Aspects of the ecology of macrobenthic abyssal key species in the South Atlantic Ocean with focus on the Isopoda Crustacea: Malacostraca

Dissertation

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We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time.
Through the unknown, remembered gate
When the last of earth left to discover
Is that which was the beginning.

T.S. Eliot (Four Quartets)

It was as if nature, centuries into the scientific revolution, had managed to save some of her best secrets for last.

William J. Broad (The Universe Below)

Thesis short summary

Trophic interactions of deep-sea ecosystems have to date been subject to a relatively limited number of studies. Therefore, the major aim of this thesis is to elucidate trophic interactions of common macrobenthic invertebrates in the Southern Ocean deep-sea, applying a multi-disciplinary approach utilising the analyses of fatty acid (FA) compositions, stable isotope ratios and gut contents, as well as estimates of biomass and production.

The study is based on material collected during the SYSTCO (SYSTem COupling in the Southern Ocean) cruise conducted during the austral summer 2007/08. A special focus was laid on the role of isopods within the ecosystem. However, not only macrobenthic invertebrates are included in the study, but also certain compartments of the meiofauna (nematodes and copepods) as well as megafauna (fish), in order to gain insights into trophic contexts of different benthic, benthopelagic and infaunal groups.

The results of my thesis show that the feeding strategies displayed by Southern Ocean macrobenthic organisms (chapters 4-6), as well as other ecosystem compartments (meiofauna, chapter 3, and megafauna, chapter 7) are complex, manifold and taxon-specific, often even species-specific. However, as diverse the feeding habits in the abyssal might be, some underlying trends are indicated by the results of this thesis.

For example, low FA contents were found in almost all organisms analysed (chapters 5 and 6), with few exceptions. Additionally, the predominance of the polyunsaturated FAs 20:5(n-3) and 22:6(n-3), together with the saturated FA 16:0 found in many analysed organisms, reflects the dominance of phospholipids, further pointing towards a low dependence on lipid reserves. This can be seen as an indication that lipids are not accumulated for energy storage, and that feeding occurs throughout the year, supporting the idea of the existence of a permanent food reservoir in the deep-sea.

However, in the majority of analysed organisms, FA alcohols were detected in varying proportions (chapters 5 and 6). These are indicative of wax esters (WE), a lipid class typically used for long-term storage. The FA component of WE is largely derived from the diet, whereas the fatty alcohols are derived from the animal's internal biosynthesis. Possibly the storage of wax esters indicates a general evolutionary mechanism developed to survive long starvation periods (e.g. found in higher latitude herbivorous copepods). If this is seen as such a survival strategy of deep-sea organisms periodically experiencing long starvation intervals, the "food-bank" hypothesis would have to be rejected. Thus, the generally low lipid content, pointing to a lack of lipid storage and the co-occurrence of wax esters as long-term energy storage remains somehow contradictive. The distinct mechanisms underlying these metabolic processes need to be addressed in future studies.

One noteworthy result of this thesis is that for many organisms thought to be carnivorous, equivocal results are found both in FA and stable isotope analyses (chapters 6 and 7). The findings seem to indicate that many organisms, even if their primary feeding strategy is based on predation or scavenging, might display a high degree of opportunism, utilising other food sources if prey or carrion is not available. This strategy is presumingly of advantage in an environment as the deep-sea, where food falls or prey organisms may occur extremely patchy. In this study, animals thought to be top-predators (e.g., bigger fish) are in some cases not found within the maximum range of $\delta^{15}N$ values. Besides opportunistic feeding,

another reason for this lower-than-expected $\delta^{15}N$ enrichment might be the decoupling from the food web based on sedimented and frequently recycled organic matter. This would apply to predating/scavenging organisms capable of moving freely in the abysso-pelagic environment such as fish in contrast to those more restricted to the benthic realm such as e.g. predating or scavenging gastropods. Similar scenarios have also been suggested by previous studies.

A feature that has been discussed to play an important role in the nutrition of deep-sea organisms is the ingestion of bacteria, which are very abundant at the deep-sea floor. However, in this study, indications for feeding on bacteria based on typical FA (e.g., 15:0, 17:0, 15:1 and 17:1) were generally only found in minor proportions (chapters 5-7).

On the contrary, another FA has been found to be important in the FA composition of many organisms analysed in this study: 20:4(n-6), arachnidonic acid (AA). Enhanced levels of this particular FA compared to other ecosystems have been previously found for deep-sea organisms (see chapters 4-6). Its source, however, is still under discussion. Macroalgae (specifically red algae), known to contain high amounts of this FA, have been suggested to be the source of 20:4(n-6) also in deep-sea settings. Another possible source might be foraminiferans, which have been reported to sometimes contain high proportions of AA. For some deep-sea organisms, as e.g. some polychaete (chapter 5) or isopod (chapter 6) species, selective feeding on foraminiferans has previously been reported. These protozoans are capable of selective feeding on certain compartments of detritus and accumulating PUFA, thereby providing a more valuable dietary resource compared to detritus. However, the question if the original source of AA is synthesis within foraminiferans or if it is taken up with their food cannot be answered. Nevertheless, as foraminiferans are a major element in deep-sea environments which can comprise a substantial proportion of benthic biomass, they most probably play a significant role in the ecosystem.

Data on life strategies and feeding habits of deep-sea isopods still remain scarce. This thesis could show that a variety of food sources are exploited by these peracarid crustaceans (chapter 6). Feeding on foraminiferans, as mentioned, could be an important link in carbon cycling in deep-sea ecosystems. Additionally, isopods seem to contribute a substantial proportion of biomass in the Southern Ocean deep-sea, apparently depending on the characteristics of the investigated area (chapter 8). The high degree of taxon-specificity has been shown both for feeding strategies (chapters 4-7) as well as biomass and production estimates (chapter 8). This again highlights the importance of a high taxonomic resolution in ecosystem studies.

The results presented in this thesis provide insights into certain abyssal benthic ecosystem processes. However, they also suggest that we still have to learn much more on the ecology of the organisms inhabiting the vast deep-sea areas on our planet. This knowledge will ultimately help to understand the driving mechanisms underlying evolutionary developments, selecting forces canalising distribution patterns and ecological interactions. The increasing interest in the deep-sea due to climatic changes and exploitation of resources demands an improved understanding of deep-sea ecosystem functioning. This will help predicting or at least understanding changes which are, to a great extent, induced by human impact.

Chapter 1

General Introduction

R/V *Polarstern* in the Antarctic ice during the ANDEEP-SYSTCO cruise.

Chapter 1 General Introduction

1.1 Aims of the study

Trophic interactions of deep-sea ecosystems have to date been subject to a relatively limited number of studies. Therefore, the major aim of this thesis is to elucidate trophic interactions of common macrobenthic invertebrates in the Southern Ocean deep-sea, applying a multi-disciplinary approach utilising the analyses of fatty acid compositions, stable isotope ratios and gut contents, as well as estimates of biomass and production.

The study is based on material collected during the SYSTCO (SYSTem COupling in the Southern Ocean) cruise conducted during the austral summer 2007/08. A special focus was laid on the role of isopods within the ecosystem. However, not only macrobenthic invertebrates are included in the study, but also certain compartments of the meiofauna (nematodes and copepods) as well as megafauna (fish), in order to gain insights into trophic contexts of different benthic, benthopelagic and infaunal groups.

A concise introduction into the characteristics of the investigated area and its faunal components is given in this general introduction, while the main results are summarised in chapter 2. In the following chapters, the single approaches are presented more in detail, based on manuscripts either published, submitted or in preparation for submission.

In chapter 3, the reaction of meiofaunal organisms to a sedimentating phytoplankton bloom at an abyssal site situated at the Polar Front is described. In chapter 4, the results of stable isotope analyses conducted on various benthic organisms from several deep-sea as well as one shelf station allows to gain a general picture of the trophic structure of the studied area. Major components of the macrofauna are further investigated by applying the analyses of fatty acid compositions on polychaetes (chapter 5) and peracarid crustaceans (chapter 6), while feeding mechanisms in Antarctic demersal fish are studied by a combination of fatty acid and gut content analyses (chapter 7). A more detailed look is taken on the role of isopods in the abyssal food web by estimating biomass and secondary production in five common families (chapter 8). Finally, the role of deep-sea research in context with recent global developments, as well as general features found in this study are discussed in chapter 9.

1.2 Southern Ocean oceanographic features

In a simple definition, the Southern Ocean comprises the waters extended south of the Polar Front (50°S in the Atlantic and Indian sectors and 60°S in the Pacific sector) (Dell, 1972; Clarke, 1996). The present investigation area (Weddell Sea) spans northwards to the Polar Front and southwards to the Antarctic shelf ice edge (Figure 1). It comprises the Atlantic-Indian deep-water basin, bounded to the north by the Atlantic-Indian Ridge, which is partly restricting the flow of bottom water (Knox, 2007).

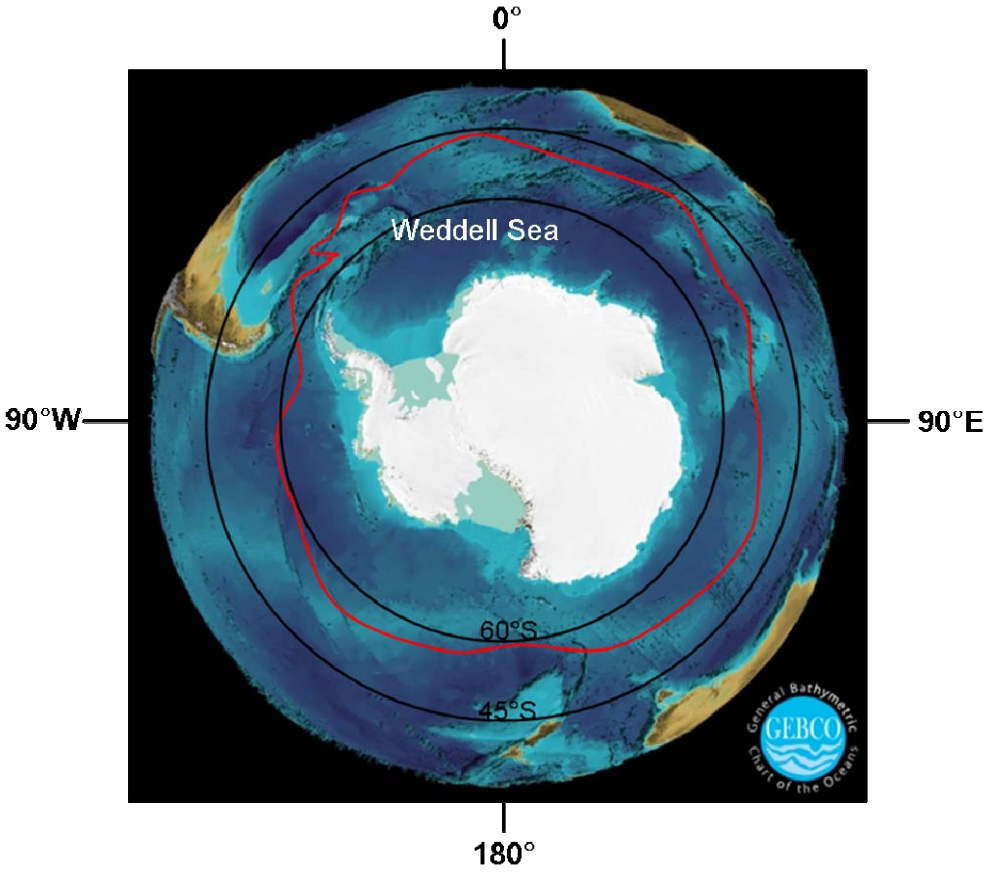

Fig 1 3-D visualized map of Antarctica and the Southern Ocean; map by Martin Jakobsson (GEBCO, General Bathymetric Chart of the Oceans). Polar Front indicated by red line.

One general characteristic of the Southern Ocean is its cold water. The Polar Front, being its northern boundary, is characterised by a steep surface temperature gradient of 3-4°C (Figure 2), as well as abrupt changes of other physical parameters like salinity. Northward-flowing Antarctic Surface Water sinks beneath warmer Subantarctic Surface Water, generating a transition zone. Surface water temperatures in the Polar Front Zone rarely exceed 8°C in summer and 3°C in winter, and decrease southwards down to -1.9°C (Knox, 2007).

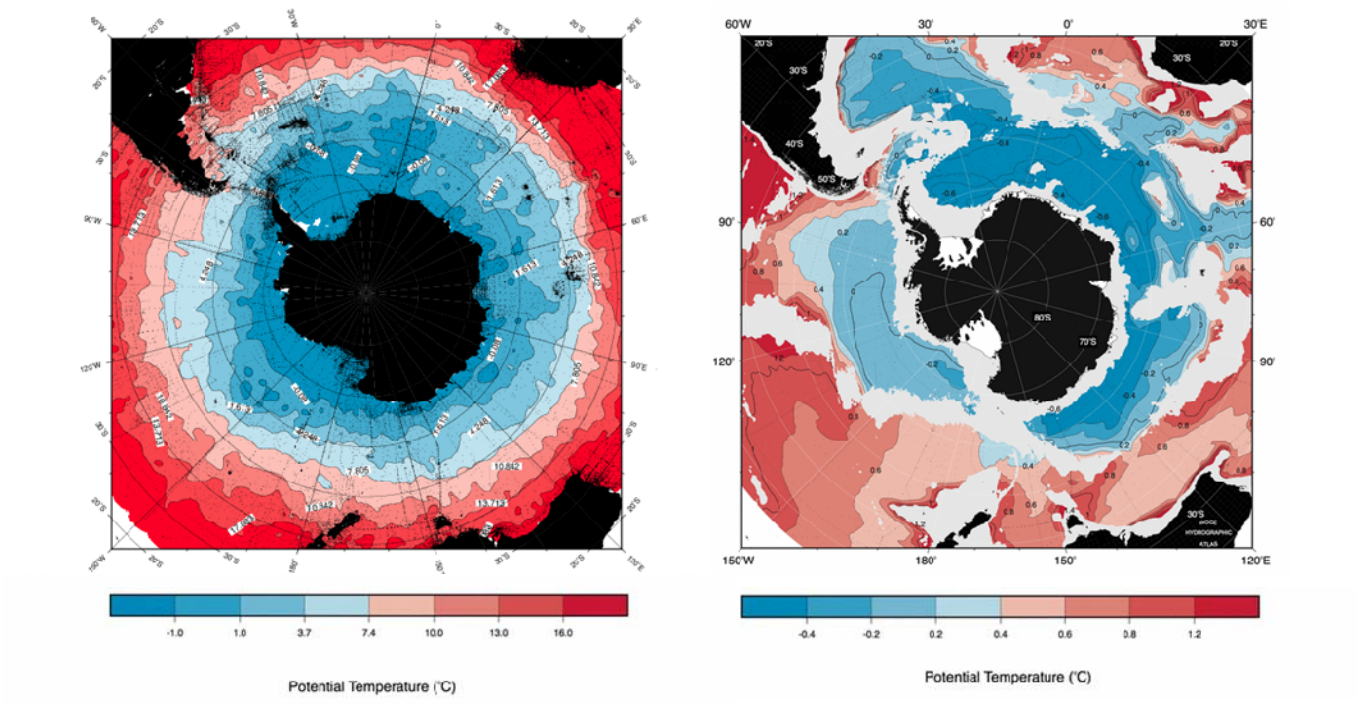

Fig 2 Surface (left) and bottom (right) temperatures in the Southern Ocean. *Source: www.bodc.ac.uk*

In the Southern Ocean, primary production is controlled by unique features present in Polar Seas, including the alteration between the dominance of darkness during one half of the year and the dominance of light during the other half, as well as the seasonal variation of ice coverage. It is therefore characterised by a strong seasonal discontinuity with a short phytoplankton bloom peak in late spring. Gross primary production in the Southern Ocean is comparably high, and the Weddell Sea can be divided into provinces with differing production levels: highest values have been measured in the marginal ice zone (mean value of 1.76 g C m^{-2} day^{-1}), followed by production in the open ocean (mean value of 0.87 g C m^{-2} day^{-1}), coastal areas (0.70 g C m^{-2} day^{-1}) and lowest production rates under the pack ice (mean value of 0.36 g C m^{-2} day^{-1}) (v. Bröckel, 1981; 1985; El-Sayed and Taguchi, 1981; Mathot et al., 1992).

The continental shelf of the Weddell Sea is comparably deep with average depths of 500-600 m, reaching down to maximum depths of over 1.200 m (Anderson, 1999). This is at least

partly due to the isostatic equilibrium adjustment of the continent responding to the great mass of the Antarctic ice sheets (Knox, 2007). It is characterised by intense seasonality and high organic carbon fluxes (Isla et al., 2006), as the water-column production is transmitted to the shelf floor in intense pulses of particulate organic matter (Bathmann et al., 1991; Fischer et al., 2000). Besides primary production, detrital fallout from pack ice melting and sometimes considerable quantities of continental debris transported by ice moving off the Antarctic continent might be an additional feature influencing the food supply to the sea floor (Dayton, 1990; Knox, 2007). Some Southern Ocean localities show deviating characteristics compared to the surrounding ocean due to special topographic or oceanographic features and have to date only been subject to few studies. One example is Maud Rise, sampled during this study, which regularly appears as a region of reduced ice coverage (De Steur et al., 2007), and intermediate to high values of annual primary production rates (Wefer and Fischer, 1991).

1.2.1 The Southern Ocean deep-sea

The abyssal region of the oceans is defined as the vast sea-floor areas lying between 2000 and 6000 meters depth, covering 54% of the Earth's surface (Gage and Tyler, 1991). Some general features account for most abyssal areas, regardless of their geography, including the covering with fine sediments, the absence of *in situ* primary production (except for cold seeps and hydrothermal vent ecosystems) and low temperatures (Gage and Tyler, 1991; Smith and Demoupoulos, 2003).

The majority of deep-sea ecosystems depends on primary production in the upper water layers, and the quantity and quality of food based on its sedimenting remains reaching the sea floor are crucial for benthic organisms (Tseytlin, 1987; Graf, 1989, 1992; Gooday and Turley, 1990; Paterson et al., 1998; Bühring and Christiansen, 2001; Smith et al., 2008). The discovery of marine snow in the late 1970ies illustrated how particulate organic matter forms aggregates and sinks at increased velocities (Trent et al., 1978). These aggregates are constantly changed on their way to the seafloor by decomposition processes via the activity of bacteria and other organisms forming the microbial loop (Azam et al., 1983). As it has been shown that the organic flux arriving on the sea floor decreases inversely with water depth (Buesseler, 2007), abyssal ecosystems and their benthic production are seen as 'food limited'. Also in marine Polar regions, the numerical abundance, biomass and distribution of organisms forming the benthic community are directly influenced by variations in food supply (Grebmeier and Barry 1991 and references therein). These are in turn dependent on changes in multiple, interdependent factors including hydrography, ice coverage, light,

temperature, nutrient availability and the structure of the pelagic food web (Grebmeier and Barry 1991; Bathmann et al., 1997; Piepenburg, 2005; Clarke and Arntz 2006).

In some cases, seasonal changes in nutrient supply to the deep-sea benthic community were observed. For example, „nepheloid layers“, layers of fresh organic material providing rich food sources for benthic organisms (Billett et al., 1983), were associated with phytoplankton blooms in the upper ocean. Employing benthic chamber landers, some authors observed rapid responses of deep-sea benthic fauna to increased inputs of organic material (Aberle and Witte, 2003, Witte et al., 2003a, b; Moodley et al., 2005; Bühring et al., 2006).

Nevertheless, the benthic fauna does not necessarily exhibit seasonal variability dependent on phytoplankton blooms. This can be assigned to the importance of rather small particles like bacteria, nano- and picoplankton and protozoans, food sources that are present throughout the year (Kojima and Ohta, 1990; Arntz et al., 2005). The described accumulation of organic material above the seafloor can often be decoupled from seasonal pulses of primary production in the photic layer, thereby providing a more permanent food reservoir buffering the benthic system. This might partly be due to relatively slow degradation resulting from limited microbial activity allowing the development of such a persistent “food bank” for benthic organisms as documented for the shelf off the Antarctic Peninsula (Mincks et al., 2005; Smith et al., 2006). Additionally, topographical features like depressions and submarine canyons can act as detritus traps that fuel patches of intense secondary production (Vetter, 1995).

Accompanying phytoplankton remains, also the remains of zooplankton and nekton, including fecal pellets and carcasses, contribute to the flow of organic matter to the sea floor. In this context, one factor characteristic for the Southern Ocean is the high abundance of euphausiids, whose sinking decomposing bodies and exuviae can provide a constant flow of nutrients to the seafloor (Sokolova, 1997). For example, a molt production by *Euphausia superba* of 0.18 C g m^{-2} yr^{-1} has been estimated (Nicol and Stolf, 1989). However, also copepods are an abundant zooplankton component in the investigated area and can contribute considerably to Southern Ocean zooplankton production and thereby carbon fluxes to the sea floor (Boysen-Ennen et al., 1991; Bathmann et al., 2000).

Besides sedimentation from the upper-water layers, horizontal distribution by bottom currents plays an important role in the distribution of detritus (Sokolova, 1997). The friction between the seabed and the flow over it generates a vertically homogeneous, although horizontally inhomogeneous, layer of varying thickness capped by a region of strong density gradients. The thickness of this benthic boundary layer (BBL) is limited by the attenuation of turbulent mixing, which extracts energy from the flow and the effects of the Earth’s rotation. It is a region above the seabed which is probably well-mixed. Biologically, the BBL can be defined

as the sediment community and assemblage of organisms in the overlying water column associated with the bottom (within 100 m above the seabed). There is a migration of primarily benthic animals into the water column to feed, breed, or escape predation, whereas primarily pelagic animals such as fish feed at the BBL (Smith and Hinga, 1983; Cartes and Maynou, 2001). Therefore, the BBL forms an important physical structure over the seabed which is modified by the bottom topography and in turn affects the distribution of animals and particles near the seabed. Especially the epibenthos and suprabenthos (mainly mysids, isopods and amphipods with swimming capacity) seems to play a key role in energy transfer in the BBL (Cartes et al., 2002), and it has been shown that benthic organisms can significantly increase the flux of particles across the sediment-water interface (Graf and Rosenberg, 1997).

In general, the Southern Ocean benthic environment is characterised by mainly constant conditions, including low, stable temperatures, low salinity fluctuations and physical barriers; however, it is also exposed to highly fluctuating features, such as organic matter fluxes (due to highly seasonal primary production governed by the light regime and ice coverage), iceberg scours in shallow regions and regionally strong bottom currents (Knox, 2007).

One feature that distinguishes deep-sea ecosystems from those in shallow waters are the differences in processes connected with initial carbon cycling. While in shallower waters, microbial degradation (mainly bacteria) accounts for rapid assimilation and respiration of organic material reaching the sea floor (Middelburg et al., 2000; Moodley et al., 2005) at abyssal depths this uptake has been observed to happen significantly slower. In this case the key players are, in contrast to the shallower-water bacteria-dominated degradation, dominated by the meio- and macrofauna (Witte et al., 2003a, b; Sweetman and Witte, 2008). One possible explanation for this finding is that the strong selection for efficient foraging behaviours in food-limited environments favours the larger organisms (Lauermann et al., 1997; Smith et al., 2008).

1.3 Southern Ocean benthos

The structure of benthic communities in the Southern Ocean is closely related to the unique present and historic geological and oceanographic features of the Antarctic continent and its surrounding seas. First of all, the Antarctic continent has been isolated from other continents for a comparatively long time span, completed by the opening of the Drake Passage around 23 Ma. This resulted in the development of the Antarctic Circumpolar Current, completely isolating Antarctica from other continents and to date seen as the feature that, to a great extent, isolates the Antarctic marine fauna from the surrounding oceans. The seafloor of the Weddell Sea, however, probably dates back as far as to the Middle Jurassic about 160-150 Ma (Livermore and Hunter, 1996). As temperatures cooled, the ice began to spread and since about 15 Ma, the continent has been mostly covered with ice (DeConto and Pollard, 2003). By the Late Miocene - Early Pliocene (ca. 10 Ma), the West Antarctic ice sheet had formed and was much thicker than it is today (Shackleton and Kennett, 1975). Two distinct intervals of cooling have been reported (2.5 and 0.7 Ma), followed by a steadily increasing coolness interrupted by climatic oscillations up to the present time (Hays, 1969).

In the context of glaciation, pack-ice cover must be considered an important evolutionary factor, and most likely influenced evolutionary developments in the Southern Ocean, mainly by preventing primary production in large areas. For example, it has been hypothesized that the eurybathic distributions (occurrence across wide depth ranges) found in many Southern Ocean species likely is an adaptation to the oscillation between glacial and interglacial periods in the past (Brey et al., 1996). Glaciation would have enhanced habitat similarities between coastal and deep-sea areas, facilitating faunal shifts between those habitats allowing shelf species to migrate to deeper waters (polar submergence) and *vice versa* (polar emergence) (Hessler and Wilson, 1983; Wilson and Hessler, 1987; Brandt, 1991; 1992). Additionally, the degree of endemism found in the Southern Ocean in many benthic groups is exceptionally high, indicative for an active speciation during the long isolation of Antarctica (Clarke and Crame, 1997; Brandt et al., 2007a).

Another effect of the ice coverage is that, by preventing new production in the water column, it could have stimulated suspension feeders to rely more on resuspended and advected material. This feeding strategy which served during glaciation is possibly still maintained by benthic suspension feeders in the Southern Ocean, despite the fact that under present conditions fresh algal food is available during certain periods of the year (Arntz et al., 2005). This possibly led to the fact that the Weddell Sea shelf and slope benthic communities are generally dominated by sessile suspension feeders. Most abundant taxa include sponges, bryozoans, echinoderms and polychaetes and have been shown to be rich both in terms of abundance and diversity (Gerdes et al., 1992; Arntz and Gutt, 1999).

Compared to this, macrobenthic abundances and biomass in the abyssal Weddell Sea are generally lower than those found on the shelf (Linse et al., 2007). Until recently, comparatively low sampling efforts led to the view that the Antarctic deep-sea was relatively species poor. This changed profoundly after the investigations of the expeditions ANDEEP I and II in 2002 and ANDEEP III in 2005, revealing a remarkable biodiversity in the studied area. The general trend was found that abundance and biomass generally decreased with depth, whereas species richness mostly increased. The mechanisms underlying these diversity patterns in deep-sea macrobenthos have been and are subject to many discussions and hypotheses. Nyssen et al. (2005) suggested that the variability in life history strategies (i.e., habitat preferences and exploited food sources) in the Southern Ocean supported the adaptive radiation and diversification of trophic roles for groups such as amphipods. Gage (1996) reasoned that the absence of large topographic barriers and the heterogeneity of the faunistic communities explain the high species diversity in the Southern Ocean.

The meiofaunal component of the Southern Ocean deep-sea benthos has been shown to comprise species compositions typical for bathyal and abyssal sediments, with nematodes and copepods being the dominant taxa (Gutzmann et al., 2004). In terms of standing stocks, the Southern Ocean meiofauna seems to be significantly higher compared to other deep-sea areas both concerning abundance (e.g., $20x10^6$ nematode individuals m^{-2}) and biomass (up to 15 g nematode dry weight m^{-2}) (Herman and Dahms, 1992).

Besides geological features, another factor postulated to strongly influence biodiversity and community structure in the deep-sea is food availability. In the Southern Ocean, high particulate organic carbon (POC) fluxes, partly controlled by sea-ice cover and mesoscale hydrography, influence the strength of pelago-benthic coupling and are thought to create benthic ‘biodiversity hotspots’ (Piepenburg, 2005; Rex, 2005; Brandt et al., 2007b). In general, the decreasing food input with increasing depth is thought to lead towards the dominance of detritus feeders in biota of deeper ocean regions (e.g., Levin et al., 2001). Also in the abyssal Southern Ocean with its strong seasonal discontinuity of primary production and thereby food input to the sea floor as described above, the major feeding strategies displayed by benthic organisms are considered to be adaptive to these conditions. For example, the numbers of scavenging organisms has been reported to be higher than in benthic communities elsewhere in the world (Arnaud, 1977). Additionally, omnivorous and opportunistic feeding has been shown for many species (e.g., Dearborn, 1967). However, it was also found that many benthic organisms might partly bypass the nutritional supplement from pelagic production and utilize alternative food sources provided year-round (Drazen et al., 2008).

Some other features assumed to be typical for Antarctic poikilotherms are also closely related to the physical and biological environment. It has for example been shown that polar marine invertebrates show a reduced basal metabolism, causing characteristics such as slow growth and longevity resulting in large size, but also adapted reproductive strategies such as brooding and seasonal breeding (e.g., White, 1977; Clarke, 1980; Brey, 1995; Barnes et al., 2007). Furthermore, oxygen supply in the tissues may determine thermal tolerance and thereby maximum size of organisms ('polar gigantism') due to better oxygenation and the architecture of the vascular system in cold water as described by Chapelle and Peck (1999).

1.3.1 Sampling area

Five stations in the eastern Weddell Sea have been sampled utilising various gear, including an epibenthic sled (EBS), a boxcorer (BC), a multiple corer (MUC), an Agassiz Trawl (AGT) (for sampling gear see picture on page 35) and a water sampler with CTD (conductivity-temperature-depth data logger), yielding the meio-, macro- and megabenthic animals as well as sediment and particulate organic matter (POM) samples used in this study. The positions of all stations are indicated in the maps presented in the relevant chapters.

One station was situated in ca. 3000 m depth within the transition zone at the Antarctic Convergence and was sampled twice, firstly during a phytoplankton bloom (station PS71/13) and again six weeks later (station PS71/85). The sediment consisted of very fine, light brown diatomaceous ooze, and the fauna comprised a fairly rich macrofauna with polychaetes, isopods and bivalves being the most dominant groups (Bathmann, 2010).

The Central Weddell Sea (PS71/33) was sampled in ca. 5340 m depth. Here the sediment consisted of very fine and soft homogeneous grey-brown clay containing many small foraminiferans with only few stones. It was mainly colonized by soft bottom dwellers and burrowing animals. Species richness for the deep Weddell Sea has been reported to be lower than for the slope regions (Linse et al., 2007), and this was confirmed for this station in the process of sorting EBS and AGT samples (Wilmsen and Schüller, pers. com.).

The shelf station PS71/48, situated in ca. 600 m depth, comprised very compact sediment, and the macro- and megafauna were found to be very rich. The hard bottom was covered by sessile animals (mainly poriferans, accompanied by spicule mats), as well as foraminiferans.

Station PS71/17 was situated at the slope close to the Antarctic continent in ca. 2100 m depth: The sediment was characterised by very fine grey clay with sand and stones, and a very rich benthic fauna was encountered.

The plateau of the sea mount Maud Rise was sampled in ca. 2150 m depth (PS71/39), and the sediment consisted of light brown foraminiferous ooze with many stones. Brandt et al. (in

press) reported that Maud Rise showed distinct differences in benthic fauna composition compared to surrounding deep-sea basins.

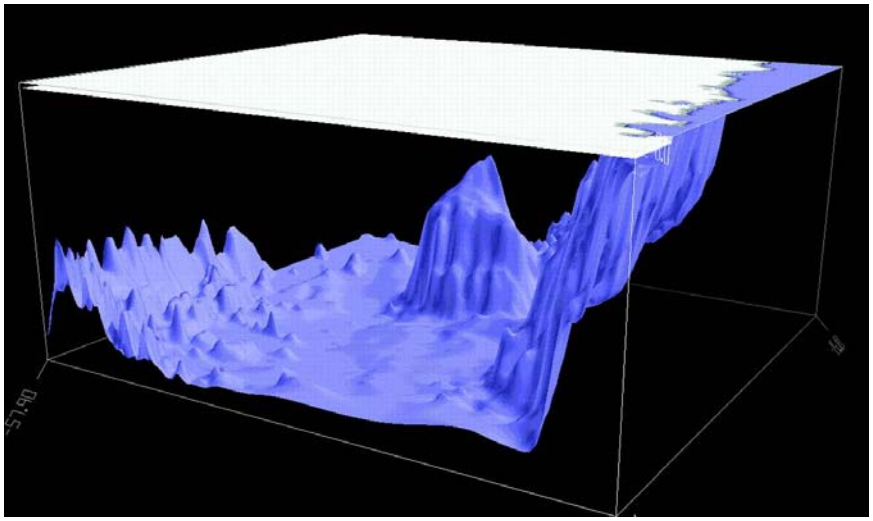

Fig 3 Perspective view from the southwest of the sea-floor bathymetry (blue shading) in the eastern Weddell Sea. Map by Holland (2001).

Generally, in the Weddell Sea, the peracarid fauna has shown to be one of the most abundant groups besides polychaetes, echinoderms and molluscs (Piepenburg et al., 2002; Brandt et al., 2007a, b; Kaiser et al., 2007) and likely plays an important role in ecosystem processes and food-web dynamics.

1.3.2 Isopoda

Peracarida (Crustacea: Malacostraca) belong to the most abundant and diverse groups inhabiting the Antarctic shelf, slope and deep-sea (Arntz et al., 1997; Brandt et al., 2007a; b; Kaiser et al., 2007) and are represented in the Southern Ocean with the orders Amphipoda, Isopoda, Cumacea, Mysidacea and Tanaidacea. It has been suggested that their remarkably high abundance and diversity is a result of a combination of different factors. These include physiological and life strategy features that are highly advantageous in the deep-sea environment. They have for example well-developed chemoreceptors, helpful in detecting potential food sources (Rehm, 2009), and their reproductive strategy of brood care in a ventral brood pouch (marsupium) is thought to be of advantage in terms of larval survival compared to dispersal strategies (Brandt, 1999; Arntz et al., 2005). Furthermore, it was shown that deep-sea isopods can synchronise their breeding intensity with seasonal primary production patterns by releasing their juveniles at the time the organic detritus deposition

started (Harrison, 1988; Brandt et al., 1994), thereby providing a rather long and well-protected developmental phase.

Southern Ocean isopods are especially rich in both abundance and diversity, and display diverse species-specific life forms, including burrowing and swimming forms; however, most are benthic bottom dwellers. They developed various feeding strategies, spanning from filter feeding to predating and scavenging, but most species were previously considered to be generalized deposit feeders (Wolff, 1962). Recently it has been shown that they display rather diverse feeding behaviours with distinct preferences, as for example certain types of foraminiferans observed in many deep-sea isopod species (Svavarsson et al., 1993; Elizalde et al., 1999; Guðmundsson, 2000; Brökeland et al., 2010). However, information on the specific diets as well as the role in the food web of Antarctic peracarid crustaceans especially in deep-sea settings still remains scarce.

Some information on the displayed feeding mechanisms can be derived from the isopods highly variable morphology. One feature found in many predating or scavenging species is the adaptation of the digestive systems toward a rapid uptake of high volumes of food, like found in some Cirolanidae and Aegidae and/or the modulation of mouthparts like reduced maxillae found in some Anthuridae or piercing mandibles present in some Gnathiidae, Paranthuridae and Bopyridae. Other species have adapted a hemi-sessile, filter feeding life style filtering small particles with their setous legs (Wägele et al., 1981). In some cases it has been suspected that bacteria and fungi can contribute substantially to isopod nutrition, as they preferentially selected food particles colonised by these microorganisms (Findlay et al., 1984; Costantini and Rossi, 1995).

However, with morphological features less implying their feeding mode, the preferred food sources of many deep-sea isopods are more difficult to identify. One method is the investigation of stomach contents, often revealing various diet components, like e.g., foraminiferans, diatoms, tintinnids coelenterates, nematodes, radiolarians and sponge spicules in the guts of deep-sea isopods (Wolff, 1962; Svavarsson, 1993). Still, in many cases these investigations deliver only unsatisfying results due to the fact that most of the food available for deep-sea organisms consists of degraded material and these organisms are possibly often exposed to starving intervals. Also, *in vivo* observations of feeding behaviour face strong restraints, as it is extremely difficult to obtain living specimens from the deep-sea to conduct according experiments on them.

Thus, alternative methods for investigating the diets and feeding preferences of marine organisms (and especially deep-sea representatives), as the analysis of fatty acid (hereafter FA) composition or measuring stable-isotope ratios gain more and more importance.

1.4 Tools for the investigation of ecologic aspects: applied methods

1.4.1 "Traditional" Methods

Gut content analyses

One traditionally used method to identify the diet composition of an animal is to analyse its gut contents. Besides identifying the ingested objects, additional information on the feeding habits of the investigated organism can be obtain by estimating the degree of gut filling and the state of the ingested dietary items (digestive stage).

However, this method faces some restraints: (1) it can only provide information on recently ingested food items; (2) due to differing structures of ingested items (e.g., soft-tissue versus hard tests), the importance of more rapidly digested ones might be underestimated compared to slowly digested ones; and (3) guts, especially those of deep-sea organisms, are often found empty, e.g. due to long starving intervals or regurgitation during retrieval of the samples (often found in fish with gas bladders).

Based on these facts, gut content analyses of deep-sea organisms rather provide a qualitative tool, and can help elucidate certain feeding interactions, but can hardly be used as a quantitative tool. In this study, gut content analyses have been conducted mainly on fish (chapter 7), but also on some isopods (Figure 4) to identify ingested items.

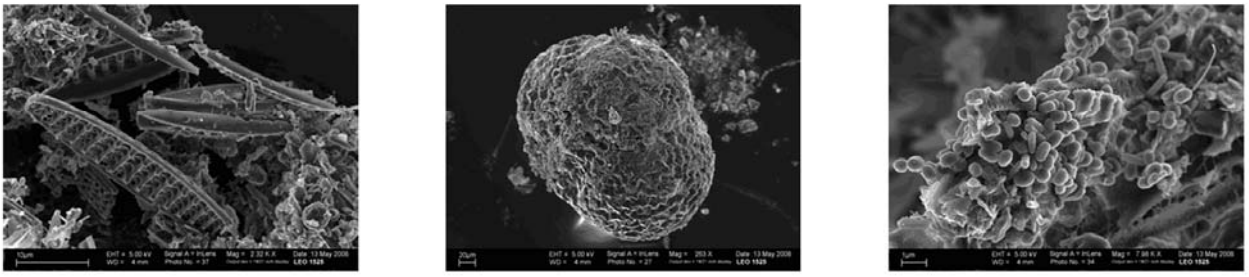

Fig 4 Scanning electron microscope (SEM) pictures of items found in the gut of the deep-sea isopod *Eurycope* spec. (family Munnopsidae). From left to right: diatom frustules, foraminiferan and unidentified colony (possibly bacteria).

Biomass and production estimates

Biomass is a measure that is traditionally used to estimate the trophic importance and position of a group of organisms. It can be deduced from the average weight of a population or taxonomic group and is presented in different measures, as e.g., wet weight, dry weight, ash free dry weight or in terms of carbon content. Secondary production represents one of the major pathways of energy flow and its measurement plays a crucial role in the quantification of ecosystem dynamics (Edmondson, 1974). It can be analysed with methods

based on a variety of parameters such as growth or mortality of identifiable cohorts or size-frequency classes (e.g., Hynes-Hamilton and Coleman, 1968; Benke, 1984; Crisp, 1984). As these and other parameters need to be taken into account, production rates are often difficult to estimate. This holds especially true for remote areas such as the Southern Ocean deep-sea, where low sampling effort prevents the knowledge on many factors (e.g. growth of identifiable cohorts, basic life histories, mean annual biomass or mean annual abundance). Nevertheless, the limited ecological studies conducted in deep-sea ecosystems so far indicate that benthic organisms most likely play an important role in carbon consumption on the deep-sea floor, and estimates on their biomass and production rates can help defining the energy flow in these settings (Gage, 1992; Cartes and Sorbe, 1999).

Therefore, in this study, two empiric models have been used to estimate production:

Empirical model of Brey (1990), developed for marine benthic invertebrates (Crustacea):

$$\log P = -0.614 + 1.022 \log B - 0.360 \log W$$

where P = annual production, B = mean annual biomass (AFDW, ash free dry weight, g/m^2), W = mean individual weight (AFDW, g), obtained as B/D ratio, D = mean annual density (ind. /m^2).

Another empirical model was suggested by Tumbiolo and Downing (1994), including temperature and water depth as factors:

$$\log P = -0.18 + 0.97 \log B - 0.22 \log W_m + 0.04 T_b - 0.014 Tb \log (Z+1)$$

where P = annual production, B = mean annual biomass (dry weight (DW), g/m^2), W = mean individual weight (DW, g), obtained as B/D ratio, D = mean annual density (ind. /m^2), T = environmental temperature (°C).

1.4.2 Fatty acid trophic markers

The analyses of lipid and fatty acid (FA) composition of marine organisms has become a well-established and widely used tool and was recently intensively reviewed (Dalsgaard et al., 2003; Bergé and Barnathan, 2005).

Lipids are major sources of metabolic energy and essential materials for forming cells and tissue membranes, thereby playing an important role in physiology. FAs are the main constituent of most lipids and released from ingested lipid molecules during digestion, but are not degraded like other nutrients. Therefore, most FAs pass into the circulation intact and are generally taken up by tissues the same way. Since a relatively limited number of FAs can be biosynthesized by animals, it is possible to distinguish dietary *vs*. non-dietary components.

Once taken up by tissues, FAs are either used for energy or re-esterified primarily to triacylglycerols, and stored in adipose tissue. Although some metabolism of FAs occurs within the predator, such that the composition of predator tissue will not exactly match that of their prey, FAs can be deposited in adipose tissue with little modification and in a predictable way.

However, the utilization of FAs as trophic markers faces some restraints, as single FAs cannot be assigned to single species, FAs are not necessarily metabolically stable and turnover rates are variable between certain FAs and additionally underlie species- and temporal specific changes Dalsgaard and St. John 2004).

FAs are referred to by the standard nomenclature of carbon chain length:number of double bonds, and the location (n-x) of the double bond nearest the terminal methyl group (for example 20:5(n-6), having 20 carbon atoms, five double bonds and 6 carbon atoms between terminal methyl group and the first double bond). FAs can be subdivided into saturated FAs (SFA), including those without any unsaturated linkages, monounsaturated FAs (MUFA), having a single double bond and polyunsaturated FAs (PUFA) with two or more double bonds.

As numerous studies demonstrated that specific FA patterns are passed from food source to consumer (e.g., Graeve et al., 1994; Falk-Petersen et al., 2000; Auel et al., 2002), FA signatures (quantitative distribution of all FAs measured in a consumer/predator or prey sample) have been used qualitatively to infer trophic levels and spatial and temporal differences in diets both within and among species. Utilising them for dietary analyses requires an understanding of the characteristics of food source FA signatures and to which extend they differ in a given ecosystem. Furthermore, an understanding of how ingested fatty acids are metabolized and deposited in various tissues of the predator is important for the interpretation of FA compositions. Not all FAs are suitable for providing information about diet due to predator metabolism, as certain FAs could arise from biosynthesis only or a combination of diet and biosynthesis. However, many FAs generally arise from diet only and are highly indicative of differences in various prey organisms (Iverson et al., 2004).

Many authors have explored the utility of FAs as trophic markers of dietary composition also in polar marine settings, as e.g. for copepods (e.g., Graeve et al., 1994; Kattner and Hagen, 1995), euphausids (e.g., Phleger et al., 1998; Stübing et al., 2003), amphipods (Graeve et al., 2001; Nyssen et al., 2005) or fish (Iverson et al., 2002; Drazen et al., 2009).

The most commonly applied concept is the FATM (Fatty Acid Trophic Markers) concept. It is based on the described fact that major primary producer taxa have distinctive FA profiles that may be, to varying degrees, transferred conservatively to consumers (St. John and Lund, 1996, Auel et al., 2002). In marine food webs, primary producers provide the basic FA

patterns by synthesizing algal FAs in their chloroplasts (Bergé and Barnathan, 2005). The main phytoplankton groups, such as diatoms, cryptophytes, dinoflagellates, chlorophytes and cyanobacteria, can be distinguished based on the presence and especially the ratios of particular FAs.

However, not all fatty acids provide equal information about diet due to predator metabolism. For instance, if short- or medium-chained fatty acids (i.e. < 14 carbons) are found in predator adipose tissue, these could arise only from biosynthesis, since any of these consumed in the diet would be immediately oxidized. In contrast, fatty acids with n-6 or n-3 double bonds or components such as 22:1(n-11) generally arise only from diet. Other fatty acids arise from a combination of diet and biosynthesis. For instance, fatty acids such as 16:0, 16:1(n-7), 18:0, 18:1(n-9), may arise to some extent from biosynthesis in the predator, but are also highly indicative of differences in various prey (Iverson et al. 2004).

Still, some FAs are of particular interest in their function as biomarkers for certain types of ingested food, and are widely used for the interpretation of an organism's FA composition. Examples are the phytoplankton markers 20:5(n-3), 16:1(n-7), 18:1(n-7) and 22:6(n-3) (Nichols et al., 1984, 1991; Sargent et al., 1995) or certain FA ratios like 20:5(n-3)/22:6(n-3) (Dalsgaard et al., 2003) and 18:1(n-9)/18:1(n-7), which can be used to distinguish carnivores from herbivores (e.g. Falk-Petersen et al., 1998, 2000; Graeve et al., 1997; Auel et al., 2002).

Generally, PUFA (e.g., 20:5(n-3), 22:6(n-3) or 20:4(n-6)), almost exclusively synthesized by plants, play an important role in the metabolic and physiological processes in marine organisms. As they are essential for all organisms, while very few animals have the capability of synthesizing them *de novo,* food rich in PUFA provides a valuable dietary resource (Brett and Müller-Navarra, 1997). Especially at low temperatures they are of major importance for regulating cell membrane properties (Hazel, 1995), and membrane fluidity is an important factor animals have to regulate to guarantee membrane function. In crustaceans, membrane fluidity has been shown to be regulated by increasing the proportion of unsaturated FAs (Farkas, 1979; Pruitt, 1990).

Fatty acid alcohols, found in various marine organisms, and also in this study, are indicative of wax esters (WE), a lipid class typically used for long term storage (Lee et al., 2006). The FA component of WE is largely derived from the diet, whereas the fatty alcohols are derived from the animal's internal biosynthesis (Sargent and Henderson, 1986). The storage of wax esters can be seen as a mechanism of surviving long starvation periods, like in higher latitude herbivorous copepods (e.g., Sargent and Falk-Petersen, 1988; Hagen and Schnack-Schiel, 1996)

Still it has to be kept in mind that the FA pattern is influenced by various factors, e.g. species specific metabolic processes, and knowledge on such processes in deep-sea organisms is scarce.

1.4.3 Stable isotope ratios

Another approach to infer dietary source and trophic position, and thereby characterize an organism's trophic niche, is to use stable isotope ratios. Isotopes display atoms of the same element with the nucleus containing the same number of protons, but differing numbers of neutrons, resulting in different atomic masses. The difference to spontaneously degrading radioactive isotopes is that stable isotopes persist in nature, where carbon (C) and nitrogen (N) isotopes are very abundant. They are widely used in ecological research, and their isotopes are the light isotopes ^{12}C and ^{14}N and the heavy isotopes ^{13}C and ^{15}N (Sulzmann, 2007).

Compared to conventional dietary analyses which only provide a measure of ingested food, stable isotope analysis of food web structure has the advantage of providing time-integrated averages of assimilated foods and, thus, represents a complimentary method of delineating patterns of trophic structure and energy flow (Hobson et al., 1995 and references therein). The value of measuring naturally occurring stable isotopes of carbon and nitrogen within marine food webs is based on the observation that these isotopes often undergo predictable step-wise enrichments between trophic levels.

The nitrogen isotope composition of animal tissue is generally more enriched in the heavy isotope relative to its food due to preferential excretion of ^{14}N (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; Vanderklift and Ponsard, 2003). Studies have shown that the stepwise ^{15}N enrichment in animal tissue for each trophic level can be used to determine the number of trophic levels in ecosystems and to interpret the trophic position of species or taxonomic groups relative to others (Wada et al., 1987, Hobson and Welch, 1992; Post, 2002; Struck et al., 2002; Bergmann et al., 2009). In contrast, the ratio of carbon isotopes changes little, as carbon moves through food webs, and differences of 0‰ to 1‰ are observed between consumers and their food (Peterson and Fry, 1987; Post, 2002). Therefore, differences in the carbon isotope composition of an organism can be indicative for food sources that are isotopically different (DeNiro and Epstein, 1978), and distinct carbon isotope discrepancies between certain groups of primary producers can be traced throughout marine food webs (Fry and Parker, 1979; McLeod and Wing, 2009). This ratio can for example be used as an indicator of sources of primary productivity in systems with isotopically distinct sources like phytoplankton and ice algae (Hobson et al., 1995).

However, also the use of stable isotope ratios in food-web studies has to be applied with caution. It has been shown that the isotopic compositions as well as tissue turnover rates can vary strongly between different types of tissues (Tieszen et al., 1983; Gannes et al., 1997), and it is therefore recommendable to use whole organisms for the analysis.

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Chapter 2

Summary of main Results

Gear used for sampling of macrobenthic organisms during the ANDEEP-SYSTCO cruise. Upper left: Agassiz Trawl, lower left: box corer; upper right: multiple corer; lower right: epibenthic sled.

Chapter 2 Summary of main Results

Compared to other ecosystems, relatively few studies have to date addressed trophic interactions of deep-sea ecosystems. However, previous studies have shown that complex mechanisms underlie general life-, and specifically feeding strategies, most likely due to the special features of the deep-sea environment described above. The multi-disciplinary approach applied in this thesis allowed to gain insights on ecologic mechanisms and feeding strategies which are summarised here and presented in detail in the following chapters. The methods utilised are the analyses of FA compositions, stable isotope ratios and gut contents, as well as estimates of biomass and production and abundance measurements.

2.1 The deep Antarctic benthic food web

Indeed, this study confirms the manifold aspects that contribute to the shape of the Southern Ocean deep-sea ecosystem. Results obtained with the various methods applied (chapters 3-7) indicate that (i) the fauna responds to phytodetritus deposition by increased activity, (ii) feeding mechanisms are diverse and can vary both between and within taxa, (iii) some species most probably display opportunistic feeding behaviour, while others show, at least to a certain degree, distinct feeding preferences.

As described in chapter 1, food supply based on production in the upper water column is an important factor strongly influencing benthic ecosystems. To investigate the effects of settling organic matter to the deep-sea, one abyssal station was visited during (PS71/13) and after (PS71/85) a phytoplankton bloom (chapter 3). Unfortunately, the sampling yielded very irregular and diverse macrofaunal organisms whose abundances varied strongly between both sampling dates, preventing a thorough comparison of the before- and after scenarios. However, for meiofauna (defined as organisms passing a 1 mm mesh and being retained on a 32 µm mesh for the deep-sea) and bacteria such a comparison was possible due to the high abundances of bacterial cells, nematodes and copepods. Additionally, FA compositions of POM and sediment were taken into account. The comparison of the findings before and after the remains of the bloom had settled to the ocean floor (visible as a greenish fluff layer on the sediment surface) by the time of the second visit yielded remarkable results and showed that both bacteria and meiofauna responded to this input of organic material. Instead of increasing overall abundances, this reaction was rather displayed by enhanced respiratory activity (meiofauna and bacteria) and vertical migration (meiofauna) to the sediment surface. In terms of reproduction it was shown that the deep-sea copepods did not react with an immediate reproductive effort to the sudden food input, as the number of egg-carrying

females or the number of nauplius larvae did not increased during the investigated time span. In terms of FA composition, enhanced signals of phytoplankton FA markers (20:5(n-3) and 22:6(n-3)) were detected in bottom water POM as well as in the first centimetre of the sediment at the second visit. Accordingly, the degree of degradation of FAs (e.g. represented by the ratio of 18:1(n-9) to 18:1(n-7) and lower amounts of PUFA) was higher before the input of the fresh organic matter.

As mentioned above, this case study could not be accomplished for macro- or megafaunal organisms. However, information on their feeding strategies and trophic position was analysed by utilising different methods at four abyssal and one shelf station.

To gain a broader picture of the ecosystem structure, stable isotope ratios were measured in animals sampled at the Weddell Sea shelf and deep-sea, including predating or scavenging (26 species or taxonomic groups), omnivorous feeding (20 species or taxonomic groups) and filter or deposit feeding (18 species or taxonomic groups) organisms. It was aimed at sampling as comprehensive as possible, including all types of benthic organisms (except infauna); nevertheless, as benthic communities display strong variability and patchy distribution (e.g. Thurston et al., 1994; Rice and Lambshead, 1994; Linse et al., 2007), sampling of the entity of benthic organisms is practically impossible. However, concerning the macrofaunal community, the sampling of organisms can be seen as relatively representative for the specific community.

The stepwise trophic level enrichment based on $\delta^{15}N$ values appears to be in the lower range of comparable studies with 2.5‰ enrichment per trophic level. The analysed animals occupied four trophic levels both in the shelf ($\delta^{15}N$ range: 2.3 ‰ – 11.8‰) and deep-sea ($\delta^{15}N$ range: 4.7‰ – 12.8‰) systems. Trophic positions derived from $\delta^{15}N$ ranges measured in this study generally agree well with the feeding types assumed for the investigated organisms based FA composition, morphology, gut contents or previously published information. Animals classified as filter- or detritus feeding ranged in the first (on the shelf expanding into the second) trophic level based on their $\delta^{15}N$ values with few exceptions (chapter 4). This group includes Bryozoa, Bivalvia, some Polychaeta, Ostracoda, Cumacea, some Tanaidacea, few Isopoda species, one Decapoda species and Holothuria. Organisms covering the second and third trophic level based on their $\delta^{15}N$ values generally were omnivorous feeders and include some Polychaeta (*Ophelina* spec.), Pycnogonida, Mysidacea, many Isopoda, some Tanaidacea, one Amphipoda species and one Decapoda species. The highest trophic level was reached by organisms that mainly display carnivorous feeding, including two species of Gastropoda, some Polychaeta, most Amphipoda, some Isopoda and all Pisces.

The spread of isotopic values within deposit feeding organisms can probably be explained by differences in selectivity towards certain detritus components. Selectivity for more freshly deposited material (e.g. algal remains) would result in lower trophic positioning, as this material has not been reworked in the same extent as longer deposited material, and is therefore isotopically lighter. A similar mechanism probably accounts for the omnivorous animals, in some groups showing varying $\delta^{15}N$ values with intermediate levels typical for an omnivorous lifestyle, and higher levels indicating that carnivory can be displayed occasionally.

The strong transitions between $\delta^{15}N$ ratios of organisms with different feeding types found in this study can depend on a variety of factors. Such wide ranges in $\delta^{15}N$ ratios in most benthic taxa of Antarctic food webs indicate feeding across a range of trophic levels, due to a high amount of omnivorous feeders, the ability of vertical niche expansion, and the 3-dimensionality of the Antarctic benthos.

To elucidate feeding strategies, FA compositions were analysed in selected macro- and megafaunal organisms, including Bivalvia, Polychaeta, Pycnogonida, Ostracoda, peracarid crustaceans (Cumacea, Tanaidacea, Isopoda and Amphipoda), Holothuroidea and fish. Additionally, FA patterns of sediment, POM and foraminifera as potential food sources besides the analysed metazoan organisms were investigated. The results mirror the diversity of diet composition and feeding habits, as e.g., shown for shelf and abyssal polychaetes (chapter 5). Within the analysed polychaetes belonging to 18 families, the most prominent FAs found were 20:5(n-3), 16:0, 22:6(n-3), 18:1(n-7), 20:4(n-6), 18:0, 20:1(n-11) and 18:1(n-9). The differing importance of these FAs in the individual FA profiles reflects the diverse feeding habits displayed by members of this group. Feeding patterns are relatively consistent within families at the deep stations, while the FA composition differed between the deep and the shelf stations within the same family. POM and sediment FA composition of the sampled stations are generally found not to be reflected in the animal's FA patterns, as the proportions of PUFA are significantly higher in the polychaetes than in both sediment and POM samples. For those polychaetes with high ratios of 20:5(n-3) and 22:6(n-3), a selective feeding on fresh phytoplankton components of the detritus on the sea floor is suggested, while markers for omnivorous and carnivorous feeding (e.g., 18:1(n-9), 20:4(n-6) and 20:1(n-11)) indicate feeding on various dietary items, including detritus and different prey organisms (e.g., deep-sea zooplankton and possibly foraminiferans). In the cases where information on feeding habits is available, the described habits are generally reflected in the FA patterns of the deep-sea polychaete families. However, in some cases, more specific indications on diet components could be derived from interpreting the FA compositions of the polychaetes.

Comparable results were obtained by analysing the FA composition of peracarid crustaceans (chapter 6). Individuals belonging to the order Isopoda, Amphipoda, Cumacea and

Tanaidacea showed FA profiles generally varying considerably between taxa. The very high 18:1(n-9)/n-7) ratios found in most amphipods strongly indicate a carnivorous or necrophagous component to their diet, but are not pronounced enough to assume that they display an obligate feeding mode. This supports the hypothesis that there might be no strict obligate necrophageous species in the scavenging amphipod guild, but that the amphipods rather act as facultative scavengers, employing predation, and possibly detrivory, when carrion is unavailable (Blankenship and Levin, 2007). Indications found in one amphipod species possibly hints to ingestion on foraminiferans, a feeding strategy previously reported for certain amphipod species (De Broyer et al., 2004).

Generally, the isopods originating from shallower waters show comparatively high ratios of 18:1(n-9) to (n-7), reflecting a carnivorous input to their diet. For the majority of isopods originating from deeper waters, the FA patterns are not dominated by a certain marker FA, and indicate, in some cases, diet preferences but also a high degree of omnivory. These include for example the ingestion of small invertebrates, feeding on phytodetritus or preferential ingestion of foraminiferans.

All cumaceans analysed show a dominance of the FAs 20:5(n-3) and 18:1(n-7) as well as low 18:1(n-9) to (n-7) ratios, strongly indicating a diet depending on phytodetritus. The low 22:6(n-3) to 20:5(n-3) ratios additionally supports a basal trophic level of this group, what is also displayed in the stable isotope analysis.

The few Tanaidacea analysed in this study all have very differing FA compositions, indicating diverse diet compositions, including foraminiferans and phytodetritus.

Peracarid crustaceans, especially amphipods, but also polychaetes were found to be important diet components of the fish investigated in this study (chapter 7). Knowing the pathways of energy transmission from the lower trophic levels to the higher predators is an important prerequisite for the understanding of the quantitative functioning of marine ecosystems. Therefore, the dietary composition of five Antarctic demersal families sampled at the Weddell Sea shelf and deep-sea was investigated by comparing gut contents and FA patterns. Most prominent fatty acids found were 20:5(n-3), 16:0, 22:6(n-3) and 18:1(n-9), being also very abundant FAs in both amphipods and polychaetes sampled at the same stations (chapters 5 and 6).

The results of the gut content analyses on the investigated fishes shows that the majority of them shares a similar diet, with the main components being amphipods and polychaetes, as previously reported for many Southern Ocean benthic and benthopelagic fishes. In spite of the strong overlap of dietary composition found in the gut content, however, the FA composition reveals differences between the analysed species, and in certain cases also within species. The respective gut content is not always mirrored in the FA composition of

the same fish individual, indicating that the contents found in the guts provide only a snapshot of their diet. In several species, the FA patterns are more distinct between fish of different size than of different species, indicating an ontogenetic transition from planktivory to benthic feeding. This assumption is based on the measured values for zooplankton markers (20:1 and 22:1) being clearly higher in juveniles than in the larger individuals of the same species.

The overall relatively similar diet composition indicates that the different fish species at least to a large extend compete for the same food resource. One possible reason for the preferred ingestion of amphipods and polychaetes could be their exposed position when moving on the sea floor instead of being burrowed within the sediment like many other benthic taxa.

Besides diet investigations, biomass and production estimates can help to study the flow of energy within a food web. Therefore, abundant abyssal isopod families were used as model organisms to provide an example of such calculations (chapter 8). The measurement of secondary production plays a crucial role in the quantification of ecosystem dynamics, as production is one of the major pathways of energy flow (Edmondson, 1974). Secondary production in aquatic invertebrate populations can be analysed with methods based on a variety of parameters such as growth or mortality of identifiable cohorts or size-frequency classes (e.g., Hynes-Hamilton and Coleman, 1968). To obtain this information, certain prerequisites must be given, such as sampling at regular time intervals or good understanding of life histories (e.g. method by Banse and Mosher (1980) relying on the body weight of animals at their first sexual maturity). As measuring most of these parameters in a sufficient quantity, especially in deep-sea settings, is often difficult, time-consuming and expensive to conduct, empiric models can be used to estimate production e.g., developed by Brey (1990), considering mean annual biomass (B) and mean individual body mass (W) to estimate production in marine benthic invertebrates. However, various environmental parameters have been shown to influence growth rates, specifically temperature and water depth (Morin and Bourassa, 1992; Tumbiolo and Downing, 1994; Cartes et al., 2002). Therefore adjusted models accounting for these factors were developed.

To obtain information on one of the most diverse and often highly abundant groups within the deep-sea benthos, size and weight measurements were conducted for the most abundant isopod families sampled in the Weddell Sea during the ANDEEP-SYSTCO expedition to provide a dataset as a basis to conduct biomass and production estimates. Two empirical models were used to calculate annually production and P/B rates and the respective results compared.

The results obtained with the two models do not differ significantly from each other, and the lower values estimated by the Tumbiolo and Downing model can be assigned to the low

ambient temperatures. In general, biomass estimates of the analysed isopod species are relatively high. The highest individual biomass values are measured for the Munnopsidae and the lowest values for the Desmosomatidae and Haploniscidae. However, with the Desmosomatidae being dominant in terms of abundance at two of the sampled stations, here they make up the major proportion of calculated isopod biomass. Estimated individual production yielded highest values in the Munnopsidae and lowest values in the Desmosomatidae; however, again, depending on abundance, family-production estimates were highest for the Desmosomatidae at two of the sampled stations.

2.2 Isopoda in the deep Antarctic benthic food web

The results from the stable isotope analyses show that in some cases isopods of the same family (Munnopsidae) can cover several trophic levels, and FA results confirm the diversity of feeding habits displayed by these peracarid crustaceans (chapter 6). Feeding strategies range from mainly depending on phytodetritus (Macrostylidae), foraminiferivory (Munnopsidae), omnivory (Haploniscidae) to carnivory (Stenetriidae).

The indications for a preferred ingestion of foraminifera found in munnopsid isopods support results from previous studies. It seems possible, that species-specific preferences for different kinds of foraminifera exist; however, to elucidate such feeding interactions, further studies with high taxonomic resolution for both isopods and foraminiferans including appropriate methods are needed.

A surprising result of the stable isotope analysis were the comparably high stable isotope $\delta^{15}N$ value found in *Chaetarcturus* cf. *bovinus; Antarcturus bovinus* (Brandt and Wägele, 1988) and *Dolichiscus* cf. *meridionalis* (reaching up to 12.4‰), indicating high trophic position (chapter 4). This is in clear contrast to the reported filter-feeding lifestyle of these isopods, which suggests a low trophic position (Wägele, 1987). One explanation could be that they supplement their diet by predating on other organisms. However, comparable scenarios with very high $\delta^{15}N$ values have been found in some cases for other filter feeders, namely sponges (Iken et al., 2001; Janussen, pers. com.). This effect could have different causes, e.g., symbiotic bacteria capable of metabolising highly refractory material, which is then assimilated by the sponge, or the direct ingestion of highly suspended, N-rich material. Also Mintenbeck et al. (2007) detected a significant increase in $\delta^{15}N$ with water depth in suspension feeders in the Weddell Sea shelf and slope ecosystem. As suspension feeders at greater depth are restricted mostly to the fine POM fraction, they depend on small particles originating from fragmentation of large particles either in the water column or on the sediment surface made available by re-suspension. Further studies on this matter are needed to elucidate the mechanisms underlying this finding.

Concerning biomass and production estimates calculated for three abyssal sites, clear differences are found between the five isopod families studied (chapter 8). Highest biomass and production levels were found in the Munnopsidae, and their comparably high individual weights can be assigned to their rather compact body shape, in some cases accompanied by large body sizes. In the Desmosomatidae and Haploniscidae the lowest biomass values were estimated, while highest P/B ratios were calculated for the Desmosomatidae. Biomass estimates for the five investigated abundant isopod families can reach up to 37% of the estimated total Antarctic abyssal macrobenthic biomass values calculated by Brey and Gerdes (1998). Especially Munnopsidae with their high biomass and production values seem to play a key role in energy transfer.

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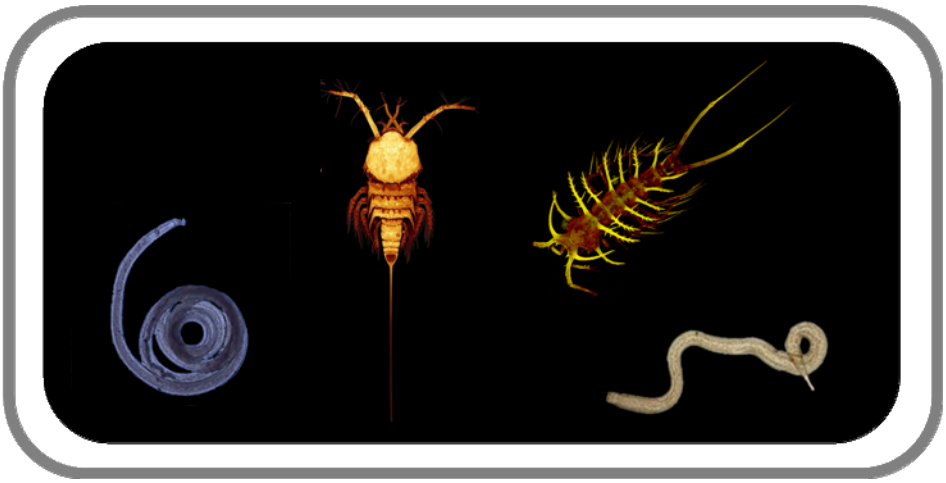
Chapter 3

Antarctic deep-sea meiofauna and bacteria react to the deposition of particulate organic matter after a phytoplankton bloom



Meiofaunal organisms: copepods (middle) and nematodes (sides).

Chapter 3 Antarctic deep-sea meiofauna and bacteria react to the deposition of particulate organic matter after a phytoplankton bloom

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Abstract

During the RV Polarstern cruise ANT XXIV-2 to the Southern Ocean and the Weddell Sea in 2007/2008 sediment samples were taken during and after a phytoplankton bloom at 52°S 0°E. The station located at 2960 m water depth was sampled for the first time beginning of December 2007 and revisited end of January 2008. Fresh phytodetritus originating from the observed phytoplankton bloom in the water column had reached the sea floor by the time of the second visit. Abundances of bacteria and most major meiofauna taxa did not change considerably between the two sampling dates. In the copepods, the second most abundant meiofauna taxon after the nematodes, the enhanced input of organic material did not lead to an observable increase of reproductive effort. However, a significant migration of meiofauna towards the sediment surface could be observed after the remains of the phytoplankton bloom reached the sea floor. Vertical shifts in meiofauna distribution between December and January could be explained by changing porewater oxygen concentration, total sediment fatty acid content and pigment profiles measured during our study. Higher oxygen consumption after the phytoplankton bloom has to be attributed to an enhanced respiratory activity of the living benthic component, as neither meiofauna nor bacteria reacted with an increase in individual numbers to the food input from the water column. Based on our results we assume that low temperatures and ecological strategies are the underlying factors for the delayed response of benthic deep-sea copepods to the modified environmental situation in terms of egg and larval production.

Keywords: Deep-sea sediments; Meiofauna; Bacteria; Vertical migration; Benthic organic carbon flux; Sediment community oxygen consumption (SCOC); Chloroplastic pigments; Fatty acids; Southern Ocean

1 Introduction

Carbon fixation by phytoplankton and the subsequent cascade of grazing, export to deeper water layers, and sedimentation on the seafloor, often referred to as the “biological pump” (Sarmiento and Le Quere, 1996), represents one of the major CO_2 sinks on earth and is the major energy source for abyssal life. The intensity of primary production in the euphotic zone, often thousands of meters above the seafloor, is directly coupled with the ecosystem structure and function in the abyss (Gooday and Turley, 1990; Graf, 1989, 1992; Sibuet et al., 1989; Smith et al., 2008; Tseytlin, 1987). Food limitation towards the abyss leads to a shift in community biomass distribution in benthic animals from the larger macro- and megafauna, which are dominating the biomass in shallower areas, to the smaller size classes of meiofauna and bacteria (Rex et al., 2006). The energy flow between the compartments of the ecosystem in the abyss therefore differs from the shelf and slope zones of the oceans.

Despite their low abundances in the abyssal deep-sea, macrofauna may nevertheless play a considerable role in the initial processing of fresh phytoplankton from the water column (Levin et al., 1999; Moodley et al., 2002; Witte et al., 2003a, b). Nonetheless, bacteria are the most important component for remineralisation and react immediately (Cahet and Sibuet, 1986; Moodley et al., 2002; Witte et al. 2003a) or with a distinct time lag (depending e.g. on water depth; Witte et al. 2003b) to the experimental deposition of organic matter. Likewise, foraminifera are important for both remineralisation and as intermediate link in the energy flow from phytodetritus to small metazoans (Gooday et al., 1996; Koho et al., 2008; Moodley et al., 2002; Nomaki et al., 2008; Witte et al., 2003b; Würzberg et al., in press).

The smallest components of metazoan life in the deep-sea are meiofauna; benthic animals classically defined as passing a 1 mm mesh and being retained on a 32 µm mesh for the deep-sea. In shallow water habitats meiofauna can significantly contribute to the regulation of benthic turnover and serve as food for secondary consumers (Coull, 1988; Giere, 1993). The reaction of deep-sea metazoan meiofauna to food input was investigated in several natural and experimental studies (Baguley et al., 2008; Danovaro et al., 2000; Gooday et al., 1996; Guilini et al., 2010; Ingels et al., 2010; Moodley et al., 2002; Shimanaga et al., 2000; Witte et al., 2003b) that unanimously report on the lack of response or considerable time lags between food presentation and measureable reactions, such as incorporation of food. Although respiration rates and oxygen consumption of benthic communities (SCOC) almost immediately increase when fresh food is available (e.g. Witte et al. 2003b), there is no evidence that meiofauna is involved in this. To date, only few studies that included the reaction of metazoan meiofauna to food input were carried out for abyssal depths (e.g. Baguley et al., 2008; Cahet and Sibuet, 1986; Ingels et al., 2010; Witte et al., 2003b).

While there is still very little known about the benthic microbial communities in the Southern

Ocean (De Wit et al., 1997), meiofauna communities of Antarctic deep-sea regions have been studied more intensely over the last years (Gutzmann et al., 2004; Herman and Dahms, 1992; Vanhove et al., 1995, 2004). However, both the reason for their success and their role as potential trophic link between sedimented organic matter and higher level consumers is still not known.

During the RV Polarstern-expedition ANT XXIV/2 to the Southern Ocean, the aim of the ANDEEP-SYSTCO project (ANTarctic benthic DEEP-sea biodiversity: colonisation history and recent community patterns – SYSTem COupling; Brandt and Ebbe, in press) was to link biological processes occurring in the water column to the functioning of benthic compartments of the deep Southern Ocean. Therefore, a deep-sea station located at the 0° meridian at 52° S (Fig. 1) was sampled while a phytoplankton bloom was ongoing in the water column and revisited after the remains of the bloom had settled to the ocean floor (visible as a greenish fluff layer on the sediment surface). This unique observation in the Southern Ocean deep-sea would allow new insights into the dynamics of the seasonal food supply to the benthic system and the subsequent activities of the benthic organisms. We were able to combine benthic C-flux measurements, oxygen penetration depth, oxygen consumption, pigment content, fatty acid composition in the sediment and bottom water particulate organic matter (POM), with bacterial and metazoan meiofauna abundances. Thus, it was possible to obtain an integrated view of seasonally induced processes at the Southern Ocean deep-sea floor.

With regard to previous studies on the population response of deep-sea meiofauna to food input (e.g. Danovaro et al., 2000) we did not expect metazoan meiofauna to react with immediate increase of reproduction to the enhanced organic matter supply directly after the settling event. However, as this had not been investigated before in the Southern Ocean we looked for changes in reproductive effort possibly triggered by the input of unforeseeable food in this otherwise adverse environment. Copepoda with their externally carried egg sacs and their easily recognisable offspring, the nauplius larvae, perfectly meet the purposes of a model organism for the study of the reaction of benthic meiofauna communities.

With our investigation we wanted to test the following hypotheses:

Meiofauna and bacteria in oligotrophic Antarctic deep-sea environments react immediately to seasonally deposited food input with (1) enhanced motile and respiratory activity and (2) visible reproductive effort (increase of bacterial cell numbers, production of eggs in copepods, increase of number of copepod nauplius larvae).

2 Materials and Methods

2.1 Selection of study area and study dates

During the RV Polarstern-expedition ANT XXIV/2 continuous measurements of chlorophyll a content in the upper water column were carried out using standard methods based on fluorescence. When enhanced chlorophyll a values indicated a local phytoplankton bloom (Herrmann and Bathmann, 2010), it was decided to start the sampling at this position in order to have a sufficient time lag between initial sampling and revisiting the station on the way back to South Africa. The selected station was located at 52°S between the Polar Front (PF) and the South Antarctic Circumpolar Current Front (SACCF) (Fig. 1).

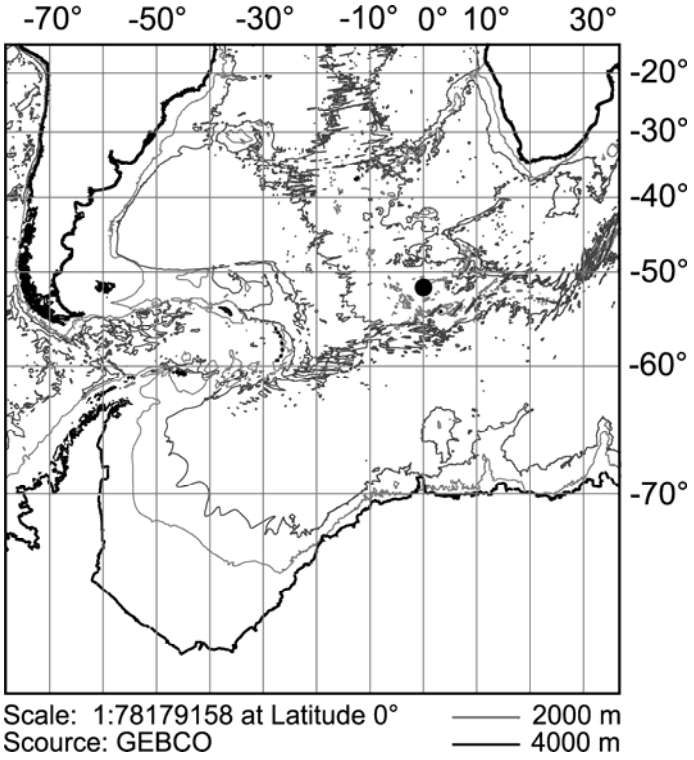

Fig 1 Map showing the location of stations PS 71/13 and PS 71/85 at 52°S 0°E in the Southern Ocean. During the RV Polarstern cruise ANT XXIV/2 the site was visited twice, before and after a phytoplankton bloom had reached the sea floor.

The first deep-sea sediment sampling took place the 5th and 6th of December 2007 during the phytoplankton bloom (Station PS 71/13, between 52° 0.41' S, 0° 1.08' E and 52° 2.25' S, 0° 1.11' W, 2963–2990 m). The site was revisited and sampled again the 26th and 27th of January 2008, 52 days after the bloom was observed in the surface water layer (Station PS 71/85, between 52° 1.14' S, 0° 0.07' E and 52° 1.53' S, 0° 0.16' E , 2964–2995 m; see also Tab. 1 and chapter 2.5). The gear deployed for this study were a multicorer, a free-falling lander system equipped with oxygen microprofiler systems and a carousel bottle water sampler.

2.2 Sample collection and storage

The multicorer (MUC, internal core diameter 9.4 cm, 69.4 cm^2) was deployed two times at each sampling date (Tab. 1). Sediment cores were used for meiofauna and bacteria countings as well as for measurements of biotic and abiotic sediment factors.

For the meiofauna community analysis three cores per deployment were sliced (0–1, 1–2, 2–3, 3–4, 4–5, 5–7, 7–10, 10–15, and 15–20 cm sediment depth) and preserved in a borax-buffered formaldehyde-seawater solution to a final concentration of 4%. Sediment for bacteria counts was subsampled from one core per MUC-deployment to a depth of 5 cm using 10 ml-syringes with cut off tips (diameter 1.4 cm). Syringe samples were immediately frozen at -20°C.

One core per sampling date was immediately cut into 1 cm sediment horizons (the first centimeter cut in two slices 0–0.5 and 0.5–1 cm) to a depth of 25 cm and frozen at -80°C for pigment analyses. Later in the laboratory these samples were stored at -30°C. A second core was sliced (0–1, 2–5 and 6–10 cm) and stored at -80 °C for fatty acid analysis. Only the solid component of this sediment core was sampled, while the supernatant was discarded.

Bottom water was taken by means of a carousel bottle water sampler. At station PS 71/13 water was sampled 39 m above ground and at station PS 71/85 36 m above ground. Samples of particulate organic matter (POM) were collected by filtering 14 (station 13) respectively 18 (station 85) litres of water to a precombusted (4h for 400 °C) GF/C filter (approx. 1.2 µm retention size). Filtering was conducted at 300 mbar and stopped when a clear colouring appeared on the filter. Two filters per station were frozen at -80°C for analysis of fatty acid composition.

2.3 Bacteria and meiofauna sample processing

The syringe samples for bacterial counts were sliced (0–1, 1–2, 2–3, 3–4, 4–5 cm sediment depth) just before further analysis. Total bacterial counts were performed using acridine orange direct count (AODC) (variant on Hobbie et al., 1977). Replicate (n = 2) sediment samples of ca. 0.5–1 g were transferred into sterile test tubes and fixed to a final volume of 5 ml with prefiltered (0.2 µm pore size) and buffered 2% (v/v) formalin after thawing. Tetrasodium pyrophosphate was added to a final concentration of 5 mM and the samples were incubated in the dark for 15 min. The samples were then sonicated for 3 minutes with a 30 second interval each minute, during which they were shaken manually. After centrifugating the samples for 3 min at a maximum of 400 rpm the supernatants were diluted 20 times with sterile seawater. For AODC, the samples were stained for 5 min with an acridine orange working solution of 0.025% (w/v) and filtered on Millipore polycarbonate 0.2 µm-pore-size filters which were stained in an irgalan black solution (Van Duyl and Kop, 1990). Filters were washed 3 times with 5 ml of sterilized Milli-Q water and mounted on microscope slides. Filters were analyzed using epifluorescence microscopy (Zeiss Axioskop 50). For each slide at least 10 optical fields were observed and at least 200 cells were counted per filter.

The fixed meiofauna samples were washed with tap water through a 32 µm mesh sieve (no upper sieve size used). Meiofauna and organic material were extracted from remaining sand particles by centrifugation with a colloidal silica polymer as the flotation medium (H. C. Stark, Levasil 200/40%, ρ = 1.17) and kaolin to cover heavier particles (McIntyre and Warwick, 1984). Centrifugation was repeated three times at 4000 rpm for six minutes respectively. After each centrifugation the floating matter was decanted and rinsed with tap water. The supernatant containing the meiobenthic organisms was thereafter stained with Rose Bengal before manually sorting to a higher taxon level using a Leica MZ 12.5 stereo microscope. The individual numbers of higher taxa, copepod nauplii, and copepods carrying eggs were counted and abundance values taken for further analyses.

For the interpretation of the vertical distribution bacteria and meiofauna individual numbers were converted into relative abundances per sediment horizon. In order to obtain these values, the sum of individuals of the complete core was taken as 100 % and percentages per slice calculated.

2.4 Sediment parameters

Pigment analyses were performed by high performance liquid chromatography (HPLC). For analytical preparation, 1 cm^3 of sediment was mixed with 100 µl of internal standard

(canthaxanthin) and 1 ml of glass beads (1 mm diameter). This mixture was extracted 3 times with 3 ml acetone in a cell mill for 3 minutes. After centrifugation (10 minutes at 4000 U min^{-1} and 0°C) the extracts were unified and concentrated on an Alltech C18™ solid phase extract clean column. Pigments were eluted with 100% acetone and further concentrated under nitrogen atmosphere in the dark to a final volume of 0.3 ml. Finally, pigments were measured with a Waters™ HPLC system according to Hoffmann et al. (2006).

Fatty acid analyses were carried out for three random subsamples (ca. 50–100 mg) per depth layer (0–1, 2–5 and 6–10 cm). Extraction was performed with minor modifications as described by Folch et al. (1957) using ultrasonic disruption in dichloromethane:methanol (v:v/ 2:1) and a washing procedure with 0.08% aqueous KCl solution. Fatty acid composition was determined with modifications as described by Kattner and Fricke (1986). Fatty acids were converted to their methyl ester derivatives (FAME) using 3% sulphuric methanol. The composition was analysed with a gas chromatograph (HP 6890A) equipped with a programmable temperature vaporizer injector (Gerstel® CIS4plus) and a DB-FFAP column. FAMEs and free alcohols were detected by flame ionisation and identified by comparing retention times with those derived from standards of known composition. For quantification of fatty acids 23:0 was used as internal standard.

2.5 In situ and ex situ measurements of oxygen micro profiles

At both sampling dates a lander system equipped with a 3D- (station PS 71/13-2) and a 1D-oxygen microprofiler system (PS 71/85-1) was deployed. The two lander stations were located in close vicinity to the stations sampled with the MUC (Tab. 1).

The 3D-oxygen microprofiler system is not restricted to driving sensors vertically into the sediment but is able to displace its sensor array (up to 12 Clark type oxygen microsensors) horizontally in order to measure cascades of microprofiles over a target area of approximately 30 x 35 cm. The 1D-microprofiler was equipped with up to 5 pressure compensated Clark type oxygen sensors that were pre-calibrated according to Sauter et al. (2001). During approximately 5–6 hours at the sea floor, the sensors were lowered through the water-sediment interface into the sediment with a vertical resolution of up to 0.25 mm. For porosity determination, a resistivity sensor (formation factor probe) was used. Additional *ex situ* oxygen measurements were performed in the laboratory on board using sediment cores collected with the MUC (see Sachs et al., 2009).

Oxygen microprofiles were obtained as raw data sets from both *in situ* and *ex situ* measurements (*in situ*: mV, *ex situ*: pA values) and had to be translated to oxygen values via the following steps: Correction of sensor drift if necessary, adjustment of sensor height relative to the water/sediment interface, translation of raw signal into oxygen concentration

on the basis of a two point calibration (bottom water oxygen concentration by Winkler titration, and sensor zero reading from oxygen-free water.

Table 1 Deployments of the lander and the multicorer at the 52°S station during the SYSTCO expedition (RV Polarstern cruise ANT XXIV-2). Sampling date, position (latitude and longitude), water depth (according to winch rope length), sediment description and cores used for this study are given.

Station Code/Location	Date	Lat	Long	Depth [m]	Sediment (MUC)	Core distribution (MUC)
52° S						
Lander						
PS 71/13-2	05.12.2007	52° 0.41' S	0° 1.08' E	2990		
MUC						
PS71/13-12	06.12.2007	52° 2.22' S	0° 1.04' W	2963	foraminiferan/ diatom ooze	3 cores meiofauna 2 cores oxygen/sediment 2 cores sediment analyses 3 syringes sediment analyses
PS71/13-14	06.12.2007	52° 2.25' S	0° 1.11' W	2970	foraminiferan/ diatom ooze	3 cores meiofauna 2 cores oxygen/sediment 2 cores sediment analyses 3 syringes sediment analyses
52° S revisited						
Lander						
PS 71/85-1	26.01.08	52° 1.14' S	0° 0.07' E	2995		
MUC						
PS71/85-5	26.01.08	52° 1.20' S	0° 0.20' E	2965	foraminiferan/ diatom ooze with greenish flufflayer	3 cores meiofauna 2 cores oxygen/sediment 1 core sediment analyses 3 syringes sediment analyses
PS71/85-7	27.01.08	52° 1.53' S	0° 0.16' E	2964	foraminiferan/ diatom ooze with greenish flufflayer	3 cores meiofauna 1 core sediment analyses 3 syringes sediment analyses

For the determination of organic carbon fluxes to the seafloor, at first the diffusive oxygen uptake was calculated from the porewater oxygen microgradient at the sediment surface using the software PROFILE of Berg et al. (1998). The oxygen uptake was then transferred to the amount of carbon aerobically respired using a modified Redfield ratio according to Anderson and Sarmiento (1994). Whereas the organic carbon flux reflects a “snapshot” of food supply at the time of measurement, oxygen penetration depth (OPD) changes much more slowly on a time scale of years, in particular in the oligotrophic deep Southern Ocean. Therefore OPD was determined as a long term measure of carbon supply to the seafloor.

For a more detailed description of the methods see Sauter et al. (2001) and Sachs et al. (2009).

2.6 Data analysis

Principal component analysis (PCA) was used to detect and visualise patterns in the composition of individual fatty acids in sediment and bottom water samples (PRIMER v6 package; Clarke and Gorley, 2006).

Meiofauna abundances are represented by median values as well as minima and maxima to describe the range of data. Pairwise *t*-tests on the two stations (PS 71/13 versus PS 71/85) were carried out for relative abundance data of each sediment horizon, for percent of copepods with eggs per total copepods and for percent of nauplii per total copepods (SigmaPlot 11). When *t*-tests could not be applied because of failing tests on normality and equal variance a Mann-Whitney Rank Sum test was used instead.

Multivariate meiofauna community analyses were carried out on abundance data of higher taxa and copepod nauplii from the first centimetre of sediment using the PRIMER v6 package (Clarke and Gorley, 2006). Bray-Curtis similarity analysis was conducted and visualised with the aid of non-metric multi-dimensional scaling MDS. The factor “station” was applied for the analysis of similarities ANOSIM (one-way analysis).

3 Results

3.1 Sediment parameters and bottom water POM

The assumption that the phytoplankton observed in the water column at the beginning of December should have been sunken to the deep-sea floor by end of January was first confirmed visually. Fluffy green material was observed on the sediment surface in all multicorer samples during the second visit (station PS 71/85).

Chlorophyll-a (Chl-a) content at the sediment surface (0–0.5 cm) was eight times higher at the end of January (41.02 ng g^{-1} TG) compared to the values measured beginning of December (5.13 ng g^{-1} TG; Fig. 2B). The content of phaeopigments (Phaeo: sum of phorbid-a, p-phorbid-a, phytin-a and p-phytin-a) had increased 33 times by the end of January (1334.85 ng g^{-1} TG) compared to the values from December (40 ng g^{-1} TG; Fig. 2C). Pigment content was gradually declining with sediment depth and so was pigment quality. Between 3 and 5 cm sediment depth the values of the revisited station equalled those of the first sampling date.

Pore-water oxygenation showed a steeper decrease within the first centimetres of the sediment after the organic material had settled (Fig. 2A). This indicates enhanced sediment community oxygen consumption (SCOC) after organic matter deposition (0.400 mmol O_2 m^{-2} d^{-1} before and 1.102 mmol O_2 m^{-2} d^{-1} after the bloom). Carbon fluxes derived from oxygen measurements were found to be moderate to low at the beginning of December (station PS 71/13; 3.3 mg C m^{-2} d^{-1}). After 7 weeks fluxes were elevated by a factor of ~3 when the second visit to the site took place (station PS 71/85; 9.1 mg C m^{-2} d^{-1} after the bloom; Fig. 2A). The values obtained *in situ* at both stations were confirmed by laboratory measurements carried out on sediment cores from the MUC. The differing fluxes were accompanied by comparable maximum penetration depths of the oxygen (OPD) at the two sampling dates. The OPDs of several decimetres (42–47 cm) indicated a low long-term (in terms of several years) average flux of organic matter to the seafloor at this site (see also Sachs et al., 2009).

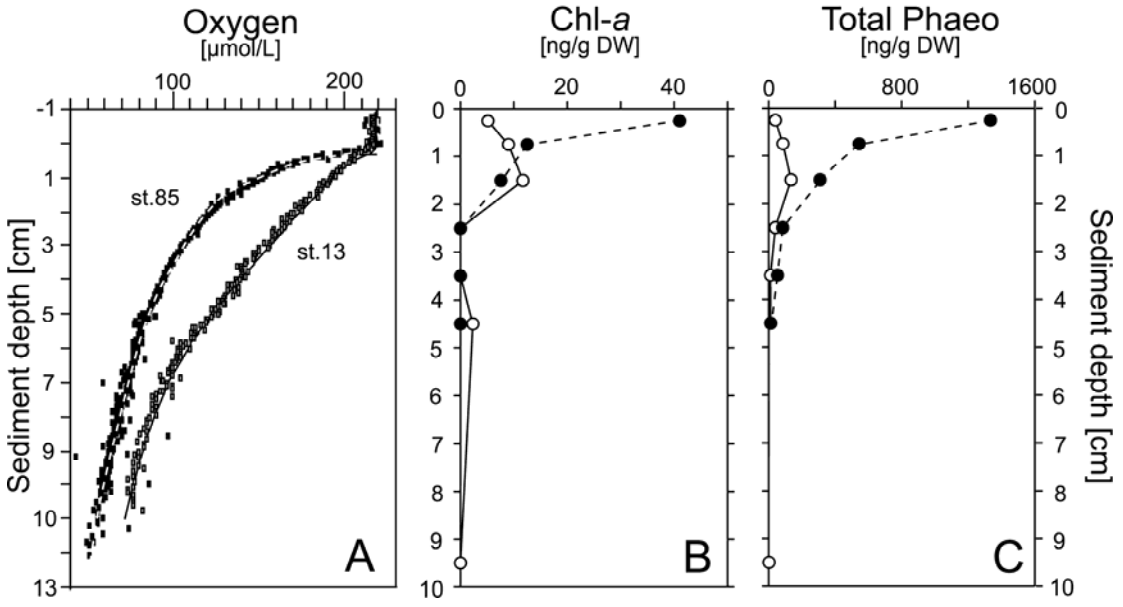

Fig 2 Seasonal changes in porewater oxygen and pigment profiles at the two studied locations south of the Polar Front at 52°S 0°E, ~3000 m depth: A. Oxygen content in the sediment before (st. 13) and after phytoplankton bloom (st. 85), benthic C_{org} fluxes derived from (A) increased by a factor of ~3 (station PS 71/13: 3.3 mg C m^{-2} d^{-1}; station PS 71/85: 9.1 mg C m^{-2} d^{-1}); B. Content of chlorophyll-a and C. Total phaeopigments before (white dots; station PS 71/13) and after phytoplankton bloom (black dots; station PS 71/85).

Total sediment fatty acid content (Fig. 3) for the three analysed sediment layers 0–1, 2–5 and 6–10 cm of station PS 71/13 decreased from 0.84 µg g^{-1} to 0.38 and 0.38 µg g^{-1}, respectively. For station PS 71/85 values from 1.01 µg g^{-1} to 0.25 and 0.19 µg g^{-1} were measured (µg fatty acid g^{-1} dry sediment, mean of three subsamples for each layer). The ratio of long-chain (> C21) to short-chain fatty acids was low, especially in the deeper sediment layers (2–5 and 6–10 cm; Tab. 2). The same accounts for the proportion of polyunsaturated fatty acids (PUFA) compared to monounsaturated (MUFA) and saturated fatty acids (SFA). PUFA content was highest in the first sediment centimetre when the station was revisited (Fig. 4). The fatty acids that were generally dominant in the sediment samples were 16:0, 18:1(n-9) and 18:0, followed by 18:1(n-7) and 16:1(n-7) (Tab. 2).

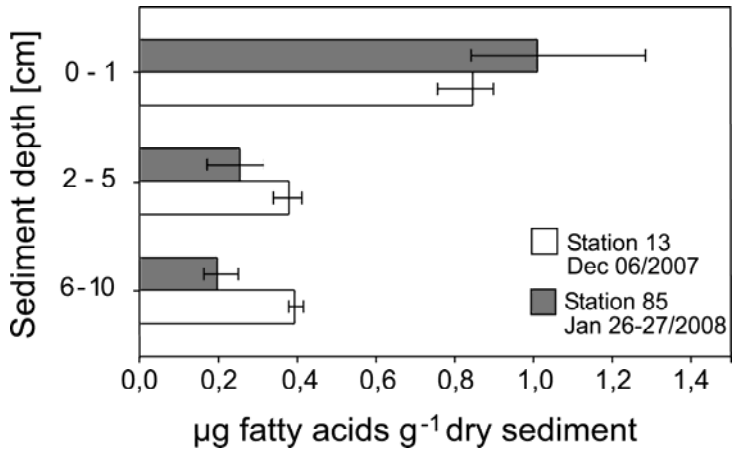

Fig 3 Total fatty acid content of sediment layers 0–1 cm, 2–5 cm and 6–10 cm at stations PS 71/13 and PS 71/85 (µg fatty acid g^{-1} dry sediment). Mean values (box), maximum and minimum (right and left end of bar) of three subsamples per sediment horizon given.

Phytoplankton fatty acid markers (e.g. 20:5(n-3), 22:6(n-3)) were detected in higher amounts in the first centimetre after the phytoplankton bloom occurred (Tab. 2). The ratio of 18:1(n-9) to 18:1(n-7) was higher at the first and lower at the second sampling date after the phytoplankton bloom. The bacterial marker fatty acids 15:0 and 17:0 were most abundant in the first sediment centimetre at station PS 71/85.

The findings for the composition of the individual fatty acids are visualised by a PCA (Fig. 5) where the two first components (PC1, PC2) together explain 93% of the variation between the different sediment samples. The main contributors that explain the separation of the sediment samples of station PS 71/13 and PS 71/85 are 16:0 (-0.615), 18:1(n-9) (-0.489), 18:0 (-0.484) and 18:1(n-7) (-0.223) for PC1 and 18:1(n-9) (-0.788), 18:1(n-7) (-0.302), 18:2(n-6) (-0.273), 20:5(n-3) (-0.253) for PC2. The most visible differences were detected between the samples of the first sediment centimetre of the two investigated stations.

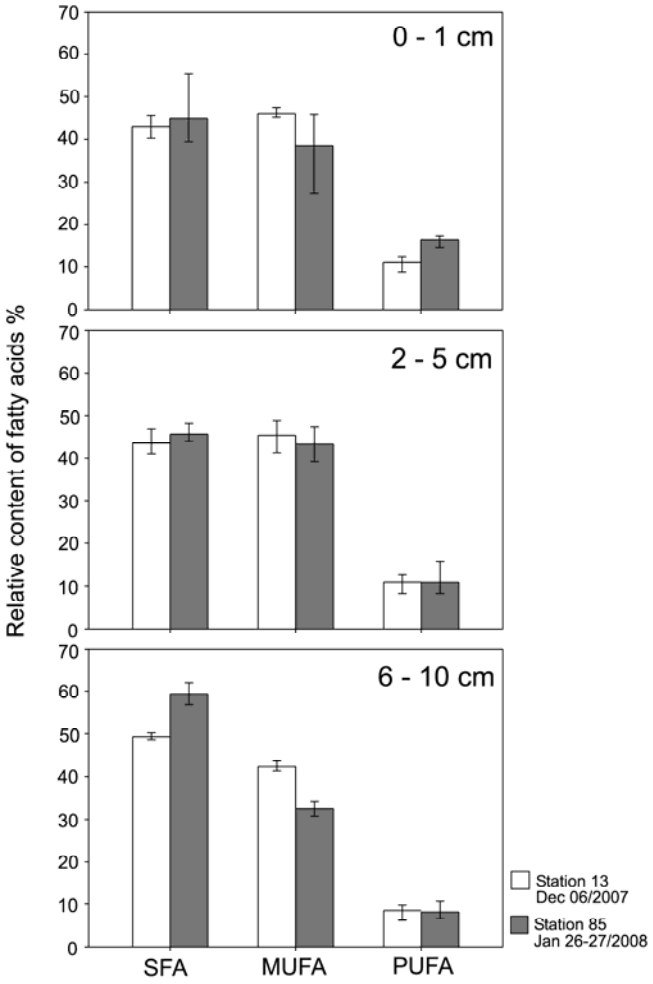

Fig 4 Proportion of saturated (SFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids in A. 0–1 cm; B. 2–5 cm; and C. 6–10 cm sediment depth for stations PS 71/13 and PS 71/85. Fatty acids that contributed less than 2% of total fatty acids were not taken into account. Results are presented as % of total fatty acids. Mean values (box), maximum and minimum (upper and lower end of bar) of three subsamples per sediment horizon given.

The total fatty acid content of the bottom water POM samples was relatively even at both sampling dates (stat. 13: 0.073 µl/l^{-1}, stat. 85: 0.064 µl/l^{-1}). Most abundant fatty acids were 16:0, 18:0, 18:1(n-9) but during the second visit (station 85), phytoplankton marker fatty acids (e.g. 20:5(n-3), 22:6(n-3)) adopted a more prominent role (Tab. 2).

Table 2 Fatty acid composition (mean of subsamples) of bottom water particulate organic matter (µg l^{-1}) and sediment (0–1, 2–5, 6–10 cm; µg g^{-1} dry sediment) for stations PS 71/13 and PS 71/85.

	Bottom water POM		**Sediment horizons**					
	[µg l^{-1}]		**[µg g^{-1} dry sediment]**					
Fatty acids	**13**	**85**	**13 0-1 cm**	**13 2-5 cm**	**13 6-10 cm**	**85 0-1 cm**	**85 2-5 cm**	**85 6-10 cm**
14:0	0,004	0,0026	0,0206	0,0183	0,0176	0,0392	0,0101	0,0089
15:0	0,003	0,0016	0,0191	0,0085	0,01	0,0253	0,0061	0,0053
16:0	0,0256	0,0218	0,2115	0,0989	0,1097	0,234	0,0725	0,0633
16:1(n-7)	0,0004	0	0,0565	0,042	0,0168	0,0534	0,0216	0,0082
16:1(n-9)	0,0067	0,0019	0,0419	0,0263	0,0262	0,035	0,0198	0,0134
17:0	0,0013	0,0006	0,0203	0,0057	0,0114	0,0426	0,0032	0,0033
18:0	0,0161	0,0162	0,1389	0,0438	0,0447	0,1571	0,029	0,0269
18:1(n-7)	0	0	0,0673	0,0283	0,0218	0,0827	0,0167	0,0067
18:1(n-9)	0,01	0,0062	0,1889	0,0622	0,0873	0,1477	0,0432	0,0363
18:2(n-6)	0,0024	0,0023	0,0299	0,0221	0,0241	0,0613	0,0117	0,0109
20:4(n-6)	0	0	0,0171	0,0053	0,0106	0,0378	0,0083	0,0046
20:5(n-3)	0,0007	0,0026	0,0169	0,0057	0,0038	0,052	0,0079	0,0066
22:5(n-3)	0,0017	0,0061	0,0164	0,0103	0,0087	0,034	0,0041	0,0026
22:6(n-3)	0,0008	0,0023	0	0,0014	0	0,0075	0	0

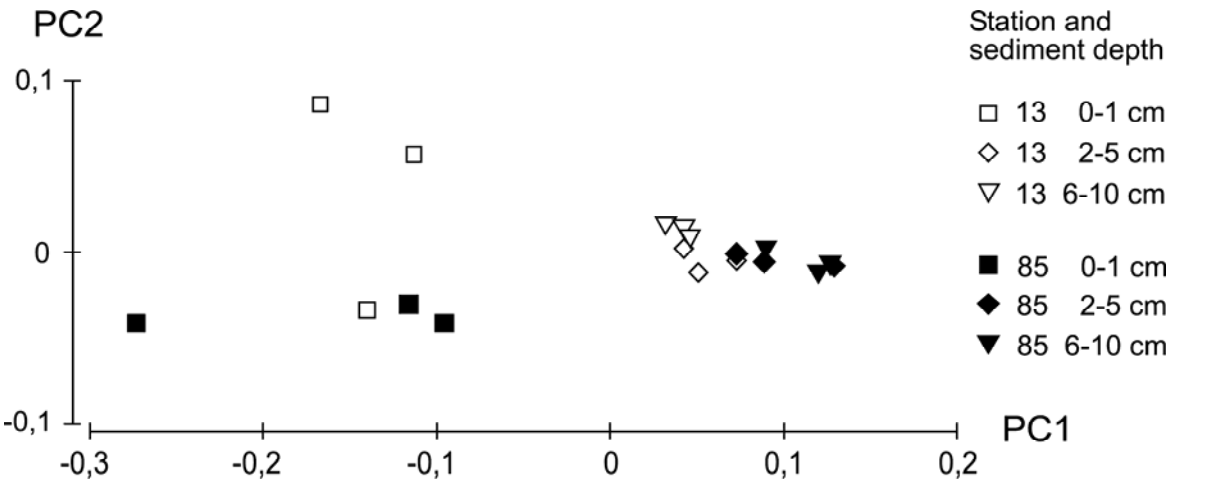

Fig 5 Principal component analysis of the individual fatty acid composition of the sediment (0–1 cm, 2–5 cm, 6–10 cm) at stations PS 71/13 and PS 71/85. The first two components together explain 93% of the variation observed (PC1 = 86.8%, PC2 = 6.1%).

3.2 Bacterial countings

In total, the first station PS 71/13 had a higher standing stock of bacteria (7.92×10^8 and 1.47×10^9 cells in 5 cm^{-3} sediment from 0–5 cm depth) than station PS 71/85 (6.47×10^8 and 3.35×10^8 cells 5 cm^{-3} sediment from 0–5 cm depth). Station PS 71/85 showed in all except two sediment horizons (sample 85-5, 0–1 cm: 4.12×10^8 cells cm^{-3}; 4–5 cm: 3.37×10^7 cells cm^{-3}) lower numbers of bacteria than both respective samples of station PS 71/13 (Tab. 3). Bacterial numbers gradually decreased with sediment depth in the two cores of station PS 71/13 but the decline was not as abrupt as in the cores from station PS 71/85. The plot of the relative abundances of bacteria versus sediment depth (Fig. 6) shows that after the blooming event end of January a higher percentage of bacteria was found in the upper centimetre of the sediment as compared to the first sampling date. Contrary to station PS 71/13, at station PS 71/85 relative bacterial density reached a minimum already in the 2–3 cm layer. The minimum at station PS 71/13 was reached in deeper horizons.

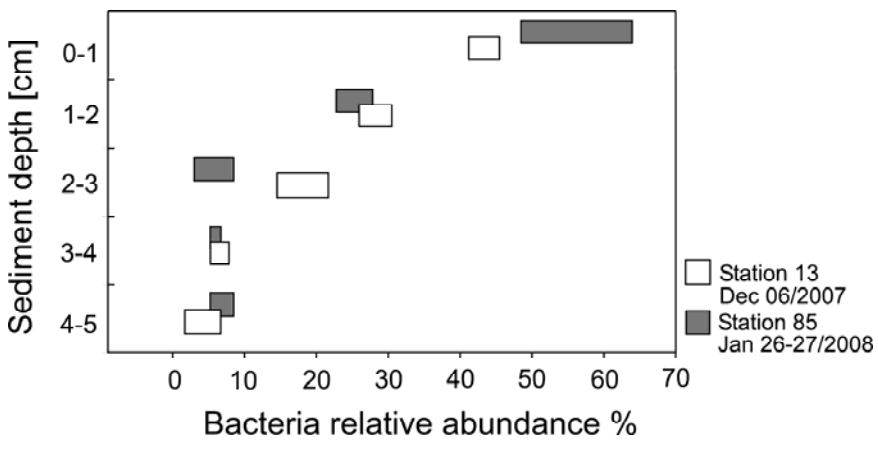

Fig 6 Relative abundances of bacteria in 5 sediment horizons of subsamples taken from MUC cores sampled at 52°S 0°E: station PS 71/13 (white boxes), before the decaying phytoplankton reached the sea floor; station PS 71/85 (grey boxes), after the settlement event. Left and right border of boxes represent the values obtained from the 2 subsamples taken per horizon and sampling date.

3.3 Meiofauna abundances and community analysis

The total number of meiofauna organisms varied between 10,120 and 4,111 individuals per core (0–20 cm sediment depth). At station PS 71/13 a median of 788.14 ind. 10 cm^{-2} (min. 662.99 ind. 10 cm^{-2}; max. 1458.26 ind. 10 cm^{-2}) and at station PS 71/85 a median of 658.95 ind. 10 cm^{-2} (min. 592.38 ind. 10 cm^{-2}; max. 725.09 ind. 10 cm^{-2}) was counted for the complete sediment profiles (Tab. 4). There was no statistical difference between the total number of individuals of the two sampling dates (Mann-Whitney Rank Sum test, p = 0.065).

Table 3 Total number of procaryote cells per cm^3 sediment from 5 sediment horizons sampled at 52°S 0°E (2963–2970 m) during the Polarstern cruise ANT XXIV-2: station PS 71/13 (2 deployments), 12/06/2007, before the phytoplankton bloom reached the sea floor and station PS 71/85 (2 deployments), 01/26–27/2008, after the settlement of the bloom.

Total no. of bacteria per cm^3 sediment Sediment depth [cm]	Station PS 71/13-12	PS 71/13-14	PS 71/85-5	PS 71/85-7
0–1	3,57E+08	6,08E+08	4,12E+08	1,62E+08
1–2	2,06E+08	4,46E+08	1,47E+08	9,30E+07
2–3	1,15E+08	3,17E+08	1,97E+07	2,82E+07
3–4	6,00E+07	7,70E+07	3,45E+07	2,26E+07
4–5	5,29E+07	2,72E+07	3,37E+07	2,85E+07
Total in 5 cm^3	7,92E+08	1,47E+09	6,47E+08	3,35E+08

Nematoda were the most abundant taxon with a relative abundance on average of 83.1% followed by copepod nauplii (counted separately to elucidate ecological aspects, 8.1%) and Copepoda (including adults and copepodids, 5%). Other taxa found were Annelida, Ostracoda, Rotifera, Tantulocarida, Gastrotricha, Tardigrada, Loricifera, Isopoda, Kinorhyncha, Tanaidacea, Bivalvia, Acari, Amphipoda, Cumacea and Gastropoda (order indicates decreasing total individual numbers with a maximum of 0.84% of occurrence).

Metazoan meiofauna showed a migration tendency towards the sediment surface after the phytoplankton remains had reached the sea floor (Fig. 7). This finding is supported by the results of the pairwise *t*-tests for the relative meiofauna abundances. In the first centimetre of the sediment the difference between the mean values of the two stations was greater than would be expected by chance and was statistically significant (p = 0.040).

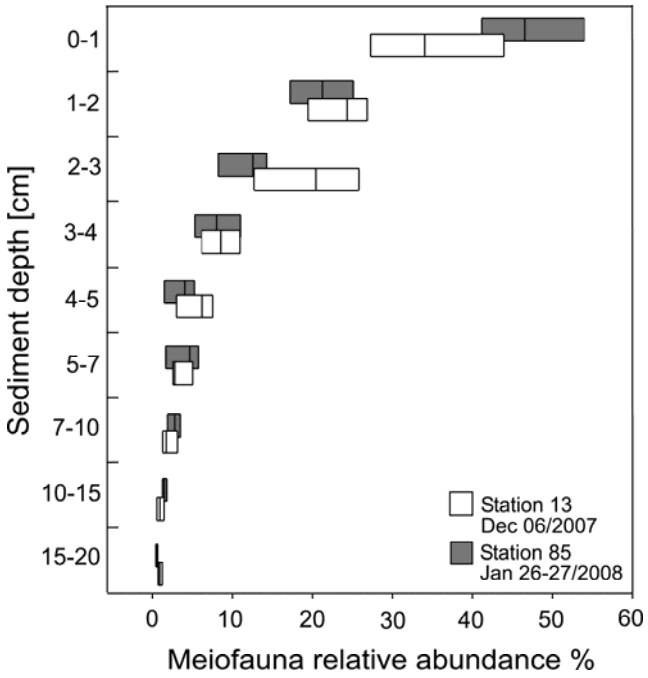

Fig 7 Relative meiofauna abundances in 9 sediment horizons from MUC cores sampled at 52°S 0°E: station PS 71/13 (white boxes, 6 MUC-cores included), before the phytoplankton bloom reached the sea floor and station PS 71/85 (grey boxes, 6 MUC-cores), after the settlement event. Boxes indicate median value (vertical black line within the box) and 25th and 75th percentile (left and right border of box).

Table 4 Median individual numbers (Med) of total meiofauna, major meiofauna taxa, copepods with egg sacs and copepod nauplii per MUC-core (69.4 cm^2) from six cores per station (0–20 cm sediment depth, minima (Min) and maxima (Max) included). Two MUC deployments were carried out at each sampling date at 52°S 0°E (2963–2970 m): station PS 71/13 (12/06/07) before and station PS 71/85 (01/26–27/08) after the decaying phytoplankton reached the sea floor.

Station	PS 71-13			PS 71-85		
Individuals per core	**Med**	Min	Max	**Med**	Min	Max
Acari	0	0	2	0	0	1
Amphipoda	0	0	0	0	0	1
Annelida	37	22	54	50	36	70
Bivalvia	1	0	2	1	0	2
Copepoda (adults and copepodids)	292.5	192	339	258.5	201	313
therein copepods with egg sac	7	5	11	3.5	2	11
Copepod nauplii	439	308	540	397	348	643
Cumacea	0	0	0	0	0	1
Gastrotricha	7	3	9	11	5	16
Gastropoda	0	0	0	0	0	1
Isopoda	3	1	4	2.5	1	5
Kinorhyncha	1.5	0	4	3	0	6
Loricifera	2.5	1	5	5	1	8
Nematoda	4621.5	3909	8528	3794	3210	4024
Ostracoda	33.5	27	37	25	18	44
Rotifera	46	19	78	14	2	21
Tanaidacea	1.5	0	3	3	0	5
Tantulocarida	1.5	0	3	16	2	119
Tardigrada	3	1	10	10	3	17
Total individuals	5469.5	4601	10120	4573	4111	5032
% Copepoda with eggs	2.42	1.79	4.4	1.54	0.73	3.51
% nauplii per Copepoda	157.6	135.09	176.56	162.68	139.76	205.43

Additionally, meiofauna individual numbers decreased more steeply within the first three centimetres in most of the cores from PS 71/85 as compared to the earlier sampling date PS 71/13 (Fig. 7). Pairwise *t*-tests of the different sediment horizons showed that Nematoda are mainly responsible for the observed pattern, while Copepoda (Fig. 8; adults and copepodides) and copepod nauplii did not follow the migration tendency to the sediment surface.

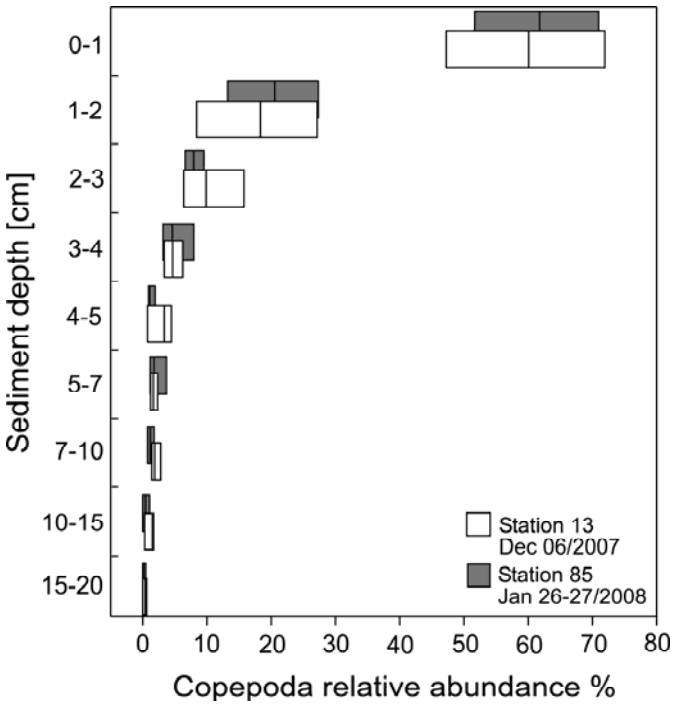

Fig 8 Relative copepod abundances in 9 sediment horizons from multicorer cores sampled at 52°S 0°E: station PS 71/13 (white boxes, 6 MUC-cores included), before the phytoplankton bloom reached the sea floor and station PS 71/85 (grey boxes, 6 MUC-cores), after the settlement event. Boxes indicate median value (vertical black line within the box) and 25th and 75th percentile (left and right border of box).

No differences in the meiofaunal community composition (0–1 cm horizon, selected because of significant differences in *t*-test, standardised by total) were observed before and after the phytoplankton bloom settled (Fig. 9). This result is confirmed by an analysis of similarity (ANOSIM) (absolute individual numbers; Global R = 0.067; p = 0.22). Although the highest nematode densities were observed beginning of December 2007 (Station PS 71/13, Tab. 4), this had no influence the meiofaunal community structure as a whole. Individual numbers of most of the major taxa did not change considerably between the two sampling dates.

For the copepods, the second most abundant taxon after the nematodes, favourable changes in the environment did not lead to a visual increase of the reproductive effort during the experimental time. Copepods with eggs (Fig. 10), expressed as a percentage of total copepods (Tab. 4), were less in January (median 1.54 %) than in December (median 2.42 %). The nauplii, the first larval stages of copepods, did not increase in total number either but

their percentage as compared to total copepods was slightly higher after the blooming event (Tab. 4). However, a *t*-test for the relative numbers of copepods with eggs and a Mann-Whitney Rank Sum test for the number of nauplii per copepods did not detect statistically significant variations between station PS 71/13 and station PS 71/85.

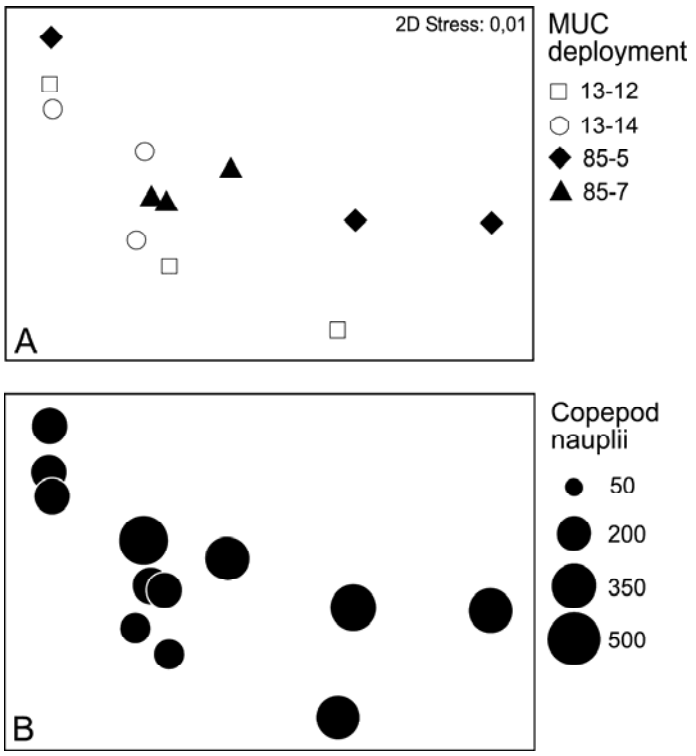

Fig 9 (A) MDS of the Bray Curtis similarity of the meiofauna community data (standardised by total) from the 0–1 cm sediment horizon of single MUC-cores sampled at 52°S 0°E before (station PS 71/13) and after (station PS 71/85) the decaying phytoplankton reached the sea floor. (B) Individual numbers of copepod nauplii per core shown as bubble plot.

4 Discussion

4.1 Changes in the sediment

Oxygen penetration depth (OPD) is a long term indicator for organic carbon supply to the ocean floor. The sediments of the abyssal Southern Ocean are generally well oxygenated and show great OPDs (Sachs et al., 2009). Thus, the variation in pore-water oxygen depth distribution obtained by the measurement of oxygen micro profiles was important for the understanding of input and recycling of organic material into this deep-sea system.

Different carbon fluxes derived from oxygen measurements before and after the phytoplankton bloom coincided with nearly similar OPDs at both dates. The observed bloom beginning of December and the concurrent carbon flux measurements at the seafloor clearly showed the correlation of surface production with benthic fluxes. Topographic characteristics of the sediment surface in station PS 71/13 may have accounted for an observed subsurface variability of the oxygen profiles of the first station (3D profiler). This is however unlikely as the meiofaunal and bacterial distributions of relative abundances with depth follow the same patterns as the oxygen profiles in both stations (see below).

Results of the pigment analyses clearly showed that the phytoplankton bloom observed in the water column at the beginning of December had reached the seafloor at 3000 m water depth by the end of January. The high concentration of chlorophyll-a and the amount of the material indicated that there was a relatively short time span between settlement and sampling. Phytodetritus forms aggregates that can settle at a rate of 100–150 m per day (Gooday, 1993 and references therein). As expected, pigment content was gradually declining with sediment depth. However, only low rates of vertical mixing were observed which is typical for deep-sea sediments with low abundances of macrofauna (compare Witte et al., 2003a, b).

The fatty acid content of the deeper sediment layers (2–5 and 6–10 cm) was higher at station PS 71/13 than at station PS 71/85. This indicates a patchy input of organic matter during former sedimentation events. Results on patchily distributed standing stocks of bacteria and meiofauna in the investigated deep-sea area may validate these findings (compare 4.2). However, the difference between the fatty acid content observed in the first centimetre and the amount in the deeper sediment layers was more pronounced in station PS 71/85 than in station PS 71/13. On the one hand the high content of fatty acids in the first centimetre of station PS 71/85 indicates the recent input of organic material. On the other hand the discrepancies between station PS 71/85 and station PS 71/13 regarding the deeper sediment layers indicate a lower organic input during previous sedimentation events at station PS 71/85. The total fatty acid content of the bottom water POM samples showed no strong differences between both sampling dates and was in the same range as values measured in 3000 meters depth in the Bellingshausen Sea (Antarctica) by Fileman et al. (1998).

Fatty acids are known to be selectively degraded in the marine environment (Reemtsma et al., 1990) and the total concentration of fatty acids is markedly reduced with water depth. However, in our study significant levels of labile fatty acids were found at the deep-sea floor, originating from the sedimentation of partially degraded material from surface water layers into the deep ocean (Fileman et al., 1998). The ratio of long-chain (> C21) to short-chain fatty acids is, due to degradation processes, generally low in marine sediments (Naganuma et al., 2001). This is also confirmed by this study and most pronounced in the deeper sediment layers (2–5 and 6–10 cm). The higher content of polyunsaturated fatty acids (PUFA) during the second visit indicates the increased abundance of components rich in these fatty acids from organisms or plant remains. Generally, PUFA are almost exclusively synthesized by plants and very few animals have the capability of synthesizing them *de novo*. Given that they are essential for all organisms, most animals depend on ingesting them with their food (Brett and Müller-Navarra, 1997).

Although the organic fluff layer on top of the sediment was not included in the fatty acid

analysis enhanced signals of phytoplankton fatty acid markers (20:5(n-3), 22:6(n-3)) were detected in the first centimetre of the sediment at station 85. Together with the clearly increased amounts of these fatty acids in bottom water POM during the second visit this substantiates the visual findings and the results from the pigment analyses. Accordingly, the degree of degradation of fatty acids (e.g. represented by the ratio of 18:1(n-9) to 18:1(n-7)) was higher before the input of the fresh organic matter.

Increased numbers of bacteria were to be expected for station 85 when the enhanced amount of bacterial marker fatty acids 15:0 and 17:0 is regarded. Heterotrophic bacteria are particularly abundant in marine sediments (Sargent et al., 1987) and colonize and decompose settling particulate matter (Azam et al., 1983; Pfannkuche and Lochte, 1993). They are known to synthesize odd-numbered branched fatty acids such as 15:0, 17:0, 15:1 and 17:1 and large amounts of 16:1(n-7) (Dalsgaard et al., 2003 and references therein). Additionally, aggregates of phytodetritus harbour a rich bacterial and cyanobacterial flora (Gooday, 1993 and references therein). However, the patchy distribution of bacterial cells (compare 4.2) does not completely reflect the findings from the fatty acids.

4.2 The use of relative abundances for bacteria and meiofauna data

As indicated by the results for the fatty acids there is also evidence for patchily distributed standing stocks of bacteria and meiofauna in the investigated deep-sea area. During our expedition it became clear that food availability was differing on medium scales: an additional *in situ* measurement of oxygen microprofiles was carried out 12 nautical miles south of 52°S at station PS 71/84 (water depth 3004 m). At the same day fluxes were found to be approximately 20 % lower (7.7 mg C $m^{-2}d^{-1}$) at station PS 71/84 than at station PS 71/85 (Sachs et al., 2009). There is a possibility that even at smaller scales a slightly poorer pre-bloom food bank in the sediment at station 85 compared to the nearby station 13 had an effect on the abundances of benthic organisms. Absolute individual numbers of bacteria and meiofauna can be quite variable between different deployments and even between the cores of the same MUC deployment (compare Tab. 3, 4; for meiofauna see also Gutzmann et al., 2004). Therefore we decided to use relative abundances of bacteria and meiofauna in order to detect differences which otherwise would be obscured by the absolute numbers found at stations 13 and 85.

4.3 Reaction of bacteria to food input

The absolute numbers of bacteria found in the sediment samples during this study were comparable but to the lower end of previous reports from the deep-sea (Rex et al., 2006,

Danovaro et al., 2008). The higher relative abundances in the uppermost sediment horizon after the settlement of the bloom could be the result of higher bacterial growth due to the change in nutrient conditions on the sediment surface. However, a possible additional input of bacterial cells associated with descending phytodetritus has to be taken into account (e.g. Grossart et al. 2006, Pfannkuche and Lochte, 1993). Thus, our hypothesis that bacteria in oligotrophic Antarctic deep-sea environments react with immediate visible reproductive effort to unexpected food input cannot be validated conclusively.

Recent findings indicate that reproduction may not be the first reaction of Antarctic benthic deep-sea bacteria to food input (D. Pearce, pers. comm.). Bacteria on Subantarctic deep-sea sites near Crozet Island did not increase in number but rather enhanced their activity in areas with high input of organic carbon. In our study the pore-water oxygenation showed a steep decrease within the first sediment centimetres after the phytoplankton bloom. This enhanced sediment community oxygen consumption (SCOC) indicates a higher respiratory activity which can be attributed among others to benthic bacteria. This is supported by Smith et al. (2001) who investigated SCOC and ATP of the surface sediment as indicator of microbial biomass during an 8-year time-series at a station in the North Pacific. They concluded that although there were clear seasonal fluctuations in food fluxes, there was no obvious correlation between SCOC and ATP. Luna et al. (2002) found a larger fraction of active bacterial cells in deep-sea sediments after experimental nutrient enrichment in a microcosm experiment. In all, it is possible that an enhanced respiratory activity of the bacteria was partly responsible for the increased oxygen consumption at station PS 71/85 after the phytoplankton bloom had settled to the bottom. However, the fluorochrome acridine orange (AO) bacterial counting technique used here does not allow to discriminate between living, dead, active or dormant cells.

Bacterial abundance was lower after the bloom than before. One explanation for the lower bacterial abundance at station PS 71/85 is that there was a generally lower standing stock of bacteria (see 4.2). Less food input during previous blooming events may have lead to this situation. A second possibility is that bacteria may have been ingested by active foraminifera. In a mesocosm experiment Koho et al. (2008) simulated a diatom bloom and studied the reaction of deep-sea foraminifers and bacteria from the Portuguese continental margin from 900 m water depth. They showed that in the moment the foraminiferal reproduction and growth peaked, the bacterial activity was even lower than in the untreated controls. Hence, they concluded that some species of foraminifers fed on phytoplankton and others exclusively on benthic bacteria. Additionally, foraminiferan species that lived in the deeper sediment layers did not necessarily move to the surface in order to feed on phytodetritus but benefited from the food input by feeding on the growing bacterial biomass (Koho et al. 2008). In our case this means that foraminiferan activities may be responsible for a decrease in

number of benthic bacteria, especially in the deeper sediment layers. Foraminifera in general play an important role in benthic food webs. There are biochemical evidences that at bathyal sites foraminifera are trophic links between phytodetritus, sediments and benthic metazoans (Nomaki et al., 2008; Suhr et al., 2003; Würzberg et al., in press).

In all, the observed shift in relative numbers of bacteria in the sediment horizons may have been produced by an input of phytodetritus associated bacteria, the grazing of active foraminifera on bacteria in deeper layers or even a shift in community abundance towards the first centimeter. Nonetheless, the observed oxygen consumption at station PS 71/85 supports our hypothesis that bacteria react with enhanced (respiratory) activity to a food pulse from the water column.

4.4 Reaction of meiofauna to food input

The meiofauna individual numbers found during our case study (592.4–1458.3 individuals per 10 cm^2) and the dominance of the Nematoda (83.1 %) are comparable to the data previously reported from about 2000 to 5000 m depth in the Southern Ocean and the Weddell Sea (Gutzmann et al., 2004; Herman and Dahms, 1992; Vanhove et al., 1995, 2004).

After the blooming event a significantly higher percentage of meiofauna organisms was found in the first sediment centimeter than before. This must be the result of a vertical migration as benthic meiofauna and especially nematodes are not found in the phytoplankton of the free water column. Thus, the hypothesis that meiofauna reacts with enhanced motile activity to food input can be accepted.

There are three possible explanations for the observed differences in vertical distribution.

Firstly, meiofauna may migrate upwards in order to feed on the fresh organic material on the surface. This is supported by the fact that vertical shift in meiofauna distribution between the sampling in December (station PS 71/13) and January (station PS 71/85) matched the pigment profiles obtained during our study. Higher pigment contents were reflected in higher relative meiofauna abundance in the first centimetre. Secondly, meiofauna may as well concentrate in the first centimetre of the sediment in order to feed on degraded material and bacteria. The meiofauna shift towards the sediment surface in January (station PS 71/85) matched the higher relative numbers of bacteria at that sampling date. Thirdly, meiofauna may avoid deeper sediment layers due to oxygen depletion. The observed shift matched the changing porewater oxygen concentration detected during our study and reflects the steep depth gradient in oxygen concentration observed in January (station PS 71/85). Nonetheless, the measured OPD was still comparable, strengthening the assumption that the migration

towards upper sediment layers in our study was mainly due to the enhanced availability of organic material.

At the Porcupine Abyssal Plain, Gooday et al. (1996) sampled before (April) and after a spring bloom (July). Meiofauna did not migrate towards the sediment surface after the phytodetrital pulse and, contrary to the foraminifera from the same samples, metazoan meiofauna did not exploit the detrital food rapidly. In our study we showed that deep-sea meiofauna indeed can move towards a newly available food source. However, it still remains unclear how the meiofauna exploits these resources. In the Cretan Sea (Mediterranean) bathyal meiofauna communities reacted with considerable time lag to food input (Danovaro et al., 2000). There, meiofauna rather utilized increased bacterial biomass resulting from pulses in particulate organic matter than the refractory organic material itself. Recent experimental findings from the Arctic deep-sea (Guilini et al., 2010) confirm the unclear feeding situation for benthic deep-sea nematodes (compare Witte et al., 2003b). Guilini et al. (2010) explain the very limited accumulation of ^{13}C-labeled carbon during a feeding experiment with a passive uptake of ^{13}C-labeled substrates by the nematodes, rather than via bacterivory. Ingels et al. (2010) found very low uptake rates as well. However, they observed a preference of bacteria over phytoplankton in Arctic and Antarctic abyssal nematode communities in a pulse-chase experiment.

In the bathyal Sagami Bay, Shimanaga et al. (2000) detected seasonal changes in the vertical distribution of Copepoda that were related to the amount of chloroplastic equivalents (CPE) available in the sediment. The most abundant taxon, the Nematoda, did however not react to this input of organic matter. These findings are in contrast to the results of this study where the measured difference in vertical distribution of the meiofauna community is mainly due to migrating nematodes. However, we did not slice our samples in the same narrow vertical steps applied by Shimanaga et al. (2000). Moreover, the sediments in Sagami Bay showed an OPD between 0.8 and 2.3 cm depending on the season. This is a very thin oxygenated layer compared to the situation we encountered in the Antarctic.

The situation in the abyss at 52°S is comparable to the findings of Franco et al. (2008) who monitored the reaction of meiofauna to phytoplankton deposition at a shallow water station with permeable sediments in the North Sea. The authors detected significant differences in the vertical distribution of nematodes in the upper 5 cm as a probable result of an upward migration of the animals towards their food source (Franco et al., 2008). Although this study has been carried out at a shallow water station, the investigated sediment was described to have highly permeable sediments (redox values > 100 mV at all sediment depths; Vanaverbeke et al. 2004), comparable to our study site. Thus, nematodes in the deep-sea may show the same migration reaction to enhanced food availability on the sediment surface.

4.5 Copepod reproductive effort

At 52° S the meiofauna did not react immediately with visible reproductive effort in terms of enhanced egg production in copepods or increasing number of copepod nauplius larvae to the seasonal but highly patchy food input. Before visible responses in numbers of eggs and larvae can be detected, copepods need time to incorporate nutrients and produce eggs. Contrary to foraminiferans that can raise their metabolic activity very rapidly there is a higher energetic expense of egg production in combination with slower rates of somatic growth in metazoans (Gooday et al., 1996). Additonally, embryos of benthic copepods have a development time that depends on environmental temperature, egg size and adult size (Veit-Köhler and Brey, submitted). In mediterranean bathyal meiofauna communities a time lag of two months between food input and a reaction in terms of increased community density, copepod nauplii, and individual biomass of higher meiofauna taxa (Nematoda, Copepoda, Polychaeta) was observed (Danovaro et al., 2000).

The lag period for the conversion of ingested food to egg production has been studied for many pelagic copepod species and summarised by e.g. Tester and Turner (1990), Bunker and Hirst (2004) and Kuijper et al. (2004). For marine benthic copepods such generalising studies do not exist. However, we observed that all gravid females of benthic deep-sea copepods carried only few but large eggs (Fig. 10). Based on this observation and our results we can conclude that because of the low environmental temperatures and the generally low and unpredictable food supply the prevailing reproductive strategy of the benthic deep-sea copepods is the production of few large yolk-rich eggs that enable few well equipped nauplii to survive even under adverse conditions (Hirst et al., submitted; Veit-Köhler and Brey, submitted). The time needed for the production of these yolk-rich eggs as well as the long embryonal development time explain why benthic deep-sea copepods do not react with immediate population growth to a sudden food input.

Fig 10 Female copepod of the genus *Mesocletodes* (Argestidae) with egg sac containing four large eggs attached to abdomen. The individual was collected with the MUC at station PS 71/85 (1–2 cm sediment depth) and belongs to *Mesocletodes* sp. 32, a widely distributed species of deep-sea copepods (Menzel, submitted). The specimen was stained with Congo red and visualised as described by Michels and Büntzow (2010); photograph by Jan Michels.

4.6 Benthic organisms and sediment community oxygen consumption (SCOC)

The enhanced oxygen consumption, higher concentrations of fatty acid degradation products in the sediment and particularly the population shifts at the sediment surface indicate a higher bacterial and metazoan respiratory activity by the end of January. These findings are in line with the study of Witte et al. (2003a, b) who reported considerable increases in SCOC shortly after artificial phytodetritus pulses in the Sognefjord (1265 m depth, OPD 16.8 mm, SCOC plus 25% from 3.6 to 4.5 mmol O_2 m^{-2} d^{-1} within 3 d) and the Porcupine Abyssal Plain (PAP, 4800 m depth, OPD 15 cm, SCOC nearly doubled from 0.44 to ~0.8 mmol O_2 m^{-2} d^{-1} within 2.5 d). The initial oxygen consumption measured in our study (0.400 mmol O_2 m^{-2} d^{-1}) is comparable to the situation found at PAP. However, after the phytoplankton bloom SCOC nearly tripled in our case (1.102 mmol O_2 m^{-2} d^{-1}). The two sites studied by Witte and co-workers contrasted in the time required by the bacteria to start incorporation of the organic material. While at their slope station bacteria immediately fed on the labelled detritus (within three days), it took them eight days to double their activity at the PAP deep-sea station (measured indirectly through the extracellular enzyme activity). However, at both locations members of the macrofauna were among the first benthic organisms that ingested the fresh food. Thus, bacteria were not responsible for the initial increase of SCOC in the Porcupine Abyssal Plain. Representatives of the macrofauna such as Amphipoda, Cumacea, Isopoda, Tanaidacea and Gastropoda were scarce in our MUC-samples (lower sieve size 32µm, no upper size limit). As the MUC is not a convenient gear for sampling larger and more motile macrofauna, biomass of this size class and thus the contribution of the macrofauna to the observed oxygen consumption cannot be estimated from our samples.

We can only speculate how long the fresh food had been available for the benthic communities at 52° S before the second sampling took place. The total time span of our case study was 52 days. We detected migration tendencies and/or shifts in abundance in the meiofauna and the bacteria. It is possible that by the end of January the reaction of the metazoan benthic organisms was triggered by a preceding use of the organic material by bacteria and foraminifera according to Moodley et al. (2002) and Koho et al. (2008). Another explanation is that bacteria may have reacted to an initial degradation of the material by macrofauna (Witte et al. 2003b). In their study nematodes (as representatives for the meiofauna) reacted with considerable time lag. In an *ex situ* pulse-chase experiment Moens et al. (2007) added labeled freeze-dried cyanobacteria to sediment cores from a 227 m deep Antarctic site. They found evidence that although remineralisation started immediately and rates were comparable to studies from deep-sea sites, nematodes were generally marked negligibly and increased only after a distinct lag period of 16 days. The most elaborate experiment in order to test bacteria as food source for deep-sea nematodes has recently been carried out by Guilini et al. (2010). They found that although different bacterial

functional groups were marked by different ^{13}C-labeled substrates, nematodes did not incorporate the label via the bacteria nor did they take up considerable amounts of the labeled substrates directly within seven days.

The absence of measureable uptake of labeled food does not mean that organic matter had not been used. Mere benthic respiration may play an important role (Relexans et al., 1996; Levin et al., 1999; Guilini et al., 2010). Bacteria (through assimilation and respiration) and Foraminifera were the key players in a short-term benthic response to an experimental input of marked diatoms in a benthic chamber experiment at a deep-sea site in the Northeast Atlantic (Moodley et al., 2002). The initial SCOC of 0.48 and 0.53 mmol O_2 m^{-2} d^{-1} in the benthic chambers doubled after the injection of labeled diatoms. However, with a rate of 45% the major signal of benthic processing of the added carbon was recorded as respiration (recovered as CO_2). Baguley et al. (2008) reported for two deep stations (3545 and 3400 m) in the Gulf of Mexico that the meiofauna respiration of 0.5 and 0.3 mg C m^{-2} d^{-1} accounted for 8–13 % of the whole sediment community respiration of 3.9 mg C m^{-2} d^{-1} at both stations. They estimated meiofauna respiration allometrically via biomass and abundance (mean values 875 and 635 ind. 10 cm^{-2}) which is comparable to our study (single cores 1,458.26–592.38 ind. 10 cm^{-2}). With a total sediment community respiration of 3.3 mg C m^{-2} d^{-1} the pre-bloom situation in our study is comparable to the two stations with similar depth presented by Baguley et al. (2008).

We assume that the upward migration would not take place if meiofauna and especially Nematoda would not feed on the freshly available food or a food source related to this input of organic matter such as bacteria, fungi, ciliates or labile material. The settlement of the phytodetritus must have occurred already ~3 to 25 days before the sampling took place (according to Witte et al., 2003b and the sinking rate of phytodetritus of 100–150 m d^{-1} given by Gooday, 1993). This is supported by the fact that at station PS 71/85 a strong reaction in terms of SCOC was observed. As the phytodetritus was still clearly visible on the sediment surface forming a green fluff layer we suppose that the remineralisation process was still at its beginning. It has been assumed that meiofauna is important in diagenesis, deep-sea carbon budgets and global biogeochemical cycles (Baguley et al., 2008). However, to date empirical data supporting speculated feeding habits, food preferences, assimilation and respiration rates, and in general the significant role of deep-sea metazoan meiofauna are lacking.

5 Conclusions

- Meiofauna and bacteria in the abyssal Southern Ocean react to the settlement of a phytoplankton bloom to the seafloor at 52°S with enhanced respiratory activity and vertical migration (meiofauna) to the sediment surface. Vertical distributions reflect the changing sediment situation, e.g. enhanced C-flux, increased SCOC, pigment contents and fatty acid distribution.

- During the experiment no increase of cell numbers of bacteria was observed. This is in line with previous findings.

- It is confirmed that in terms of reproduction deep-sea copepods only react with a distinct lag to a sudden food input. The reproductive effort of benthic copepods, e.g. the number of egg-carrying females or the number of nauplius larvae, did not increase during the investigated time span.

- Pelagobenthic coupling in the deep Southern Ocean is still poorly understood. Reworking, incorporation and respiration of sedimented material by different benthic compartments should be followed over longer time periods. A more frequent sampling is important but logistically hardly feasible.

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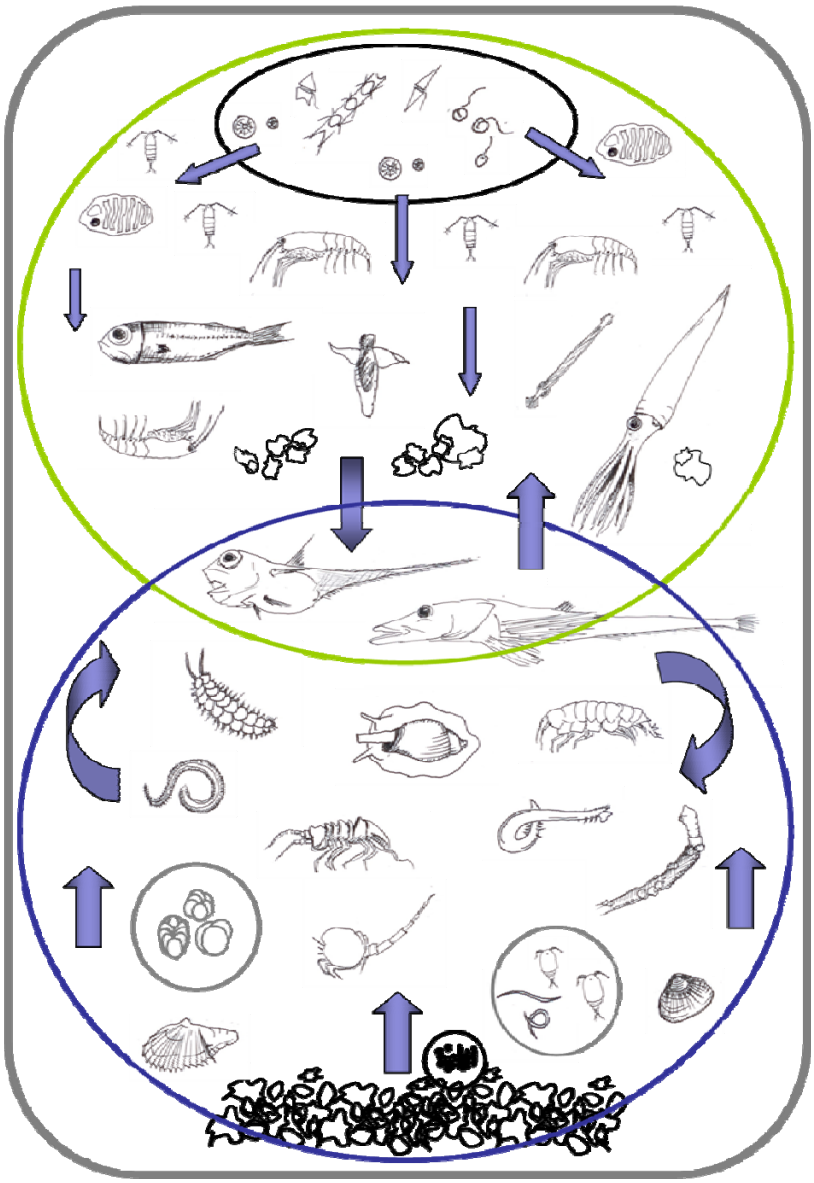
State of the manuscript and own contribution:

I conducted the POM and sediment fatty acid analyses and relevant data interpretation. The manuscript was written based on discussions of all authors and has been submitted to Deep-Sea Research II.

Chapter 4

Southern Ocean benthic food webs: evidence for shelf and deep-sea ecosystems from stable isotope C and N data



Components of the Antarctic food webs; green circle: Pelagial; blue circle: Abyssal. Blue arrows indicate carbon fluxes. Images not scaled.

Chapter 4 Southern Ocean benthic food webs: evidence for shelf and deep-sea ecosystems from stable isotope C and N data

Abstract

The benthic food web structure of the Weddell Sea shelf and deep-sea was investigated in the austral summer 2006/07 using carbon and nitrogen stable isotope tracers. The analysed organisms were classified according to their feeding habits based on fatty acid marker analyses, gut content analyses or published information as filter or deposit feeding (18 species or taxonomic groups), omnivorous feeding (20 species or taxonomic groups) and predating or scavenging (26 species or taxonomic groups). Fatty acid compositions measured in this study vary strongly between taxonomic groups indicating different feeding strategies. Generally, the trophic position estimated based on $\delta^{15}N$ values reflects these feeding habits assumed for the organisms. However, some exceptions were found and the reasons for these deviations are discussed. The analysed animals occupy wide $\delta^{15}N$ ranges covering four trophic levels both in the shelf (2.3‰ – 11.8‰) and deep-sea (4.7‰ – 12.8‰) systems. Comparably low $\delta^{15}N$ values were measured for the highest trophic levels (including fish and predating/scavenging amphipods) and possible reasons are discussed.

Keywords: Southern Ocean food webs; stable isotope ratios, $\delta^{15}N$, $\delta^{13}C$, fatty acids, deep-sea ecosystem, shelf ecosystem, feeding strategies

1 Introduction

The Southern Ocean is characterised by unique habitats shaped by physical and biological features. The Antarctic continental shelf is large and deep, as being depressed by the weight of the continental ice; and can reach more than 1000 m in depth, increasing the distance from the seabed to the euphotic zone by a factor of 3-4 compared to continental shelves elsewhere in the world. Coastal waters are of major importance to the Southern Ocean marine ecosystem, as maximum summer chlorophyll standing crops are frequently much greater in coastal than in open waters, and nutrient levels are often depleted further. The pelagic fauna appears to be broadly similar to that elsewhere. Resulting from the highly seasonal phytoplankton blooms, a key feature of the ecology of the Antarctic benthos is the combination of a low inorganic sedimentation with a strongly seasonal phytodetrital flux. In general, it appears that the organic matter reaching the continental shelf seabed has a long half-life, leading to a food bank for deposit feeders (Clarke and Arntz, 2006). Abundance, biomass and distribution patterns of benthic organisms have been shown to be strongly influenced by variations in food supply from the upper water column. This sedimentation of

organic matter depends on multiple factors such as hydrography, ice coverage, light, temperature and the structure of the pelagic food web (e.g., Grebmeier and Barry, 1991). Deep-sea benthic faunas have been reported to be capable of reacting rapidly to the input of organic material (Billett et al., 1983; Aberle and Witte, 2003; Moodley et al., 2005). However, benthic organisms might partly be decoupled from this seasonal food input, as bacteria, nano- and picoplankton and protozoans present throughout the year can provide alternative food sources (Kojima and Ohta, 1990; Orejas et al., 2001; Arntz et al., 2005; Smith et al., 2006).

The region above the sea floor is often referred to as the benthic boundary layer (BBL), characterised by being a well-mixed layer of varying thickness restricted by a strong density gradient (Smith and Hinga, 1983). In terms of faunal features the BBL can be seen as the sediment community and assemblage of organisms in the water column within 100 m of the seabed, including primarily benthic animals migrating into the water column e.g. to breed, and primarily pelagic animals such as fish which feed within the BBL (Gage and Tyler, 1991). It appears to be a region of elevated grazing rates and activity (Cartes et al., 2002), forming an important physical structure affecting the distribution of animals and particles near the seabed.

In the present investigation area, polychaetes, peracarid crustaceans, echinoderms and molluscs belong to the most abundant groups of benthic invertebrates, and the surprisingly high diversity of the deep-sea Southern Atlantic Ocean benthos has been explored recently (Brandt and Hilbig, 2004; Brandt et al., 2007 a, b). Besides the mentioned groups, representatives of other groups of crustaceans, as well as Bryozoa, Pycnogonida and fish were analysed in the present study to gain information on trophic pathways and feeding mechanisms utilising analyses of stable isotope C and N ratios and, in some cases, for their FA composition.

The application of methods like analysing FA patterns or stable isotope ratios is to date widely used in ecologic studies, as they provide, compared to conventional dietary analyses, time-integrated averages of assimilated foods (Hobson et al., 1995). Especially the naturally occurring stable isotopes of nitrogen can be used to elucidate patterns of trophic interactions within marine food webs. This is due to the fact that the heavy isotope accumulates in a predictable way with increasing trophic level. Generally, the nitrogen isotope content of animal tissue is step-wise enriched in the heavy isotope relative to its food due to preferential excretion of ^{14}N (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; Vanderklift and Ponsard, 2003). The ^{15}N enrichment in animal tissue for each trophic level can be used to determine the number of trophic levels in ecosystems and to investigate the trophic position taxonomic groups relative to others (Wada et al., 1987; Hobson and Welch, 1992; Post, 2002; Bergmann et al., 2009). The ratio of carbon isotopes, however, has

been shown to change little with increasing trophic level, and differences in the range of 0‰ to 1‰ between consumers and their food have been reported (Peterson and Fry, 1987; Post, 2002). In some cases, distinct carbon isotope ratios have been reported for certain groups of primary producers, which then can be traced throughout marine food webs (DeNiro and Epstein, 1978; Fry and Parker, 1979; McLeod and Wing, 2009) and be used as an indicator of sources of primary productivity in systems with isotopically distinct sources like e.g., phytoplankton vs. ice algae (Hobson et al., 1995).

However, the isotopic signature of a consumer alone is generally not sufficient to infer trophic position or carbon source without an appropriate isotopic baseline. Although every baseline will suffer from some temporal and spatial variation between the baseline and the secondary consumer of interest, the baseline should integrate isotopic changes at a time scale near that of the secondary consumer, cover the same sampling time period, and capture the spatial variability contributing to the isotopic signature of the secondary consumer (e.g. long-lived primary consumers such as snails and mussels) (Post 2002 and references therein). Based on the N ratio of such a baseline organisms, trophic levels can be calculated.

The estimation of trophic levels is widely applied in stable isotope studies and can, to a certain degree, characterize the functional role of organisms within, and allow estimates of energy or mass flow through ecological communities. Trophic levels, however, cannot account for complex interactions as food webs, which are in turn more difficult to construct comprehensively (see review by Post, 2002).

In the present study, results of an isotopic survey on organisms and sediments are used to define trophic levels of Southern Ocean shelf and deep-sea benthic organisms. The aim of this study is to provide a comprehensive isotope dataset, which, in combination with the analyses of FA composition and published information on feeding habits of benthic organisms is used to obtain information on the food web structure and trophic pathways on the Weddell Sea shelf and deep-sea.

2 Material and Methods

2.1 Sampling

The studied material originates from four stations (PS71/13, PS71/17, PS71/33 and PS71/39) sampled during the ANDEEP-SYSTCO project (see chapter 1 for a description of the stations' characteristics and sampling methods).

Sediment samples were treated as described in chapter 3; only the upper two sediment centimetres were taken into account.

2.2 Stable isotope analyses

As different tissue types have been show to have varying isotopic compositions, whole organisms were used. In case of larger animals (fish or Holothuroidea), muscle or body wall tissues, respectively, were used as homogenization of whole bodies was not practicable. Prior to stable isotope analysis, all samples were homogenized with a mortar. Visible calcareous parts of animals (shells) were removed (Bivalvia, Gastropoda, Ostracoda), or carbonate was extracted (sediments, Holothuria, Bryozoa, Cumacea) by acidification with 5% HCl for $\delta^{13}C$ analyses. $\Delta^{15}N$ analyses were always conducted on non-acidified samples. Analyses were conducted according to lab protocols established by C Mayr (Munich). Samples were weighed into tin capsules using an ultra scale and combusted in a continuous Helium flow in an elemental analyzer (NC2500, Carlo Erba, Italy) at 1080°C in the presence of chromium oxide and silvered cobalt oxide. Nitrogen oxide and excess oxygen were reduced by passing over copper wires at 650°C, and water vapour was trapped with $Mg(ClO_4)_2$. The remaining gases (N_2 and CO_2) were separated via a GC column at 45°C, and N_2 and CO_2 passed successively via a ConFloII interface into the isotope ratio-mass spectrometer (Delta Plus, Thermo-Finnigan, Germany). Carbon and nitrogen contents were determined by comparing the peak area vs. sample weight ratio of each individual sample. Calibration was conducted using the elemental standards Cyclohexanone-2,4-dinitrophenylhydrazone ($C_{12}H_{14}N_4O_4$) and Atropine ($C_{17}H_{23}NO_3$, both Thermo Quest, Italy). Additionally, a lab-internal organic standard (Peptone) was used for final isotopic calibrations. Isotope values are reported in ‰ deviation relative to international standards (AIR for nitrogen and VPDB for carbon). Analytical precision typically was 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$ (one standard deviation). Element concentrations are given as weight percentages relative to dry weight and have an analytical error of less than 5% of the given value. Statistical tests were carried out with the software PASW Statistics 17.0 (SPSS).

The nitrogen and carbon isotopic composition of natural samples is given as delta value (δ) representing the isotope ratio of the heavy to the light isotope in per mil relative to an international standard and is defined as $\delta\,{}^{y}X = (R_{sample}/R_{standard} - 1)\,1000$ with R being the ratio of the heavier to the light isotope ($^{15}N/^{14}N$ and $^{13}C/^{12}C$, respectively) and ^{y}X being the heavier isotope (i.e. ^{15}N, ^{13}C).

Based on this nomenclature, the simplest model for estimating the trophic position of a secondary consumer (Post, 2002) is:

$TL = 1 + (\delta^{15}N_{secondary\ consumer} - \delta^{15}N_{baseline}) / \Delta_n$

Whereas 1 is the trophic position of the organism (1 for primary producers) used to estimate $\delta^{15}N_{baseline;}$ $\delta^{15}N_{secondary\ consumer}$ (or any higher consumer) is measured directly; Δ_n is the enrichment in $\delta^{15}N$ per trophic level. Different values of Δ_n have been reported in literature (Peterson and Fry, 1987; Hobson et al., 1995; Post, 2002). Here, a fractionation of 2.54 per

mil suggested by Vanderklift and Ponsard (2003) based on a major review of 134 Δ_n estimates was used.

3 Results

3.1 Fatty acid (FA) composition of analysed groups:

For information on interpretation of FA trophic markers, see explanations in chapters 5-7.

The FA composition of the sediment and particulate organic matter (POM) indicates that little fresh algal material is available on the top or within the first few centimetre of the sea floor sediment, but the organic material rather consists of relatively degraded components (see chapters 3 and 5).

The animals analysed show strongly varying FA compositions, which can be assigned to the ingestion of different dietary spectra (Table 1). Both holothurian species investigated for their FA composition seem to have slightly different feeding habits. In Holothuroidea species 3, the dominant FAs 20:5(n-3) (44.2% of total FAs), 20:4(n-6) (7.7% of total FAs), 16:1(n-7) (5.5%) and 22:6(n-3) (5.3% of total FAs) indicate feeding on relatively fresh phytodetritus, while in *Taeniogyrus contortus*, 20:4(n-6) is the most prominent FA with 37.2±2.1% of total FAs, followed by 20:5(n-3) (21.1±2.2% of total FAs), 22:1(n-7) (9.3±0.8% of total FAs) and 22:6(n-3) (6.3±0.4% of total FAs). Within the bivalves, the most prominent FAs in declining order were 22:6(n-3) (27.1%±6.9 of total FAs), 16:0 (10.2±2.0% of total FAs), 20:5(n-3) (7.5±0.8% of total FAs) and 18:1(n-7) (6.2±0.9% of total FAs), indicating the utilisation of mainly strongly degraded material. Most dominant FAs in the Pycnogonid species 1 and 2 were quite similar, with high values for 20:5(n-3), 16:0, 22:6(n-3) and 18:1(n-7), indicative for the ingestion of phytodetritus. The third species showed somehow different FA pattern, with 20:4(n-6) being the dominant FA, followed by 20:5(n-3), 16:0 and 22:6(n-3), and additionally having a distinctly higher ratio of 18:1(n-9) to (n-7), possibly hinting towards a carnivorous component of their diet. The dominant FAs in the analysed Ostracoda were 22:6(n-3), 20:5(n-3), followed by 18:1(n-9) in one species and 18:4(n-3) in the other, as well as 16:0 in both and strongly propose the ingestion of degraded organic material.

Based on the occurrence of FA markers (this chapter and chapters 5-7), gut content analyses (for fish, chapter 7) and/or additional published information, the analysed species or taxonomic groups were classified into three feeding groups: (1) filter- or detritus feeding, (2) omnivorous feeding and (3) predating or scavenging, for both shelf (Table 2a) and deep-sea stations (Table 2b).

Table 1 Station, number and fatty acid composition (given as % of total fatty acids) of analysed Antarctic deeps sea and shelf benthic organisms

	BIVALVIA (station 39)		**PYCNOGONIDA** (station 48)			**HOLOTHUROIDEA** (station 48)		**OSTRACODA** (station 48)	**CUMACEA** (station 48)
	Vesicomya sirenkoi	*Nucula* spec	species 1	species2	species3	species3	*Taeniogyrus contortus*	Ostracoda spec.	Bodotriidae spec.
	(n=4)	(n=1)	(n=1)	(n=1)	(n=1)	(n=1)	(n=5)	(n=3)	(n=1)
14:0	0.5±0.87	4.1					0.2±0.41	3.6±0.95	1.2
15:0	0.5±0.55								
16:0	11.3±1.50	8.0	18.4	20.0	15.2	3.6	2.4±0.32	10.6±0.13	15.9
16:1(n-9)	1.3±1.42				2.1			0.7±0.97	
16:1(n-7)	1.6±1.06	7.4	2.9	3.1		5.5	1.1±0.86	10.0±0.46	10.5
16:1(n-5)	1.3±1.35	2.8					0.2±0.46		
16:2(n-4)	1.6±1.15		2.6	1.8	1.2				
16:4(n-1)	0.6±1.07								
17:0	1.1±0.67		1.2		1.1		0.9±0.75		
18:0	6.4±3.14	4.7	3.8	3.5	5.9	4.8	2.6±0.69	2.4±0.20	4.9
18:1(n-9)	2.6±0.96	5.2	5.7	6.1	7.2	3.2	1.6±0.18	17.2±8.79	14.5
18:1(n-7)	6.5±0.79	5.4	6.5	5.9	3.4	4.2	2.6±0.56	7.7±1.68	12.3
18:1(n-5)	2.2±0.42	2.0							
18:2(n-6)	1.1±0.64							1.6±0.34	2.1
18:3(n-6)							1.3±0.68	0.9±1.22	
18:4(n-3)	1.2±1.42					1.4		5.6±4.66	1.8
20:0	1.4±1.04	1.7				1.0	3.1±0.68		
20:1(n-11)			1.9	4.1		2.7	1.8±0.17		1.2
18:5(n-3)/20:1(n-9)	2.5±0.92	19.5	5.7	8.8	6.8	3.6	0.6±1.30	3.0±0.99	
20:1(n-7)	4.6±1.23	5.2	4.2	1.7	1.6	2.7	1.3±0.78		
20:2(n-6)	1.0±0.57			1.2		2.1	1.6±0.22		
20:3(n-6)						1.3	8.7±13.89		
20:4(n-3)						1.6			
20:4(n-6)	4.8±0.57	2.5	9.0	5.7	20.4	7.7	34.8±5.60	1.1±0.81	4.8
20:5(n-3)	8.0±0.81	7.2	22.0	20.8	15.9	44.2	16.8±7.10	18.1±2.24	19.8
22:1(n-11)	2.0±0.38		1.1				3.8±2.42		
22:1(n-9)	0.3±0.54		1.1	1.6	2.0	1.6			
22:1(n-7)			1.2	1.4	1.1	3.5	8.2±2.59		1.4
22:5(n-3)	3.5±0.58	2.4	4.8	5.8	1.9				1.8
22:6(n-3)	32.3±4.08	21.7	7.6	8.5	14.3	5.3	6.3±0.43	17.5±4.10	7.9

Table 2a Classification to three feeding types based on fatty acid analyses or literature information for organisms found at the shelf station

Feeding type	Taxon	Taxon	Reference
Filter feeding or detritivorous	Bryozoa	Bryozoa spec.	Gage, 1992; Demidkova, 2010
	Holothuroidea	*Taeniogyrus contortus*	This chapter, Hansen, 1975; Billett, 1991
		Echinopsolus splendidus	
		Holothuroidea spec. 3	
		Psolidium spec.	This chapter
	Ostracoda	Ostracoda spec.	This chapter
	Cumacea	*Nannastacidae* spec.	Chapter 6
		Bodotriidae spec.	
		Diastylidae spec.1	
		Cumacea spec.	
	Isopoda	*Chaetarcturus* cf. *bovinus*	Wägele, 1987
		Dolichiscus cf. *meridionalis*	Wägele, 1987
		Antarcturus bovinus	Wägele, 1987
		Edotia pulchra	Wägele, 1991
Omnivorous	Pycnogonida	Pycnogonida spec. 1	This chapter; Fry, 1965; Chimenz Gusso and Gravina, 2001; Fahrenbach and Arango, 2007
		Pycnogonida spec. 2	
		Pycnogonida spec. 3	
	Polychaeta	*Pionosyllis epipharynx*	Chapter 5
	Tanaidacea	*Neotanais spec.*	Chapter 6
		Tanaidacea spec.	
	Isopoda	*Cuspidoserolis cf. johnstoni*	Luxmoore, 1981
	Amphipoda	Amphipoda spec.1	Chapter 6
Predating or scavenging	Gastropoda	*Harpovoluta charkoti*	Hain, 1990; Arnaud, 1976-1978
	Polychaeta	Polyonidae spec.	Chapter 5; Fauchald and Jumars, 1979
		Travisia kerguelensis	
		Nereis cf.*atlantica*	
	Isopoda	*Accalathura gigantissima*	Wägele, 1991
		Natatolana occulta	DeBroyer et al., 2004; Nyssen et al., 2005
		Natatolana intermedia	
		Stenetrium weddellensis	Chapter 6
		Glyptonotus antarcticus	Clarke, 1979
		Notoxenus cf *spinifer*	Chapter 6
	Amphipoda	*Abyssorchomene* spec.	Chapter 6
	Pisces	*Trematomus bernacchii*	Chapter 7
		Trematomus scotti	
		Artedidraco orianae	
		Macrouridae spec.	
		Bathydraco antarcticus	

Table 2b Classification to three feeding types based on fatty acid analyses or literature information for organisms found at the deep stations

Feeding type	Taxon	Taxon	Reference
Filter feeding or detritivorous	Bivalvia	*Nucula* spec.	This chapter
		Vesicomya sirenkoi	This chapter, Krylova and Sahlig, 2010
	Polychaeta	*Flabelligeridae* spec.	Chapter 5
		Spionidae spec.	
	Tanaidacea	*Apseudomorpha* spec.	Chapter 6
	Decapoda	Decapoda spec.	No information available
Omnivorous	Polychaeta	*Opheliidae* spec.	Chapter 5
	Tanaidacea	*Neotanais* spec.	Chapter 6
		Tanaidacea spec.	
	Isopoda	*Munnopsidae* spec. 1	Chapter 6
		Munnopsidae spec. 2	
		Munneurycope spec.	
		Betamorpha spec.	
		Eurycope spec.	
		Ischnomesidae spec.	
		Syneurycope spec.	
	Mysidacea	Mysidacea spec. 1	Grossnickle(1982); Jerling and Wooldridge (1995)
Predating or scavenging	Gastropoda	*Aforia lepta*	Hain, 1990
	Polychaeta	*Polyodontidae* spec.	See chapter 5
		Bathyglycinde spec.	
	Isopoda	*Accalathura gigantissima*	Wägele, 1991
		Cuspidoserolis spec.	Luxmoore, 1981
		Serolis spec.	Luxmoore, 1981
		Storthyngura cf. gigantea	No information available
	Amphipoda	*Lysianassidae* spec. 1	Chapter 6
		Lysianassidae spec. 2	
		Eurythenes spec.	
	Pisces	*Macrouridae* spec.	Chapter 7
		Bathydraco spec	

3.2 Stable isotope C and N ratios

The isotopic values measured for the sediment show distinct differences between the stations, most pronounced for $\delta^{13}C$. Here, the northernmost station (PS71/13), situated at the Polar Front, has significantly (t-test $P<0.05$) lower values than the other stations. Regarding the $\delta^{15}N$ higher values than at both other stations were found at station PS71/33, situated in the Weddell Basin. Unfortunately, for the shelf station PS71/48, no sediment samples were available for analyses due to a limited deployment of gear.

As found in previous studies, the overall correlation between organisms' $\delta^{13}C$ and in $\delta^{15}N$ is weak, meaning that no stepwise enrichment of ^{13}C was observed. Additionally, increasing evidence that $\delta^{13}C$ is biased by the individual lipid content of the organisms limits the interpretation possibilities of this value. As samples were not defatted prior to isotope analysis, and the individual lipid contents of the investigated organisms were not measured, prohibiting the application of a correction factor, this study focuses on the $\delta^{15}N$ values measured.

The benthic animals analysed spanned about 13.8‰ (14.4‰ – 28.2‰) in $\delta^{13}C$ and 9.5‰ in $\delta^{15}N$ (2.3‰ – 11.8‰) at the shelf and 11.3‰ (17.9‰ – 29.2‰) in $\delta^{13}C$ and 8.1‰ in $\delta^{15}N$ (4.7‰ – 12.8‰) at the deep-sea stations (Table 3). The range of $\delta^{15}N$ enrichment steps measured in this study seems to be at the lower end than the 2.5-3.4‰ assumed in most studies and are assumed to be 2.54‰ based on the evaluation of numerous data sets by Vanderklift and Ponsard (2003). Based on this enrichment steps, four trophic levels are covered by the shelf as well as by the deep-sea organisms.

The overall $\delta^{15}N$ pattern of all organisms together mostly mirrors the feeding classifications based on FA and/or gut content analyses as well as published information (Fig. 1), regardless of their origin (depth/station). However, some deviations can be observed and will be elucidated and discussed in detail. The filter feeding or detritivorous group generally covers the first and second trophic level. Within this group, the Cumacea inhabit a unique position, as they have the lowest $\delta^{15}N$ values measured in the whole study, including sediment samples, and additionally show comparably high $\delta^{13}C$ values. According to their $\delta^{15}N$ values, they seem to obtain a trophic position one trophic level lower than the other detritivores examined.

Of the four analysed holothurians, two have comparably higher $\delta^{15}N$ values compared to the other two species and to other detritivorous groups. The biggest inconsistency, however, is found in the isopod *Antarcturus bovinus*, showing one of the highest isotope $\delta^{15}N$ values (12.4‰) of all organisms analysed. This is in clear contrast to its presumed filter-feeding lifestyle (Wägele, 1987). Other organisms classified as filter feeding or detritivorous are bryozoans, bivalves, some polychaetes, some decapod crustaceans and, besides cumaceans, some other peracarid crustaceans (isopods and tanaidaceans).

The group of animals classified as omnivorous feeders takes in a rather narrow range of $\delta^{15}N$ values with variations also within one taxon in some cases. They span over the second and third trophic level. Assumed omnivores are some polychaetes, the Pycnogonidae, some decapod and peracarid (isopods, amphipods, tanaidaceans and mysidaeceans) crustaceans.

The third and fourth trophic levels are occupied with carnivorous feeders. Again, intra-taxonomic variation can be observed. The carnivorous group with lower $\delta^{15}N$ values includes many isopods, amphipods, some polychaetes, some fishes and the gastropod *Aforia lepta*.

Gathered in the group with the highest $\delta^{15}N$ values are mainly species for which necrophagy has been described (Isopoda: *Natatolana* spec, Amphipoda: *Eurythenes gryllus*; Gastropoda: *Harpovoluta charkoti*; Fish: Macrouridae spec.).

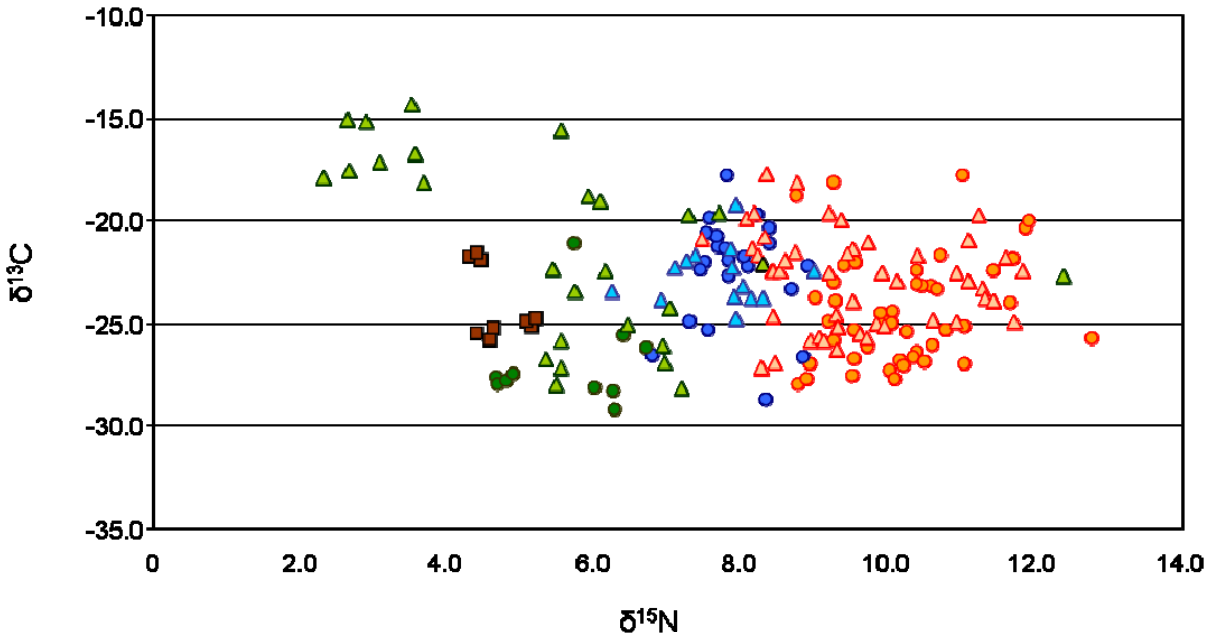


Fig 1 Results for $\delta^{13}C$ and $\delta^{15}N$ values (in ‰) of all analysed sediments and organisms together, regardless of their origin (station): circles (deep stations) and triangles (shelf station) indicate sample depth; the colours green (filter or detritivorous feeding), blue (omnivorous feeding) and orange (predating or scavenging) indicate different feeding types; squares represent sediments samples (only deep stations sampled).

Table 3: Identification, tissue type analysed, number of samples analysed (N) and number of pooled individuals per sample (N pooled, if applicable), station, $\delta^{15}N$ and $\delta^{13}C$ values and estimated trophic level (TL) for all analysed organisms. If present, shells were removed (Bivalvia, Gastropoda, Ostracoda) or de-calcification was conducted (Bryozoa, Holothuria, Cumacea) prior to analyses.

Taxon (1)	Taxon (2)	Tissue	N	N pooled	Station	$\delta^{15}N$ ‰	$\delta^{13}C$ ‰	TL
Bryozoa	Bryozoa div.	complete	3	n.a.	PS71/48	6.2±0.8	-26.0±0.7	2.3±0.3
Bivalvia	*Nucula* spec.	complete	1	4	PS71/39	6.0	-28.1	1.5
	Vesicomya sirenkoi	complete	4	22	PS71/39	4.8±0.1	-27.2±0.2	1.0±0.0
Gastropoda	*Aforia lepta*	complete	1		PS71/85	7.5	-20.9	2.1
	Harpovoluta charkoti	complete	2		PS71/48	11.6/11.8	-21.8/-22.4	3.7/3.8
Polychaeta	*Nereis* cf. *atlantica*	complete	1		PS71/48	8.3	-27.1	3.1
	Flabelligeridae spec.	complete	1		PS71/39	6.7	-26.3	1.8
	Ophelina spec.	complete	9		PS71/39	7.9±0.3	-21.4±0.6	2.2±1.1
	Bathyglycinde spec.	complete	1		PS71/33	9.4	-22.2	2.8
	Pionosyllis epipharynx	complete	1		PS71/48	7.9	-24.8	2.9
	Polyodontidae spec.	complete	1		PS71/39	9.5	-27.6	2.9
	Polyonidae spec.	complete	1		PS71/48	9.5	-23.9	3.6
	Spionidae spec.	complete	1		PS71/39	6.4	-25.6	1.8
	Travisia kerguelensis	complete	1		PS71/48	7.9	-24.8	3.6
Ostracoda	Ostracoda spec.	complete	1		PS71/48	5.5	-28.0	2.0
Tanaidacea	*Apseudomorpha* spec.	complete	1		PS71/33	5.7	-21.2	1.4
	Neotanais spec.	complete	1		PS71/39	7.8	-17.9	2.2
	Tanaidacea spec.	complete	1		PS71/39	7.6	-19.9	2.1
Cumacea	*Bodotriidae* spec.	complete	2		PS71/48	2.6/2.6	15.1/17.6	1.0/1.0
	Diastylidae spec.	complete	1		PS71/48	3.7	-18.1	1.3

	Cumacea spec.	complete	1		PS71/48	2.3	-17.9	1.0
	Nannastacidae spec.	complete	4		PS71/48	3.3±0.3	15.9±1.3	1.1±0.1
Isopoda	*Accalathura gigantissima*	complete	5		PS71/48	10.0±0.9	-21.3±1.1	3.7±0.3
	Accalathura gigantissima	complete	1		PS71/13	11.0	-17.9	3.5
	Antarcturus bovinus	complete	1		PS71/48	12.4	-22.7	4.7
	Chaetarcturus cf. *bovinus*	complete	2		PS71/48	7.3/7.7	19.7/19.7	2.7/2.8
	Dolichiscus cf. *meridionalis*	complete	1		PS71/48	8.3	-22.1	3.1
	Cuspidoserolis cf. *johnstoni*	complete	1		PS71/48	7.9	-19.2	2.9
	Cuspidoserolis spec.	complete	1		PS71/17	9.5	-21.9	2.9
	Serolis spec.	complete	2		PS71/48	10.4/10.6	-22.5/-23.2	3.2/3.3
	Edotia pulchra	complete	1		PS71/48	5.6	-15.6	2.0
	Eurycope spec.	complete	1		PS71/17	8.2	-23.4	2.5
	Eurycope spec.	complete	1		PS71/39	8.7	-19.8	2.4
	Betamorpha spec.	complete	1		PS71/39	7.9	-22.5	2.2
	Munneurycope	complete	1		PS71/39	6.8	-26.6	1.8
	Munnopsidae spec. 1	complete	1		PS71/39	7.5	-22.1	2.1
	Munnopsidae spec. 2	complete	1		PS71/39	9.0	-22.4	2.7
	Syneurycope spec.	complete	1		PS71/13	6.3	-12.3	1.6
	Ischnomesidae spec.	complete	1		PS71/13	7.6	-12.3	2.1
	Natatolana oculata	complete	10		PS71/48	9.2±1.2	-23.0±1.8	3.4±0.5
	Natatolana intermedia	complete	3		PS71/48	9.0±0.9	-22.5±0.5	3.4±0.3
	Notoxenus cf spinifer	complete	2		PS71/48	8.8/9.3	-18.1/-18.8	3.3/3.5
	Stenetrium weddellensis	complete	7		PS71/48	8.6±0.5	-19.8±1.6	3.2±0.2
	Storthyngura cf. *gigantea*	complete	1		PS71/33	10.7	-23.4	3.3
	Glyptonotus antarcticus	complete	1		PS71/48	9.5	-21.9	3.5

Amphipoda	Amphipoda spec. 1	complete	9		PS71/48	7.6±0.6	-22.6±0.9	2.8±0.2
	Lysianassidae spec.1	complete	4		PS71/39	11.4±0.4	-22.5±1.1	3.2±0.2
	Lysianassidae spec.2	complete	12		PS71/39	9.6±0.5	-24.9±1.2	2.9±0.2
	Eurythenes gryllus	complete	10		PS71/33	10.9±1.0	-24.7±2.7	3.4±0.4
Mysidacea	*Mysidacea* spec.	complete	2		PS71/39	8.3/8.8	-26.6/-28.7	2.4/2.6
Decapoda	*Nematocarcinus* spec.	complete	2		PS71/17	7.3/7.5	-25.0/-25.3	2.0/2.1
	Decapoda spec.	complete	2		PS71/39	6.3/6.3	-28.3/-29.2	1.6/1.6
Pycnogonida	Pycnogonida spec.1	complete	1		PS71/48	7.9	-23.7	2.9
	Pycnogonida spec.2	complete	1		PS71/48	6.9	-23.8	2.5
	Pycnogonida spec.3	complete	1		PS71/48	9.0	-22.5	3.3
Holothuroidea	*Psolidium* spec.	body wall	2		PS71/48	5.5/5.7	-23.5/-27.1	2.0/2.1
	Holothuroidea spec.3	body wall	5		PS71/48	5.8±0.3	-21.7±2.9	2.1±0.1
	Echinopsolus splendidus	body wall	1		PS71/48	7.2	-28.2	2.6
	Taeniogyrus contortus	body wall	2		PS71/48	7.0/7.0	-24.3/-26.9	2.5/2.6
Pisces	Macrouridae spec.	muscle	5		PS71/48	9.5±1.0	-25.3±1.46	3.5±0.4
	Macrouridae spec.	muscle	3		PS71/39	10.0±0.4	-26.9±0.2	3.0±0.1
	Macrouridae spec.	muscle	2		PS71/17	10.0/11.1	-24.9/-25.2	3.0/3.5
	Trematomus bernacchii	muscle	6		PS71/48	9.5±0.3	-25.5±0.4	3.5±0.1
	Trematomus scotti	muscle	4		PS71/48	11.1±0.4	-24.3±0.6	4.2±0.1
	Artedidraco orianae	muscle	1		PS71/48	11.1	-21.0	4.2
	Bathydraco spec.	muscle	5		PS71/39	9.9±1.0	-27.2±0.6	3.0±0.4
	Bathydraco antarcticus	muscle	1		PS71/48	11.3	-23.5	4.3

4 Discussion

Benthic communities display strong variability and patchy distribution (e.g. Thurston et al., 1994; Rice and Lambshead, 1994), making sampling of the entity of benthic organisms practically impossible. However, concerning the macrofaunal community, the sampling of organisms in this study can be seen as relatively representative for the specific community. For meio- and megafaunal organisms, the sampling was less representative, and can only provide examples for the respective fauna. Additionally, especially for the deep-sea, the patchy occurrence often only yields low sample numbers (see discussion in chapter 4), therefore sometimes only one or few individuals were available for analyses.

The benthic system is supplied with organic material sinking down from the pelagic environment, including phytoplankton and zooplankton remains, faecal pellets and carcasses of larger organisms. During sinking, this material is degraded by bacteria, which can alter its isotopic signature before reaching the sea floor (Mako and Estep, 1984). Resulting from this, surface sediments as the repository of this organic matter have been shown to be ^{13}C enriched compared to water column or ice-associated POM (Iken et al., 2005) what has also been shown to have the effect that benthic food chains generally tend to be longer compared to pelagic ones. These processes can also be responsible for differences between deep-sea and shelf benthic systems, as well as higher-productivity and lower-productivity areas, as in the latter, the coupling between pelagic production and benthic consumers is tighter, resulting in lower isotopic enrichment. The extent of primary productivity also has an influence on the heavy isotope enrichment of phytoplankton and can lead to different isotope values at the base of the food chain (Goericke et al., 1994).

4.1 Filter feeding or detritivorous feeding type

Representatives of this feeding type sampled at deep stations span over the first, while those sampled at the shelf station expand into the second trophic level (Fig. 2). The spread of isotopic values within deposit feeding organisms could be explained by differences in selectivity towards certain detritus components. Selectivity for more freshly deposited material (e.g. algal remains) would result in lower trophic positioning, as this material has not been reworked in the same extent as longer deposited material, and is therefore isotopically lighter. At the deep stations, bivalves (*Vesicomya sirenkoi* and *Nucula* spec.), some polychaetes (Flabelligeridae spec. and Spionidae spec.), one decapod species and one Tanaidacean species (*Apseudomorpha* spec.) were classified to this feeding type. At the shallow station, this group includes Bryozoa, Holothuria (spec. 3, *Taeniogyrus contortus*, *Psolidium* spec. and *Echinopsolus splendidus*), Cumacea (families Nannastacidae, Diastylidae, Bodotriidae and one unidentified specimen), Ostracoda and two Isopod species (*Edotia pulchra* and *Antarcturus bovinus*).

Molluscs have been shown to have lower diet-tissue isotopic discrimination for ^{15}N than other organisms, related to their excretion of primarily ammonia (Vanderklift and Ponsard, 2003). Such lower discrimination would result in lower tissue $\delta^{15}N$ values and hence lower TL estimates if a fixed fractionation value is used.

The genus *Vesicomya*, occurring in very high abundances at the Maud Rise station (PS71/39), is presumably a filter/detritus feeder, as specimens are characterised by non-reduced guts, while a symbiosis with chemoautotrophic bacteria like in other representatives of their family has not yet been proved (Krylova and Sahlig, 2010). The results of the FA analyses support this theory, as bacterial markers have only been found in relatively small amounts, but FAs indicative for feeding on degraded organic material (22:6(n-3) and 16:0) take the dominant proportion. The proportion of diatom typical FA markers was comparably low, indicating that the bivalves rather utilise degraded material than fresh algal remains. The low $\delta^{15}N$ values measured for this species (4.8±0.09‰) confirm a very basal trophic position and therefore *Vesicomya sirenkoi* are utilised as the baseline organism (TL 1.0) for the deep stations. The analysed specimens of *Nucula* spec. have a FA composition comparable to *Vesicomya sirenkoi*, except that higher values of 18:5(n-3)/20:1(n-9) and 20:1(n-7) were found. The source for these FAs remains ambiguous, as they can be typical for zooplankton such as copepods, and an ingestion of motile prey seems unlikely for the bivalves. However, a somehow different trophic strategy of *Nucula* spec. compared to *Vesicomya sirenkoi* is supported by the distinctly higher $\delta^{15}N$ value (TL 1.5).

The feeding on phytodetritus described for polychaetes of the families Spionidae and Flabelligeridae indicated by their FA composition (see chapter 5) is mirrored in their relatively low trophic position (TL 1.8 in both), as is also the case for the tanaidacean genus *Apseudomorpha* (TL 1.4), for which feeding on phytodetritus has been indicated by their FA composition with high values of phytoplankton markers (see chapter 6).

The phylum Bryozoa (moss animals) consists of sessile, active, suspension-feeding forms that tend to form hydroid-like branched colonies in the deep-sea, rather than the encrusting colonies common on hard surfaces in shallow water (Gage, 1992). In bryozoan species from the Sea of Okhotsk, the main FAs were 16:0, 18:0, 22:6(n-3), and 20:5(n-3) (Demidkova, 2010). The presence of the FA markers that are characteristic of microalgae, protozoans, and detritus in bryozoan lipids would suggest a relatively low trophic position, but compared to e.g bivalves, the bryozoans occupie a slightly higher trophic position (TL 2.3±0.3).

Most deep-sea holothurians are deposit feeding, consuming surficial (uppermost few millimetres) sediment (Hansen, 1975; Billett, 1991). In Holothuria spec. 3, high values of phytodetrital marker FAs support this feeding mode. Strikingly high amounts of 20:4(n-6) as found in this study for *Taeniogyrus contortus* have also been detected by other authors studying the FA composition of deep-sea holothurians (Bühring et al., 2002; Hudson et al.,

2004). For the remaining two species, no FA analyses could be conducted. The holothurian species also show species-specific diverging isotopic values, and higher $\delta^{15}N$ values were found in individuals of *Taeniogyrus contortus* (TL 2.5 and 2.6) and *Echinopsolus splendidus* (TL 2.6), while lower values were measured in the other two species *Psolidium* spec. (TL 2.0 and 2.1) and Holothuroidea spec. 3 (TL 2.1±0.1). Such species-specific differences have also been observed in holothurians from the NE Atlantic (Iken et al., 2001), and the differences could be due to the fact, that some holothurians are indeed capable of selective feeding on certain compartments of detritus (e.g., remains of macroalgae), influencing the trophic position.

The FA pattern found in the Ostracoda strengthens the assumption that the analysed specimens obtain a detritivorous feeding style, as indicated by the low trophic position (TL 2.0).

Phytodetritivory is obtained by many peracarid crustaceans. High proportions of phytoplankton FA markers are e.g. found in the Cumacea (see chapter 6), and within the comparison of isotopic values, this group takes in a position distinct from all other groups ($\delta^{15}N$ of 3.5±1.1‰ and $\delta^{13}C$ of -16.5±1.4‰). Comparably low $\delta^{15}N$ values for Cumaceans even lower than in according sediment or POM samples have also been found in studies conducted in other ecosystems (e.g., Vizzini and Mazzola, 2002; Iken et al., 2005). Moreover the size fraction of the ingested POM may play a role, as different size fractions show isotopic variations (Rau et al., 1983).

This finding can most likely be explained by the fact, that these organisms utilise a food source distinct from the other organisms analysed, as for example fresh alga or a very fine POM fraction. This indicates a strong link to the pelagic environment, which can also account for other motile animals included in this study (e.g. fish), but is more visible in the case of cumaceans, as they inhabit a very low trophic level.

Based on the indications for phytodetritus feeding (see chapter 6), the Bodotriidae have been chosen as a baseline organism for the shelf station (TL 1.0).

Within the Isopoda, two species with differing lifestyles were assigned to the filter or detritus feeding group. Idoteidae (*Edotia pulchra)* are reported to feed commonly on herbivorous (phytodetritus), explaining the low $\delta^{15}N$ value (TL 2.0). On the contrary, comparably high stable isotope $\delta^{15}N$ values found in *Chaetarcturus* cf. *bovinus, Dolichiscus* cf. *meridionalis* and *Antarcturus bovinus* would indicate relatively high TL (2.7, 3.1 and 4.7, respectively), which is in clear contrast to the observed filter-feeding lifestyle of these isopods (Wägele, 1987). One explanation is a supplementary diet by predating on other organisms. However, comparable scenarios with very high $\delta^{15}N$ values have been found for filter feeding sponges (e.g. Iken et al., 2001), and the effect could have different causes (e.g. symbiontic bacteria

capable of metabolising highly refractory material, which is then assimilated by the sponge, or the direct ingestion of highly suspended, N-rich material). Also Mintenbeck et al. (2007) detected a significant increase in $\delta^{15}N$ with water depth in suspension feeders in the Weddell Sea shelf and slope ecosystem. As suspension feeders at greater depth are restricted mostly to the fine POM fraction, they depend on small particles originating from fragmentation of large particles either in the water column or on the sediment surface made available by re-suspension.

The Decapoda species sampled at station PS71/39 could not be further identified. Therefore, no assumptions on feeding habits could be made and they are classified as detritivorous feeders according to their $\delta^{15}N$ values (TL of 1.6 in both individuals).

4.2 Omnivorous feeding style

Within the benthos, omnivores have been shown to be generally enriched over filter feeders (Hobson et al. 1995 and references therein). At the deep station, polychaetes (*Ophelina* spec.), Mysidacea, Isopoda (*Betamorpha* spec., *Munneurycope* spec., Munnopsidae sp., *Eurycope* spec., *Syneurycope* spec. and Ischnomesidae spec.), Tanaidacea (Tanaidacea spec. and *Neotanais* spec.) and Decapoda (*Nematocarcinus* spec.) were assigned to the group of organisms with an omnivorous feeding style. At the shelf station, this group includes one polychaete species (*Pionosyllis epipharynx*), three Pycnogonid species (not further identified), Isopoda (*Cuspidoserolis* cf. *johnstoni*) and one amphipod species (Amphipod spec. 1).

Omnivory has been assumed for the polychaetes *Ophelina* spec. (Opheliidae) and *Pionosyllis epipharynx* (Syllidae) based on their FA composition and previous studies (see chapter 5), what is reflected in their intermediate stable isotope N values (TL 2.2±1.1 and 2.9, respectively).

Pycnogonidae are known to obtain feeding types from detritivory to carnivory, often on coeloenterates, and in some species on bryozoans (Prell, 1909; Fry, 1965; Gusso and Gravina, 2001; Fahrenbach and Arango, 2007). Two of the three analysed specimens, each belonging to a different species, show intermediate $\delta^{15}N$ values (TL 2.5 and 2.9), indicating an omnivorous lifestyle with the ingestion of detritus as indicated by their FA composition. For one individual, a higher $\delta^{15}N$ value (TL 3.3) than in the other investigated specimens was measured. This indicates tendencies to carnivorous feeding, what is further strengthened by its FA pattern with a high 18:1(n-9) to (n-7) ratio. The origin of the comparably high 20:4(n-6) values, as also found in the investigated holothurians, remains ambiguous.

The amphipod species (Amphipod sp. 1) assigned to this feeding group was classified according to its FA pattern (see chapter 6). The moderate $\delta^{15}N$ values measured (TL 2.8±0.2) seem to confirm the omnivorous lifestyle.

Mysids are generally considered omnivorous (Grossnickle, 1982; Jerling and Wooldridge, 1995), also indicated for the individuals analysed in this study (TL 2.4 and 2.6).
Decapoda of the genus *Nematocarcinus* have been described to be predating or scavenging, but also displaying opportunistic omnivorous feeding (Allen et al., 2000); however, the $\delta^{15}N$ values (TL 2.0 and 2.1) more likely indicate a detritivorous feeding mode.

4.3 Predating or scavenging feeding style

Organisms classified as predating or scavenging span over more than two trophic levels, and surprisingly, some of the organisms thought to be top-predators (bigger fish) are not found at the maximum range of $\delta^{15}N$ values. This lower-than-expected ^{15}N enrichment of predating/scavenging organisms capable of moving freely in the abysso-pelagic environment such as fish compared to those more restricted to the benthic realm such as e.g. predating/scavenging gastropods indicates that they are partly decoupled from the food web based on sedimented and frequently recycled organic material, as suggested by other authors (e.g., Mahaut et al., 1990; Iken et al., 2001).
Included in this feeding group at the deep stations are one gastropod (*Aforia lepta*) polychaetes (*Bathyglycinde* spec. and Polyodontidae spec.), three species of Amphipoda (Amphipoda species 1 and 2 and *Eurythenes gryllus*), four species of Isopoda (*Storthyngura* cf. *gigantea*, *Serolis* spec., *Cuspidoserolis* spec. and *Accalanthura gigantissima*) and two fish species (Macrouridae sp. and *Bathydraco* spec.). At the shelf station, one gastropod species (*Harpovoluta charkoti*), three polychaete species (Polyonidae spec., *Nereis* cf. *atlantica* and *Travisia kerguelensis*), seven isopod species (*Accalathura gigantissima*, *Natatolana intermedia*, *Natatolana occulta*, *Stenetrium weddellensis*, *Glyptonotus antarcticus* and *Notoxenus* cf*. spinifer*) and five fish species (*Trematomus scotti*, *T. bernachii*, Macrouridae spec., *Bathydraco* spec. and *Bathydraco antarcticus*) were classified as predating/scavenging.
The gastropod *Harpovoluta charkoti* is very abundant in the Weddell Sea down to 600 m, and the mode of feeding has been described to be mainly necrophageous (Arnaud 1976-1978, 1979; Hain 1990). This is in agreement with the high $\delta^{15}N$ values found (TL 3.7 and 3.8). *Aforia lepta* belongs to the suborder Toxoglossa, characterised by the possession of teeth in which poisonous glands terminate, and their predatory lifestyle. However, the individual analysed for this study has relatively low $\delta^{15}N$ values (TL 2.1) compared to other organisms classified as carnivores. This is most likely due to the lower tissue $\delta^{15}N$ values related to their excretion mode (Vanderklift and Ponsard, 2003), an argument which has to be taken into account for all other molluscs as well.
The $\delta^{15}N$ values measured for the polychaetes in some cases confirm the assumed carnivorous diet component (see chapter 5) for *Nereis* cf. *atlantica* (3.1), *Travisia*

kerguelensis (3.6) and Polyonidae spec. (TL 3.6), but possibly indicate partly omnivorous feeding in *Bathyglycinde* spec. (TL 2.8) and Polyodontidae spec. (2.9).

The Amphipoda species analysed in this study show strong species-specific variations in their $\delta^{15}N$ ratios, which are reflected also in their FA composition (see chapter 6). Some species, as *Eurythenes gryllus*, known to be at least mainly scavenging, have $\delta^{15}N$ values indicating a trophic level of 3.4±0.4, while others show lower average values (Amphipoda spec. 1: 2.8±0.2, *Lysianassidae* spec.1: 3.2±0.2, *Lysianassidae* spec.2: 2.9±0.2). However, it has been shown that within the scavenging guild of lysianassoid amphipods, each species employed alternate foraging modes, including detrivory or predation, to supplement necrophagy (Blankenship and Levin, 2007), what could explain lower-than expected TL.

The same scenario probably accounts for the representatives of the isopod families Cirolanidae (*Natatolana occulta* and *Natatolana intermedia*) and Chaetiliidae (*Glyptonotus antarcticus*), classified as scavenging isopods, and often found in baited trap systems (Clarke, 1979; DeBroyer et al., 2004; Nyssen et al., 2005). Thus, higher $\delta^{15}N$ values than measured in this study (ranging from 9.0 to 9.5‰) would be expected; however, even lower $\delta^{15}N$ values have been measured for *Natatolana* sp. (6.8±0.4‰) and *G. antarcticus* (6.3‰) from the Antarctic Peninsula shelf (Nyssen et al., 2005) indicating that they display rather facultative than obligate scavenging.

Serolidae (including *Cuspidoserolis* cf. *johnstoni* and Serolis spec.) are predators, feeding on a variety of small invertebrates (Luxmoore, 1981), and also the predator *Accalathura gigantissima*, belonging to the isopod family Paranthuridae, has been observed to feed on other crustaceans (e.g. amphipods) by using its stinging mouthparts to suck out their prey (Wägele, 1991), and a relatively high $\delta^{15}N$ value (TL 3.5) confirms a high trophic position.

For the isopods *Stenetrium weddellensis* and *Notoxenus* cf. *spinifer*, a carnivorous input to their dietary spectrum has been indicated by their FA composition (see chapter 6) and is confirmed by relatively high $\delta^{15}N$ values (TL 3.2±0.2 and 3.3/3.5, respectively).

The feeding habits of *Storthyngura* cf. *gigantea* are basically unknown, but the overall morphology and the comparably enormous size (up to several centimetres; Malyutina, 2003) would support the assumption that they are predators, as indicated by high $\delta^{15}N$ values (TL 3.3).

The analysed fish species have been shown to prey on different other organisms, mainly amphipods and polychaetes, but also gastropods and fish (see chapter 7). The $\delta^{15}N$ values indicate TL between 3.0 and 4.2 are in agreement with their carnivorous lifestyle, but certain differences within genera are observed. For the example of the Macrouridae and Bathydraconidae, these differences seem to be at least partly dependent on the fish body size (Fig. 3), as the longer the fish, the higher the $\delta^{15}N$ value. The Trematoidae seem to show

species-dependent differences, as for *Trematomus scotti*, higher values were measured than for *T. bernachii*; for the assumption of size-dependent changes, the sample size is too small. The occurrence of lower-than-expected $\delta^{15}N$ values mentioned previously have also been found in studies on macrourid fish from the North Pacific (Drazen et al., 2008) and from the North Atlantic (Iken et al., 2001), suggesting that for these top predators, lower $\delta^{15}N$ values may be the result of bypassing the benthic food web by scavenging on nekton carrion from upper water layers. This might be a common feature especially in deep-sea fishes, meaning that the populations of these abyssal fishes are only weakly linked to benthic trophic dynamics but closely coupled to processes within the pelagic realm.

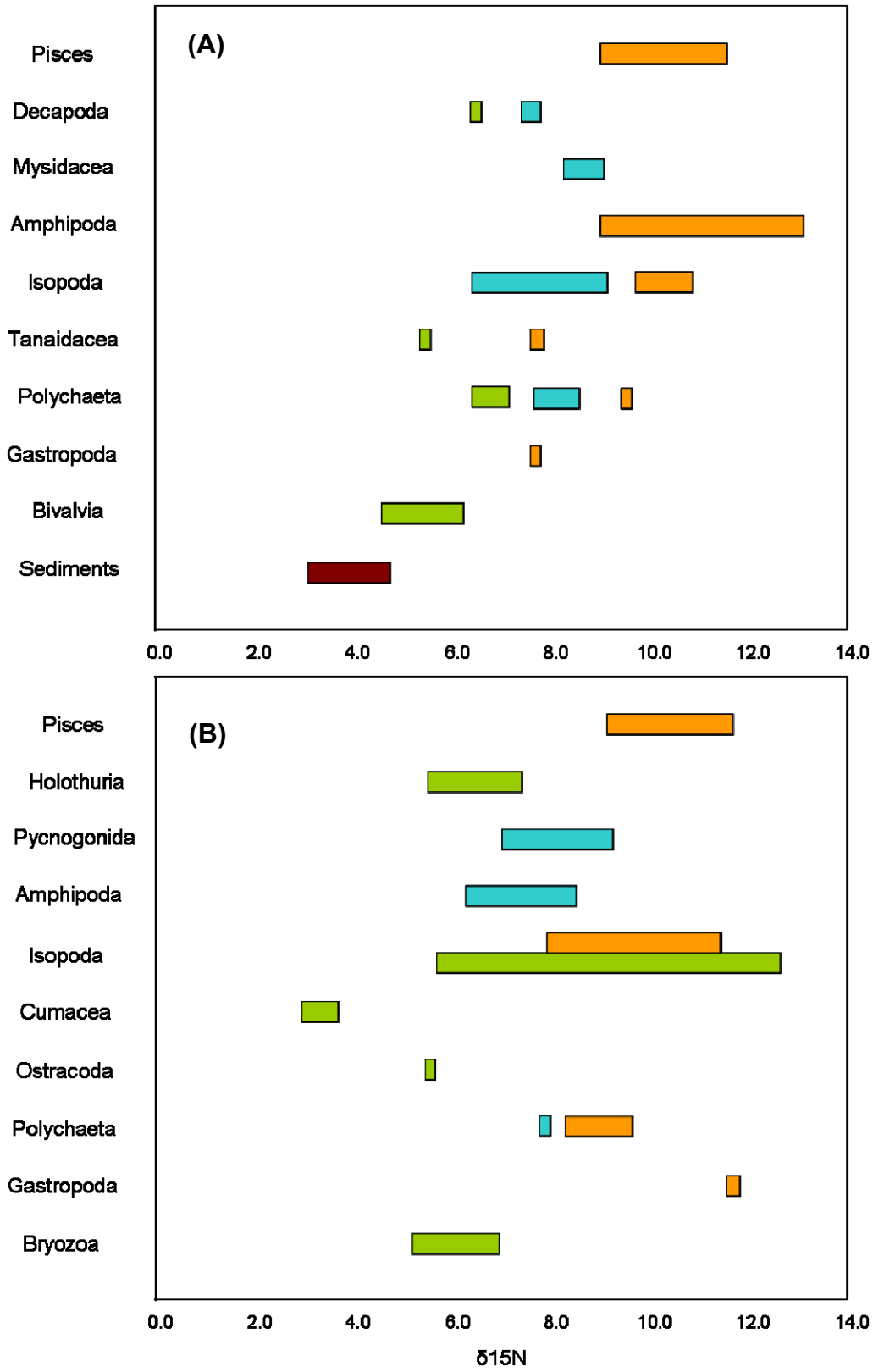


Fig 2 Isotopic ranges of $\delta^{15}N$ for Antarctic benthic deep-sea (A) organisms and sediments (brown) and shelf (B) organisms. Colours indicate anticipated feeding style (green: filter/detritus feeding; blue: omnivorous feeding; orange: predating/scavenging).

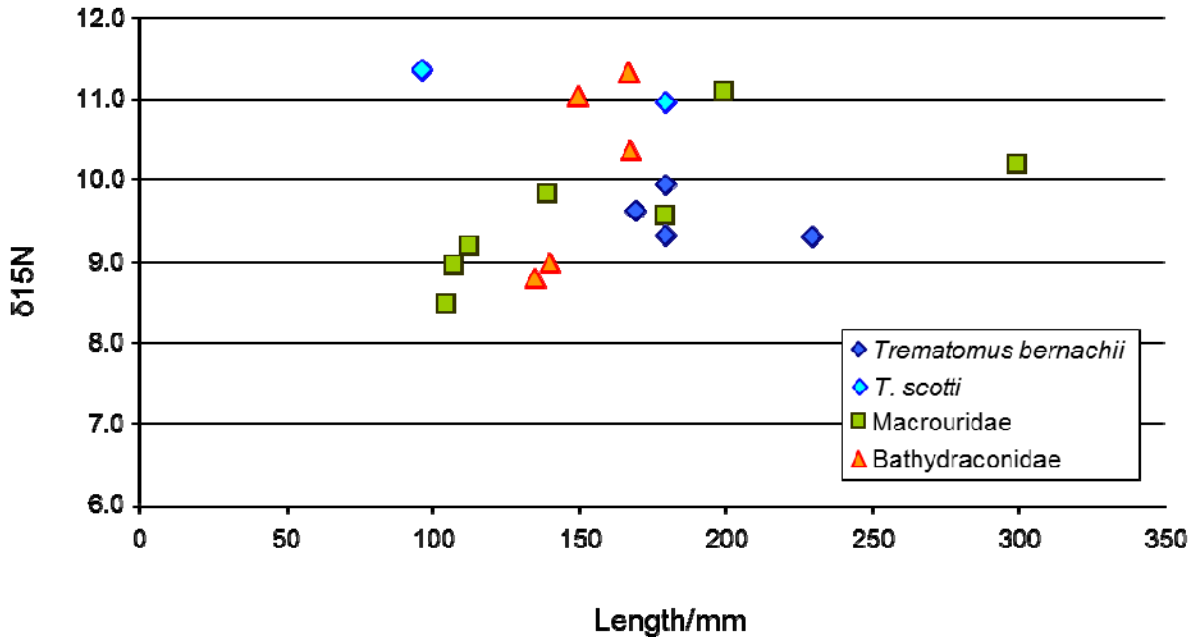


Fig 3 Fish body length (in mm) *versus* $\delta^{15}N$ ratios (in‰).

5 Conclusions

In this study, narrower trophic ranges than e.g. in an Arctic deep-sea system (4.6-17.7‰) (Iken et al., 2005) or Northeast Atlantic (Iken et al., 2001) were detected. However, at least in the latter, much higher baseline (POM and sediment) $\delta^{15}N$ values were measured. The reasons are latitudinal differences in the nitrogen isotopic composition of nitrate and nitrogen supply. In N-S transects in the southern Ocean the $\delta^{15}N$ values of nitrate can vary by several permill and is dependent on the nitrate concentration (Sigman et al., 1999). These isotopic changes in the nitrate source will be carried over to the primary producer and, thus, must cause site-specific differences in the entire food chain.

The strong transitions between $\delta^{15}N$ values of organisms with different feeding types found in this study can depend on a variety of factors. Such wide ranges in $\delta^{15}N$ ratios in most benthic taxa of Antarctic food webs indicate feeding across a range of trophic levels and are partly due to a high amount of omnivory and the ability of vertical niche expansion.

Also processes of nitrogen assimilation and excretion can have an influence on consumer-diet ^{15}N enrichment. Ammonotelic organisms show lower ^{15}N enrichment than ureotelic or uricotelic organisms. This mechanism can also cause differences among taxonomic classes: molluscs and crustaceans have been shown to generally yield lower ^{15}N enrichment, possibly due to the fact that these organisms excrete mainly ammonia (Vanderklift and Ponsard, 2003).

Differences in $\delta^{13}C$ values are generally coupled with the source of primary production. It has e.g. been shown that ice algae can be isotopically heavier compared to phytoplankton, resulting in differences in $\delta^{13}C$ values, what could be caused by either local differences in the availability of CO_2 for photosynthesis or be related to the thickness of diffusive boundary layers that ultimately determine the rate of CO_2 or HCO_3^- diffusion. Well-defined boundary layers such as those associated with littoral or epontic algae lead to an entrapment of otherwise normally expelled or discriminated ^{13}C. The subsequent enrichment in ^{13}C of carbon available for photosynthesis would thus result in higher $\delta^{13}C$ values of ice algae carbon. Algae occurring in pelagic or turbulent water conditions are expected to have reduced boundary layers and consequently decreased $\delta^{13}C$ values.

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State of the manuscript and own contribution:
I conducted the fatty acid analyses analyses and related data interpretation, as well as the stable isotope analyses. The manuscript was written based on discussions with Dr. Christoph Mayr (Munich) and is currently prepared for submission.

Chapter 5

Diet insights of deep-sea polychaetes derived from fatty acid analyses

Polynoid (right) and scalibregmatid (left) polychaetes sampled in the Antarctic deep-sea during the ANDEEP-SYSTCO cruise.

Chapter 5 Diet insights of deep-sea polychaetes derived from fatty acid analyses

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Abstract

The fatty acid (FA) composition of representatives belonging to 18 polychaete families from the Southern Ocean shelf and deep-sea (600 to 5337 m) was analysed in order to identify trophic biomarkers and elucidate possible feeding preferences. Total FA content was relatively low with few exceptions and ranged from 1.0 to 11.6 % of total body dry weight. The most prominent FA found were 20:5(n-3), 16:0, 22:6(n-3), 18:1(n-7), 20:4(n-6), 18:0, 20:1(n-11) and 18:1(n-9). For some polychaete families and species FA profiles indicated selective feeding on certain dietary components, like freshly deposited diatom remains (e.g. Spionidae, Fauveliopsidae and Flabelligeridae) or foraminiferans (e.g. Euphronisidae, Nephtyidae and Syllidae). Feeding patterns were relatively consistent within families at the deep stations, while the FA composition differed between the deep and the shelf stations within the same family. Fatty alcohols, indicative of wax ester storage, were found in almost all families (in proportions of 0.0 to 29.3 % of total FA and fatty alcohols). The development of this long term storage mechanism of energy reserves possibly displays an evolutionary strategy.

Key words: Deep-sea, fatty acids, polychaetes, Southern Ocean benthos

1 Introduction

The pioneering investigations of the expeditions ANDEEP I & II in 2002 and ANDEEP III in 2005, studying the biodiversity and potential origin of taxa which have radiated in the Southern Ocean deep-sea, revealed a remarkable biodiversity. The mechanisms underlying this high diversity in deep-sea macrobenthos still lack satisfactory explanation (Gage, 1996). Polychaetes, as shown for other deep-sea regions (Hessler and Sanders, 1967; Thistle et al., 1985; Alongi, 1992, Borowski and Thiel, 1998; Hutchings, 1998; Brandt and Schnack, 1999; Kröncke and Türkay, 2003), take an important role in terms of abundance and diversity in the

Southern Ocean deep-sea, including the Weddell Sea sampled in this study (Piepenburg et al., 2002; Brandt et al., 2007a, b; Schüller et al., 2009). Previous studies demonstrate that benthic polychaetes adopt an important ecological role, as they are major contributors to the resuspension of organic matter via bioturbation (Reichardt, 1987; Levin et al., 1997; Hutchings, 1998). They exhibit a wide variety of feeding modes, ranging from surface deposit or suspension feeding to carnivory and scavenging (Fauchald and Jumars, 1979). Nonetheless, ecological studies on Southern Ocean deep-sea polychaetes are very limited.

The deep-sea ecosystem is dependent on primary production in the upper water layers, making the quantity and quality of food reaching the sea floor crucial for benthic organisms (Tseytlin, 1987; Graf, 1989, 1992; Gooday and Turley, 1990; Paterson et al., 1998; Bühring and Christiansen, 2001; Smith et al., 2008). In marine polar regions, the numerical abundance, biomass and distribution of organisms forming the benthic community are directly influenced by variations in food supply (Grebmeier and Barry, 1991, and references therein). These are in turn related to changes in multiple, interdependent factors including hydrography, ice coverage, light, temperature, nutrient availability and the structure of the pelagic food web (Grebmeier and Barry, 1991; Bathmann et al., 1997; Clarke and Arntz, 2006; Arrigo et al., 2008). In the Southern Ocean, the primary production is characterised by a seasonal discontinuity with a short phytoplankton bloom peak in late spring. In addition to sedimentation from the upper water layers, bottom currents (horizontal distribution) play an important role in the distribution of detritus (Sokolova, 1997). “Nepheloid layers”, layers of fresh organic material providing rich food sources for benthic organisms (Billett et al., 1983), are associated with phytoplankton blooms in the upper ocean. Although rapid responses of deep-sea benthic fauna to increased inputs of organic material have been observed (Aberle and Witte, 2003; Witte et al., 2003; Moodley et al., 2005; Bühring et al., 2006), the accumulation of organic material on the seafloor can be decoupled from seasonal pulses of primary production in the photic layer by providing a more permanent food reservoir buffering the benthic system, as documented for the shelf off the Antarctic Peninsula (Mincks et al., 2005; Smith et al., 2006).

The basis of benthic deep-sea food webs consists of degraded material and some abyssal organisms are possibly exposed often to starving intervals, consequently classic approaches (gut content analyses) to identify the composition of their diet rarely deliver satisfying results. Additionally, it is difficult to obtain living specimens from the deep-sea for conduct feeding experiments. The analysis of fatty acid (hereafter FA) composition has become an established tool to elucidate the feeding behaviour of organisms and can help to gain insights into deep-sea animals’ diets. The FA marker concept relies on the fact that certain FA are incorporated into consumers in a conservative manner, thereby providing information on an organism’s diet (e.g. Dalsgaard et al., 2003; Lee et al., 2006). The FA

pattern is also influenced by various factors (e.g. species specific metabolic processes), but knowledge on such processes in deep-sea organisms is scarce. Thus, one aim of this study was a general characterisation of the FA composition of deep-sea polychaetes based on results obtained in previous FA studies conducted on other benthic organisms. These provided evidence, for example for holothurians, for bentho-pelagic coupling (Hudson 2004), links to the epipelagic zone for various benthic taxa (Bühring and Christiansen, 2001) or different dietary preferences in deep-sea copepods (Laakmann et al., 2009).

Some FA that function as biomarkers for the type of ingested food are of special interest, and are widely used for the interpretation of an organism's FA composition. Examples are the phytoplankton markers 20:5(n-3), 16:1(n-7), 18:1(n-7) and 22:6(n-3) (Nichols et al., 1984, 1991; Sargent et al., 1995) or certain FA ratios like 20:5(n-3)/22:6(n-3) and 18:1(n-9)/18:1(n-7) (Dalsgaard et al., 2003), which can be used to distinguish carnivores from herbivores (e.g. Falk-Petersen et al., 1998, 2000; Graeve et al., 1997; Auel et al., 2002). Another noteworthy FA is 20:4(n-6), which has shown to be an important component in foraminiferans (Gooday et al., 1992; Suhr et al., 2003) and possibly points towards the ingestion of these protozoans. Generally, polyunsaturated fatty acids (PUFA, e.g. 20:5(n-3), 22:6(n-3) or 20:4(n-6)) that are almost exclusively synthesized by plants, play an important role in regulating cell membrane properties (Farkas, 1979; Pruitt, 1990; Hazel 1995). As they are essential for all organisms, yet very few animals have the capability of synthesizing them *de novo*, food rich in PUFA provides a valuable dietary resource (Brett and Müller-Navarra, 1997).

In this study, we analysed and compared the FA composition of members of 18 polychaete families to gain information on their general biochemical composition, as well as on the proportion of specific fatty acids to compare this information with feeding types previously described (e.g. Fauchald and Jumars, 1979). For this we applied multivariate analyses (i.e. discriminant analysis, as well as principle component analyses [PCA]) to identify dietary differences based on FA patterns. This will provide a starting point for future comparisons, which could be particularly helpful if the feeding type of an organism is unknown.

2 Material and Methods

2.1. Study area

The studied material was sampled during the ANDEEP-SYSTCO project on board of RV *Polarstern*, expedition ANT XXIV/2 from 28.11.2007 to 4.2.2008. The material was collected at five stations located roughly along the Greenwich meridian, in the Weddell and Lazarev Seas, ranging from 600 to 5337 m depth (Fig. 1). The sampled stations are situated in different regimes and therefore exhibit heterogeneous characteristics concerning faunal

composition, carbon fluxes and sediment structure. In general, carbon export rates reported for the Southern Ocean are low to moderate (Fischer et al., 2000). In terms of average primary production, the Weddell Sea can be divided in a northern-central province of low production (<300 mg m^{-2} day^{-1}) and a south-eastern coastal province of elevated production (400-700 mg m^{-2} day^{-1}) (v. Bröckel, 1981, 1985; El-Sayed and Taguchi, 1981). In terms of production (P) and biomass (B), Brey and Gerdes (1998) concluded that in the high Antarctic Weddell Sea and Lazarev Sea the macrozoobenthos biomass decreases from 26.83 g C m^{-2} in the 100–300 m stratum to 0.16 g C m^{-2} in the 1500-4300 m stratum. Community production decreases accordingly with depth (from 4.83 g C m^{-2} $year^{-1}$ to 0.09 g C m^{-2} $year^{-1}$), annual P/B ratio, however, increases with depth from 0.18 $year^{-1}$ in the 100-300 m stratum to 0.55 $year^{-1}$ in the 1500-4300 m stratum.

Details on sediment characteristics and faunal composition are available for all stations employed in this study (Bathmann, 2010). Station PS71/17 (southern Lazarev Sea) was characterised by very fine grey clay with sand and stones. The polychaete diversity found at this station was highest of all stations sampled, but general species richness and composition lay within the range of expectation formed on experiences from ANDEEP III samples (Schüller et al., 2009).

One station was located in the Central Weddell Sea (PS71/33), the sediment consisting of very fine and soft homogeneous grey-brown clay containing many small foraminiferans with only few stones. It was mainly colonized by soft bottom dwellers and burrowing animals. Species richness for the deep Weddell Sea has been reported to be lower than for the slope regions (Linse et al., 2007), and pre-sorting of epibenthic sledge (EBS) and Agassiz Trawl (AGT) samples on board yielded only 127 polychaete specimens belonging to 19 families compared to over 300 at station PS71/17 (25 families) suggesting this station to be of lower polychaete abundance but probably comparable diversity (Wilmsen and Schüller, pers. com.).

At station PS71/39 (Maud Rise), the sediment consisted of light brown foraminiferous ooze with many stones. Maud Rise regularly appears as a region of reduced ice coverage (De Steur et al., 2007), and intermediate to high values of annual primary production rates are reported (Wefer and Fischer, 1991). Brandt et al. (unpublished data) observed that Maud Rise showed distinct differences in benthic fauna composition compared to surrounding deep-sea basins, and in the case of polychaetes (especially the tube-dwelling, suspension-feeder fraction) is unique compared to stations sampled during ANDEEP. The over-all polychaete community at Maud Rise is characterized by high abundances of few species with wide distribution ranges in the Southern Ocean, giving rise to the assumption that the community is one of generalists and opportunists rather than specialists.

The shelf station PS71/48 comprised very compact sediment, and the hard bottom was covered by sessile animals (mainly poriferans, accompanied by spicule mats), as well as foraminiferans. The Antarctic continental shelf is large, deep (500-1000 m), and characterised by intense seasonality and high organic carbon fluxes (Isla et al., 2006). The water-column production is transmitted to the shelf floor in intense pulses of particulate organic matter (Bathmann et al., 1991; Fisher et al., 2000).

Station PS71/85 was situated at the Antarctic Convergence and the sediment consisted of very fine, light brown diatomaceous ooze. The faunal composition comprised a fairly rich macrofauna with polychaetes, isopods and bivalves being the most dominant groups. Fisher et al. (2000) reported for this region organic carbon fluxes with lower temporal variability as compared to the polar coastal environments. The peak sedimentation was almost as high as in the coastal environments, despite much lower daily primary production in the Polar Front Zone.

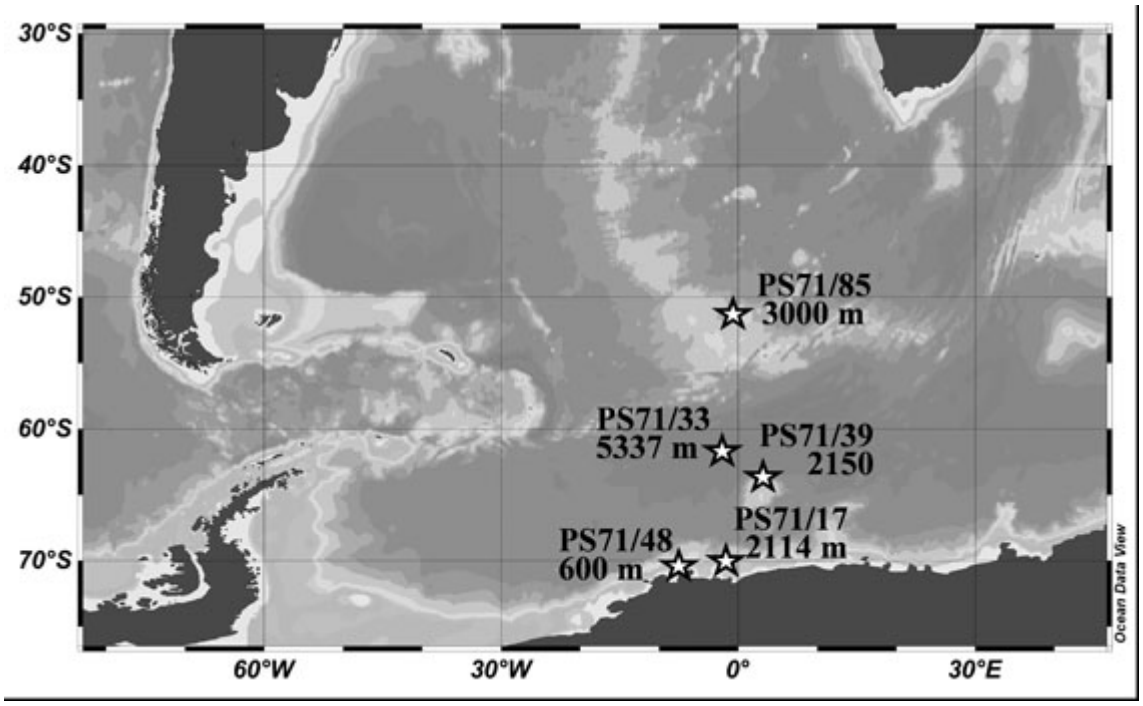

Fig 1 Stations sampled during the ANDEEP-SYSTCO expedition ANT XXIV/2 from 28.11.2007 to 4.2.2008.

2.2. Sampling

A total of 79 polychaete individuals analysed for this study were obtained by an EBS (Brandt and Barthel, 1995; Brenke, 2005), an AGT and a Rauschert-dredge (Stransky, 2008). Sorting of the samples was conducted either in climate chambers (0-2°C) or on ice and stopped within 1 h after retrieval to guarantee for freshness of the material. The aim of sorting was to collect as many polychaetes of different families as possible that could be accurately identified within the short timeframe given. All samples were sorted to the highest taxonomic level possible, with one to 22 replicates per family; digital pictures were taken of each specimen. The samples were frozen and stored at -80°C prior to analysis.

Sediment samples were taken by a multiple corer (MUC), cut into 1 cm slices and immediately frozen at -80 °C. Later in the laboratory, one subsample (125-250 mg) of the first sediment centimetre from each deep station was randomly analysed for fatty acid composition. Bottom water was taken by means of a water sampler with CTD (conductivity-temperature-depth data logger), sampled as close to the bottom as possible without endangering the gear. Samples of POM (particulate organic matter) from the bottom water were obtained by filtering different volumes to a precombusted (400°C for 4h) GF/C filter (approx. 1.2 µm retention size). Filtering was conducted at 300 mbar and stopped when a clear colouring appeared on the filter (volumes of 11.5-18 litres). Per deep station, 2-3 filters were analysed for their fatty acid composition. No sediment and POM data are available for the shelf station due to limited deployment of gear (see Table 1 for sediment and filter information).

Table 1 Sediment and particulate organic matter (POM) for ANDEEP-SYSTCO samples. Number of samples, station, sample volumes (in litres for POM, in mg for sediment samples), layer (meters above ground for POM, sediment layer for sediment samples), amounts of saturated (SFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids in % of total FA, and proportions of the ten most abundant fatty acids (of the polychaete samples) in % of total FA.

Sample	N	Station	Volume	Layer	SFA	MUFA	PUFA	16:0	16:1ω7	18:0	18:1ω9	18:1ω7	20:1ω11	20:4ω6	20:5ω3	22:5ω3	22:6ω3
Filter	3	PS71/17	16 L	247m	48±2	33±2	19±3	27±3	1±0	14±1	25±4	2±0	1±0	1±0	2±2	3±2	4±4
	2	PS71/33	11.5 L	1m	57±2	29±1	14±2	29-35	1-1	12-13	17-18	1-1	1-1	1-1	1-1	2-3	1-3
	3	PS71/39	16 L	42m	68±3	24±3	9±1	40±4	1±0	16±3	14±5	1±0	1±0	1±0	1±0	2±1	2±1
	3	PS71/85	18L	9m	64±3	19±3	17±3	32±4	1±0	22±4	13±4	1±0	1±0	1±0	3±1	7±4	3±1
	-	PS71/48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sediments	1	PS71/17	250 mg	1.cm	34	50	18	22	13	6	9	14	-	3	3	2	2
	1	PS71/33	199 mg	1.cm	28	69	9	15	2	10	39	9	-	1	1	1	1
	1	PS71/39	200 mg	1.cm	34	58	11	19	4	11	31	7	-	1	1	1	1
	1	PS71/85	125 mg	1.cm	46	28	29	21	3	19	13	4	-	3	3	2	2
	-	PS71/48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

2.3. Fatty acid analyses

Prior to the lipid analysis samples were freeze dried, weighed and allowed to extract in dichloromethane-methanol (v:v/2:1) for at least 48 h. Lipid extraction was performed with minor modifications as described in Folch et al. (1957) using ultrasonic disruption in dichloromethane:methanol and a washing procedure with aqueous KCl solution. The analysis of fatty acid composition was performed with modifications as described in Kattner and Fricke (1986). Fatty acids were converted to their methyl ester derivatives (FAME) in sulphuric methanol and analysed using a gas chromatograph (HP 6890A) equipped with a programmable temperature vaporizer injector (Gerstel® CIS4plus) and a DB-FFAP column. The use of a large volume injector allows a measurement of very low lipid amounts. FAMEs and fatty alcohols were detected by flame ionisation and identified by comparing retention times with those derived from standards of known composition. For quantification of fatty acids tricosanoic acid was used as internal standard.

2.4. Statistical analysis

Some families were represented by small sample sizes or only one individual due to the constraints of sampling in the deep-sea, while others had sufficient numbers to allow statistical testing. FA with proportions lower than 0.5% of total FA were excluded prior to the analyses. To evaluate family differences, a discriminant analysis was conducted based on ten fatty acids (FA) for families with more than one individual. These FA were chosen for the analyses due to their average abundance (>3% of all FA). Wilk's λ was used to indicate the power of the discriminant analysis to separate groups (smaller values indicating greater success).

To identify feeding differences based on FA pattern, a principal component analysis (PCA) was conducted for the same ten variables (fatty acids) used in the discriminant analysis. The polychaetes at the four deep stations had relatively similar FA compositions within the families, thus one PCA was conducted for the polychaetes of all deep stations, and one for those from the shelf station. The PCA was performed based on the correlation matrix with eigenvalues >1 extracted. A one-way ANOVA with post-hoc test was used to test for significance of differences in proportions in saturated (SFA), monounsaturated (MUFA) and polyunsaturated FA (PUFA). All analyses were performed using the SPSS statistical software package.

3 Results

3.1. Biochemical composition of sediments and POM

One sediment sample per station was analysed to give an impression of the fatty acids that are present in the polychaetes' environment. The sediment FA were dominated by MUFA, while PUFA made up the smallest proportion (Fig. 2). POM, which was retained by filtrating bottom water, contained mainly SFA. The FA 18:1(n-9) was dominant in most samples of both sediment and filtrated bottom water, while typical phytoplankton markers like 20:5(n-3) and 22:6(n-3) were not prevalent in either. Typical bacterial biomarkers (such as 15:0, 17:0, 15:1 or 17:1) as well as the FA 20:4(n-6) were also only found in minor proportions. FA composition of polychaetes differed from POM and sediment in having significantly much higher proportions of PUFA ($P < 0.05$). Variations in FA proportions within groups with specimen numbers ≥3 are given as standard deviations.

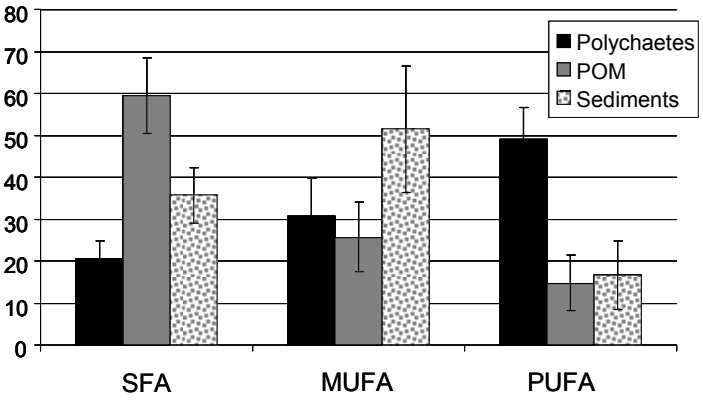

Fig.2 Proportion of saturated (SFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids (in % of total fatty acids) of sediment, particulate organic matter (POM) and polychaete samples. Error bars indicate standard deviations.

3.2. General fatty acid composition of polychaetes

The most prominent FA found in the polychaetes were 20:5(n-3), 16:0, 22:6(n-3), 18:1(n-7), 20:4(n-6), 18:0, 20:1(n-11) and 18:1(n-9) (Table 2). Total FA contents were comparatively low, with values varying between taxa from 1.0 to 5.1% of body dry weight. One exception was one specimen of Goniadidae (*Bathyglycinde* sp.), with a FA proportion of 11.6% of total dry weight. Fatty alcohols were found in most analysed polychaetes, in varying proportions from 0 to 29.3 % of total FA and fatty alcohols. The highest values occurred in the families Capitellidae, Opheliidae, Flabelligeridae and Sigalionidae.

The discriminant analyses on the most abundant FA show a clear separation between the different families as well for the deep (91% correct classification of families) as for the shelf stations (100% correct classification of families) (Fig. 3a and b).

Table 2 Ratios of fatty acids (A=18:1(n-9)/18:1(n-7) ratio, B=20:5(n-6)/22:6(n-6) ratio), amounts of saturated (SFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids (FA) in % of total FA, total fatty alcohols (TA, in % of total FA and fatty alcohols), total FA content (TFA, in % of total body dry weight) and proportion of the ten most abundant FA in all samples (in % of total FA) for all analysed ANDEEP-SYSTCO polychaetes. Specimens of one family are presented for each station they were sampled. For groups with specimen numbers ≥ 3, average results with standard deviations are given.

Family	Species	N	St	A	B	SFA	MUFA	PUFA	TA	TFA	16:0	16:1ω7	18:0	18:1ω9	18:1ω7	20:1ω11	20:4ω6	20:5ω3	22:5ω3	22:6ω3
Acrocirridae	*Acrocirridae* spec	1	17	0.33	7.17	15	33	52	11.9	1.4	6	3	5	2	5	12	4	29	3	4
Capitellidae	Capitellidae spec.	1	85	0.26	13.41	18	33	49	29.3	1.2	6	3	5	2	6	10	5	33	5	2
Euphrosinidae	*Euphrosinidae* sp.	5	48	0.35±0.05	3.36±056	20±1	22±2	58±2	10.2±2.1	1.3±0.1	7+/-1	2+/-0	10+/-1	3+/-0	8+/-1	1+/-0	20+/-2	17+/-3	4+/-1	5+/-1
Fauveliopsidae	*Fauveliopsidae* sp.	3	17	0.46±0.05	1.33±0.18	29±9	28±13	42±4	3.8±1.5	0.8±0.4	11+/-2	2+/-1	15+/-7	6+/-2	13+/-6	3+/-0	5+/-2	15+/-1	8+/-4	11+/-2
Flabelligeridae	*Flabelligeridae* sp.	1	39	1.04	1.6	18	28	54	23.0	1.2	8	3	7	3	3	5	1	26	4	17
Flabelligeridae	*Flabelligeridae* sp.	1	48	0.23	0.55	17	53	30	3.6	1.0	8	6	8	3	11	7	2	3	7	5
Goniadidae	*Bathyglycinde* spec.	1	33	0.03	0.99	15	57	28	4.7	11.6	13	6	2	1	33	5	1	13	5	7
Maldanidae	Maldanidae spec.	1	39	0.24	0.87	18	36	46	2.3	2.3	13	6	3	3	11	4	8	12	5	13
Nephtyidae	*Nephtyidae* sp.	1	17	0.69	3.73	20	28	52	1.1	3.4	11	4	5	5	7	2	25	12	3	3
Nephtyidae	*Nephtyidae* sp.	1	17	2.62	14.30	25	24	51	1.0	2.6	17	3	4	12	4	2	24	14	3	1
Nephtyidae	*Aglaophanus* spec	1	48	0.69	1.01	22	21	57	1.7	2.1	10	1	10	4	5	7	4	20	3	20
Opheliidae	*Ammotrypanella* cf.*arctica*	1	39	0.35	2.55	18	28	54	18.9	1.6	13	1	3	2	6	10	4	29	3	12
Opheliidae	*Kesun abyssorum*	1	33	0.42	2.67	13	59	28	4.4	4.6	6	4	3	9	23	11	3	9	4	3
Opheliidae	*Kesun abyssorum*	1	39	0,31	3.04	17	38	46	20.1	1.5	8	3	8	2	8	9	11	15	7	5
Opheliidae	*Ophelina breviata*	1	48	0.72	4.23	22	34	45	8.8	1.2	15	2	4	5	7	9	4	26	2	6
Opheliidae	*Ophelina breviata*	1	48	0.61	1.65	21	36	44	1.1	1.2	14	1	5	5	9	12	11	10	1	6
Opheliidae	cf. *Ophelina* sp.	14	39	0.97±0.79	6.48±0.38	17±1	36±5	47±4	20.7±1.6	1.5±0.1	13+/-1	2+/-1	3+/-0	6+/-5	6+/-1	11+/-0	4+/-0	30+/-3	2+/-0	5+/-0
Opheliidae	*Travisia kerguelensis*	1	48	0.77	3.55	21	43	35	12.2	1.0	12	10	7	5	6	12	12	11	2	3
Opheliidae	*Travisia kerguelensis*	1	48	0.51	3.22	21	48	31	11.8	1.1	11	9	6	4	8	12	11	10	2	3
Opheliidae	*Travisia kerguelensis*	1	85	0.63	3.06	28	26	46	11.6	1.6	10	1	16	2	4	4	3	20	8	7
Orbiniidae	Orbiniidae spec.	1	48	1.17	1.26	22	19	59	1.6	2.2	11	1	8	5	5	5	3	23	2	19
Phyllodocidae	Phyllodocidae spec.	1	48	0.46	1.36	20	19	61	2.2	3.2	7	1	10	3	6	3	2	27	3	20
Polynoidae	Polynoidae sp.	1	39	1.0	0.74	23	26	52	4.9	2.0	12	2	5	7	7	5	4	17	2	23
Polynoidae	Polynoidae sp.	7	48	1.25±0.26	0.86±0.14	24±3	26±3	51±3	5.5±0.7	1.8±0.2	12+/-1	2+/-1	6+/-1	8+/-1	6+/-1	7+/-2	3+/-1	19+/-4	3+/-1	22+/-2
Polyodontidae	*Polyodontidae* sp.	5	39	1.49±0.13	0.81±0.05	18±2	30±3	52±3	4.9±1.2	2.9±0.2	12+/-1	2+/-1	5+/-0	10+/-2	7+/-1	3+/-1	4+/-1	16+/-1	2+/-0	20+/-1
Polyodontidae	Polyodontidae sp.	1	85	1.45	0.82	20	39	41	7.5	4.2	13	5	5	15	11	1	3	14	2	17

Scalibregmatidae	*Axiokebuita millsii*	1	48	0.38	16.65	18	53	29	1.8	4.4	7	3	5	8	21	12	5	17	2	1
Scalibregmatidae	Scalibregmatidae spec.	1	39	0.28	4.65	18	37	46	2.3	1.9	5	3	9	3	9	13	6	16	2	3
Sigalionidae	Sigalionidae spec.	1	33	0.27	0,89	16	30	54	14.9	2.2	7	2	6	3	12	4	2	19	5	21
Spionidae	Spionidae sp.	5	17	0.11±0.05	2.23±0.28	21±5	30±4	50±8	3.1±0.6	1.7±0.1	9+/-1	2+/-2	5+/-2	1+/-0	15+/-3	4+/-1	2+/-0	26+/-5	6+/-1	11+/-1
Spionidae	Spionidae sp.	4	48	0.09±0.01	1.60±0.09	20±2	30±3	50±2	13.3±1.9	1.5±0.1	8+/-0	1+/-0	7+/-2	1+/-0	15+/-1	6+/-0	3+/-0	21+/-1	6+/-0	13+/-0
Spionidae	Spionidae sp.	1	48	0.89	12.87	14	29	56	1.3	1.0	6	5	8	4	5	8	9	39	3	3
Syllidae	*Pionosyllis epipharynx*	5	48	2,10±0.55	2.26±1.15	25±2	20±2	55±4	2.2±0.0	2.9±0.6	17±1	4±2	7±0	7±1	4±1	3±3	7±3	25±2	3±0	13±3
Syllidae	*Eusyllis kerguelensis*	1	48	6.85	2.13	27	17	56	1.2	1.4	17	1	8	7	2	1	9	28	5	13
Syllidae	*Eusyllis kerguelensis*	1	48	3.32	1.27	24	21	55	1.1	1.1	16	1	7	10	3	2	10	23	4	14
Syllidae	*Trypanasyllis gigantea*	1	48	9.25	2.15	23	18	59	1.5	2.7	9	1	10	6	10	2	4	21	1	17
Syllidae	*Trypanasyllis gigantea*	1	48	0.59	2.26	21	27	52	2.8	1.4	12	3	5	9	3	2	9	22	10	1
Syllidae	*Brania rhopalophora*	1	48	2.28	1.15	20	38	42	8.6	5.0	12	9	6	19	8	1	5	14	3	14
Terebellidae	*Eupistella grubei*	1	48	0.46	1.30	23	34	43	3.2	3.8	18	17	2	5	11	1	1	14	9	11

PCA for the polychaetes from deep stations (Fig. 4a) explained 49 % of variance in the first 2 componets (26 and 23 %, respectively). In order to classify different feeding types based on trophic markers, polychaetes were assigned to the four quadrants defined by these first two components. FA were defined as characteristic for the respective quadrant, if loadings on at least one of the two relevant PCs were ≥0.4 or ≤-0.4, respectively (Table 3). This leads in turn to transitions in the importance of a respective FA within the quadrant. The first feeding type (quadrant 1) is reflected by increased levels of the marker FA 18:1(n-9) and 20:4(n-6) as well as 16:1(n-7), with the Polyodontidae, Nephtyidae and some Opheliidae (i.e. *Travisia kerguelensis*) grouping in this area. The next feeding type (quadrant 2) is characterised by 16:1(n-7) and 22:6(n-3) as well as 18:0, 18:1(n-7) and 22:5(n-3). The families Fauveliopsidae, Goniadidae, Maldanidae and two Opheliidae (i.e. *Kesun abyssorum*) are situated in this area of the plot. The third quadrant with the Spionidae, as well as the Flabelligeridae and Capitellidae individuals is characterised by 22:6(n-3) and 22:5(n-3) as well as 20:5(n-3). The last group has increased values for 20:5(n-3) and 20:1(n-11), and in this area of the plot, the other Opheliidae (cf. *Ophelina* sp.) specimens and the Acrocirridae and Scalibregmatidae individuals are located.

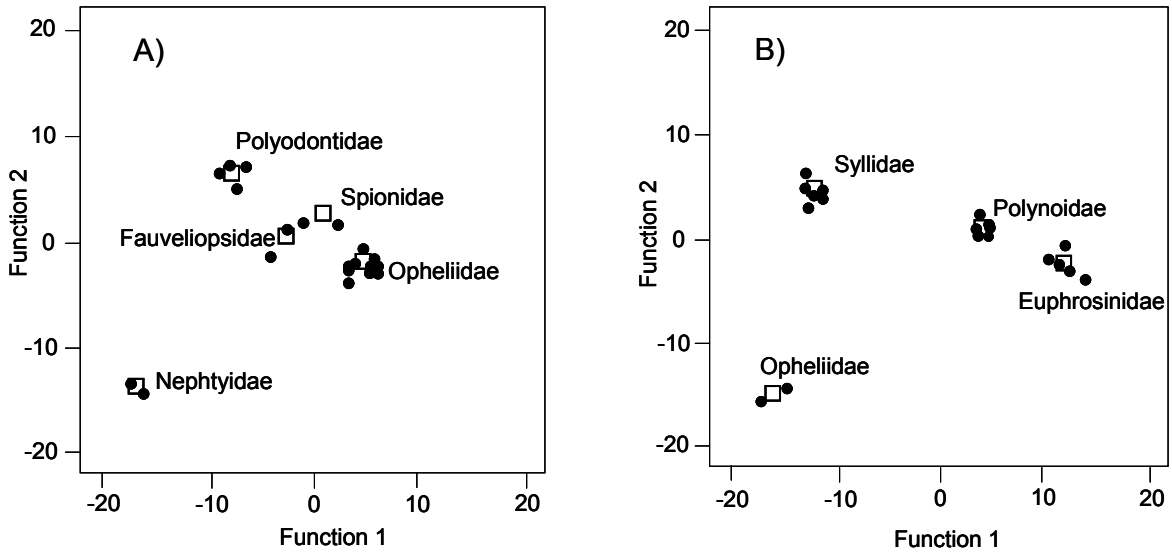

Fig 3 Discriminant analysis on the 10 most abundant fatty acids found in the polychaetes analysed at the deep (A) and shelf (B) stations. Plot of the individuals belonging to polychaete families with n>2 (circles), as well as group centroids (squares) for the first and second discriminant functions (of five (A) and four (B) significant ($p<0.001$) functions). These first 2 functions accounted together for 67.4% of the variance in the discriminant analysis of five species (total n = 19) for A), and 41.3 % of the variance for four species (total n = 19)
Species were separated with 91% (71 of 78 cases) in A) and 100% (78 of 78 cases) of all original grouped cases, and 91.5% and 100% of cross-validated grouped cases, respectively, correctly classified (Wilk's $\lambda < 0.001$).

In the PCA conducted for the shelf station (Fig. 4b), the two first components accounted for 47 % of variance (28 and 19 %, respectively). Three groups, again with transitions between them, can be distinguished. The first group (i.e. the Syllidae and a single Terebellidae specimen) in quadrant 1 is characterised by the markers 18:1(n-9) in the former and 22:5(n-3) in the latter. The second group with the Euphrosinidae is allocated on the transition between the second and third quadrant and is thus primarily characterised by only the first component, i.e. 20:4(n-6) and 18:0 (Table 3). The third group includes all families in the third and fourth quadrant (i.e. Polynoidae, Opheliidae, Orbiniidae, Flabelligeridae, Scalibregmatidae, Nephtyidae and Phyllodocidae) with high loadings of 18:1(n-7) and 20:1(n-11) on component 2. Differences within this group are due to component 1 with high values of 22:6(n-3) and 18:1(n-9) for the Polynoidae and Opheliidae (*Ophelina breviata).*

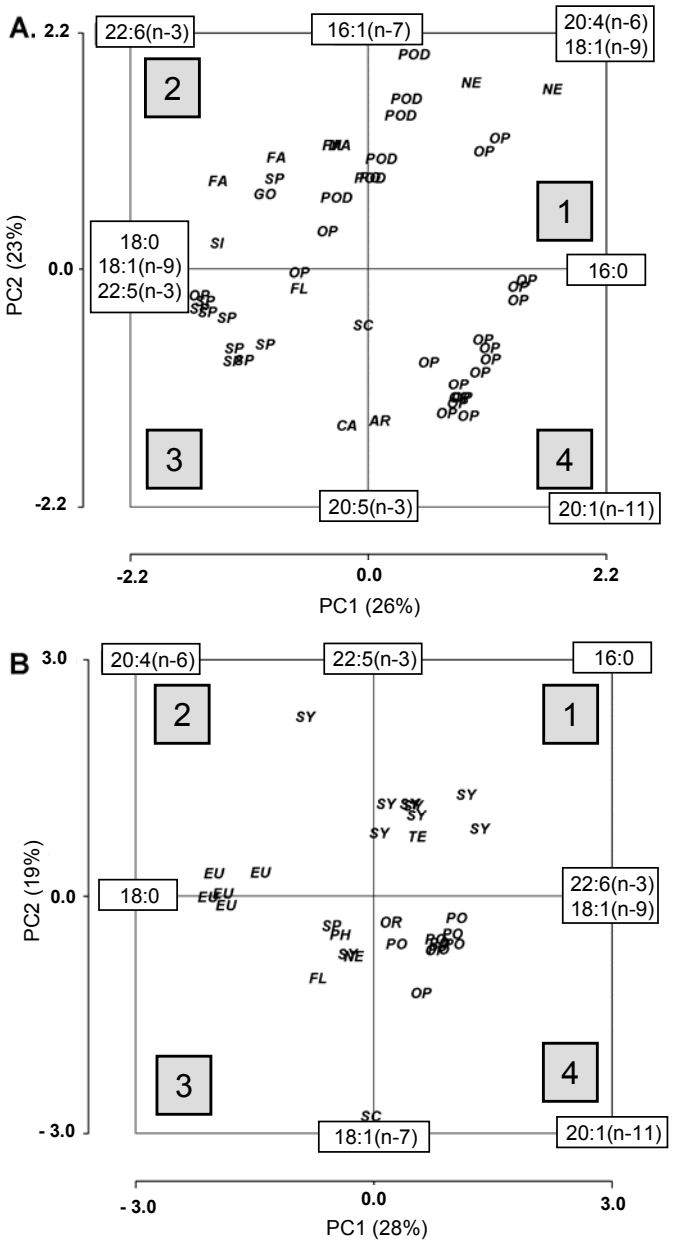

Fig 4 Principal component analyses (PCA) of polychaetes according to their relative fatty acid composition at the deep (A) and shelf (B) stations. Sample plot for the principal components PC1 and PC2 (outer axes). The fatty acid (FA) positions determining the overall pattern are indicated by names of the respective FA in the corners of the plot. Quadrant numbers referred to in the text are given in the grey boxes. Loadings of the FA used are given in Table 3. Abbreviations of the polychaete families' names: AR = Acrocirridae, CA = Capitellidae, EU = Euphrosinidae, FA = Fauveliopsidae, FL = Flabelligeridae, GO = Goniadidae, MA = Maldanidae, NE = Nephtyidae, OP = Opheliidae, OR = Orbiniidae, PH = Phyllodocidae, POD= Polyodontidae, PO = Polyonidae, SC = Scalibregmatidae, SI = Sigalionidae, SP = Spionidae, SY = Syllidae, TE = Terebelidae.

Table 3 Loadings of the first two components of the 10 fatty acids used for the prinicipal component analyses (PCA) conducted for the deep and shelf stations. Only if the loadings of at least one of the two relevant principal components (PC) were ≥0.4 or ≤-0.4 are included in the analysis (bold numbers).

Stations	Component	16:0	16:1ω7	18:0	18:1ω9	18:1ω7	20:1ω11	20:4ω6	20:5ω3	22:5ω3	22:6ω3
deep	PC 1	**0.61**	0.18	**-0.52**	**0.52**	**-0.55**	**0.50**	**0.42**	0.18	**-0.82**	**-0.50**
	PC 2	0.23	**0.57**	0.23	**0.52**	0.11	**-0.65**	**0.39**	**-0.90**	-0.23	**0.38**
shelf	PC 1	**0.72**	0.25	**-0.71**	**0.67**	-0.13	0.35	**-0.79**	0.10	-0.29	**0.63**
	PC 2	**0.51**	0.23	-0.06	0.27	**-0.69**	**-0.78**	**0.40**	0.21	**0.52**	-0.04

3.3. Fatty acid composition of the polychaete families

Euphrosinidae: Five specimens were analysed at the shallowest station. They all showed similar FA patterns with 20:4(n-6) being the most dominant, followed by 20:5(n-3), 18:1(n-7) and 18:0. Their fatty alcohol content was 10.2 ± 2.1 % of total FA and fatty alcohols.

Fauveliopsidae: Three specimens were found at 2100 meters depth, having the highest values for the FA 18:0, 18:1(n-7), 20:5(n-3), and 16:0, with a fatty alcohol proportion of 3.8 ± 1.5 % of total FA and fatty alcohols.

Nephtyidae: Two individuals from a deep station had a FA composition dominated by 20:4(n-6), 20:5(n-3), 18:1(n-9) and 16:0, while the single specimen from the shelf station had 22:6(n-3), 20:5(n-3) and 18:0 as major FA. All family representatives had low fatty alcohol contents compared to most other families (0.7 ± 0.7 % of total FA and fatty alcohols).

Opheliidae: Within this family, 22 individuals were analysed. Of the Opheliidae from the deep stations, 14 are classified as members of the genus *Ophelina*, two as *Kesun abyssorum* and one as *Ammotrypanella* cf. *arctica* and *Travisia kerguelensis* each. Four specimens were collected at the shallow stations, namely two specimens of *Ophelina breviata* and two of *Travisia kerguelensis*. All Opheliidae have 20:5(n-3), 16:0 and 20:1(n-11) as major components. Only in *A.* cf. *arctica was* 22:6(n-3) a prominent proportion with 12% of total FA, while it is comparably low in the others. One of the two *K. abyssorum* from a deep station, as well as two specimens of *T. kerguelensis* from the shallow station, show high values (11-12% of total FA) of 20:4(n-6). Of the Opheliidae from the shelf station, the major FA found in the two *O. breviata* were 20:5(n-3), 16:0, 20:1(n-11) and 18:1(n-7). Most dominant FA in *T. kerguelensis* were 20:1(n-11), 16:0 and 20:4(n-6), followed by 20:5(n-3). The proportion of fatty alcohols varies strongly in this family, from 1.1 % of total FA and fatty alcohols in one *O. breviata* to 20.5 ± 1.5 % in cf. *O.* sp.

Polynoidae: Of the eight specimens analysed, only one origins from a deep station. The FA with the highest proportions are 22:6(n-3), 20:5(n-3), 16:0 and 18:1(n-9) at all stations. Fatty alcohols were found in all members of the family, with 5.2 ± 0.7 % of total FA and fatty alcohols.

Polyodontidae: Five specimens were collected at Maud Rise, one individual at the Antarctic Convergence. All had 22:6(n-3), 20:5(n-3), 16:0 and 18:1(n-9) as dominant FA, while the fatty alcohols made up to 7.5 % of total FA and fatty alcohols.

Scalibregmatidae: Two individuals were analysed for their FA composition. The dominant FA in *Axiokebuita millsii*, sampled at the shelf station, as well as the Scalibregmatidae specimen from a deep station were 18:1(n-7), 20:5(n-3) and 20:1(n-11).

Spionidae: A total of ten spionids was analysed, whereof nine originate from a depth of ca. 2000 meters. Their FA composition was dominated by 20:5(n-3), followed by 18:1(n-7) and 22:6(n-3). The single specimen from the shelf station also had 20:5(n-3) as the clearly dominant FA, but in this case accompanied by 20:4(n-6), 20:1(n-11) and 18:0. All Spionidae from Maud Rise (n=4) had much higher fatty alcohol proportions (13.3 ± 1.9 % of total FA and fatty alcohols) than the individuals from the shelf (1.3 %) and the deep station close to the continent (3.1%± 0.6).

Syllidae: Ten individuals, belonging to four species (*Eusyllis kerguelensis*, n=2; *Pionosyllis epipharynx*, n=5; *Trypanosyllis gigantea*, n=2; *Brania rhopalophora*, n=1) were analysed. FA 20:5(n-3), 22:6(n-3) and 16:0 are common in all, 20:4(n-6) and 18:1(n-9) were also found in high proportions, especially in *Trypanosyllis gigantea* and *Pionosyllis epipharynx*. Fatty alcohol contents were low (1.1-2.8 % of total FA and fatty alcohols), with the exception of the *Brania rhopalophora* specimen that had 8.6 % total FA and fatty alcohols.

Other families (specimen numbers <2): The FA patterns of the single Acrocirridae and Capitellidae specimens were dominated by 20:5(n-3) and 20:1(n-11) together with 18:4(n-3) in the former, and 18:1(n-7) in the latter. In the single specimens of Sigalionidae, Flabelligeridae, Phyllodocidae, Orbiniidae and Maldanidae, 20:5(n-3), 22:6(n-3) as well as 18:1(n-7) and 16:0 were the dominant FA. The single specimen of *Eupistella grubei* (Terebellidae) had 16:0 followed by 16:1(n-7) and 20:5(n-3) as dominant FA. *Bathyglycinde* sp. (Goniadidae) originating from ca. 5000 m depth had the highest total FA content found in this study (11.6%), as well as the highest percentage of all investigated polychaetes for 18:1(n-7). Other major FA found in *Bathyglycinde* sp. were 20:5(n-3), 16:0 and 20:1(n-7). Fatty alcohols proportion varied between families, with the lowest values in the Phyllodocidae and Orbiniidae (2.2 and 1.6 % of total FA and fatty alcohols, respectively) and the highest values in the Flabelligeridae and Capitellidae (23.0 and 29.3 % of total FA and fatty alcohols, respectively).

4 Discussion

4.1. Feeding ecology

Fatty acid markers have been used in numerous studies to determine the diet of organisms (Dalsgaard et al., 2003 and references therein) and were also successfully applied in several benthic studies (e.g. Graeve et al., 2001; Drazen et al., 2008a, b). However, applying the FA marker approach to benthic deep-sea organisms has some constraints, since sinking particulate organic matter and its FA composition are constantly changed on their way through the water column to the seafloor by decomposition processes (Azam et al., 1983; Reemtsma et al., 1990) and sometimes its origin remains ambiguous. Nevertheless, significant levels of labile typical marker FA can be found at the deep-sea floor indicating the sedimentation of partly undegraded material into the deep ocean (Fileman et al., 1998) and/or an autochthonous production of markers at the sea floor. This allows a rough classification of different trophic niches based on trophic markers. In order to identify feeding types as well as selective feeding behaviour of 18 polychaete families we applied a trophic biomarker approach, by performing multivariate analyses on the general FA patterns and interpretation of specific FA in light of their potential dietary origin.

Indications for selective feeding behaviour were found by comparing FA patterns of polychaetes, sediment and POM samples. The latter two are dominated by SFA and monounsatured FA, while showing an absence of typical indicators of fresh phytodetritus (e.g. 20:5(n-3) in diatoms, 22:6(n-3) in dinoflagellates – Nichols et al., 1984, 1991; Sargent et al., 1995), indicating that the material was exposed to strong degrading processes during sinking from upper water layers to the seafloor. The POM and sediment FA composition of the sampled stations is generally not reflected in the animal's FA patterns, as the proportions of PUFA are significantly higher in the polychaetes than in both sediment and POM samples (Fig. 2). For non-carnivorous taxa, this points either towards a selective ingestion of comparably fresh phytodetritus and/or a strong retention of these highly unsaturated FA in metabolic processes (Brett and Müller-Navarra, 1997). Both 20:5(n-3) and 22:6(n-3) are common membrane fatty acids whose proportions can be enhanced due to the low lipid content of the animals, thus their interpretation as biomarkers has to be handled with caution here. This taken into account, still the indication for a selective feeding on fresh diatom components of the detritus on the sea floor based on high ratios of 20:5(n-3) and 22:6(n-3) cannot be discounted.

FA patterns of polychaetes were highly variable, but relatively consistent within families from similar depths with only a few exceptions (namely the Opheliidae, in which species seem to have developed different feeding preferences while having a similar lifestyle, e.g. subsurface deposit feeding). This indicates a rather wide range of different food sources used by the deep-sea polychaetes but also a family specific feeding behaviour. The polychaete families

of the deep stations can roughly be divided into four groups with fluent transition according to their most relevant FA, indicating different dietary foci. The first components separate families characterised by typical markers for omnivorous and carnivorous feeding (18:1(n-9), 20:4(n-6) and 20:1(n-11)) from those with markers of phytodetritus (20:5(n-3), 18:1(n-7) and 22:6(n-3)). Allocated to the first group are the Polyodontidae, Nephtyidae and some Opheliidae (i.e. *Travisia kerguelensis*), while the Fauveliopsidae, Maldanidae, Goniadidae, Sigalionidae, Spionidae, Flabelligeridae and Capitellidae show strong signals for phytodetritus markers.

One striking point within the PCA is that no correlation is expressed between the values of 16:1(n-7) and 20:5(n-3), both widely accepted as diatom markers (e.g. Daalsgard et al., 2003). This finding could either be explained by elongation of this FA to 18:1(n-7) by the polychaetes, or it might indicate an impact of bacterial components (likely associated with the degrading detritus). Larvae of deep-sea polychaetes sampled at methane hydrates have been shown to consume considerable amounts of bacteria (Pile and Young, 2006). Heterotrophic bacteria are known to synthesize large amounts of 16:1(n-7), as well as odd-numbered branched FA such as 15:0, 17:0, 15:1 and 17:1 (Dalsgaard et al., 2003, and references therein). As these bacteria colonize and decompose settling particulate matter (Azam et al., 1983; Pfannkuche and Lochte, 1993), they are abundant in marine sediments (Sargent et al., 1987). In our analysis, no significant amounts of the other FA mentioned in this context were detected, but it cannot be excluded that high values of 16:1(n-7) found in some polychaetes are of bacterial origin.

Polychaetes from the shelf station can roughly be classified into carnivorous/omnivorous and phytodetritivorous families. The first group includes (i) the Syllidae, determined by high values of 18:1(n-9) indicating a carnivorous or detritivorous diet, (ii) the Polynoidae, Orbiniidae and Opheliidae, which are dominated by high values of 20:1(n-11) and 22:6(n-3), possibly due to the ingestion of deep-sea zooplankton and (iii) the Euphrosinidae, clearly determined by high values of 20:4(n-6), possibly ingested with foraminiferans. The second group includes the Spionidae, Phyllodocidae, Terebellidae and Flabelligeridae, with higher values of 20:5(n-3) and 18:1(n-7) a common feature, probably reflecting the importance of phytodetritus in their diet.

Although families were classified as primarily phytodetritivorous and primarily carnivorous in both habitats (shallow and deep), the FA composition of families differed to some degree between habitats. FA were aligned and families allocated differently to the respective FA in the PCA analyses for each habitat. These variances can either be attributed to a different food spectrum available at the shelf station or simply to the occurrence of differing species composition with different behaviour or metabolistic characteristics. A high carbon flux and a strong bentho-pelagic coupling have been reported for the shelf area (Bathmann et al., 1991;

Fisher et al., 2000; Isla et al., 2006), probably providing a distinct food spectrum there compared to the deep stations.

Phytodetritivorous families

High proportions of 20:5(n-3) and 22:6(n-3) are found in the Spionidae, Acrocirridae, Capitellidae, Fabelligeridae and Terebellidae. The FA patterns of the Spionidae and Acrocirridae are relatively similar; both families belonging to the order Spionida that are generally considered to be surface deposit- or filter-feeders. According to the dominance of 20:5(n-3) and 18:1(n-7), it seems likely that the animals preferably ingest food patches that are of higher nutritional value (e.g. freshly deposited phytodetritus) instead of degraded organic material, as shown by Kishlinger and Woodin (2000) for spionid polychaetes. Other authors have also shown that Spionidae are capable of selective feeding to some degree (Jumars et al., 1982), and to differentiate among food patches when offered natural and organic enriched sediments (Fauchald and Jumars, 1979). The FA patterns of the motile or sessile non-jawed Fauveliopsidae, tubiculous Terebellidae (*Eupistella grubei)* and the discretely motile Flabelligeridae are in good agreement with their subsurface or surface deposit-feeding lifestyle, and a diet consisting mainly of phytodetritus (Fauchald and Jumars, 1979).

Interestingly, we found indications that the Phyllodocidae and Goniadidae reflect the typical FA pattern of phytodetritovorous families, although only a single specimen of each was available. Members of these families were originally thought to be hunting carnivores or scavengers, with Goniadidae having distinct jaws (Fauchald and Jumars, 1979), however, high values for 18:1(n-7) and 20:5(n-3) indicate a diet based on phytodetritus. More analyses as to how FA pattern and feeding ecology within these families are related are needed to clarify this trophic signal.

Carnivorous families

For some families studied, the carnivorous input to their diet is reflected in their FA patterns. The ratio between 18:1(n-9) and 18:1(n-7) is often used to distinguish carnivores from herbivores (e.g. Graeve et al., 1997; Falk-Petersen et al., 1998, 2000; Auel et al., 2002). This ratio needs to be interpreted very carefully, as higher values of 18:1(n-7) can be indicative of diatoms, but the degree to which 18:1(n-9) is synthesized can differ between species, and the ratio has been reported to change due to starvation (Daalsgard et al., 2003). High values for the 18:1(n-9)/18:1(n-7) ratio were measured namely in the Syllidae, Polyodontidae, Nephtyidae and, to a lower degree, Polynoidae, which is concordant with the carnivorous feeding type of these families. Members of these families are considered as free-living burrowers or vagile carnivores, feeding on small invertebrates including molluscs,

crustaceans, polychaetes, hydroids, bryozoans, and other colonial invertebrates (Fauchald and Jumars, 1979).

Very high values of 20:4(n-6) were found in the Euphronisidae, some Opheliidae (*Travisia kerguelensis* and *Kesun abyssorum*), Nephtyidae and the Syllidae. This FA is an important FA in some foraminiferan species, with proportions up to 21 % (Gooday et al., 2002; Suhr et al., 2003; Würzberg, unpublished data). We propose that these polychaetes ingest considerable amounts of this FA in foraminiferans, since it was not found in comparably high amounts in the analysed sediment samples, thereby indicating selective feeding on this prey resource. The high values of this FA found in all specimens belonging to the families of Euphrosinidae and Syllidae is concordant with the finding of Fauchald and Jumars (1979), who reported that an unidentified Euphrosinidae species from the deep-sea Atlantic Ocean exclusively feeds on foraminiferans, and that some Syllidae may have specialized on foraminiferans in deeper water. It can be suspected that the latter family displays an opportunistic feeding mode, utilizing different food sources if no suitable prey is available. Foraminiferans themselves are capable of selective feeding on certain compartments of detritus and accumulating PUFA, thereby supplying a more valuable dietary resource compared to detritus (Suhr et al., 2003). Other authors have suggested that macroalgae (specifically red algae), which are also known to contain high amounts of this FA, could be the source of 20:4(n-6) in deep-sea holothurians (Bühring et al., 2002). Visual inspection of the sediments, however, detected no macroalgal fragments, and we propose that the probable source of 20:4(n-6) in the polychaetes' diet are foraminiferans.

Another common FA found in considerable proportions [reaching 12-13 % of total FA in the Acrocirridae, Opheliidae (cf. Ophelina sp., Travisia kerguelensis) and Scalibregmatidae] in most of the analysed polychaetes was 20:1(n-11), being especially pronounced in some Opheliidae and Scalibregmatidae, as well as in some Polynoidae. This FA has been reported to be particularly common in calanid copepods (Sargent and Whittle, 1981) and within deep-sea zooplankton species in general (Pond et al., 2000), that could be ingested either with detritus, by filtrating or by active hunting. The single individuals of Capitellidae and Acrocirridae have a higher amount of 20:1(n-11) [(in addition to high values of the diatom markers 20:5(n-3) and 18:1(n-7)], but based on the morphology and lifestyle of these organisms, an indirect ingestion of zooplankton remains seems more likely than active hunting. Similarly high values of 20:1(n-11) recorded for the polychaete *Travisia* sp. (Opheliidae), as well as for some Ophiuridae (Echinodermata), sampled in the Pacific Ocean were attributed to direct feeding on copepod remains (Drazen et al., 2008a, b).

4.2. Energy reserves and lipid storing strategies

The total FA content found in the polychaetes analysed was relatively low (1-11.6 % of total body dry weight). This finding could suggest that lipids are not accumulated for energy storage, and that feeding occurs throughout the year (Bühring and Christiansen, 2001), thereby supporting the theory of a permanent food reservoir in the deep-sea (Mincks et al., 2005; McClintic et al., 2008). However, fatty acid alcohols were found in almost all analysed polychaetes that are indicative of wax esters (WE), a lipid class typically used for long term storage (Lee et al., 2006). The FA component of WE is largely derived from the diet, whereas the fatty alcohols are derived from the animal's internal biosynthesis (Sargent and Henderson, 1986). The storage of wax esters can be indicative of an evolutionary mechanism of surviving long starvation periods, like in higher latitude herbivorous copepods (Lee et al., 1971; Sargent and Falk-Petersen, 1988; Hagen and Schnack-Schiel, 1996; Martynova et al., 2009). In the case of copepods, wax esters are accumulated which primarily contain fatty alcohols dominated by 14:0 and 16:0 (omnivorous or carnivorous copepods) or 20:1(n-9) and 22:1(n-11) (herbivorous calanid copepods) (Brett et al., 2006). In the polychaetes analysed in this study, 18:1 alcohols were dominant in most families. The ability to reduce larger amounts of 18:1(n-7) and 18:1(n-9) has previously been reported in the Southern Ocean, e.g. from the euphausiid *Thyssanoessa macrura* (Kattner et al., 1996) and the deep-sea copepod *Pareuchaeta barbata* (Laakmann et al., 2009).

The generally low lipid content, pointing to a lack of lipid storage and the co-occurrence of wax esters as long term energy storage remains somehow contradictive. The distinct mechanisms underlying these metabolic processes need to be addressed in future studies.

5 Conclusion

By analysing their FA composition, we show that previously reported feeding habits were generally reflected in the FA patterns of the deep-sea polychaete families. This will be helpful in future studies of FA composition of deep-sea invertebrates, especially where feeding type is uncertain. For example, feeding on phytodetritus was confirmed based on the marker 20:5 (n-3) (e.g. in the Spionidae, Flabelligeridae of Fauveliopsidae). The FA patterns (e.g. the 18:1(n-9) to 18:1(n-7) ratio) found in this study support the carnivorous tendency in the Polynoidae, Syllidae, Polyodontidae and Nephtyidae, but also indicate that these families are not facultative carnivores. For these later families an opportunistic feeding mode is suggested that includes other food sources if their preferred prey items are not available.

In some cases, more specific indications on diet components could be derived from interpreting the FA compositions. In several samples analysed deep-sea zooplankton seems to be an additional food source, supplementing the omnivorous diet of these polychaete species. For example, the high values of 20:4(n-6) hint to a distinct preference for

foraminiferans in the Euphrosinidae, Nephtyidae and some species of Opheliidae and Syllidae. Foraminiferans are normally very abundant in deep-sea samples (Levin, 1991, Gooday et al., 1992) and probably play a central role in the rapid initial processing of fresh organic carbon in deep-sea sediments (Moodley et al., 2002). These protozoans are capable of selective feeding on certain compartments of detritus, thereby supplying a more valuable nutritional resource due to PUFA enrichment compared to detritus (Suhr et al., 2003) and most likely represent an important link between to higher trophic levels. It is probable that the importance of foraminiferans as a food source for benthic invertebrates is a factor that is characteristic of the deep-sea environment.

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Chapter 6

Fatty acid patterns of Southern Ocean shelf and deep-sea peracarid crustaceans and a possible food source, foraminiferans

Peracarid crustaceans (upper left: amphipod, upper right: cumacean; lower left: tanaidacean; lower right: isopod) sampled in the Antarctic deep-sea during the ANDEEP-SYSTCO cruise.

Chapter 6 Fatty acid patterns of Southern Ocean shelf and deep-sea peracarid crustaceans and a possible food source, foraminiferans

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Abstract

In order to elucidate the feeding behaviour of macrobenthic peracarid crustaceans from the Antarctic shelf and deep-sea, the fatty acid composition of individuals belonging to the order Isopoda, Amphipoda, Cumacea and Tanaidacea, as well as one potential food source, foraminiferans, was analysed. Multivariate analyses of the FA composition revealed distinct differences between taxonomic groups, with transitions between the groups in some cases. Fatty acids of Cumacea were characterised by phytoplankton markers such as 20:5(n-3) (up to 30% of total fatty acids) suggesting a diet based on phytodetritus. High values of the fatty acid 20:4(n-6) were found in some munnopsid isopods (up to 21% of total fatty acids) and some tanaidaceans (up to 19% of total fatty acids), possibly reflecting the ingestion of foraminiferans, as indicated by high levels of the respective fatty acid in the foraminiferan samples (up to 21% of total fatty acids). Most of the analysed amphipods display high values of t 18:1(n-9) (up to 37 % of total fatty acids), widely used as an indicator for a carnivorous component in the diet. According to the fatty acid trophic markers found in this study, the analysed peracarid crustaceans can be classified into three dietary groups: 1) mainly phytodetritivore, 2) mainly omnivore (in some cases with indications for foraminiferivory) and 3) mainly carnivore.

Key words: Deep-sea, fatty acid, Peracarida, Foraminifera, Southern Ocean benthos

1 Introduction

Peracarid crustaceans belong to the most abundant and most diverse groups inhabiting the Southern Ocean shelf and deep-sea floor (Hessler and Thistle, 1975; Wilson, 1998; Brandt, 2007 a, b). The question about the causes for the high degree of diversity in this group still remains unanswered. A possible reason could be the specialisation for certain types of food, but, on the first glance, in the deep-sea, which is considered to be a relatively homogenous habitat with limited food availability, selective feeding does not appear to be very promising, if

not unreasonable (MacArthur and Pianka, 1966; Lehmann, 1976). However, besides the possession of a ventral brood pouch (marsupium), another characteristic feature specific for peracarid crustaceans are very good chemoreceptors (aesthetascs), which can be of particular help in finding preferred food items (Rehm, 2009). Selective feeding has been reported for some members of this group of crustaceans. While most cumaceans and tanaidaceans are generally regarded as non-selective deposit-feeders (Dennell, 1937; Bückle-Ramirez, 1965; Mendoza, 1982; Messing, 1983; Kudinova-Pasternak, 1981, 1991; Gage and Tyler, 1991; Cartes et al., 2001; Błazewicz-Paszkowycz and Ligowski, 2002), the feeding modes of isopods and amphipods are very diverse and include the whole spectrum from suspension-feeding to necrophagy (Cartes and Sorbe, 1998; Dauby et al., 2001). Deep-sea isopods were previously considered to be generalized deposit feeders (Wolff, 1962), but recently they have been shown to have a more manifold feeding behaviour with distinct preferences, as for example foraminiferans (Svavarsson et al., 1993; Gudmundsson, 2000).

However, information on the specific diets as well as the role in the food web of Antarctic peracarid crustaceans especially in deep-sea settings still remains scarce. This is at least partly due to low sampling effort and, in case of deep-sea organisms, the difficulties of *in vivo* experiments. Additionally, the often empty guts or homogenous material within the guts (e.g. Iken et al., 2001; Brökeland et al., 2010) of most macrobenthic invertebrates make a clear identification of the dietary composition difficult. Especially for small abyssal invertebrates alternative methods to identify the origin of their gut contents are needed to shed light on feeding strategies and food web relationships. One approach to identify food sources is to analyse their fatty acid (hereafter FA) composition, what has become an established tool to gain information on food preferences and feeding history (e.g. Sargent and Whittle, 1981; Graeve et al., 1997; Dalsgaard et al., 2003), since FAs of potential food items have specific signatures that are not degraded during digestion, and can accumulate in the tissues of consumers. Such FAs can function as biomarkers for certain types of ingested food, and are used for the interpretation of an organism's FA composition. Examples are the diatom markers 20:5(n-3), 16:1(n-7) and 18:1(n-7) (Volkman et al., 1989; Dunstan et al., 1994; Graeve et al., 1994; Sargent et al., 1995; Zhukova and Aizdaicher, 1995) or 18:1(n-9), indicative for carnivorous feeding, if accompanied by low 18:1(n-7) levels (e.g. Falk-Petersen et al., 1998, 2000; Auel et al., 2002). For example, in arctic shelf invertebrates, Graeve et al (1997) found a clear gradient from low 18:1(n-9) to (n-7) ratios in suspension feeders, via predatory decapods, to higher ratios in scavenging amphipods. The 18:1(n-7) isomer is derived by chain elongation from 16:1(n-7), typical for phytoplankton (especially diatoms), and higher proportions of this FA are presumably indicative of herbivory (e.g. Sargent and Whittle, 1981; Graeve et al., 1997, Falk-Petersen et al., 1998; Auel et al., 2002). Besides the 18:1(n-9) to (n-7) ratio, also the 22:6(n-3) to 20:5(n-3) ratio can be help to determine the

degree of carnivory, increasing towards higher trophic levels as 22:6(n-3) is highly conserved through the food web (Dalsgaard et al., 2003).

Still controversial is the origin of 20:4(n-6), which is common in macroalgae (e.g. in polar Rhodophyta, Graeve et al., 2002), but has also been shown to be an important FA in bacteria (Nichols et al., 1997), fungi (Kendrick and Ratledge, 1992; Eroshin et al., 1996) or foraminiferans (Gooday et al., 1992; Suhr et al., 2003). Foraminiferans are a major element in benthic sediments also in the deep-sea and can comprise up to 50 % of benthic biomass (Snider et al., 1984; Gooday et al., 1992), including the easily overlooked, soft-shelled species which can account for 10 to 20% of total foraminiferans (Gooday, 2002). Thus, they most probably play a significant role in carbon cycling, especially in polar environments, where calcareous and agglutinated foraminiferans often constitute a substantial proportion also in terms of biomass of benthic communities (Basov, 1974; DeLaca et al., 1981; Thiel, 1983; Smith et al., 2002). They are commonly one of the most important consumers of fresh phytodetritus, especially in deep-sea settings (Gooday et al., 1988, 1990, 1992; Moodley et al., 2002), and given the fact, that they can very rapidly utilize sinking fresh organic material from the surface (Linke et al., 1995; Nomaki et al., 2006, 2008, 2009), their role in deep-sea food webs must be considerable.

Foraminiferans have been shown to contain higher amounts of unsaturated FAs (PUFAs) than the surrounding sediment (Suhr et al., 2003). This class of FAs is essential for all organisms, and PUFAs like 20:5(n-3), 22:6(n-3) or 20:4(n-6) are almost exclusively synthesized by plants, while few animals have the capability of synthesizing them *de novo*, making food rich in PUFA a valuable dietary resource (Brett and Müller-Navarra, 1997). Thus, foraminiferans have the potential to represent an important trophic link especially in deep-sea food webs.

In this study, the FA patterns of individuals belonging to four groups of peracarid crustaceans, namely the order Isopoda, Amphipoda, Cumacea and Tanaidacea were analysed, to gain information on their general FA composition and detect possible group specific differences. Additionally, a potential food source, foraminiferans, was analysed to obtain information on their role in the diet of the investigated crustaceans.

2 Material and Methods

2.1 Sampling

The studied material originates from the RV *Polarstern* cruise ANT XXIV/2 taking place from November 28th 2007 to February 4th 2008 in course of the ANDEEP-SYSTCO project.

Samples were collected at six stations located roughly along the Greenwich meridian, ranging from 488 to 5337 m in depth (Figure 1).

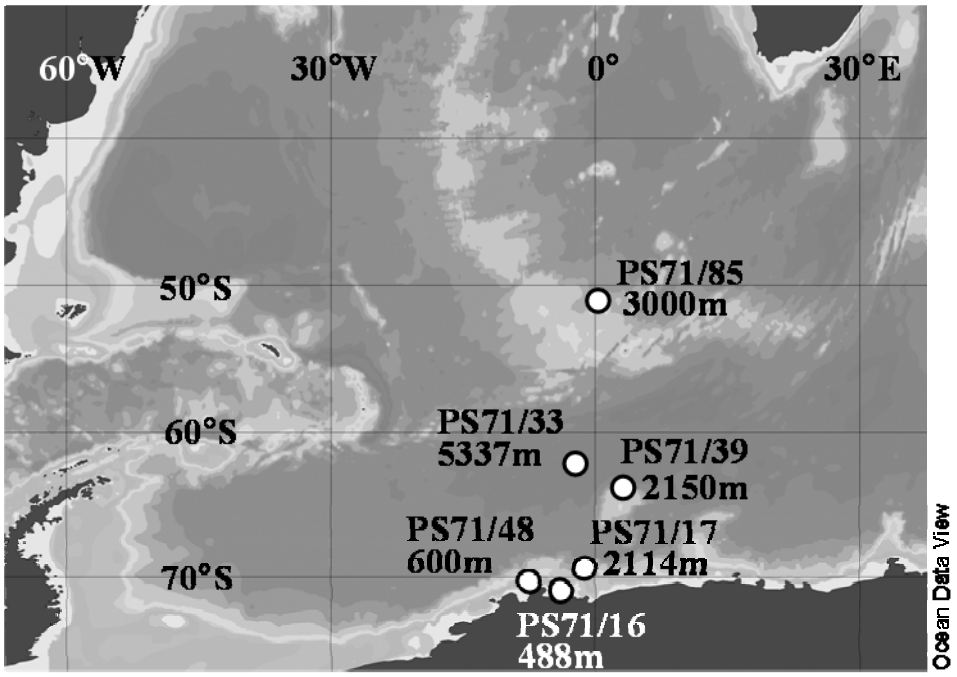

Fig 1 ANDEEP SYSTCO stations (RV *Polarstern* cruise ANT XXIV/2) sampled for this study.

Macrobenthic samples were taken by an epibenthic sled (Brandt and Barthel, 1995; Brenke, 2005), a deep-water trawl, a Rauschert-dredge (Stransky, 2008), as well as a baited trap system. Sorting of the samples was conducted either in climate chambers (0-2°C) or on ice and stopped within 1 h after retrieval to guarantee for freshness of the material. All samples were sorted to the highest taxonomic level possible and digital pictures were taken as vouchers for each specimen to allow for latter confirmation by specialists of the original identification. The samples were frozen and stored individually at -80°C until analysis for which whole animals were used. Foraminifera were collected together with the surrounding sediment by means of a multiple corer (Barnett et al., 1984) and frozen immediately at -80°C. After the cruise, the sediment samples were thawed in the lab and carefully centrifuged to allow for quicker sorting of the foraminiferans. Per station, live agglutinated foraminiferans with clearly identifiable protoplasm (indicated by a greenish-brownish colouring) were picked until 20-30 individuals were gathered which were pooled as one sample. The samples were immediately frozen again at -80°C until analyses. Due to time constraints to guarantee freshness of the samples, no further taxonomic classification was conducted and the samples represent a species mixture, but it was observed in course of the sorting process that most of the picked foraminiferans belong to the genera *Vanhoefenia*, *Bulimina*, *Nonionella* and *Miliolida*, as well as some saccaminids and gromids.

2.2. Fatty acid analyses

Prior to the FA analysis all samples were freeze dried, weighed and allowed to extract in dichlormethane-methanol (v:v/2:1) for at least 48 h. Lipid extraction was performed with minor modifications as described in Folch et al. (1957) using ultrasonic disruption in dichloromethane:methanol and a washing procedure with aqueous KCl solution. The analysis of FA composition was performed with modifications as described in Kattner and Fricke (1986). FAs were converted to their methyl ester derivatives (FAME) in sulphuric methanol and analysed using a gas chromatograph (HP 6890A) equipped with a programmable temperature vaporizer injector (Gerstel® CIS4plus) and a DB-FFAP column. The use of a large volume injector allows a measurement of very low lipid amounts. FAMEs and fatty alcohols were detected by flame ionisation and identified by comparing retention times with those derived from standards of known composition. The FAs 18:5(n-3) and 20:1(n-9) can not be distinguished according to their retention times and are therefore presented together. For quantification of FAs tricosanoic acid was used as internal standard.

2.3 Statistical analyses

FAs with proportions lower than 0.5 % of total FA were excluded prior to the analyses. To identify feeding differences based on FA pattern, a principal component analysis (PCA) was conducted for the dominant (> 3% of total FAs in at least one group) ten variables (FAs). The PCA was performed unrotated based on the correlation matrix and eigenvalues >1 were extracted. The first two components together explain 46.9% of variance (PC1 29.7%, PC2 17.2%).

3 Results

3.1 General fatty acid composition

In total, 50 individual animals belonging to the four investigated peracarid crustacean order as well as six pooled samples of foraminiferans have been analysed.

The total FA content was generally low (1.0 to 4.4 of individual dry weight, DW) with some exceptions within the Amphipoda with comparably high values (up to 15.5% of DW). FA alcohols, indicative of wax ester storage, were found in all groups, but generally in relatively low amounts (0 – 5% of total FAs). The peracarid FAs were mainly made up by monounsaturated FAs (MUFA) and polyunsaturated FAs (PUFA), while in foraminiferans, no clear dominance of one saturation type FA proportion can be seen (Table 1 and 3).

Table 1 Numbers, sampling depth, total fatty acid content (TFA, in % of total body dry weight), total fatty alcohols (TA, in % of total fatty acids and fatty alcohols), ratios of fatty acids (A=16:1(n-7)/16:0 ratio, B=18:1(n-9)/18:1(n-7) ratio, C=22:6(n-6) /20:5(n-6) ratio)), amounts of saturated (SFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids (in % of total fatty acids for all analysed peracaridean and foraminiferan samples. For groups with specimen numbers ≥ 3, average results with standard deviations are given, for groups with specimen numbers = 2, minimum and maximum values are given.

Taxon	Family	Species	N	Depth/m	DW/mg	TFA	TA	A	B	C	SFA	MUFA	PUFA
Amphipoda	Lysianassidae	*Eurythenes gryllus*	5	2114	0.35±0.09	3.4±2.30	2.2±0.52	0.3±0.28	2.5±0.88	1.2±0.28	17.5±3.75	38.1±11.98	44.3±9.82
		Abyssorchomene sp.	1	600	3.51	15.5	5.1	0.1	11.6	0.5	20.5	58.8	20.8
		Abyssorchomene spp.	4	3000	0.65	6.7±3.97	2.4±1.56	0.9±0.33	4.9±1.83	1.1±0.25	16.8±2.29	57.0±9.19	26.2±9.65
		Lysianassidae sp.	1	2114	0.36	1.15	1.0	0.1	1.7	1.8	21.5	28.3	60.5
Isopoda	Munnopsidae	*Eurycope* sp.	2	2150	0.24/6.21	1.4/1.9	6.0/12.2	0.1/0.1	1.4/1.5	0.9/1.2	15.0/15.8	29.2/47.6	36.6/55.8
		Betamorpha sp.	2	2150	1.05/0.89	1.2/1.3	1.5/2.9	0.1/0.1	1.4/1.5	0.9/1.2	13.2/12.2	26.2/26.8	60.7/61.0
		Syneurycope sp. 1	3	3000	2.54±0.66	1.1±0.1	1.9±1.13	0.4±0.12	1.2±0.50	0.9±0.14	15.2±0.51	37.9±3.84	46.9±3.48
		Syneurycope sp. 2	1	5337	1.77	1.0	2.8	0.2	1.2	0.9	10.6	33.2	56.2
		Ilyarachna sp.	1	5337	3.58	1.0	3.4	0.6	0.8	0.7	7.0	41.2	51.8
	Haploniscidae	*Haploniscus* sp.	1	3000	0.13	1.7	0.5	0.5	2.0	1.6	7.1	26.5	66.5
		Chaulioniscus sp.	1	5337	1.09	2.7	2.2	0.6	2.2	0.9	12.2	54.0	33.7
		Mastigoniscus sp.	1	3000	0.22	1.1	0.1	0.5	1.3	0.9	17.2	43.6	39.3
	Macrostylidae	*Macrostylis* sp. 1	1	2150	0.69	3.7	1.9	0.3	0.7	0.9	17.3	45.5	37.2
		Macrostylis sp. 2	1	5337	2.50	2.9	3.5	0.9	0.8	0.4	7.6	43.7	48.7
	Arcturidae	*Chaetarcturus* cf. *bovinus*	1	600	10.95	1.0	2.4	0.4	1.7	0.5	17.7	36.9	45.4
	Ischnomesidae	*Ischnomesus* sp.	1	2150	2.15	1.0	5.0	0,4	1,0	1,3	22.2	30.3	47.5
	Paramunnidae	*Notoxenus* cf *spinifer*	3	488	2.94±1.05	1.7±0.3	1.5±0.9	0.2±0.1	2.0±0.3	0.6±0.1	14.8±0.93	36.8±1.93	48.4±1.43
	Stenetriidae	*Stenetrium weddellensis*	6	600	7.60±2.78	3.2±1.0	3.1±1.6	0.5±0.3	2.5±1.0	0.6±0.2	20.1±2.32	44.1±2.51	35.8±1.92
Cumacea	Leuconidae	*Leuconidae* sp. 1	1	488	0.73	1.1	1.1	0.1	0.9	0.5	17.7	32.1	50.2
		Leuconidae sp. 2	2	2114	0.78/0.50	1.0/1.34	2.0/2.72	0.2/0.5	0.7/0.7	0.5/0.5	20.0/22.83	26.3/33.32	53.8/43.81
		Eudorella sp.	1	488	0.43	1.1	0.3	0.2	1.0	0.4	19.2	33.9	46.9
	Bodotriidae	*Bodotriidae* spp.	3	600	18.45±2.19	1.3±0.27	0.1±0.18	0.2±0.18	0.8±0.37	0.2±0.06	17.4±3.52	39.7±0.90	42.9±2.63
	Nannastacidae	*Nannastacidae* sp.	2	600	7.20/5.12	2.1/2.5	0.1/1.2	1.0/1.3	1.2/1.6	0.2/0.2	21.5/23.5	46.8/50.2	29.2/33.2
	Diastylidae	*Diastylidae* sp.	1	600	11.05	1.1	0.1	1.5	1.1	0.2	16.1	45.8	38.1
Tanaidacea	Metapseudidae	*Apseudomorpha* sp.	1	5337	5.43	4.4	1.9	4.8	0.6	1.6	14.4	66.8	18.8
	Neotanaidae	*Neotanais* sp.	1	2150	3.46	1.1	1.5	0.4	1.8	1.0	14.7	43.1	42.2
	Apseudidae	*Apseudes* sp.	1	3000	0.33	1.0	1.4	0.1	1.0	0.5	21.9	44.1	34.0
	Agathotanaidae	*Paranarthrura* sp.	1	3000	0.13	1.4	2.4	1.6	0.3	0.6	24.7	28.9	46.4

Table 2 Numbers and proportions of the ten most abundant fatty acids in all samples (in % of total fatty acids) for all analysed peracarid samples. For groups with specimen numbers ≥ 3, average results with standard deviations are given, for groups with specimen numbers = 2, minimum and maximum values are given.

Taxon	Family	Species	N	14:0	16:0	16:1(n-7)	18:0	18:1(n-9)	18:1(n-7)	18:2(n-6)	20:4(n-6)	20:5(n-3)	22:6(n-3)
Amphipoda	Lysianassidae	*Eurythenes gryllus*	5	1.8±1.59	12.8±2.76	3.6±2.60	3.7±1.38	19.6±7.07	7.8±1.09	4.6±3.87	3.2±1.50	14.3±3.66	17.2±6.22
		Abyssorchomene spp.	4	1.7±0.70	14.0±1.82	7.5±4.13	2.1±1.12	36.8±3.48	7.5±3.67	1.4±0.32	2.1±1.99	10.5±3.64	10.5±5.37
		Abyssorchomene sp.	1	7.3	14.2	19.3	1.1	30.0	6.0	1.8	1.2	11.2	7.4
		Lysianassidae sp.	1	1.0	11.0	1.0	7.1	13.1	7.5	6.2	9.2	13.6	23.8
Isopoda	Munnopsidae	*Eurycope* sp.	2	1.1/1.2	10.3/11.8	1.0/3.7	3.2/5.6	15.0/21.4	10.5/14.2	1.0/1.6	6.3/14.6	16.5/23.2	14.8/18.0
		Betamorpha sp.	2	0.7/1.1	9.7/10.2	1.0/1.2	2.4/3.0	13.0/14.4	9.5/9.6	1.4/1.7	17.6/21.0	17.2/18.4	15.8/20.4
		Syneurycope sp. 1	3	1.2±0.22	11.3±0.39	4.3±1.27	3.4±0.49	15.9±4.36	12.2±1.61	1.3±0.25	5.8±1.77	19.2±4.52	16.4±2.71
		Syneurycope sp. 2	1	<1.0	6.7	3.4	3.9	11.1	17.4	1.6	7.8	18.2	19.9
		Ilyarachna sp.	1	<1.0	5.2	3.0	1.8	15.4	18.1	1.1	11.9	18.0	12.5
	Haploniscidae	*Chaulioniscus* sp.	1	1.0	9.4	5.3	2.8	26.1	12.0	1.7	3.8	13.0	11.3
		Mastigoniscus sp.	1	1.1	12.5	6.8	4.7	16.6	12.7	1.6	4.6	14.6	13.4
		Haploniscus sp.	1	0.6	4.2	2.0	2.9	12.6	6.5	<1.0	2.6	24.1	39.7
	Macrostylidae	*Macrostylis* sp. 1	1	1.8	12.7	5.3	2.8	11.5	15.6	1.1	9.7	13.6	12.6
		Macrostylis sp. 2	1	1.0	6.0	3.4	1.5	10.5	13.8	1.0	3.7	9.7	6.9
	Arcturidae	*Chaetarcturus* cf. *bovinus*	1	1.1	12.8	4.7	4.9	20.5	11.7	<1.0	5.9	26.1	11.8
	Ischnomesidae	*Ischnomesus* sp.	1	<1.0	15.4	6.5	6.9	11.7	12.1	1.0	4.6	18.4	24.5
	Paramunnidae	*Notoxenus* cf *spinifer*	3	1.1±0.11	11.5±0.78	2.5±1.14	3.3±0.33	20.0±0.92	10.4±1.37	1.0±0.04	7.7±1.02	22.7±2.14	14.0±1.24
	Stenetriidae	*Stenetrium weddellensis*	6	2.5±1.18	15.0±2.27	6.4±3.70	2.4±0.60	24.6±2.61	10.6±2.43	1.0±0.06	4.0±0.53	16.7±2.70	10.3±1.10
Cumacea	Leuconidae	*Leuconidae* sp. 1	1	<1.0	14.4	1.2	3.3	15.0	16.0	<1.0	3.4	29.8	15.5
		Leuconidae sp. 2	2	<1.0/3.2	11.8/12.3	4.9/6.7	9.0/4.4	12.2/8.0	18.2/11.6	1.4/2.5	6.6/5.2	21.1/22.4	9.5/11.4
		Eudorella sp.	1	1.0	15.1	3.4	4.1	15.4	15.1	1.0	3.0	27.6	11.1
	Bodotriidae	*Bodotriidae* spp.	3	1.1±0.09	12.3±3.57	3.4±3.41	4.7±0.64	14.4±2.42	22.2±6.88	1.0±0.05	5.6±1.31	29.2±3.69	6.9±0.72
	Nannastacidae	*Nannastacidae* sp.	2	4.4/4.6	15.1/16.4	16.8/20.3	2.0/2.5	13.4/19.0	11.2/11.8	1.0/1.4	2.0/2.1	19.0/19.1	3.4/3.4
	Diastylidae	*Diastylidae* sp.	1	1.2	12.8	19.0	2.1	13.4	12.2	1.8	4.1	24.0	3.7
Tanaidacea	Metapseudidae	*Apseudomorpha* sp.	1	5.6	5.9	28.4	1.3	16.7	9.3	1.0	3.9	7.5	7.4
	Neotanaidae	*Neotanais* sp.	1	1.4	10.0	4.3	3.3	14.4	13.9	1.7	15.7	15.2	6.9
	Apseudidae	*Apseudes* sp.	1	4.7	9.8	15.2	6.2	4.9	14.7	<1.0	9.4	14.6	8.6
	Agathotanaidae	*Paranarthrura* sp.	1	1.2	13.7	1.8	9.8	7.0	11.4	3.6	18.9	5.0	8.2

The FA composition varies between, and partly within peracarid order (Table 2). The PCA conducted on all peracarid individuals mirrors these differences and separates the peracarid order with transitions between the groups according to the loadings of the respective FA (Figure 2). The first two components together explain 46.9% of variance (PC1 = 29.7%, PC2 = 17.2%).

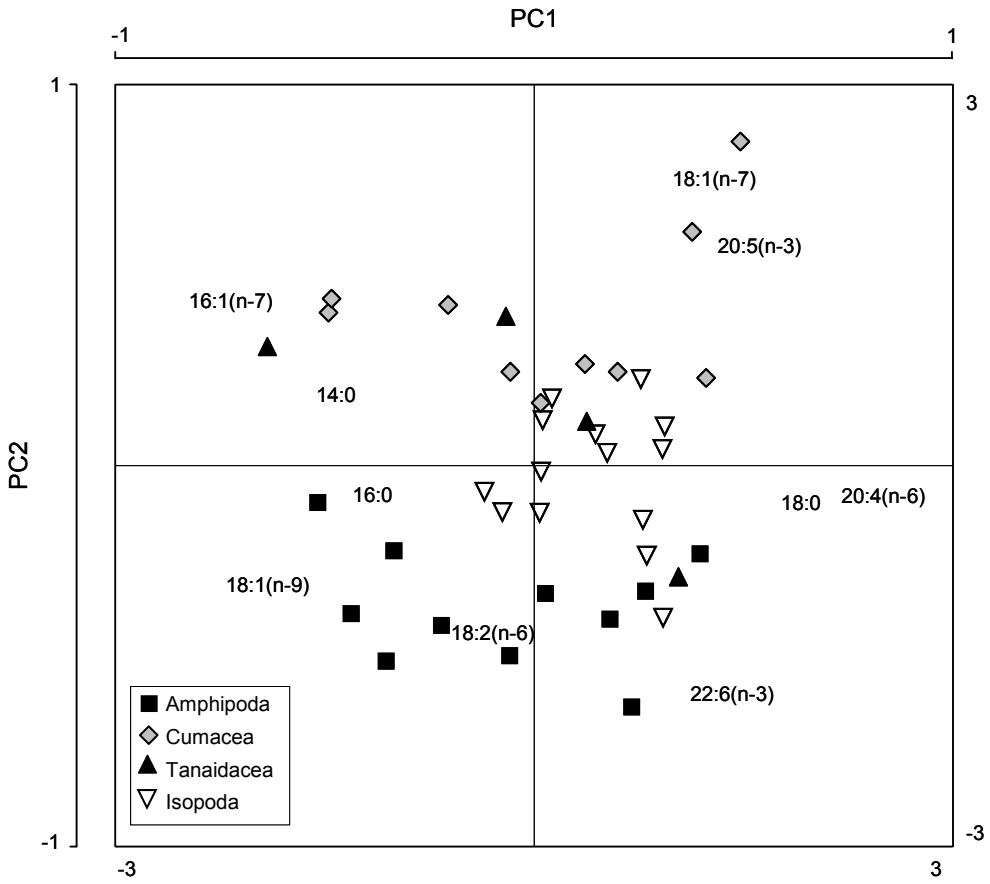

Fig.2 Principal component analysis of all peracarid crustacean individuals according to their relative fatty acid composition. Sample plot for principal components PC1 (explaining 29.7% of variance), and PC2 (explaining 17.2% of variance) for individual specimens (inner axes) and loadings of the single fatty acids (outer axes).

The Cumacea are located between the upper left and upper right of the plot, dominated by positive loadings of the FAs 20:5(n-3), 18:1(n-7) and16:1(n-7). The Amphipoda are situated parallel to this group, from the lower left to the lower right of the plot, distinguished from the others by high loadings of the FAs 18:1(n-9), 18:2(n-6) and 22:6(n-3). The Isopoda individuals are situated around the centre of the plot, showing strong transitions to both other groups and are not dominated by specific FA. However, the individuals located at the right middle of this central group are characterised by high loadings of 20:4(n-6) and 18:0 (Munnopsidae). The four Tanaidacea specimens do not group together, as two individuals

appear together with the Cumacea group (*Apseudes* sp. and *Apseudomorpha* sp.), and the remaining two within the Isopoda/Amphipoda (*Paranarthrura* sp. and *Neotanais* sp.).

3.2 Foraminifera

The FA compositions of foraminiferans (Table 3) varied between the samples. The FA 16:0 played a dominant role in all analysed foraminiferans with up to 28.8% of all FAs, followed by 18:1(n-9), 18:0 and 20:4(n-6); the latter can reach comparably high levels in some samples (up to 21% of all FAs). FA alcohols (2.1-5.4% of total FAs) were present in all foraminiferan samples.

Table 3 Proportions of the ten most abundant fatty acids in all samples (in % of total fatty acids) for all analysed pooled foraminiferan samples.

Sample no	14:0	16:0	16:1ω7	18:0	18:1ω9	18:1ω7	18:2 ω 6	20:4ω6	20:5ω3	22:6ω3
1	1.4	16.3	1.7	7.8	7.0	11.3	2.0	20.5	2.8	2.5
2	3.8	25.5	6.5	11.6	17.2	3.5	4.0	5.7	3.2	1.4
3	3.1	28.8	1.0	14.9	10.4	5.3	2.7	8.4	1.0	3.8
4	1.9	15.8	1.1	12.0	9.7	7.0	3.7	8.1	4.4	8.4
5	1.0	17.6	1.0	17.7	12.9	5.3	4.6	11.8	3.5	3.9
6	3.0	24.4	1.0	10.1	17.3	6.4	5.2	5.7	1.0	1.0
7	4.7	17.1	7.4	3.8	12.6	18.7	2.0	4.7	4.2	2.0

3.3 Amphipoda

The analysed ten specimens from deeper waters and one from a shelf station were identified as: *Eurythenes gryllus*, *Abyssorchomene* spp. and Lysianassidae sp. The highest overall FA contents of all studied peracarids were found within this group (up to 15.5% of dry weight) in *Abyssorchomene* sp. The FA composition between specimens varied, but in general the dominant FAs found were 18:1(n-9), followed by 22:6(n-3) and 16:0 (Figure 3a), determining the positioning within the PCA plot. Most of the analysed amphipods have comparably high ratios of 18:1(n-9) to (n-7), reaching up to 11.6. These are accompanied by high 22:6(n-3) to 20:5(n-3) and low 16:1(n-7) to 16:0 ratios. Some amphipods have comparably high levels of 20:4(n-6) (up to 15.6% of total FAs). FA alcohols were found in all analysed amphipods, with values of 1.0-5.1% of total FAs.

3.4 Isopoda

In total, 25 isopods belonging to six families originating from the depths between 488 to 5340 m were analysed for their FA composition. The total FA content was low, ranging from 1.0 to 3.7% of body dry weight. The FAs 22:3(n-6), 20:5(n-3), 18:1(n-7) and 18:1(n-9) are prominent in the majority of isopods, but no general pattern can be observed for the whole group (Figure 3b). This is reflected by a mainly central position within the PCA plot with only slight transitions of some families, due to phytoplankton markers (both Macrostylidae), the potential foraminiferan marker 20:4(n-6) (most Munnopsidae), and the indicators for carnivorous tendencies 18:1(n-9), 22:3(n-6) and a high 18:1(n-9) to (n-7) ratio (*Stenetrium weddellensis* and *Haploniscus* spec.). FA alcohols were found in most isopods, with the highest value of all peracarid samples in *Eurycope* spec. (12.2% of total FAs).

3.5 Cumacea

Most of the ten sampled Cumaceans were obtained from shallower depths (488-600 m), while only two specimens origin from deeper waters. Sampled and analysed were the families Bodotriidae, Leuconidae, Nannastacidae and Diastylidae. The average FA content was lowest of all analysed groups, ranging from 1.1- 2.5% of total DW. The dominant FA in this group was 20:5(n-3), with individual levels ranging from 19.0–29.2% of all FAs, determining the position in the upper area within the PCA plot. Further dominant FAs were 18:1(n-7), 18:1(n-9) and 16:0 (Figure 3c). The 18:1(n-9) to (n-7) and 22:6(n-3) to 20:5(n-3) ratios are low.

3.6 Tanaidacea

In total, four specimens each belonging to a different genus were collected, all originating from deep waters. The total FA content ranged from 1.0 to 4.4% of total DW. A strong variability between the genera was found, and no single FA takes a dominant role in all samples (Figure 3d). This is also reflected in the PCA analysis, as each individual is located in another area of the plot. Prominent FA in all tanaids, however, are 18:1(n-7) with levels ranging from 9.3-14.7% of total FAs, followed by 16:1(n-7), 20:4(n-6) and 20:5(n-3). Striking are the high levels of 20:4(n-6) (15.7 and 18.9% of total FAs) found in *Neotanais* spec. and *Paranarthrura* spec.; however, higher values of 20:5(n-3) in the former determine the positioning in another area of the PCA plot. The highest levels of 16:1(n-7) (28.4% of total FAs) and the highest 16:1(n-7) to 16:0 ratio (4.8) of all samples in this study were found in *Apseudomorpha* spec.

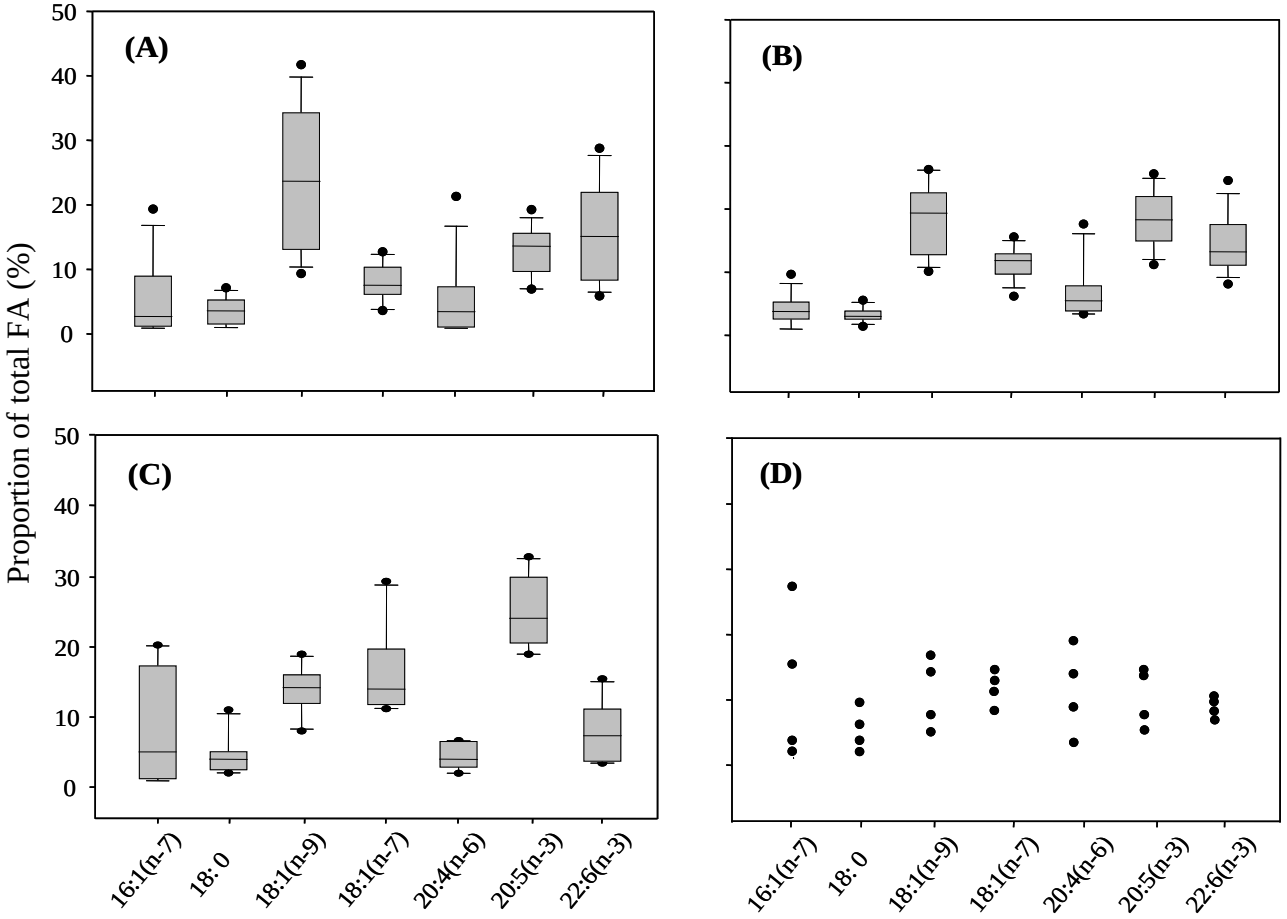

Fig 3 Fatty acids responsible for the main differences between taxonomic groups (loadings > 0.6 in the Principal Component Analysis conducted for the peracaridean samples). Median, 10th, 25th, 75th and 90th percentiles and standard deviation are given for (A): Amphipoda (n=13), (B): Isopoda (n=25) and (C): Cumacea (n=10). For (D): Tanaidacea individual values are given according to small sample size (n=4).

4 Discussion

4.1 Fatty acid composition and marker fatty acids

Generally, benthic species have relatively low lipid contents compared to some zooplankton species (Clarke and Peck, 1991), which was also found in our study. Lipids are apparently not accumulated for energy storage indicating that the investigated animals have the possibility of feeding throughout the year (Bühring and Christiansen, 2001).

The predominance of the polyunsaturated FAs 20:5(n-3), 22:6(n-3) together with the saturated FA 16:0 reflects the dominance of phospholipids (Sargent and Henderson, 1986; Tande and Henderson, 1988), further pointing towards a low dependence on lipid reserves.

4.2 Foraminifera

FA analyses on foraminiferans are still very limited, as these protozoans are normally of very small size, what makes the sampling of sufficient biomass for biochemical analyses difficult. Additionally, they are known to show inter-specific differences in their biochemical composition, and foraminifer taxonomy is a challenging task. Nevertheless, given their probably significant, but so far under-investigated role in deep-sea ecosystems, research in their role within the food web needs to be pushed on.

Our results show that the foraminiferans contain considerable amounts of PUFA (especially 20:4(n-6)), and it is striking that the phytoplankton typical FAs 20:5(n-3) and 22:6(n-3) only occur in comparably low amounts. This raises the question on the feeding of foraminiferans, which are thought to be mainly detritivore. However, practically nothing is known on metabolic processes and lipid biochemistry in these protozoans, which might differ strongly from the functioning of these processes in invertebrates. Still, overall FA patterns with high 20:4(n-6) and 18:1(n-9) values comparable to our results were also found in other studies. Analysing the FA composition of calcareous and agglutinated foraminiferan species, Suhr et al. (2003) found significant differences in their FA profiles as well as higher amounts of PUFAs compared to the surrounding phytodetritus, indicating selective feeding on specific components. Therefore, foraminiferans could play an important role in providing animals feeding on them with sufficient amounts of PUFA. High amounts (16%) of 20:4(n-6) have also been found in large agglutinated foraminifera from the NE Atlantic (Gooday et al. 2002) and in large Antarctic shallow water foraminiferans (up to 11.2%) by Suhr et al. (2008).

Foraminiferivory has already been described for various benthic organisms (e.g. Lipps and Ronan, 1974, Hickmann and Lipps, 1983; Herbert, 1991; Langer et al., 1995). Nomaki et al. (2008) constructed a food web model for the Japanese deep-sea (Sagami Bay) that includes foraminiferans as primary consumers, utilized by secondary consumers (e.g. copepods and polychaetes), which are themselves fed upon by predators. Elizalde et al. (1999) found that a northeast Atlantic isopod, *Munnopsurus atlanticus,* selectively ingests benthic agglutinated foraminifers and that the available POC from this source would be ten times higher than the carbon available from the sediment. It seems likely that benthic foraminifers are an important link in the trophic chain because of their high biomass.

Interpreting the importance of foraminiferans in the diet of the peracarid crustaceans by analysing and comparing their FA patterns has to be conducted tentatively. The results of this study as well as findings of other authors show that foraminiferans can have strongly varying FA compositions, most likely due to the heterogeneity of the samples (species specific FA compositions). However, besides foraminiferans, potential sources of 20:4(n-6) are very limited. It has been shown that Rhodophyta usually contain high amounts of this

PUFA, and Bühring et al (2002) suspected these algae incorporated in gelatinous material captured in the deep-sea could be the source of high 20:4(n-6) values in holothurians from the north-east Atlantic. But in the current studied area, no evidence for red algae remains has been found to date. Another source of enhanced 20:4(n-6) values could be the capability of synthesizing this FA *de novo* (Ginger et al., 2000), but this ability is very rare in the animal kingdom. Additionally, $\delta^{13}C$ data found in the study by Bühring et al. (2002) makes this pathway unlikely; therefore 20:4(n-6) is most probably ingested with food. It has been shown that bacteria (Nichols et al., 1997) and fungi (Kendrick and Ratledge, 1992; Eroshin et al., 1996), both potential dietary sources of foraminiferans, can contain enhanced levels of 20:4(n-6) and could possibly be responsible for high levels of this FA in the protozoans.

4.3 Amphipoda

In the deep-sea, the majority of amphipod species are carnivorous or scavenging (Thurston, 1990; Dauby et al., 2001). All amphipod species analysed in the present study belong to the carnivorous/scavenging family of Lysianassoidae (*Eurythenes gryllus*, *Abyssorchomene* spp. and Lysianassidae sp.). Our results with very high 18:1(n-9)/n-7) for most amphipods strongly indicate a carnivorous or necrophagous component to their diet, but are not pronounced enough to assume that they display an obligate feeding mode.

Arctic shelf amphipods have been found to have FA compositions with 18:1(n-9) to (n-7) ratios similar to our results (3.3-3.6) (Graeve et al., 1997) while in *Eurythenes gryllus* from the Porcupine Abyssal Plain values up to 18 for this ratio were reported, what in this case likely indicates a strict necrophageous diet of the analysed specimen (Bühring and Christiansen, 2001). However, it is likely that there might not be strict obligate necrophageous species in the scavenging amphipod guild, but that the amphipods rather act as facultative scavengers, employing predation, and possibly detritivory, when carrion is unavailable (Blankenship and Levin, 2007). The *Eurythenes gryllus* specimens analysed in the present study have lower 18:1(n-9) to (n-7) ratios than reported in previous studies, possibly indicating that, even though carnivorous feeding might be the preferred strategy, other food sources are utilized when prey or carrion is not available. De Broyer et al. (2001) showed for species belonging to the genus *Abyssorchomene*, that they are capable of active hunting, and pieces of flesh, sponge spicules, crustacean remains and also diatoms have been found in their guts.

It is known that many deep-sea amphipods are capable of surviving long starvation periods (up to 18 month in *Waldeckia obesa*, Coleman, 1991), and the occurrence of FA alcohols in

all analysed amphipods possibly indicates the utilization of wax esters as long time energy storage.

4.4 Isopoda

While there are some studies that analysed the general biology of isopods from Antarctic shelf waters (Dearborn, 1967; Menzies and George, 1968; White, 1972; Luxmoore, 1982), information on feeding in deep-sea isopods is still very limited. This is due to the low sampling effort of the deep-sea and the resulting high value of the samples. Specimens are rather used for taxonomic purposes, as a major part of species found is still undescribed. The FA compositions analysed in this study reveal distinct differences between some isopod species, while others have similar FA patterns. The animals originating from shallower waters, especially *Stenetrium weddellensis* have comparatively high ratios of 18:1(n-9) to (n-7), what reflects a diet with a carnivorous input. For the majority of isopods originating from deeper waters, the FA patterns are not dominated by a certain marker FA, indicating an omnivorous diet. Some Haploniscidae show relatively high 18:1(n-9) to (n-7) ratios compared to the other abyssal isopods. This could possibly be due to the ingestion of small invertebrates. The FA signatures of the two Macrostylidae have higher values of 20:5(n-3) pointing towards feeding on phytodetritus. The high levels of 20:4(n-6) found in some Munnopsidae could either be due to the direct ingestion of bacteria or fungi, or indicative for preferential feeding on foraminiferans. No typical bacteria FA markers (e.g. 15:0, 17:0, 15:1 or 17:1; Dalsgaard et al., 2003) have been found in these analysed individuals; but no statement can be made on the possible ingestion of fungi. However, foraminifer fragments have been found in the guts of a variety of isopods in previous studies (Menzies, 1956; Wolff, 1962; Wilson and Thistle, 1985; Brandt, 1997; Svavarsson et al., 1993; Gudmundsson et al., 2000), making this source of 20:4(n-6) more likely. A selective feeding behaviour of isopods on foraminiferans has also been suggested by Elizalde et al. (1999) and Cartes et al. (2000) for *Munnopsurus atlanticus*, and in a study based on gut content analyses (Brökeland et al., 2010), the food of the four investigated species of deep-sea isopods included calcareous, agglutinated as well as soft-walled foraminifers.

In most isopod samples, FA alcohols were found, possibly indicating the utilization of wax esters as long time energy storage to survive starvation periods.

4.5 Cumacea

Cumaceans typically dig in soft seabed sediments (Schram, 1986) and are thought to be mainly deposit feeders (Dennell, 1934) ore scrapers (Dixon, 1944), but some might also act

as predators or scavengers (Kaestner, 1967). Studying the gut contents of some Antarctic shelf cumaceans, Blazewicz and Ligowski (2002) found mainly diatom remains.

Our results strongly indicate a diet depending on phytodetritus for the sampled Cumaceans, taken the dominance of 20:5(n-3) and 18:1(n-7) as well as low 18:1(n-9) to (n-7) ratios. The low 22:6(n-3) to 20:5(n-3) ratio additionally supports a basal trophic level of this group.

4.6 Tanaidacea

Many tanaidaceans live in tubes or tunnels constructed from sand grains, mud, and detritus (Holdich and Jones, 1983) and are commonly classified as sediment (Kudinova-Pasternak, 1991), seston (Dennel, 1937; Lang, 1956) or detritus (Blazewicz and Ligowski, 2002) feeders. Some tanaids can emerge partially from their tubes to graze on the surrounding substratum (Johnson and Attramadal, 1982; Kudinova-Pasternak 1991), some can additionally feed on microorganisms co-existing in their tubes (Bird and Holdich, 1985, Delille et al., 1985), and a few species are suspected to be predators (Gutu, 1986).

The high levels of 20:4(n-6) found in this study for *Paranarthrura* spec. and *Neotanais* spec., but also *Apseudes* spec. possibly hint to an ingestion of bacteria of fungi, or rather the utilization of foraminiferans as preferred food items, as earlier studies suggest based on the morphology of mouthparts, that some tanaids utilize foraminiferans as a food source besides detritus (Kudinova-Pasternak, 1991). In the present study, lower values of 20:4(n-6) were only found in *Apseudomorpha* spec., accompanied by high 16:1(n-7) values, indicating that this species likely utilises phytodetritus as food. However, more samples need to be analysed to support the trend found in this study for single specimens.

5 Conclusions

Comparing the FA compositions of four orders of peracarid crustaceans, we could identify different FA patterns between the taxonomic groups, but also within one peracarid taxon. Based on FA trophic markers found in this study and the distinction in the PCA analyses, most of the peracarid crustaceans can be assigned to their respective taxonomic order with differing feeding habits: phytodetritivory is most pronounced in the Cumacea, while in the Isopoda, a more omnivorous diet (in some cases possibly foraminiferivory) is likely. In most Amphipoda strong indications for carnivory are found, while the Tanaidacea individuals show strongly varying FA patterns, placing them either between the phytodetritivore cumaceans or within the omnivore isopods. Indications for feeding on foraminiferans derived from earlier studies and comparisons of the FA signatures of potential prey and consumers suggest that some species of isopods and tanaidaceans seem to have a preference for these protozoans. Foraminiferans possibly provide an important, high-quality food source for abyssal invertebrates. We suggest that high values of the FAs 20:4(n-6) defined against high values of typical phytoplankton markers like 20:5(n-3) and 18:1(n-7) or hints for carnivory with high ratios of 18:1(n-9) to (n-7) can be used as an indication for foraminiferivory.

However, this study can only be seen as a starting point on which future investigations can build up on to elucidate the structure and mechanisms of Southern Ocean benthic food webs. Further investigations utilizing more sensitive methods to define the role of foraminiferans in the diet of peracarid crustaceans are needed.

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State of the manuscript and own contribution:

I conducted the fatty acid analyses and relevant data interpretation. The manuscript was written based on discussions of all authors and has been submitted to Deep-Sea Research II.

Chapter 7

Demersal fishes from the Antarctic shelf and deep-sea: a diet study based on fatty acid patterns and gut content analyses

Bathydraconid (upper picture) and macrourid (lower picture) fish caught in the Antarctic deep-sea during the ANDEEP-SYSTCO cruise.

Chapter 7 Demersal fishes from the Antarctic shelf and deep-sea: a diet study based on fatty acid patterns and gut content analyses

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Abstract

The gut contents and fatty acid composition of 49 fish belonging to five Antarctic demersal families (Nothoteniidae, Macrouridae, Channichtyidae, Bathydraconidae and Artedidraconidae) sampled at two stations at the Southern Ocean shelf and deep-sea (600 and 2150 m) was analysed in order to identify their main food resource by connecting trophic biomarkers with the dietary items found in the fish guts. Main food items of most analysed fish were amphipod crustaceans (e.g. in 50 % of *Trematomus scotti* guts) and polychaetes (e.g. in 80% of *Bathydraco antarcticus* guts), but also other food items including e.g. fish, other crustaceans and gastropods were ingested. The most prominent fatty acids found were 20:5(n-3), 16:0, 22:6(n-3) and 18:1(n-9). The results of gut content and fatty acid analysis indicate that all fish except the Channichthyidae share similar food resources irrespective of their depth distribution, benthic amphipods and polychaetes. A difference of the dietary spectrum can rather be observed with ontogenetic phases than between species, as high values of typical zooplankton marker fatty acids (e.g. values for 22:1(n-11) up to 7.1% of total fatty acids) indicate that younger (smaller) specimens include more zooplankton in their diet.

Key words: Deep-sea, fatty acid, benthic fish diet, Southern Ocean

1 Introduction

The Antarctic continental shelf is distinctive in being depressed by the weight of the continental ice; and heavily scoured by previous extensions of the continental ice sheet. It can exceed 1000 m in depth, what increases the distance from the seabed to the euphotic zone compared to continental shelves elsewhere in the world. Similar to other high-latitude ecosystems, the major pelagic herbivores are copepods, euphausiids and salps (Hunt et al. in press, Flores et al. in press, Brandt et al. in press). Intense pulses of particulate organic matter to the shelf floor originating from seasonal water-column production are responsible

for high organic carbon fluxes to the shelf sea floor (Bathmann et al., 1991; Fischer et al., 2000; Isla et al., 2006), where the majority of samples analysed in this study originate. Additionally, the Maud Rise seamount was sampled, regularly appearing as a region of reduced ice coverage (De Steur et al., 2007), with intermediate to high annual primary production rates (Wefer and Fischer, 1991). In marine polar regions, the structure and biomass of the benthic community depend on multiple, interdependent factors, such as hydrography, ice coverage, light, temperature and the structure of the pelagic food web regulating the food supply to the benthic realm (Grebmeier and Barry, 1991; Clarke and Arntz 2006). However, it appears that the organic matter reaching the continental shelf seabed has a long half-life, leading to a food bank for deposit feeders and thereby providing comparably stable conditions for the benthic fauna (Mincks et al., 2005; Clarke and Arntz, 2006; Isla et al., 2006).

Fish play an important role as top predators in marine systems, a fact that also accounts for the Antarctic shelf and deeper waters. Some studies investigating the diet of Antarctic fishes have been conducted, in some cases including deep-sea species, and it has been shown that there exist different feeding strategies reaching from sediment browsing to active hunting (Daniels, 1982; Gon and Heemstra, 1990; Pakhomov and Tseitlin, 1991; Gartner et al. 1997, Pakhomov, 1997).

The Notothenioidei, a suborder of the Perciformes, form the dominant component of the fish community of the Antarctic continental shelf and upper slope (DeWitt, 1971; Andriashev, 1987; Eastman and Clarke, 1998; Dettaï and Lecointre, 2004). This suborder features unique adaptations such as the presence of antifreeze proteins and the loss of haemoglobin (Eastman 1993). Nototheniids lack a swim-bladder, but achieve buoyancy by lipid storage and reduced skeletal calcification. The former is possibly also a strategy to survive long periods of limited food supply during austral winter by relying on these energy-rich deposits (Eastman 1988, 1990, 1993; DeWitt et al., 1990; Hagen et al., 2000). Four families investigated in this study belong to this suborder, including the Nototheniidae (cod icefishes), with the two species *Trematomus scotti* and *T. bernachii*, the Channichthyidae (Antarctic icefishes, *Chionodraco myersi* and *Cryodraco antarcticus*), the Harpagiferidae (plunderfishes, one individual of *Artedidraco orianae*), and also the Bathydraconidae (Antarctic dragonfishes, *Bathydraco antarcticus* and *Bathydraco* sp.). The fifth family analysed in this study are the Macrouridae (rattails), belonging to the order Gadiformes.

The traditional way of estimating fish diets is the analysis of stomach contents. However, this method faces some restraints, as it can only provide information on recently ingested food items, and more rapidly digested items might be underestimated compared to slowly digested ones. Furthermore, macrourid fishes for example have gas bladders that expand upon retrieval to the surface, often causing regurgitation. An approach that can be used in

addition to clarify which feeding sources have been utilised by an organism integrated over longer time spans is the analysis of its fatty acid (hereafter FA) composition. This method has become an established tool to gain information on food preferences and feeding history of marine organisms (e.g. Sargent, 1976; Sargent and Whittle, 1981; Graeve et al., 1994; Iverson et al., 2002), since FAs of potential food items have specific signatures that are not degraded during digestion, and can accumulate in the tissues of consumers. Some FAs can function as biomarkers for certain food categories, and help interpreting the specific FA composition of an organism. Widely used are the phytoplankton markers 20:5(n-3), 16:1(n-7), 18:1(n-7) and 22:6(n-3) (Dunstan et al., 1994; Sargent et al., 1995; Falk-Petersen et al., 1998), the indication for carnivory by high 18:1(n-9) values, accompanied by low 18:1(n-7) values (e.g. Graeve et al., 1997; Auel et al., 2002), or markers synthesized by polar calanoid copepods, such as 20:1(n-9) and 22:1(n-11) (Sargent, 1976; Hagen et al., 1993).

Knowing the pathways of energy transmission from the lower trophic levels to the higher predators is an important prerequisite to understand the quantitative functioning of marine ecosystems. The objective of this study is to (i) compare the diet composition of benthic fishes, both on the Antarctic shelf and in the deep-sea; (ii) evaluate the (short-term) diet composition from gut content analysis in the light of (long-term) results from FA analysis.

2 Material and Methods

2.1 Sampling

The studied material originates from the ANDEEP-SYSTCO expedition (ANT XXIV/2 from 28th November 2007 to 4th February 2008) on board of RV *Polarstern*. Samples were collected at two stations in the Weddell Sea; one deep-sea station (PS71/39) located on the plateau of the Maud Rise sea mount at 2150 meters depth, and one shelf station close to the Antarctic shelf ice edge in 600 meters depth (Figure 1).

The fish were caught by a deep-water bottom trawl and a Rauschert-dredge. Species were identified to species level, and the individual fish were immediately measured (for all macrourids total length, TL; for other taxa standard length, SL; both to the nearest mm). Small pieces of white muscle tissue from under the posterior dorsal fin were dissected from each fish for fatty acid analysis and frozen at -80°C. The fish bodies were frozen at -80°C for further analysis.

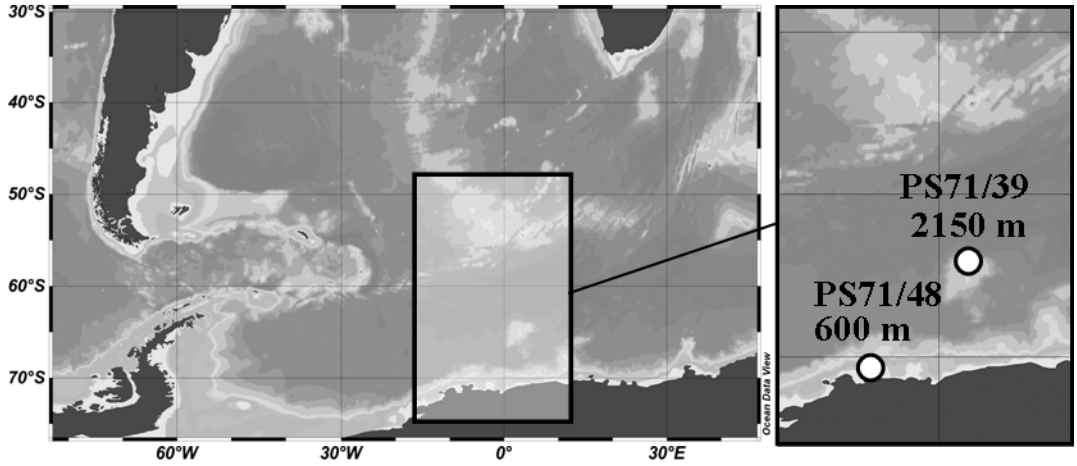

Fig 1 Map of the sampled shelf (PS71/48, 60 0m depth) and deep-sea (PS71/39, 2150 m depth) station

2.2. Gut content analyses

The fish bodies were thawed individually and wet weight (to the nearest 0.1 g) measured. Guts were removed and stomach contents of each fish sorted, prey items counted and identified to different taxonomic levels, depending on the condition of the items. The degree of gut filling was estimated visually (expressed in %). The percentage frequency of occurrence of food items (number of guts containing a particular prey item as a percentage of the total number of guts examined) was determined for each fish species.

2.3. Fatty acid analysis

Prior to the FA analysis the muscle tissue samples were freeze dried, weighed and allowed to extract in dichlormethane-methanol (v:v/2:1) for at least 48 h. Lipid extraction was performed with minor modifications as described in Folch et al. (1957) and analysis of fatty acid composition was performed with modifications as described in Kattner and Fricke (1986). For a detailed method description see chapters 5 and 6.

2.4. Statistical methods

Principal component analysis (PCA) was performed using the SPSS software package (SPSS version 16.0) to investigate the variation in fatty acid signatures between species and identify the FAs most responsible for this variation. FAs with proportions lower than 1% of total FAs

were excluded prior to analysis. Eleven FAs were chosen as variables for the analysis based on their average abundance (>3 % of all FA in at least one species).

3 Results

In total, 49 fish belonging to five species were analysed (Table 1).

The gut content analysis showed that the dietary spectrum of the majority of investigated benthic fishes strongly overlaps (Table 2). Amphipods and polychaetes were the most frequently found food items found and made up the major proportion in all investigated species except the Channichtyidae. In *Trematomus bernacchii*, additional species of small gastropods were found relatively frequently (in 38% of guts). Ostracoda were found in *Trematomus bernachii*, Macrouridae spp. and *Bathydraco antarcticus*, while calanoid copepods were only found in Macrouridae spp. Only one individual (*Cryodraco antarcticus*) was found having ingested another fish (Myctophiidae). Other food items that occurred occasionally include Decapoda, Isopoda, Ostracoda, Tanaidacea, Solenogaster, and Bryozoa.

The highest total FA content found in this study occurred in *C. myersi* (7.2% of total body dry weight (DW)), while the total FA content in all other groups was comparably lower (Table 3).The most prominent FAs found were 20:5(n-3), 16:0, 22:6(n-3) and 18:1(n-9).

The PCA reveals strong overlaps between most of the analysed individuals, but allows a separation of the analysed fish into three groups (Figure 2). The first two components together explained 58.7% of variance (PC1 = 38.1%, PC2 = 20.6%). The biggest group of individuals centeres slightly to the left side of the center of the plot, mainly determined by high loadings of 20:5(n-3) and 22:6(n-3). This group includes Macrouridae spp., *Bathydraco* sp. and *B. antarcticus* (except one individual) and most adult *Trematomus bernachii* and *T. scotti*. The second group with transitions to the first is orientated more to the upper right side of the plot mainly due to high loadings of 18:1(n-9) and 14:0, including *Chionodraco myersi*, one *B. antarcticus* individual, *Artedidraco orianae*, *Cryodraco antarcticus* and some *Trematomus* specimens.A third group expands to the lower right side of the plot, directed by higher loadings for 22:1(n-11) and 18:5(n-3)/20:1(n-9), and includes the smallest (juvenile, ≤ 60mm) specimens of Macrouridae spp., *Trematomus bernachii* and *T. scotti*.

No distinct differences could be found between representatives of the deep and shallow stations, but for a statistic comparison, the sample sizes were insufficient. One of the two Macrouridae sampled at the deeper station is located slightly apart from the main group, while the other is grouped with the macrourid individuals from the shallow station. Within the Bathydraconidae, no depth related differences are found, even though the animals sampled at the two sites belong to different species.

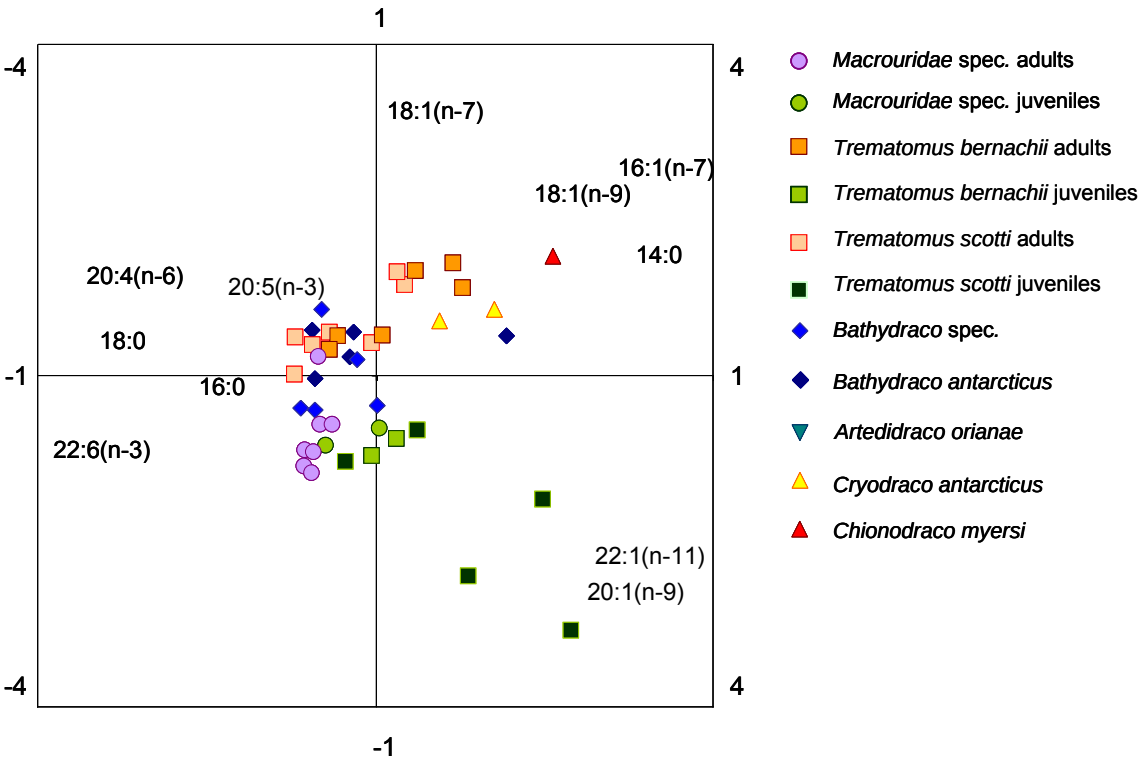

Figure 2 Principal component analyses of fish individuals according to their relative fatty acid composition. Sample plot for the principal components PC1 and PC2 for fish fatty acids (outer axes) and loadings of the respective fatty acids (inner axes).

Table 1 Numbers, depth of catch, length, and average degree of gut filling for Weddell Sea fishes sampled for gut content and fatty acid analyses. Measurement types are SL standard length, TL total length.

Family	species	N	Depth (m)	Median length (mm) (range: min – max)	Length measurement	Average gut filling (%) (range: min – max)
Nothoteniidae	*Trematomus scotti*	16	600	78 (43-126)	SL	74 (50-100)
	Trematomus bernachii	10	600	135 (57-230)	SL	52 (10-90)
Macrouridae	*Macrouridae* sp.	7	600	112 (38-200)	TL	64 (10-90)
	Macrouridae sp.	2	2150	180; 300	TL	70; 90
Bathydraconidae	*Bathydraco antarcticus*	5	600	164 (152-178)	SL	44 (20-80)
	Bathydraco sp.	5	2150	151 (135-168)	SL	42 (30-60)
Channichtyidae	*Cryodraco antarcticus*	2	600	450; 530	SL	10; 90
	Chionodraco myersi	1	600	310	SL	10
Artedidraconidae	*Artedidraco orianae*	1	600	90	SL	70

Table 2 Gut content of Weddell Sea fishes in % frequency of occurrence for food items in respective guts

	species	***Trematomus scotti***	***Trematomus bernachii***	***Macrouridae* spp.**	***Bathydraco antarcticus***	***Bathydraco* sp.**	***Cryodraco antarcticus***	***Chionodraco myersi***	***Artedidraco orianae***
Dietary item	N	16	10	9	5	5	2	1	1
Gastropoda	*Cirsonella extrema*	19							
	Eotionella spec.	13							
	Volverina hyalina	6							
Polychaeta	Polychaeta	25	20	44	20		50		100
	Polychaete remains	38	40	22	80				
Crustacea	Crustacean remains	25		44	20	80			
	amphipod remains	6	20						
	Amphipoda	50	40	44	20	40			100
	Copepoda			33					
	Decapoda	13	10				50		
	Ostracoda		10	22	20				
	Cirripedia larvae		10						
	Isopoda	6		11					
	Tanaidacea	6							
Fish	cfMyctophidae spec.						50		
Other	animal remains	25	20	22	40				
	Solenogaster	6							
	Bryozoa				20				
	parasitic nematoda	13					present		
	parasitic plathelminthes	6	20	22			present		
	sediment grains	13		11		20		100	

Table 3 Numbers of analysed fish individuals, total fatty acid content (TFA, in % of total body dry weight (DW)) and values for the 11 most abundant (>3% in at least one of the analysed groups) fatty acids (in % of total fatty acids) of muscle tissue of demersal Weddell Sea fishes.

species	N	TFA (% of DW)	14:0	16:0	16:1(n-7)	18:0	18:1(n-7)	18:1(n-9)	18:5(n-3)/ 20:1(n-9)	20:4(n-6)	20:5(n-3)	22:1(n-11)	22:6(n-3)
T. scotti	7	2.1±0.5	0.6±0.8	18.4±3.7	4.4±1.7	4.4±0.6	7.1±0.8	10.6±2.4	1.7±1.3	5.0±1.5	19.1±3.2	0.9±0.9	22.7±2.3
T. scotti juv.	5	3.3±2.0	0.6±0.7	17.2±6.0	4.3±1.5	1.9±1.7	7.5±3.6	6.1±4.3	5.6±2.5	12.2±7.8	17.4±4.8	6.8±4.1	18.4±7.8
T. bernachii	6	2.9±1.3	1.5±1.2	18.8±2.6	6.2±2.4	3.9±0.7	6.6±0.9	11.7±1.2	1.8±0.6	4.0±0.9	18.4±1.6	0.7±0.5	21.0±3.0
T. bernachii juv.	2	1.9±1.1	0.5±0.7	19.4±0.6	3.7±0.5	3.4±0.3	4.9±1.0	9.1±0.6	7.2±0.4	3.2±0.1	18.4±1.6	2.5±1.1	22.1±1.1
M. spp.	7	2.0±0.5	0.2±0.6	21.5±1.3	3.0±0.7	4.6±0.6	4.0±1.2	10.1±0.9	2.0±1.0	3.6±0.7	14.2±1.7	nd	35.3±1.9
M. sp. juv	2	1.8±0.7	nd	19.2±5.5	3.1±0.6	4.1±0.5	4.8±1.8	9.6±0.2	3.4±3.0	4.0±0.4	16.2±5.4	3.2±2.9	28.8±9.3
B. antarcticus	5	2.2±1.7	1.6±1.2	18.7±1.6	4.4±1.2	4.4±1.1	6.3±0.8	10.5±1.4	2.1±1.4	3.6±1.1	17.5±1.8	0.3±0.9	26.4±1.5
B. sp.	5	1.5±0.7	0.4±0.7	18.8±1.2	3.3±1.0	4.4±1.0	6.4±0.8	9.9±1.32	2.1±1.2	4.1±0.8	16.7±1.5	0.6±1.1	30.3±2.1
C. antarcticus	2	2.2±1.7	1.9±0.4	19.4±0.4	6.5±0.9	2.6±0.3	6.5±0.5	14.4±1.4	4.0±0.5	2.3±0.8	15.1±1.7	0.9±1.1	20.6±1.5
Ch. myersi	1	7.2	5.9	12.6	8.1	1.7	7.4	18.8	10.6	nd	10.0	7.1	8.7
A. orianae	1	2.8	2.9	19.1	7.0	4.3	7.2	11.8	1.7	6.0	16.7	0.5	18.5

4 Discussion

The results of the gut contents of the investigated demersal Weddell Sea fishes showed that the majority of them share a similar diet, with the main components being amphipods and polychaetes, similar to many Southern Ocean benthic and benthopelagic fishes (Schwarzbach, 1988; Pakhomov and Tseitlin, 1991; La Mesa et al., 1997). The relatively low FA contents found in this study reflect low overall lipid contents, what has been shown to be a general feature of benthic compared to pelagic fishes due to a lesser need for positive buoyancy (Clarke et al., 1984; Friedrich and Hagen, 1994; Phleger et al., 1999).

In accordance with the findings from the gut content analysis, the FAs 20:5(n-3), 22:6(n-3), 18:1(n-9) and 16:0 dominant in the analysed fish samples have also been shown to be the most abundant FAs in both amphipods and polychaetes sampled at the current expedition (Würzberg et al., 2010; Würzberg et al., in press). In spite of the strong overlap of dietary composition found in the gut content, however, the FA composition revealed differences between the analysed species, and in certain cases also within species depending on the body size (Figure 3). The signal from the FA markers could not in each case directly be coupled with the dietary items found in the fish stomachs. In the Macrouridae for example, calanoid copepods were found in the guts of larger specimens, and none in those of the two investigated juveniles. In contrast, in the juveniles the measured values for the zooplankton markers 20:1 and 22:1 are clearly higher than in the larger specimens. The same accounts for the *Trematomus* species; even though no copepods were found in the guts, zooplankton markers were present, and, again, occurred with the highest values in the smallest specimens.

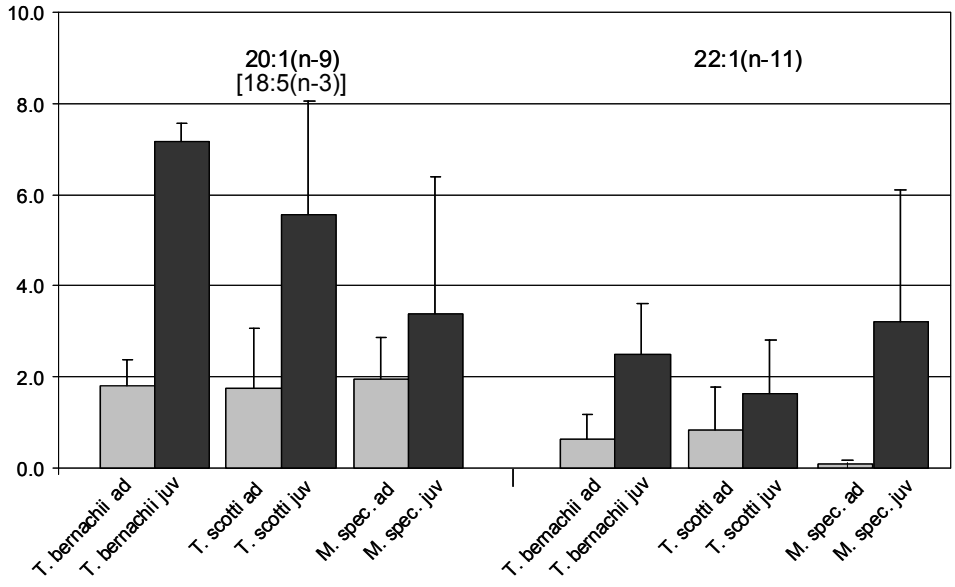

Figure 3 Selected zooplankton marker fatty acids that varied significantly between size classes for *Trematomus scotti*, *T. bernachii* and *Macrouridae* spec. in percentage of total fatty acids. Error bars indicate standard deviation

Another example is the indication for a strong carnivorous input, likely piscivory, in the Channichtyidae. The two channichthyids in our study had considerably higher values of 18:1(n-9), resulting in higher 18:1(n-9) to 18:1(n-7) ratios than all other fish in this study. As most animals are able to synthesize 18:1(n-9) from the precursor 18:0 (Dalsgaard, 2003), the increasing accumulation of this FA with increasing trophic level makes a very high trophic position of the Channichtyidae likely. Only one dietary fish was found, however, while the guts of the other individuals were almost empty. Channichthyids typically are ambush feeders of fish and euphausids (Gubsch, 1982; Iwami and Kock, 1990; Flores et al., 2004) that can survive without food for a long period of time, thriving on incidental large energy input from their prey. This explains a high proportion of empty stomachs (Skora and Neyelov, 1992; Flores et al., 2004).

The similar diet composition indicates that the different fish species compete for the same food resource. Schwarzbach (1988) also found a high (65%) overlap in prey between the investigated Weddell Sea benthos feeding fish species made up by a high proportion of amphipods and polychaetes. The ingested amphipods and polychaetes are probably a preferred food source due to their visibility when moving on the sea floor instead of being burrowed within the sediment like many other benthic taxa.

Several studies have addressed the diet composition of Antarctic Nototheniidae species and are concordant with our findings. *Trematomus scotti* adults in the Antarctic part of the Indian Ocean have been reported to mainly ingest benthic amphipods, polychaetes, and euphausids (Pakhomov and Tseitlin, 1991; Pakhomov, 1997), and also on the eastern Antarctic shelf *T. scotti* mainly fed on benthic organisms like polychaetes and amphipods (Schwarzbach, 1988). The food spectrum of *T. bernachii* has been reported to be wider, and besides polychaetes and amphipods this species has for example been found to ingest gastropods, isopods and occasionally pycnogonids, fish and fish eggs, euphausiids, mysids, decapods, echinoids, holothurians, priapulids, thaliaceans and algae (Daniels, 1982; Dewitt et al., 1990; Kiest, 1993; LaMesa et al., 2004). Also in the current study, small gastropods have only been found in the guts of *T*. *bernacchii*.

Artedidraco orianae, frequently found on the Antarctic sublittoral and continental shelf, has also been reported to mainly feed on amphipods and errant polychaetes, and, to a lower proportion, isopods (Eakin, 1990).

The Macrouridae analysed in our study as well ingested mainly amphipods and polychaetes.

Drazen et al. (2001; 2008) investigated the diet of two species of macrourids from the abyssal North Pacific utilizing stomach content and stable isotope analyses, as well as fatty acid profiles (Drazen et al., 2009). They found that smaller specimens (<150 mm pre-anal length) of the sampled two species mainly fed on crustaceans, polychaetes and holothurids,

while increasingly larger individuals (>150 mm pre-anal length) additionally utilised squid and fish and displayed scavenging. Ontogenetic changes in feeding were also found by Stowasser et al. (2009) for macrourid species from the Northeast Atlantic with the indication of a switch from active predation to scavenging occurring with increasing body size. In our study, no indications for carrion feeding (e.g. high 18 1(n-9) to 18:1(n-7) ratios) were found. This might in some cases simply depend on the size range of the sampled fish. The macrourids (up to 300 mm total length) falling into the range of carrion feeding fish, may have fed on other food items due to inavailabilty of carrion.

Information on the diet of Bathydraconidae is relatively sparse, as the guts of these fish have often been found to be empty (Skora & Neyelov, 1992), as also found in the current study. A reason for this is the rather inactive and sluggish behaviour described for Bathydraconids, as they rely on more or less motile benthic or epibenthic prey adopting a ‘‘sit and wait’’ feeding strategy (LaMesa et al., 2007). Main prey items reported are amphipod crustaceans and fish (Pakhomov, 1998; LaMesa et al., 2007). However, both amphipods (in both species) and polychaetes (in *B. sp.*) were found in the guts, and their FA composition places them within the group mainly feeding on these prey items, except for one *B. antarcticus* specimen which had higher 18:1(n-9) values. This indicates that these fish probably utilise benthic invertebrates and, occasionally, fish as dietary items.

In summary, all fish species investigated in this study, except the Channichthyidae, seem to share similar food resources. A shift of the dietary spectrum can rather be observed with ontogenetic phases than between species, indicating that younger (smaller) specimens ingest more zooplankton (e.g. calanoid copepods), while with increasing size of the fish, simultaneously the selected prey items change and amphipods and polychaetes are mainly fed upon. The ingestion of zooplankton has also previously been reported for juveniles of Antarctic *Trematomus* species (Daniels, 1982; Pakhomov et al., 1995; Barrera-Oro and Piacentino, 2007). This is reflected in the individual FA compositions found in this study, as the proportions of the long-chain FAs 20:1 and 22:1 are highest in the smaller individuals of the respective species, most pronounced in *T. scotti*, strongly indicating the ingestion of zooplankton, as they are typical components of calanoid copepods (Hagen et al. 1993, Kattner et al. 1994). However, in this study, low sample numbers and therefore insufficient size ranges did not allow testing for intra-specific changes in diet and/or FA composition with increasing fish size in this species.

5 Conclusions

Analysis of the gut content and individual FA composition of five Antarctic fishes showed that most of them share a similar food source, made up by benthic amphipods and polychaetes.

The respective gut content was not always mirrored in the FA composition of the same fish, indicating that the contents found in the fish guts provide only a snapshot of their diet. In contrast, FA patterns possibly indicated seasonal and ontogenetic changes in the diet composition. In several species, differences in the FA composition were more distinct between fish of different size than of different species, indicating an ontogenetic transition from planktivory to benthic feeding.

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State of the manuscript and own contribution:

H. Flores and me collected the fish samples and prepared them for further analyses. I conducted the fatty acid analyses and relevant data interpretation. The manuscript was written based on discussions of all authors and has been submitted to Deep-Sea Research II

Chapter 8

Comparing biomass and production estimates of Antarctic Deep-Sea isopod families

Southern Ocean deep-sea isopods: upper left: Ischnomesidae; lower left: Haploniscidae; lower right: Munnopsidae; upper right: Desmosomatidae.

Chapter 8 Comparing biomass and production estimates of Antarctic Deep-Sea isopod families

Abstract

Data are presented on morphometric measurements and biomass for five abundant isopod families from three stations in the abyssal eastern Weddell Sea. Secondary production and P/B estimates were calculated utilising two empirical models. Results for P and P/B calculated by of both empirical models differed slightly, being lower for the model including water depth and temperature as factors.

Abundance and biomass differed between stations, and highest biomass estimates were calculated for the Polar Front region (8.012 mg DW m^2 for all five isopod families together). Highest individual biomass and production values were estimated for the Munnopsidae, while the Desmosomatidae accounted for the biggest proportion of biomass at two stations due ro their high abundance rates. Compared to previous biomass and production estimates for the deep Weddell Sea, the isopod families analysed contribute a major proportion to macrobenthic biomass.

1 Introduction

Previously collected samples provided a wealth of information on the structure of the benthic community in the Southern Ocean (Brandt et al., 2007 a, b). Isopods belong to the most abundant and most diverse groups inhabiting the shelf and deep-sea floor in the present study region (Hessler and Thistle, 1975, Wilson, 1998, Brandt, 2007 a, b; Kaiser et al., 2007), likely inhabiting a key role within the ecosystem. Analyses indicated that some species were quite rare (e.g., only a few individuals present at few stations) while others were more common (abundant at higher densities at most of the sampled stations). However, more background information than available to date is needed to draw conclusions on the general biology of deep-sea isopods in order to correlate the present abundance patterns with possible implications for ecosystem and food web dynamics.

Generally, marine benthic animals can play an important link for energy flow from primary producers to fish (see chapter 7) and in the recycling of sedimented organic matter (Crisp, 1984). The measurement of secondary production plays a crucial role in the quantification of ecosystem dynamics, as production is one of the major pathways of energy flow (Edmondson, 1974).

Secondary production in aquatic invertebrate populations can be analysed with methods based on a variety of parameters such as growth or mortality of identifiable cohorts (e.g., Benke, 1984; Crisp, 1984) or size-frequency classes (e.g., Hynes-Hamilton and Coleman, 1968). To obtain this information, certain prerequisites must be given, such as sampling at

regular time intervals or good understanding of life histories (e.g. method by Banse and Mosher, 1980, relying on the body weight of animals at their first sexual maturity).

As measuring most of these parameters in a sufficient quantity, especially in deep-sea settings, is often difficult, time-consuming and expensive to conduct, empiric models have been developed to estimate production (e.g., Brey, 1990), considering mean annual biomass (B) and mean individual body mass (W) to estimate production in marine benthic invertebrates. However, various environmental parameters have been shown to influence growth rates, specifically temperature and water depth (Morin and Bourassa, 1992; Tumbiolo and Downing, 1994; Cartes et al., 2002). Therefore adjusted models were developed, interpolating these factors.

Most studies addressed broad taxonomic groups and general life strategies (e.g., Brey 1999). However, a higher resolution of taxonomic groups can help to gain information on the position of a distinct group within the food web and furthermore be applied to and compared between different sites and ecosystems. To obtain information on one of the most diverse and often highly abundant groups within the deep-sea benthos, size and weight measurements were conducted for isopods sampled in the Weddell Sea during the ANDEEP-SYSTCO expedition (*Polarstern* cruise ANT XXIV/2, November 28th 2007 to February 4th 2008). The most abundant isopod families were analysed to provide a dataset based on which biomass and production estimates can be conducted. Two empirical models were used to calculate annually production and P/B rates and the respective results are compared.

2 Material and Methods

Samples were collected at three stations in the Weddell Sea: station PS71/13 (Polar Front), PS71/17 (close to the Antarctic continent) and PS71/39 (Maud Rise plateau) (for detailed station description, see chapter 1). Samples for morphometric measurements were obtained by means of an epibenthic sled, and isopods were identified on board and in the home laboratory by specialists. Individuals with overall intact bodies were analysed for their total length, width at the widest point, and alcohol wet weight, using a Leitz microscope and an ultra scale. Prior to the measurement of preserved wet weight, excess surface moisture was removed.

Abundances (ind. m^2) were calculated for the five most frequent isopod families from the number of individuals based on the samples yielded from sampling with a box-corer (sub-sampled with a 0.9x0.9 m frame) on the respective station. Mean biomass (B, mg/m^2) was calculated for each family from the mean wet weight divided by the sampled area (WW).

As sampling, sorting and identification of macro-invertebrates are time-consuming, in practice the animals are often preserved before identification, counting and biomass

estimation. This preservation may affect weight estimates, and wet weights of benthic invertebrates reportedly decreased during the first weeks of preservation in ethanol (Howmiller, 1972; Dermott and Paterson, 1974), presumably due to water and/or lipid loss. To account for this, correction factors can be used to estimate the differences between preserved and fresh weights. However, as most benthic animals have relatively low lipid contents compared to pelagic species, and no conversion factors for deep-sea isopods are available, it was decided to calculate with the actual weight measured.

To estimate production rates and P/B ratios, two empiric models were applied:

1) Empirical model of Brey (1990), developed for marine benthic invertebrates (Crustacea):

$$\log P = -0.614 + 1.022 \log B - 0.360 \log W$$

where P = annual production, B = mean annual biomass (AFDW, ash free dry weight, g/m^2) and W = mean individual weight (AFDW, g), obtained as B/D ratio, D = mean annual density (ind./m^2).

2) Empirical model by Tumbiolo and Downing (1994):

$$\log P = -0.18 + 0.97 \log B - 0.22 \log W_m + 0.04 T_b - 0.014 Tb \log (Z+1)$$

where P = annual production, B = mean annual biomass (DW, g/m^2), W = mean individual weight (DW, g), obtained as B/D ratio, D = mean annual density (ind./m^2), T_b = Annual mean bottom temperature (°C) and Z = (depth/m).
As only (alcohol preserved) wet weight values were available for the measured samples, conversion factors developed for isopods (Brey, 2001) were used to estimate DW and AFDW to allow comparison with other studies using different units:

Crustacea: Isopoda	WM->DM	DM->AFDM	WM->AFDM	DM>C
	0.2	0.64	0.142	0.463

Mean annual bottom temperature was assumed to be -1.9°C for all stations (Knox, 2007).

3 Results

A total of 406 specimens of the five investigated isopod families caught by means of the EBS at the three sampled stations were measured for length and weight (Table 1), thereof 169 Desmosomatidae, 136 Munnopsidae, 39 Ischnomesidae, 192 Haploniscidae and 73 Macrostylidae. The data were summarized for families and stations, as the patchy

distribution of species did not yield sufficient numbers for species-specific estimates. For all isopod individuals regardless their family, the four length classes comprising individuals ranging from 1.1-3.0mm made up the major proportion. In all families except the Ischnomesidae, the size class of 1.6-2.0mm included the majority of individuals. Average length distribution and accordingly, also wet weight per individual varied only slightly between stations (Fig. 1).

Wet weights were averaged for all individuals belonging to one family, assuming that sampling provided an averaged size distribution at the given time point. Wet weight was dependent on body length in all families, showing the highest values in the Munnopsidae and lowest values in the Desmosomatidae and Haploniscidae (Fig. 2).

Table 1 Numbers of specimens belonging to the five investigated families measured for length and weight.

Family	Genus	N
Desmosomatidae	*Austroniscus* spp.	19
	Chelator spp.	5
	Desmosomatidae spp.	28
	Disparella spec.	1
	Eugerda spp.	4
	Eugerdella spp.	2
	Exiliniscus spp.	6
	Mirabilicoxa spp.	11
	Nannoniscinae spp.	14
	Pseudomesidae spec.	1
	Rapaniscus spp.	10
	Regabellator spp.	3
	Total	**104**
Munnopsidae	*Aspidarachna* spec.	2
	Betamorpha spp.	22
	Coperonus spp.	11
	Disconectes spp.	4
	Eurycope spp.	14
	Ilyarachna spp.	5
	Lionectes spec.	2
	Microcope spec.	1
	Munneurycope spp.	8
	Munnopsidae spp.	15
	Munnopsurus spp.	4
	Notopais spinosa	1
	Syneurycope spp.	14
	Total	**92**
Ischnomesidae	*Ischnomesus* spp.	**33**
Haploniscidae	*Antennuloniscus* spp.	5
	Chauliodoniscus spp.	68
	Haploniscus spp.	52
	Total	**140**
Macrostylidae	*Macrostylis spp.*	**37**
Total		**406**

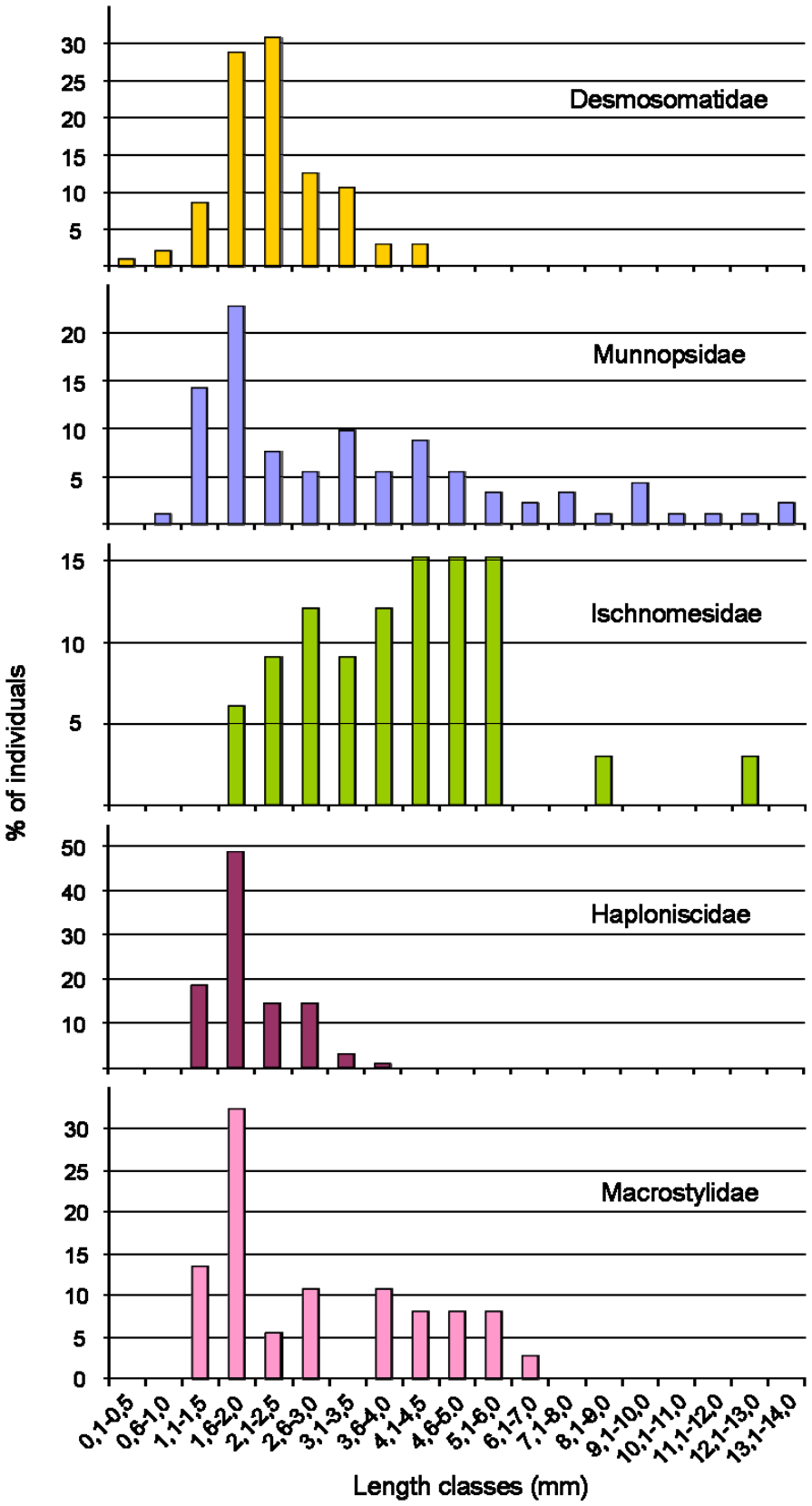

Fig 1 Length classes (0.5 mm classes, % of all individuals of one family) for the five isopod families analysed.

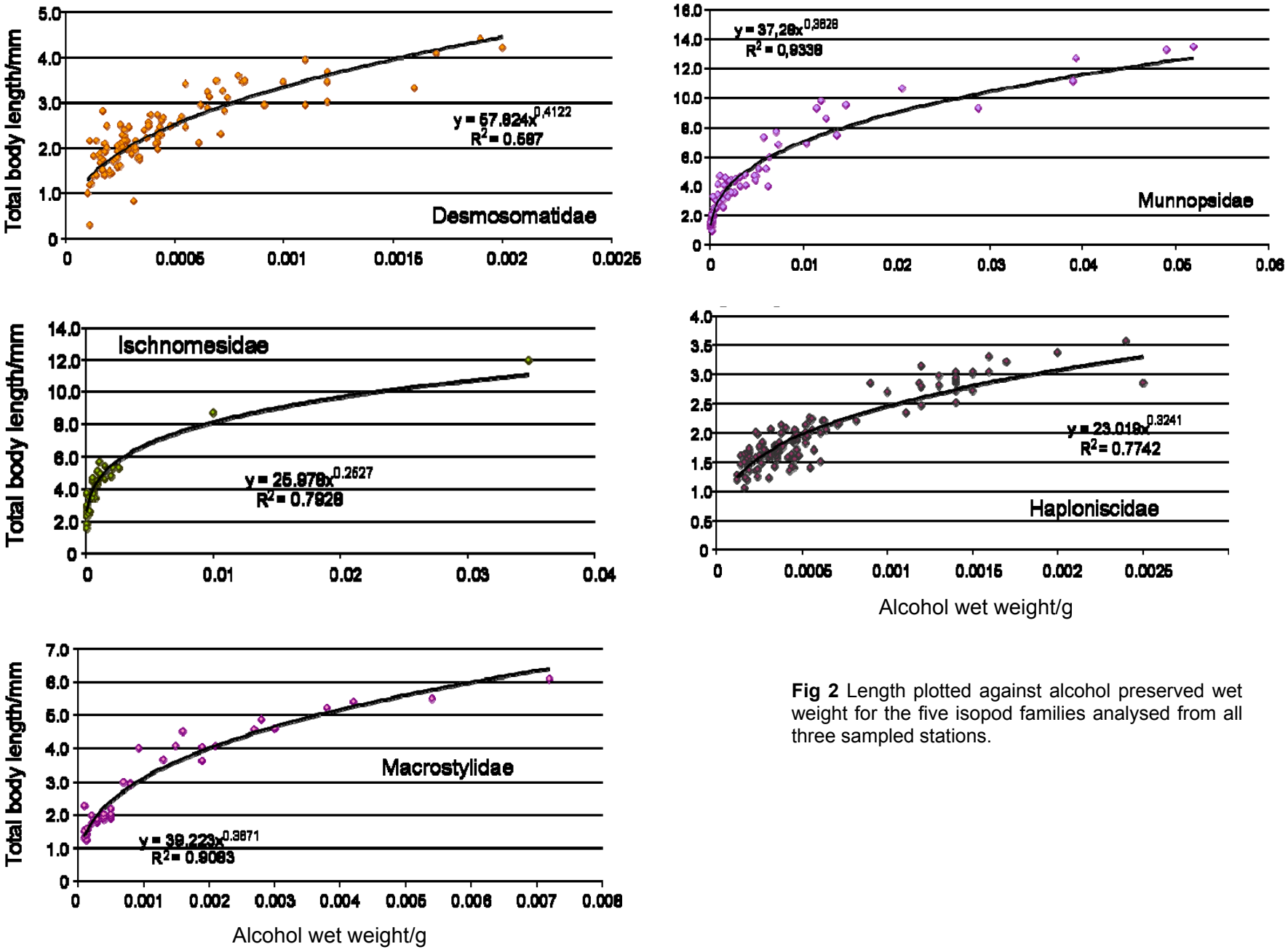

Fig 2 Length plotted against alcohol preserved wet weight for the five isopod families analysed from all three sampled stations.

Table 2 Station details, abundance, biomass, production and P/B estimates for five families of deep-sea isopods at the three sampled stations. Production and P/B estimates calculated after 1) Brey (1990) and 2) Tumbiolo and Downing (1994).

Station details	Factor	Desmosomatidae (N=104)	Munnopsidae (N=92)	Ischnomesida (N=33)	Haploniscidae (N=140)	Macrostylidae (N=37)	Sum (N=406)
PS71/13 Depth: 2997 m	estimated abundance (ind.m^2)	31.1	1.1	2.3	4.5	3.3	42.3
	B estimated biomass (mg DW m^2)	3.430	2.049	1.106	0.404	1.022	8.012
	P (mg DW, calculated from 1)	1.869	0.958	0.897	0.746	0.931	5.401
	P (mg DW, calculated from 2)	1.217	0.759	0.663	0.508	0.669	3.817
	P/B (calculated from 1)	0.545	0.467	0.811	1.847	0.910	-
	P/B (calculated from 2)	0.355	0.371	0.599	1.258	0.655	-
PS71/17 Depth: 2114 m	estimated abundance (ind.m^2)	18.9	2.2	2.2	2.2	1.1	26.7
	B estimated biomass (mg DW m^2)	1.231	0.511	0.341	0.273	0.178	2.534
	P (mg DW, calculated from 1)	1.288	0.715	0.637	0.598	0.474	3.712
	P (mg DW, calculated from 2)	0.833	0.514	0.451	0.419	0.342	1.639
	P/B (calculated from 1)	1.046	1.400	1.870	2.190	2.667	-
	P/B (calculated from 2)	0.677	1.006	1.323	1.537	1.926	-
PS71/39 Depth: 2152 m	estimated abundance (ind.m^2)	3.3	1.7	1.1	3.3	3.3	12.7
	B estimated biomass (mg DW m^2)	0.153	1.401	0.454	0.355	0.754	3.118
	P (mg DW, calculated from 1)	0.538	0.914	0.621	0.687	0.853	3.613
	P (mg DW, calculated from 2)	0.360	0.696	0.465	0.474	0.606	2.601
	P/B (calculated from 1)	3.510	0.652	1.368	1.933	1.131	-
	P/B (calculated from 2)	2.349	0.500	1.024	1.335	0.804	-

Abundances calculated from BC samples differed between stations (Table 2), and ranged from 12.7 ind./m^2 at station PS71/39, 26.7 ind./m^2 at station PS71/17 to 42.3 ind./m^2 at station PS71/13. Total estimated biomass for all isopod families together was highest at station PS71/13 (8.012 mg DW/m^2) and lowest at station PS71/17 (2.534 mg DW/m^2). The Desmosomatidae were the most abundant family at stations PS71/13 and PS71/17, while at station PS71/39, calculated abundances of all families were low and relatively even. The picture is slightly different in terms of biomass, depending on the average WW measured for the different families. At stations PS71/13 and PS71/17, the Desmosomatidae show the highest total biomass (3.430 and 0.874 mg DW/m^2, respectively) according to their high abundances. However, despite the relatively even abundances of all families, at station PS71/39 the Munnopsidae provided the highest total biomass values (1.401 mg DW/m^2), while the Desmosomatidae and Haploniscidae provided the lowest total biomass values (0.153 and 0.355 mg DW/m^2, respectively). According to this, P values were found to be highest in the Desmosomatidae at stations PS71/13 and PS71/17, while at station PS71/39 the highest P values were estimated for the Munnopsidae. The highest P/B ratios were calculated for the Haploniscidae at station PS71/13, for Macrostylidae at station PS71/17 and for the Desmosomatidae at station PS71/39.

Results for P and P/B calculated by of both empirical models differed slightly, being generally lower for the model developed by Tumbiolo and Downing (1994) compared to that of Brey (1990).

4 Discussion

Secondary production of marine benthos is an important factor in defining the energy flow in marine communities. The widely used methods to calculate secondary production include different sets of parameters such as growth or mortality of identifiable cohorts or size-frequency classes. Sampling deep-sea ecosystems, however, faces certain restraints as they are time consuming and expensive, thereby mostly preventing sampling at regular time intervals. In the Southern Ocean, additional factors such as ice coverage in winter further restrict sampling efforts. This explains why for most deep-sea invertebrates their life histories are practically unknown, including reproductive mechanisms, life span and seasonal abundance variations. Nevertheless, the limited studies on deep-sea ecosystems conducted so far indicate that benthic organisms might play an important role in carbon consumption on the deep-sea floor (Gage, 1992; Cartes and Sorbe, 1999), making estimates on their biomass and production rates valuable information.

Different empirical models for production estimates have been developed, and in this study, two different models were applied to Southern Ocean deep-sea isopods. The one developed

by Brey (1990) includes mean annual biomass (B) and mean individual body mass (W). Biomass as well as body mass showed to be the most important variables explaining variations in secondary production in marine ecosystems (Brey, 1990; Morin and Bourassa, 1992; Tumbiolo and Downing, 1994). However, various environmental parameters were found to influence growth rates, and biomass-specific production levels seem to decrease from low latitudes through subarctic zones and decrease, regardless of latitude, from shallow to deep waters, the effect of temperature being strongest in shallow waters (Morin and Bourassa, 1992; Tumbiolo and Downing, 1994). Therefore, another model including the factors water depth and temperature was also applied (Tumbiolo and Downing, 1994).

The results from these calculations have to be interpreted with strong precaution, as both empirical models need the most reliable estimation of mean annual biomass and density. However, the data available for this study can hardly fulfil this requirement. To be able to use the empirical models, we have to (a) assume that no seasonality at all takes place in the isopods life cycles and (b) we sampled a sufficient area and enough specimens to provide mean values for size distribution and biomass. Concerning (a), no statement can be made on seasonal abundance patterns in the sampling area due to limited sampling efforts. Concerning (b), it has been shown that in general, estimates of deep-sea macrofaunal abundances should be treated with care due to the patchy distribution and the “rareness” of some of these organisms. Macrobenthic abundances have been reported to often occur extremely patchy at different sites on the Weddell Sea shelf and slope, with minimum and maximum values of abundance and biomass varying between 100 to more than 47 000 ind.m^{-2}, and 0.1 and 1673 g wet weight m^{-2}, respectively (Brey and Gerdes, 1998).

Calculations based on sampling with an EBS have been shown to strongly underestimate abundances (Brenke, pers. communication), while sampling with more quantitatively working gear, as box- or multiple corers often yield low numbers of macrofaunal animals due to the small area sampled. Nevertheless, we believe that the data presented here can provide a useful tool for future studies whenever abundance estimates of the respective families of deep-sea isopods are coupled with biomass estimates and for comparison between different deep-sea areas.

The results obtained with the two models do not differ significantly from each other, and the lower values estimated by the Tumbiolo and Downing model can be assigned to the low ambient temperatures. For benthic animals in cold environments it has indeed been reported to have reduced metabolism rates (e.g., Barnes et al., 2007).

In relation to their abundance, highest biomass and production levels were found in the Munnopsidae, and their comparably high individual weights can be assigned to their rather compact body shape, in some cases accompanied by large body sizes. On the contrary, the Ischnomesidae, many specimens having large body sizes, generally show a more slender,

elongated body size. Both Macrostylidae and Haploniscidae have a rather small and delicate habitus (see chapter picture, p. 171). Concerning their life style, only sparse data is available on deep-sea isopods. Many representatives of the Munnopsidae have good swimming capabilities, theoretically enabling them to cover long distances between food patches. Members of this family have been shown to preferentially feed on foraminiferans, while Macrostylidae and Ischnomesidae seem to mainly ingest phytodetritus and Haploniscidae seem to often display omnivory (see chapter 6).

For Antarctic benthic ecosystems, high biomass values have been reported; however, benthic biomass and community production have been shown to decrease with depth, probably related to exponentially decreasing food input to the benthos with increasing water depth (Brey and Gerdes, 1998).

Compared to previously estimated values of 10-62 mg C/m^2 for total macrofauna community biomass in the bathyal (1500 – 4300 m) Weddell Sea (Brey and Gerdes, 1998), the biomass values estimated for isopods in this study are relatively high. In terms of carbon, estimated contents of the five isopod families are 3.709 mg C/m^2 at station PS71/13; 1.173 mg C/m^2 at station PS71/17 and 1.444 mg C/m^2 at station PS71/39. This would accounts for a proportion between 1.9 and 37.1% of Brey's estimate for bathyal community biomass, depending on station and if min/max values are compared.

Biomass and secondary production estimates of macrobenthic fauna from deep-sea habitats worldwide vary strongly. E.g., for a munnopsid isopod (*Munnopsurus atlanticus*), differing biomass values have been reported depending on the sampled area (Cartes et al., 2001). In the bathyal Atlantic, biomass was distinctly higher (0.803 mg DW/m^2) than in the Mediterranean (0.078 mg DW/m^2). Not enough specimens belonging to the genus *Munnopsurus* to allow any estimates could be sampled in this study, but for the example of *Ilyarachna* spp. from station PS71/13, biomass estimates show higher values (1.183 mg DW/m^2).

Generally, bathyal species have been found to show clearly lower P rates than shallow-water species, whereas P/B ratios were more similar between them (Cartes and Sorbe, 1999), or even significantly higher (Brey and Gerdes, 1998).

The values for secondary production estimated in this study are in the range of values obtained in other studies and different areas. Secondary production in bathyal suprabenthic peracarids in the western Mediterranean (Cartes and Sorbe, 1999) was found ranged from 0.129 mg DW/m^2 (cumacean) to 9.002 mg DW/m^2 (mysid). For the munnopsid isopod *Ilyarachna longicornis*, P was calculated to reach 0.286 mg DW/m^2 in the Catalan Sea (Cartes et al., 2001). The isopod P values calculated in this study lay in the range of 0.342 mg DW/m^2 to 1.869 mg DW/m^2, depending on isopod family and station.

Based on the comparison of a large dataset it was found that generally, suprabenthic crustacean P/B was significantly higher than P/B of benthic crustacean, while P/B of other invertebrates was lower than those of both other groups (Cartes et al., 2002).
P/B ratios found in this study are more in the lower range than reported by other authors and span from 0.355 to 3.510, whereas ranges between 1.56 (cumacean) and 12.64 (amphipod) have been estimated for bathyal peracarids from the Mediterranean (Cartes and Sorbe, 1999), and a P/B ratio of 5.72 for *Ilyarachna longicornis* from the Catalan Sea (Cartes et al., 2001).

5 Conclusions

With the discussed uncertainties concerning the general lifestyle and abundance estimates in mind, the calculated values of biomass and secondary production have shown to be comparably high for the deep Weddell Sea isopod families investigated in this study. Differences between families most likely depend on the respective species' habitats and general biology, especially feeding strategies. Highest overall abundances and isopod biomass values were calculated for station PS71/13, which is situated in the Polar Front region. High primary production has been reported for this area (see chapter 1), seemingly influencing abundance and biomass patterns in the deep-sea.
The highest individual (independent of overall abundance) biomass and production rates have been calculated for the Munnopsidae. It has been suggested that these isopods play a significant role in deep-sea carbon cycling via the feeding of foraminiferans, which, in turn, have been reported to be an important link in the trophic chain because of their high biomass (Elizalde et al., 1999).
It can be concluded, that the analysed isopod families play an important role in Southern Ocean deep-sea ecosystems, and that abundance patterns and faunal composition are important feature which have to be taken into account when conducting studies on ecosystem dynamics, as pronounced taxonomic differences can be seen. The results from this study provide data for comparison with isopod data from other regions or with other taxonomic groups, helping to elucidate ecologic mechanisms in deep-sea environments.

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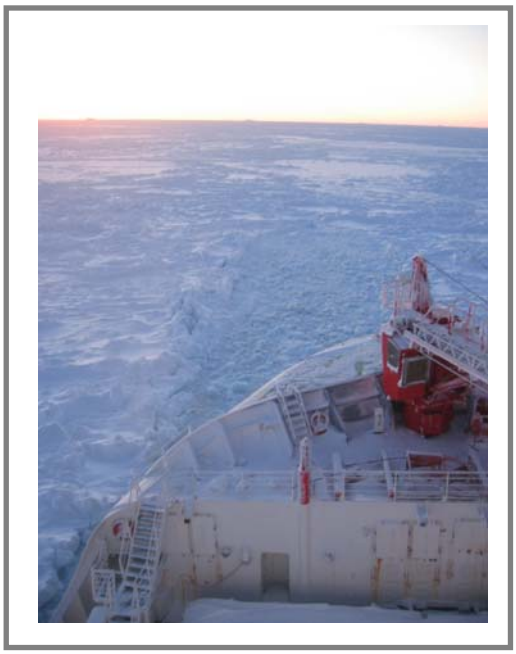
State of the manuscript and own contribution:
I conducted the morphometric measurements, calculations and data interpretation. The manuscript was written by myself, supported by discussions with Nils Brenke (DZMB Wilhelmshaven) and Angelika Brandt (University Hamburg), and is currently being prepared for submission.

Chapter 9

General Discussion



RV Polarstern breaking ice in the Southern Ocean.

Chapter 9 General Discussion

On the background of presently ongoing climate changes, ocean acidification, anthropogenic impact and potential human exploitation of deep-sea ecosystems such as deep-sea mining or waste dumping, an improved understanding of deep-sea ecosystems and ecosystem functioning is urgently needed. These ecosystems more and more get in the focus of industrial exploitation of resources as manganese nodules, petrol or deep dwelling fish – and no one can predict what consequences such an impact on the deep-sea realm could have. Climatic changes might affect also remote ecosystems as in abyssal areas, and without even knowing the status quo, it will be impossible to track occurring changes. The recent developments in the exploitation of deep-sea resources, especially the increasing oil production e.g. off Angola or in the Gulf of Mexico, have shown the urge of rapidly gaining more knowledge on these under-investigated areas. Even though studies have been addressed to investigate the persisting ecosystems, partly commissioned by the mining industry itself, it has become clear that the lack of deep-sea research efforts in the last decades cannot be caught up within the short time spans considerable for industrial interests. Furthermore, internationally agreed rules and laws for the rights on the deep-sea floor are still missing for the majority of the world's oceans, as are organs to supervise its exploitation. One outstanding exception is the Antarctic treaty, signed by several nations, explicitly stating that the Antarctic area is only to be explored for scientific reasons. This could be an exemplary model for future agreements on the handling of deep-sea matters world-wide.

It has to be kept in mind that any interpretation of the results from this thesis has to be conducted cautiously, as the relatively small samples numbers, due to sampling difficulties in deep-sea settings as described in the previous chapters, can rather be seen as snapshots from a huge environment. However, as information on the deep-sea realm and its trophic interactions remains scarce, any additional results and clues can help to elucidate the trophic mechanisms underlying these multifasceted ecosystems.

The results of this thesis show that the feeding strategies displayed by Southern Ocean macrobenthic organisms (chapters 4-6), as well as other ecosystem compartments (meiofauna, chapter 3, and megafauna, chapter 7) are complex, diverse, manifold and taxon-specific, and often even species-specific. This urges the importance of a high taxonomic resolution, if we are aiming at understanding the ecosystem and the role of an organism within. However, to date the number of taxonomists is rapidly decreasing. This is certainly mostly due to political and strategic developments in the field of biology, as new methods as e.g. molecular technics, so-called "barcoding" of organisms have experienced quite a boost. Additionally, the increasing demand for rapid results, determining the allocation of financial

funds has marginalised the field of taxonomy with its rather slow and thourough working routine. This is indeed quite alarming, as experienced taxonomists are getting fewer and fewer, leaving a gap in knowledge and preventing the education of a new generation of researchers with a taxonomic focus. But to understand the complex interactions and mechanisms underlying ecosystem dynamics, evolutionary developments and reaction to ecosystem changes, we cannot rely on the vague information obtained by studies on a very general level. To date, we are still far from knowing the majority of species inhabiting the vast deep-sea areas of our planet, including the Southern Ocean. However, results from FA analyses on a family- or species level demonstrate that there can be strong differences in feeding strategies between members of one order or one family. The present study documented that it is much too simple to e.g. classify all isopods as detritus feeding, all amphipods as scavengers (chapter 6) or all polychaetes as burrowers (chapter 5), but that ecologic studies strongly depend on cooperating taxonomists to be able to understand trophic interactions of organisms.

However, to obtain such ambitious goals, some more prerequisites have to be optimised. Still, sampling the deep-sea is laborious, expensive, time consuming, and in most cases difficult to plan as the patchy distribution and the lack of sufficient sampling gear yields basically unpredictable samples. Especially for the macrofauna, inhabiting an important role in deep-sea systems, optimised and standardised sampling methods are needed, as the EBS, while being a well-working gear, has been shown to be hardly useful to predict abundances. However, more quantitative gear (such as corers) are to date not able to sample areas large enough for reliable abundance estimates, or to yield enough macrobenthic organisms to conduct further analyses, as e.g. biochemical investigations.

As diverse the feeding habits in the abyssal might be, some underlying trends are indicated by the results of this thesis.

For example, low FA contents were found in almost all organisms analysed (chapters 5 and 6), with few exceptions. Additionally, the predominance of the polyunsaturated FAs 20:5(n-3), 22:6(n-3) together with the saturated FA 16:0 found in many analysed organisms reflects the dominance of phospholipids (Sargent and Henderson, 1986; Tande and Henderson, 1988), also pointing towards a low dependence on lipid reserves. This can be seen as an indication that lipids are not accumulated for energy storage, and that feeding occurs throughout the year (e.g., Bühring and Christiansen, 2001), supporting the idea of the existence of a permanent food reservoir in the deep-sea (Mincks et al., 2005; McClintic et al., 2008).

However, in the majority of analysed organisms, FA alcohols were detected in varying proportions (chapters 5 and 6). These are indicative of wax esters (WE), a lipid class typically

used for long-term storage (Lee et al., 2006). The FA component of WE is largely derived from the diet, whereas the fatty alcohols are derived from the animal's internal biosynthesis (Sargent and Henderson, 1986). Possibly the storage of wax esters indicates a general evolutionary mechanism developed to survive long starvation periods (e.g. found in higher latitude herbivorous copepods; Sargent and Falk-Petersen, 1988; Hagen and Schnack-Schiel, 1996). If this is true, the food-bank hypothesis would have to be rejected, if seen as a survival strategy in deep-sea organisms periodically experiencing long starvation intervals. Thus, the generally low lipid content, pointing to a lack of lipid storage and the co-occurrence of wax esters as long-term energy storage remains somehow contradictive. The distinct mechanisms underlying these metabolic processes need to be addressed in future studies.

One noteworthy result of this thesis was that for many organisms thought to be carnivorous, contradicting results were found both in FA and stable isotope analyses (chapters 6 and 7). These findings seem to indicate that many organisms, even if their primary feeding strategy is based on predation or scavenging, might display a high degree of opportunism, utilising other food sources if prey or carrions is not available. This strategy is presumingly of advantage in an environment as the deep-sea, were food falls or prey organisms may occur extremely patchy. In this study, animals thought to be top-predators (e.g., bigger fish) are in some cases not found within the maximum range of $\delta^{15}N$ values. Besides opportunistic feeding, another reason for these lower-than-expected $\delta^{15}N$ enrichment of predating/scavenging organisms capable of moving freely in the abysso-pelagic environment such as fish compared to those more restricted to the benthic realm such as e.g. predating or scavenging gastropods indicates that the fish might be partly decoupled from the food web based on sedimented and frequently recycled organic matter. This has also been suggested by previous studies (e.g., Mahaut et al., 1990; Iken et al., 1991; Drazen et al., 2008).

A feature that has been discussed to play an important role in the nutrition of deep-sea organisms is the ingestion of bacteria, which are very abundant at the deep-sea floor (Azam et al., 1983; Sargent et al., 1987; Pfannkuche and Lochte, 1993). However, in this study, indications for feeding on bacteria based on typical FA (e.g., 15:0, 17:0, 15:1 and 17:1) were generally only found in minor proportions (chapters 5-7).

On the contrary, another FA has been found to be important in the FA composition of many organisms analysed in this study: 20:4(n-6), arachnidonic acid (AA). Enhanced levels of this particular FA have been previously reported for deep-sea organisms compared to other ecosystems (see chapters 4-6). Its source, however, is still under discussion. Macroalgae (specifically red algae), known to contain high amounts of this FA, have been suggested to be the source of 20:4(n-6) also in deep-sea settings (Bühring et al., 2002). Indeed, it has been shown that remains of macroalgae originating from coastal shallow waters can be found in deep waters (Knox, 2007). Another possible source might be foraminiferans, which

have been reported to sometimes contain high proportions of AA. For some deep-sea organisms, as e.g. some polychaete (chapter 5) or isopod species, selective feeding on foraminiferans has previously been reported (chapter 6). These protozoans are capable of selective feeding on certain compartments of detritus and accumulating PUFA, thereby supplying a more valuable dietary resource compared to detritus (Suhr et al., 2003). However, the question if the original source of AA is the synthesis within foraminiferans or is taken up with their food cannot be answered. But as foraminiferans are a major element in deep-sea environments and can comprise a substantial proportion of benthic biomass, they most probably play a significant role in carbon cycling. They are commonly one of the most important consumers of fresh phytodetritus, especially in deep-sea habitats and given the fact, that they can very rapidly utilize sinking fresh organic material from the surface, their role in deep-sea food webs must be considerable.

To further elucidate the role of foraminiferans in the diet of deep-sea organisms, more advanced methods with a high resolution are needed. One possible trait could be recently developed methods, as e.g. gut content analyses utilising molecular primers.

Data on life strategies and feeding habits of deep-sea isopods still remain scarce. This thesis could show that a variety of food sources are exploited by these peracarid crustaceans (chapter 6). Feeding on foraminiferans, for example, could be an important link in carbon cycling of deep-sea ecosystems, given the important role these protozoans inhabit (see above). Additionally, isopods seem to contribute a substantial proportion of biomass in the Southern Ocean deep-sea, which might be depending on the characteristics of the investigated area (chapter 8). The high degree of taxon-specificity has been shown for both feeding strategies (chapters 4-7) and biomass and production estimates (chapter 8). This again highlights the importance of a high taxonomic resolution in ecosystem studies.

As the results of this thesis indicate that in some cases deep-sea organisms might display a rather opportunistic feeding behaviour, while others seem to be more selective, leaves the question of the reaction of deep-sea benthic faunas to any disturbances, as climatic changes or man-made impacts. However, as difficult it might be to predict any of such changes, it seems clear that the deep-sea fauna would react with drastic changes, leaving space for those creatures that can react promptly to any occurring changes, while those who are more dependent on certain food sources might be the big loosers in such a scenario.

In general, the results presented here (chapters 3-8) suggest that we still need to learn much more on the ecology of these fascinating and important organisms inhabiting the vast deep-sea areas on our planet. This knowledge will ultimately help to understand the driving mechanisms underlying evolutionary developments, selecting forces canalising distribution

patterns and ecological interactions. The increasing interest in the deep-sea due to climatic changes and exploitation of resources and subsequently ecosystem services need a much improved understanding of deep-sea ecosystem functioning in order to predict or at least understand changes which are to a great extent induced by human impact.

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