Gradients in benthic community structure and bioturbation potential along the Nordic Seas continental margin

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‘Gradients in benthic community structure and bioturbation potential along the Nordic Seas continental margin’

A thesis presented for the degree of Doctor of Philosophy (Ph.D.) at the University of Aberdeen

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November 2007
I, Mark Shields, confirm that I composed the thesis, that it has not been accepted in any previous application for a degree, that the work is my own, and that all quotations have been distinguished by quotation marks and the sources of information specifically acknowledged.
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Abstract

The Nordic Seas region, extending north from the Wyville-Thomson Ridge, west of Scotland to the Fram Strait, north of Svalbard, marks a transitional zone between the temperate North Atlantic Ocean and the polar Arctic Ocean. The influence of contrasting fluxes of organic matter on benthic community structure and function within the deep waters of the region were investigated. Previous studies have sampled the macrofaunal community throughout the region but it is difficult to draw comparisons between studies due to differences in the sampling strategy employed. Therefore samples of the macrofaunal community were collected throughout the region employing a standardised method. In the summer of 2002, during the RRS James Clark Ross 75 cruise, replicated samples were obtained with the SMBA multiple corer and the NIOZ boxcorer from four stations located at similar sampling depths along a latitudinal transect at the Norwegian Sea continental margin. Additional replicated samples were obtained with a megacorer at six stations located along two bathymetric transects across the Norwegian Sea continental margin in the summer of 2005 during the RRS James Clark Ross 127 cruise.

Contrasting fluxes of organic matter influenced benthic community structure, functional ecology and bioturbation potential. Species known to adopt the feeding strategy of the sub-surface storage of organic matter occurred in areas characterised by a seasonal input of organic matter. Species richness and diversity was highest at the Svalbard Margin, located within the marginal ice zone. Bathymetric patterns of macrofaunal biomass were comparable with previously reported global patterns. However, bathymetric patterns of macrofaunal abundance were higher than global patterns. The previously reported rapid subduction of organic matter by the sipunculan *Nephasoma* sp. and associated deep burrow networks on the Voring Plateau was linked to the species *Nephasoma lilljeborgi*.

**Keywords:** Nordic Seas, macrofauna, benthic, community structure, bioturbation, organic matter.
“Worms have played a more important part in the history of the world than most persons would at first suppose”
Charles Darwin, 1898.

But more importantly:

“Let’s move onto the yawning chasm”
John Gage, 2003 on my PhD and not, as I first believed, about my well timed yawn near the end of a rather long monthly meeting with the Deep-Sea Benthic Group.
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1 Introduction

1.1 Deep-Sea Environment

The deep sea is the most extensive habitat on the planet but its biology is the least known and explored. Information on the natural history of organisms living within the deep sea is limited due to the difficulties associated with sampling such a remote habitat. The deep sea begins at the edge of the continental shelf at a water depth below the level of effective light penetration for photosynthesis (Gage and Tyler 1991). The continental shelf varies in width from a few to hundreds of kilometres and generally extends to a water depth of 200 m, although it can extend to 500 m depth. At the edge of the shelf break, where there is a marked increase in the gradient of the sea floor is where the continental margin begin. The continental slope extends to depths of 3000 to 5000 m where there is a marked decrease in the angle of the slope and the flat and extensive abyssal plains begin. The abyssal plains are broken in several places by seamounts and submarine ridges that can form deep ocean mountain ranges that rise from the flat abyssal plains. Dissecting the abyssal plains are narrow troughs called trenches that extend down to water depths of 7000 and 11000 m.

The extreme physical properties of the deep-sea environment play a significant role in the life history of deep-sea fauna (Gage and Tyler 1991). As water depth increases there is a decrease in temperature and temperature variability, an increase in hydrostatic pressure and a decrease in nutrient flux. Typically, deep-sea fauna live long, grow slowly and produce fewer offspring than fauna living in shallower waters. The deep-sea fauna found living at the sea floor can be classified into two major groups, benthic and benthopelagic fauna. The benthic fauna are the organisms found living on or within the seabed and the benthopelagic fauna are those organisms found living in the water column immediately above the sea bed. Within each group, the fauna can be subdivided according to size,
feeding mode and in the case of the benthic fauna if the organisms are living on or within the sediment.

A number of environmental factors can influence benthic community patterns including water temperature, hydrostatic pressure, oxygen concentration, sediment heterogeneity, near bottom water flow and availability of organic matter (Carney 2005). Information on benthic communities is limited and by 1997 it was estimated that only 500 m$^2$ of sea-bed had been sampled by quantitative cores, a small proportion from a total of 270 million km$^2$ of the deep sea floor (Gage 1997). The search for new exploitable resources is expanding into the deep sea and it is essential that the biology of this remote habitat is fully understood. In order to fully understand the ecological importance and natural history of the fauna inhabiting this extreme environment sampling effort must be increased.

The oceans are a changing environment due to increasing pressure from human activity and a rapidly changing climate. It is at the poles where climatic change is most evident but how this changing climate will influence deep-sea communities remains unknown. The exploration for new hydrocarbon reserves has extended into the deep sea to the west of Norway and Scotland and already interests are growing extending exploration into Arctic waters (Bett 2001). In order to understand the impact of increasing pressures on the deep-sea fauna of the region then the most basic natural history and community pattern data is required. Any changes in benthic community patterns within the region could have a profound impact on the carbon cycle and sediment geochemistry (Berner 1980; Rhoads and Boyer 1982; Klages et al. 2003). Understanding the biology and sustainability of the deep-sea environment will allow suitable measures to be taken that will ensure available resources will be maintained for future generations.
1.2 Thesis Outline

The aim of this thesis is to enhance our knowledge and understanding of community patterns, functional ecology and bioturbation potential of the benthic macrofauna of the deep Nordic Seas region. The Nordic Seas region, extending north from the Wyville-Thomson Ridge, west of Scotland, to the Fram Strait, north of Svalbard, marks a transitional zone between the temperate North Atlantic Ocean and the polar Arctic Ocean.

It is well documented that sea ice cover is receding in the Arctic (McCarthy et al. 2001; Richter-Menge et al. 2006) due to a combination of strong natural variability in the coupled ice-ocean-atmosphere system and a changing global climate (Serreze et al. 2007). This reduction in sea ice cover is due to a dramatic shift from a “cold abundant ice” to a “warm limited ice” mode within the Arctic (Piepenburg 2005). Any change in sea ice coverage will have a profound impact on the trophic structure and energy flow of pelagic-benthic coupling, particularly at the marginal ice zones, and will result in a switch in the Arctic ecosystem (Carrol and Carrol 2003; Piepenburg 2005; Wassmann et al. 2006).

A switch from “sea-ice algae-benthos” to “phytoplankton-zooplankton” dominance would alter the supply of food for the benthos, the most important factor determining benthic community structure and function within the region (Klages et al. 2003). Ice algae provide a high quality food source for some benthic deposit feeders (McMahon et al. 2006) and any change in food quality may influence benthic community structure and activity. In shallower waters, benthic community structure can be determined by the quality of organic matter available to the community (Rosenberg 1995; Dauwe et al. 1998). In the deep sea, benthic communities are capable of selectively feeding on particles dependent on their size (Wheatcroft 1992) and age (Smith et al. 1993). Furthermore, deep-sea benthic communities can respond to the arrival of copepod faecal pellets (Graf 1989; Graf 1992) and an artificial pulse of diatoms (Blair et al. 1996; Levin et al. 1997; Aberle and Witte 2003; Witte et al. 2003a; Witte et al. 2003b). It is now understood that surface climate
variability and primary production can influence species composition and abundance of deep-sea benthic communities (Ruhl and Smith Jr. 2004). However, the response of the deep-sea benthic community to long term changes in the quality and quantity of the food source is little understood.

Potentially any change in the benthic community, either behaviourally or structurally, could alter sediment geochemistry (Klages et al. 2003). Any change in bioturbation or bioirrigation activity of the benthic fauna could influence microbial community activity, sediment pore water chemistry and particle transport. In particular, the loss or introduction of ecosystem engineers could lead to a significant change in sediment heterogeneity and the availability of resources that determine benthic community structure. However, information on the deep-sea benthic community and animal-sediment interactions within the region are limited and direct comparisons between previous studies is difficult. Therefore, the following questions were addressed within this PhD thesis:

1. How does local taxonomic and functional group composition of macrofaunal communities, drawn from a common species pool, change within specific geographical regions in relation to depth, latitude and contrasting organic matter input?

2. What are the major contributors to bioturbation within the deep Nordic Seas region?

3. With respect to the rapid burial of fresh organic matter, do recently proposed contrasts (Witte et al. 2003b) between continental margin and abyssal plain environments hold true when comparisons are made within a single ocean basin?

4. What is the geographic distribution of the sipunculan worms (*Nephasoma* sp.) associated with the rapid subduction of organic matter on the Vøring Plateau (Graf 1989)? Are these animals ‘keystone’ bioturbators throughout the Nordic Seas region?
1.3 Deep-Sea Biology

1.3.1 Organic Matter Flux

Life in the deep sea is predominantly supported by the vertical flux or lateral advection of surface produced organic matter (Gage and Tyler 1991; Tyler 1995). The quantity of organic matter reaching the sea floor is largely determined by the sedimentation of particulate organic matter from surface waters, sinking at a minimum estimated rate of between 100 and 150 m day$^{-1}$ (Billett et al. 1983). This vertical flux of organic matter is the main process connecting plankton and benthic fauna within the global carbon cycle (Wassmann et al. 1996). The input of organic matter can occur as a seasonal pulse, and may provide one of the major food sources for deep-sea benthic fauna (Lampitt 1985; Hecker 1990). Following the pulsed arrival of organic matter to the deep-sea floor the benthic community is capable of responding within days (Gooday 1988; Graf 1989).

Transport of organic matter to the deep sea is normally measured via sediment traps that only record the vertical flux. Benthic-pelagic coupling studies based on sediment traps have revealed that the energy requirements of deep-sea benthic communities cannot always be supported by the vertical flux of organic matter alone (Graf 1992; Smith Jr et al. 1998). Lateral advection may be responsible for the transport of greater volumes of organic matter to the deep sea than the vertical flux (Graf 1992). Continental margins are recognised as important areas for the cycling of organic matter, particularly due to high rates of primary productivity and associated large quantities of organic matter within the sediments (Walsh et al. 1991). Cross-shelf and down-slope transport of organic matter is believed to account for the significant quantities of organic matter observed in the sediment of the continental margins (Lampitt 1985; Hecker 1990; Lohse et al. 1998).
1.3.2 Benthic Response

Organic matter input to the deep sea can vary seasonally and annually (Pfannkuche et al. 1999) and the benthic fauna is capable of responding rapidly to the fresh arrival of organic matter to the sea floor (Graf 1989; Diaz et al. 1994; Levin et al. 1997; Aberle and Witte 2003; Witte et al. 2003b). Micro- and meiofauna show a particularly rapid response in terms of increased activity (sediment community oxygen consumption) and increased biomass in the days following sedimentation (Godoay 1988; Aberle and Witte 2003; Witte et al. 2003b). Community patterns of the larger, longer living macro- and megafauna do not always reflect seasonal fluctuations (Smith 1987; Gage and Tyler 1991). However, the seasonal input of organic matter does provide a valuable food source for some larger members of the benthic community (Graf 1989; Levin et al. 1997; Aberle and Witte 2003; Witte et al. 2003b). A larger body size and longer life span provides macro- and megafauna with a buffer against the often unpredictable seasonal input of organic matter (Peters 1986). Food availability appears to be the main factor controlling the biomass distribution of the deep-sea benthic community at various trophic levels (Sibuet et al. 1989).

The availability of resources can influence life history strategies of a species and help determine the reproductive output (Sibly and Calow 1986). Synchronization of reproduction to the seasonal input of organic matter has been observed within some deep-sea species (Lightfoot et al. 1979; Gage and Tyler 1982; Tyler et al. 1982; Tyler and Gage 1984; Tyler 1986; Young et al. 1992). Furthermore, the rapid subduction and sub-surface storage (‘caching’) of seasonally available organic matter has been proposed as a feeding strategy for some deep-sea deposit-feeders (Jumars et al. 1990). The majority of heterotrophs within the deep sea occur in the upper few centimetres of the sediment column and therefore would not have access to food stored below the sediment-water interface (Pfannkuche et al. 1999).
1.3.3 Influence of Environmental Factors

A complex combination of abiotic and biotic factors influences distribution and community patterns of the benthic fauna (Dayton 1984). Physical processes of the oceans help determine the direct and indirect input of organic matter to the sea bed (Thomsen and van Weering 2001; Rutgers van der Loeff et al. 2002). In turn, the final deposition of organic matter, and subsequent early diagenesis and solute fluxes are influenced by the benthic fauna (Diaz et al. 1994; Blair et al. 1996; Levin et al. 1997; Witte et al. 2003b).

Therefore, in order to understand and model the cycling of organic carbon arriving at the deep-sea floor an accurate estimate of the benthic metazoan abundance, biomass and community structure is required (Piepenburg et al. 1995; Christiansen et al. 2001; Klages et al. 2003).

Biomass in the deep sea generally decreases with depth and often food supply becomes the limiting factor (Rowe 1983; Gage and Tyler 1991). Surface productivity displays global patterns (Berger 1989), which in turn influences global patterns of carbon flux to the deep sea (Jahnke 1996) and carbon content of the sediments (Seiter et al. 2004). On a local scale, the influence of organic matter flux on the benthic community can be determined via the deployment of sediment traps and the measurement of sediment community oxygen consumption (Ritzarau et al. 2001; Smith et al. 2001). Often, there is no relationship between the availability of carbon and nitrogen and the abundance and biomass of the benthic fauna (Rosenberg et al. 1996; Flach 2002; Flach et al. 2002). However, benthic community biomass can provide a useful proxy of organic matter flux to the deep sea averaged over several years (Piepenburg et al. 1995; Piepenburg et al. 2001; Flach 2002).

Depth-related changes in community structure down slope of continental margins have been described by many authors (reviewed by Carney 2005). Recently in the literature, global bathymetric trends in standing stock and body size of deep-sea benthic
communities revealed the abundance of larger animals to be lower and decrease more rapidly with depth than smaller bodied animals (Rex et al. 2006). This work updated the classic review of Rowe (Rowe 1983), that first described the rapid decrease in macrofaunal abundance and biomass with increasing water depth. A combination of environmental factors potentially influences the benthic community both along and across continental margins, with no evidence of a single environmental factor controlling benthic community structure. The deep-sea floor is a complex ecosystem and the influence of the majority of environmental factors on benthic community structure are coupled either directly or indirectly (Flach 2002) and depend on the spatial scale considered (Gage and Tyler 1991).

1.3.4 Animal-Sediment Interactions

Bioturbation, the redistribution of sediment particles linked to the activity of the benthic fauna, and bioirrigation, the exchange between pore water and overlying bottom water enhanced by burrow flushing, are two complex biological processes associated with the benthic fauna. Both processes influence the cycling of elements including carbon, nitrogen and redox sensitive trace metals within the sedimentary column. Therefore, the feeding and locomotion activity of the benthic fauna strongly influences the final deposition of organic matter, and subsequent early diagenesis and solute fluxes (Berner 1980; Aller 1982; Murray et al. 2002; Burdige 2006).

Within the deep sea, the majority of the benthic macrofauna are considered to be generalists, surface deposit or sub-surface deposit feeders. Carnivores, scavengers and suspension feeders are present but are not highly abundant (Gage and Tyler 1991). All activities of the benthic fauna that displace sediment have the potential to cause non-selective particle reworking, a diffusive process that results in the random displacement of particles (Aller 1982). Mathematically, bioturbation is treated as a particle diffusion
process consisting of a series of instantaneous steps separated by finite rest periods (Wheatcroft et al. 1990). The magnitude of particle diffusion is assumed to be controlled by the activities of the benthic macrofauna and in particular by deposit feeders (Smith 1992).

In addition to non-selective transport, the benthic fauna is capable of selective particle transport. Deposit feeders selectively feed on finer particles, which can result in the displacement of particles within the sediment column (Wheatcroft 1992). Finer particles have a larger relative surface area than coarse particles and therefore provide the required daily intake of food from a lower volume of sediment consumed (Wheatcroft 1992). Sediment generally contains a low food value and so deposit feeders have to consume large volumes to obtain the required daily intake (Smith 1992). However, young food-rich particles are 10-100 times more likely to be ingested by deposit feeders than older sediment particles (Smith et al. 1993). Therefore, selective particle mixing associated with deposit feeders is a process dependent upon particle size (Wheatcroft 1992) and age (Smith et al. 1993).

The presence of burrows and tubes in the sedimentary column increases the sediment-water interface area and the selective mixing of particles can induce spatial heterogeneity (Murray et al. 2002; Meysman et al. 2006). Burrows and tubes create a complex three-dimensional transport network that alters the spatial and temporal distribution of chemical reactions within the sedimentary column (Burdige 2006). Irrigation of the burrows can create a strong concentration gradient that enhances diffusive exchange between the burrow and sediment pore water (Aller 2001). An increase in bacterial population and activity that potentially provides an additional food source for some benthic fauna is often associated with sediment immediately adjacent to burrows (Aller 1988). Recent contrasts have been drawn between the sediment mixings depths associated with the fauna of continental margin and abyssal plain communities. High
sediment mixing depths of 5-10 cm at the continental margin were linked to the presence of deep dwelling fauna (Witte et al. 2003a). In contrast, a sediment mixing depth of only 2 cm at an abyssal plain location was linked to a lack of deep dwelling fauna (Aberle and Witte 2003; Witte et al. 2003b).

1.3.5 Macrofaunal Functional Groups

The role of bioturbation on the functional ecology of benthic communities was reviewed in detail by Pearson (2001). This review considered several methods of analysing benthic community structure and function, including adaptive behaviour (Miller et al. 1992), feeding guilds (Fauchald and Jumars 1979) and bioturbatory activity (Swift 1993). When considering functional group concepts, there is a need for the most basic natural history data of the species present in benthic community studies (Pearson 2001). Often, basic natural history information is lacking from deep-sea benthic community studies due to the difficulties associated with in-situ observations. A lack of natural history information can lead to misleading interpretation of the functional ecology of benthic communities (Pearson 2001). However, functional group ecology can provide an understanding of the influence of gradients in deep-sea environmental conditions on benthic faunal distribution (Pearson and Rosenberg 1978; Rosenberg 2001).

It is important to consider the mechanical activity of the benthic fauna when considering the influence of the benthic community on bioturbation and bioirrigation. Solan et al. (2004) proposed a method of characterising bioturbation associated with the benthic fauna that considered mean body size, mobility, sediment mixing mode and abundance. This method recognised and considered that individual species can have a varying impact on the mixing depth associated with benthic fauna activity (Meysman
Five sediment mixing modes have previously been described and associated with benthic macrofauna (Figure 1.1) (Gerino et al. 2003):

1. **Biodiffusors:** Includes species responsible for the random movement of sediment particles over short distances. Major biodiffusors normally include bivalves (Maire et al. 2006, Michaud, 2005 #250).

2. **Conveyors:** Includes species that are responsible for the non-local transport of sediment particles from depth to the sediment surface. Often conveyors are described as head-down deposit feeders and transport sediment up through their guts. Major conveyors would include the polychaete families Maldanidae (Aller 1982; Levin et al. 1997) and Capitellidae (Clough and Lopez 1993; Neira and Hoepner 1994; Méndez et al. 2001).

3. **Inverse-conveyors:** Includes species that are responsible for the non-local transport of sediment particles from the sediment surface to depth. Often inverse-conveyors are described as head-up deposit feeders and transport sediment from the surface down through their guts. This behaviour has previously been associated with sipunculans (Smith et al. 1986b; Graf 1989)

4. **Regenerators:** Includes species that form large burrows and transport sediment from depth to the surface, where the sediment is then washed away. Regenerators are responsible for a high output of sediment into the water column. Once the burrow is abandoned, there is net movement of surface sediment down into the burrow. Large echiurans could be classed as major regenerators (Smith et al. 1986a; Hughes et al. 1993; Hughes et al. 1999)

5. **Gallery-diffusors:** Includes species that form a network of burrows and are responsible for the non-local downward transport of sediment particles. In addition, irrigation of the burrow network enhances solute diffusion between the burrow and
sediment pore water (Francois et al. 2001). The polychaete *Hediste diversicolor* is a representative of this group (Francois et al. 2001; Duport et al. 2006).

**Figure 1.1** Schematic representation of the biological and physical sediment reworking modes taken from Gerino et al. (2003). 1) biodiffusors, 2) conveyors, 3) inverse-conveyors, 4) regenerators and 5) gallery-diffusors (Francois et al. 2002). Size of arrow heads is representative of the intensity of particle fluxes.

Despite there being many methods proposed for analysing benthic community structure and function (Pearson 2001), there are often similarities that can be drawn between the proposed methods. For example, there are similarities in the sediment mixing modes proposed by Solan et al. (2004) and Gerino et al. (2003). However, the method of Solan et al. (2004) provides an arbitrary value for determining the bioturbation potential of
individual species and the community based on standing stock and functional ecology. Similarities between both studies are presented below:

1. Epifauna (Solan et al. 2004) = No similar mode described by Gerino et al. (Gerino et al. 2003).

2. Surficial modifiers (Solan et al. 2004) = Biodiffusors (Gerino et al. 2003) but this would be limited to only 1-2 cm sediment depth.


1.3.6 Ecosystem Engineering

Within the marine environment, bioturbators have been described as classic examples of ecosystem engineers (Levinton 1995). The phrase ecosystem engineer was coined to describe organisms that directly or indirectly alter the availability of resources for other species via the physical alteration of biotic and abiotic materials (Jones et al. 1994). Two types of ecosystem engineers can be distinguished, autogenic and allogenic. Autogenic engineers create physical structures that form an integral part of the engineered ecosystem where they live. Allogenic engineers transform resources from one state to another via mechanical alteration or other means.

All organisms alter their abiotic environment to varying degrees, but the presence and absence of ecosystem engineers can have a significantly large impact on the ecosystem (Coleman and Williams 2002; Meysman et al. 2006). The potential impact of an ecosystem engineer depends on the spatial and temporal scale of their activity patterns (Jones et al.
1994). Therefore, the scale of impact associated with ecosystem engineers is dependent on
the following six factors (Jones et al. 1994):

1. Lifetime activity of individual organisms.
3. Spatial distribution, both locally and regionally, of the population.
4. Length of time the population has been present at a site.
5. Durability of constructs, artefacts and impacts in the absence of the original
   engineer.
6. The number and types of resource flows that are modulated by constructs and
   artefacts, and the number of other species dependent on these flows.

The loss of ecosystem engineers can potentially lead to changes in how a benthic
community functions (Coleman and Williams 2002). Likewise, the introduction of
ecosystem engineers could help restore an ecosystem to a desired state (Byers et al. 2006).
Therefore, any influence ecosystem engineers would have on their ecosystem is dependent
on their density and the rate at which resources are depleted and then renewed (Gilad et al.
2004; Wright et al. 2004).

Within the marine environment, the mode of ecosystem engineering associated
with bioturbators (sediment reworking, biogenic structure building, bioirrigation) varies
between species and can determine the impact of the benthic fauna on microbial
communities and sediment geochemistry (Mermillod-Blondin and Rosenberg 2006). The
influence of bioturbation on microbial activity is known to decrease with increasing
hydrologically induced pore water flow rates (Gerino et al. 2003; Mermillod-Blondin and
Rosenberg 2006). The deep-sea floor, characterised by fine grained sediments and low
hydrological connections between pore water and free water could be classed as a
diffusion-dominated system (Covich et al. 2004). Therefore, deep-sea bioturbators could
have a significant impact on biogeochemical processes and the microbial community (Figure 1.2) (Mermillod-Blondin and Rosenberg 2006).

**Figure 1.2** The influence of ecosystem engineers on biogeochemical processes within a diffusion dominated habitat. + indicates a positive and – indicates a negative effect of bioturbation on the flow of resources for microbial activity. Differences in the flow of resources to the microbial community are depicted by difference in arrow thickness, taken from Mermillod-Blondin and Rosenberg (2006).

1.3.7 Gaps in knowledge

Within the deep sea, there is little information on the response of the benthic community to contrasting fluxes of organic matter input. Recent evidence does indicate that the abundance and composition of the benthic community can be influenced by surface climate variability and primary production (Ruhl and Smith 2004). From studies based in
shallower waters, it is now known that the quantity and quality of organic matter available to the benthic fauna can determine the functional ecology and structure of that community (Rosenberg et al. 1996). However, knowledge on the influence of the quantity and quality of organic matter on community structure and functional ecology of the deep-sea macrofauna is limited. The incorporation of organic matter within the sediment is largely determined by the activity patterns of the benthic community within the deep sea (Berner 1980). Therefore, the response of the benthic community to the availability of organic matter can have a significant impact on the geochemistry of the sedimentary column and in order to understand the influence of the benthic community on the sedimentary column it is essential to analyse the community structure and functional ecology.

1.4 Nordic Seas Environment

1.4.1 Topography and Hydrography

The Nordic Seas or GIN Seas (Greenland-Iceland-Norwegian Seas) mark a transitional zone between the temperate North Atlantic Ocean and polar Arctic Ocean. The region extends north from the Wyville-Thomson ridge, north-west of Scotland to the Fram Strait, north of Svalbard, and east from Greenland to Norway (Figure 1.3). Topography of the sea floor within the region is complex with many topographical features including deep basins, mid-ocean ridges and continental shelves. There are four deep basins, the Greenland and Boreas basins to the west and Norway and Lofoten basins to the east. Mid-ocean ridges and fracture zones separate each of the deep basins.
Two major biogeochemical provinces are distinguishable, the western Polar Domain along the Greenland coast, and the eastern Atlantic Domain extending north along the Norwegian continental margin to Svalbard (Ritzarau et al. 2001). Both provinces are influenced by the cyclonic circulation pattern characteristic of the region, driven by the inflow of Polar Water from the north via the Fram Strait and by the North Atlantic Water from the south across the Iceland-Scotland ridge (Figure 1.3). Within the Western Polar Domain, Polar Water flows southwards forming the East Greenland Current that extends from the surface waters to between 150 and 800 m water depth (Schäfer et al. 2001). Sea
ice coverage is characteristic of the province year round with water temperature varying from -1.5 °C near the surface to 0 °C near the bottom, while salinity varies from 30 psu to 34 psu over a similar depth range (Coachman and Aagaard 1974).

The warmer more saline North Atlantic Current forms the Norwegian Current that flows northwards along the Norwegian continental slope. This inflow of Atlantic Water to the Nordic Seas is one of the key components influencing the climate and ecology of the region (Drange et al. 2005). Surface water flow within the eastern Atlantic Domain is dominated by the Norwegian Current, which splits into two branches at the Bear Island Fan forming the West Spitsbergen Current flowing north along the continental slope and the North Cape Current flowing east into the Barents Sea (Olsen et al. 2003). Further north, the colder and less saline Arctic Surface Water of the East Spitsbergen Current converges with the West Spitsbergen Current off the coast of Svalbard (Schäfer et al. 2001). Steered by local bathymetry the West Spitsbergen Current continues to flow north along the margin towards the Fram Strait and branches in two at a sill separating the Yermak Plateau from the Svalbard Margin (Rutgers van der Loeff et al. 2002). One branch, deflected east, forms the North Spitsbergen Current, the second branch, formed from the remaining deeper layers of the West Spitsbergen Current continues to flow north into the Arctic Ocean (Rutgers van der Loeff et al. 2002).

1.4.2 Pelagic-Benthic Coupling

Primary production within the Nordic Seas is highly variable and location specific due to variation in temperature, nutrient supply and light availability within the region (Skogen et al. 2007). The interannual variation in primary production appears to be dependent on the North Atlantic Oscillation, sea ice cover and the transport of water into the Nordic Seas (Skogen et al. 2007). At the marginal ice zones, there is high ice-related primary
production influenced by large seasonal, interannual and spatial variation in the ice cover (Falk-Petersen et al. 2000). Primary production at the Fram Strait, located within the marginal ice zone is about 80 g C m$^{-2}$ y$^{-1}$ (Hop et al. 2006) and mean primary production for the whole Nordic Seas region is estimated at about 73 g C m$^{-2}$ y$^{-1}$ (Skogen et al. 2007). The vertical flux and lateral advection of this organic carbon from the surface waters helps to sustain the benthic fauna within the region. Diatoms appear to contribute to the most significant proportion of organic matter arriving at the sea floor and particularly heavily silicified diatom species that are less likely to suffer silica dissolution when sinking through the mixed layer (Kohly 1998).

Strong interannual variability in particle flux to the deep sea is characteristic of both biogeochemical provinces in the Nordic Seas (Wassmann et al. 1996; Wassmann et al. 2002). The strength of pelagic-benthic coupling is important for benthic fauna (Piepenburg 2005) and is generally considered weak within the Nordic Seas (Wassmann et al. 1996). Consequently, the biomass, metabolism and survival of benthic fauna appears to be sustained by a relatively constant flux of refractory organic matter, rather than by episodic inputs of fresh phytodetritus (Ritzarau et al. 2001; Sauter et al. 2001).

In the eastern Atlantic Domain, the seasonal flux of organic matter to the deep-sea floor is determined by interactions between autotrophic and heterotrophic organisms and is more typical of a temperate environment (Figure 1.4) (von Bodungen et al. 1995; Carrol and Carrol 2003). Within the Norwegian Sea, organic matter flux appears to be determined by zooplankton and in particular the copepod population (Wassmann et al. 1996). When there is strong coupling between the zooplankton grazers and phytoplankton, then the food web shifts towards fish and bird production (Aagaard et al. 1999). However, pelagic-benthic coupling occurs when zooplankton grazers are absent resulting in a food web dominated by the benthos (Aagaard et al. 1999). Organic matter arriving at the Vøring Plateau mainly consists of zooplankton faecal pellets, carcasses and hard body parts.
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(Bathman et al. 1990). In particular, the spring arrival of copepod faecal pellets is nutritionally important for some members of the benthic community (Graf 1989; Graf 1992). An additional food source for the Atlantic Domain benthos is provided from the winter outburst of dense bottom water across the Bear Island Fan from the Barents Sea (Honjo et al. 1988).

Figure 1.4 Two idealized potential primary production scenarios related to sea ice cover and associated trophic implications within the Norwegian Arctic. Thicker arrows and boxes represent primary pathways of organic carbon flow. Diagram from Carrol and Carrol (Carrol and Carrol 2003).

The presence of sea ice in polar seas strongly influences pelagic production and the sedimentation of organic matter (Honjo 1990; Smith and Sakshaug 1990). Ice edge processes enhance pelagic and/or sympagic primary production, stimulating the rapid episodic flux of particles to the sea bed (Sakshaug and Skjodal 1989; Hebbeln and Wefer 1991; Niebauer 1991; Andreassen et al. 1996; Peinert et al. 2001). The receding ice edge can induce prolonged diatom blooms (Rey and Loeng 1985; Smith and Nelson 1985)
leading to strong pelagic-benthic coupling and an increase in food supply to the benthos (Schewe and Soltwedel 2003). Sea ice algae can also contribute significantly to total primary production (Legendre et al. 1992) and represent a high-quality food source for some benthic deposit-feeders (McMahon et al. 2006). Marginal ice zones are areas of known high benthic standing stock (Grebmeier and Barry 1991; Piepenburg 2000). However, it should be noted that the degree of pelagic-benthic coupling, particularly at the marginal ice zones, can vary over relatively small spatial scales under the influence of water mass properties and primary production (Tamelander et al. 2005). Therefore in the Polar Domain, organic matter flux to the sea floor is linked to variation in sea ice coverage and the decoupling of autotrophic and heterotrophic organisms (Figure 1.4) (Carrol and Carrol 2003).

1.4.3 Benthic Response

Recently, the role of the benthic community in organic carbon cycling within the Arctic was reviewed by Klages et al. (Klages et al. 2003). Benthic carbon remineralisation within the region was found to vary both intra- and interannually and was dependent on depth and sediment properties (Klages et al. 2003). On the shelves and upper slope of the margins, echinoderms, and in particular ophiuroids, play an important role in organic carbon remineralisation (Piepenburg et al. 1995; Piepenburg 2000). Rapid subduction and storage of organic matter deep down the sedimentary column has previously been observed at the Vøring Plateau and was associated with the deep burrowing sipunculan, Nephasoma sp. (Graf 1989). Abundance and activity of the benthic fauna does not appear to be influenced by water temperatures that are close to freezing point (Klages et al. 2003). An observed northward decline in biomass and benthic activity within the Arctic was linked to a decrease in organic matter input associated with permanent ice coverage (Soltwedel et al. 2021).
The deep Arctic Ocean is extremely oligotrophic and any input of organic matter from surface derived sources is low and very patchy (Soltwedel and Schewe 1998). Availability of organic matter appears to be the most important factor influencing the structure and functioning of the benthic community within the region (Klages et al. 2003). However, the response of the benthic community to variation in the quality of available organic matter remains unknown.

1.4.4 Influence of Climate Change

The Arctic climate is changing dramatically (McCarthy et al. 2001; Richter-Menge et al. 2006) due to natural variability (MacDonald et al. 1999; Vanegas and Mysak 2000) and anthropogenic global warming (Johannesson et al. 1995; Shindell et al. 1999). Warming at a rate of ~0.01°C yr⁻¹ of the deep waters of the Nordic Seas has been linked to variations in the amount and direction of exchange of water between the deep basins of the Arctic Ocean, Greenland Sea and Norwegian Sea (Østerhus and Gammelsrød 1999). A recent report on the environmental state of the Arctic highlighted convincing evidence on the continuing reduction of sea ice extent in the region, observed during both the summer minimum and winter maximum coverage (Richter-Menge et al. 2006). Reduction in sea ice coverage has been linked to a combination of strong natural variability in the coupled ice-ocean-atmosphere system and a changing global climate (Serreze et al. 2007). Any change in sea ice coverage will have a profound impact on the trophic structure and energy flow of pelagic-benthic coupling, particularly at the marginal ice zones (Figure 1.4) (Carrol and Carrol 2003).
1.5 Nordic Seas Benthic Fauna

1.5.1 Previous Sampling

Within the Nordic Seas the benthic macrofaunal community has previously been sampled at the Vøring Plateau (Romero-Wetzel and Gerlach 1991; Jensen et al. 1992), Svalbard Margin (Weslawski et al. 2003; Wlodarska-Kowalczyk et al. 2004), Yermak Plateau (Kröncke 1994), East Greenland Margin (Schnack 1998; Piepenburg et al. 2001), Faeroe-Shetland Channel (Narayanaswamy et al. 2003; Narayanaswamy et al. 2005) and in the four deep basins of the Nordic Seas (Dahl et al. 1976). However, drawing direct comparisons between these studies is difficult due to differences in sampling methods employed and by the limited replication in some studies. Furthermore, there is often a wide time interval between studies, most notably between samples collected from the deep basins of the Nordic Seas (1975) and more recently from the Svalbard Margin (1999-2001). Sampling locations of the previous studies are provided in Figure 1.5.
Figure 1.5 The location of previous studies with sampling stations below 500 m water depth. Green circle (●) (Narayanaswamy et al. 2003; Narayanaswamy et al. 2005); blue circle (●) (Dahl et al. 1976); red triangle (▲) (Romero-Wetzel and Gerlach 1991; Jensen et al. 1992); black triangle (▲) (Schnack 1998; Piepenburg et al. 2001); black circle (●) (Thomsen et al. 1995); green triangle (▲) (Weslawski et al. 2003; Wlodarska-Kowalczuk et al. 2004); red circle (●) (Kröncke 1994).

1.5.2 Faeroe-Shetland Channel

Samples were collected from 15 stations on the West Shetland Slope between a depth range of 150 and 1000 m (Narayanaswamy et al. 2003). Stations from 150 to 300 m were sampled with the Day grab (0.1 m²), stations from 350 to 500 m with the USNEL boxcorer (0.1 m²) and stations from 550 to 1000 m with the megacorer (0.063 m²) and all samples were washed through a 500 μm mesh sieve (Narayanaswamy et al. 2003). Polychaetes were the most abundant taxon and an exponential decline in polychaete abundance and...
biomass with increasing water depth was expected to be similar to patterns described by Rowe (1983). However, an overall increase in polychaete biomass with increasing depth was observed (Narayanaswamy et al. 2003; Narayanaswamy et al. 2005). The large scale distribution of polychaete species down slope was determined by water temperature rather than depth, while sediment grain size influenced the polychaetes on a more local scale (Narayanaswamy et al. 2005).

1.5.3 East Greenland Margin

In total 81 species were recorded from 31 stations sampled between 68°N and 81°N on the East Greenland slope (Piepenburg et al. 2001). Samples were collected with the giant boxcorer, with 2 to 3 replicates per station and with sub-samples of a sediment surface area 0.0625 m² taken and washed through a 300 μm mesh sieve for macrofaunal community analysis (Piepenburg et al. 2001). Three distinct polychaete assemblages were described at shelf (200 to 400 m), mid-slope (800 to 1400 m) and deep stations (>1400 m) across two bathymetric transects at 75°N and 79°N (Schnack 1998). Polychaete species were few in number and mainly consisted of Atlantic species (Schnack 1998). Community patterns showed no correlation with sediment grain size, organic matter content, C:N ratio and Chl-a content (Schnack 1998). On the shelf, macrofaunal abundance and biomass was higher under the ice-free water of a Polynya than under permanent ice-cover (Ambrose and Renaud 1995).

1.5.4 Nordic Seas Deep Basins

Samples have previously been collected between depths of 2400 and 3800 m from 11 stations located in all four deep basins (Dahl et al. 1976). One or two samples were obtained with the Reineck boxcorer (0.06 m²) at each station and the sediment was washed
through a next of 2 mm, 1 mm and 500 μm mesh sieves for macrofaunal community analysis (Dahl et al. 1976). Compared with other deep basins in the North Atlantic the benthic fauna of the Nordic Seas region was described as having a higher macrofaunal abundance but lower number of species (Dahl et al. 1976). Abundance of fauna in the Greenland basin was higher than similar depths within the Norwegian basin. There was variability in abundance of fauna in the Lofoten basin, linked to the close proximity of the nearby Norwegian coastal shelf and productive surface waters (Dahl et al. 1976). The dominant fauna of the benthic community varied between basins and often between stations located within a single basin.

1.5.5 Vøring Plateau

The benthic community of the Vøring Plateau was sampled extensively in the late 1980s (Graf 1989; Romero-Wetzel and Gerlach 1991; Jensen 1992; Jensen et al. 1992) and in total more than 70 different taxa were sampled from 17 stations (Romero-Wetzel and Gerlach 1991). There was a single drop of the USNEL boxcorer at each station with half of the sample (0.125 m²) washed through a 500 μm mesh sieve for macrofaunal community analysis (Romero-Wetzel and Gerlach 1991). Two distinct communities were described either side of a ridge separating the north of the plateau from the south, with a higher macrofaunal abundance and species numbers reported from stations to the south of ridge (Jensen et al. 1992). Rapid subduction of freshly deposited copepod faecal pellets (Graf 1989) down a dense network of burrows (Romero-Wetzel 1987) was associated with the sipunculan, Nephasoma sp. Sediment mounds observed on the Vøring Plateau and at other locations within the Nordic Seas were linked to the enteropneust, Stereobalanus canadensis (Jensen 1992). Small elongated faecal pellets were recorded in the burrow network associated with the sediment mounds, and it appeared that a number of S.
canadensis individuals inhabited the ‘enteropneust nest’ and shared a common faecal deposit (Jensen 1992).

1.5.6 Bear Island Fan

There is little published information on the macrofaunal community at Bear Island Fan, located on the continental slope between Norway and Svalbard (Thomsen et al. 1995; Witte et al. 1997). Sea floor photographs from about 1340 m water depth revealed a high abundance of polychaete tubes, mainly associated with Oweniidae, Myriochele sp. Samples were previously collected from Bear Island Fan with a boxcorer (0.25 m$^2$) and washed through a 500 $\mu$m mesh sieve (Thomsen et al. 1995), however, to date no information on the composition of the macrofaunal community has been published from these samples.

1.5.7 Svalbard Margin

The macrofaunal community has been sampled along a depth gradient from 200 to 3000 m at 79°N on the Svalbard Margin (Weslawski et al. 2003; Wlodarska-Kowalczuk et al. 2004). A single sample was obtained at each station, stations between 200 and 500 m were sampled with a Van Veen grab (0.1 m$^2$) and sub-samples (0.1 m$^2$) from a boxcorer provided samples from stations >500 m with all samples washed through a 500 $\mu$m mesh sieve (Weslawski et al. 2003; Wlodarska-Kowalczuk et al. 2004). From Macrofaunal abundance, biomass and species richness decreased with depth across the margin (Wlodarska-Kowalczuk et al. 2004). Multivariate analysis revealed four distinct macrofaunal communities on the shelf (<370 m), shallow slope (~500 m), deep slope (~1500 m) and on the rise (>2000 m) (Wlodarska-Kowalczuk et al. 2004). Both the shelf and rise benthic communities were dominated by polychaetes, although species
composition of the polychaete fauna differed between the shelf and rise. The most abundant fauna on the slope were two species of bivalve, *Yolidiella lucida* and *Thyasira dunbari*. A number of species of crustaceans, ophiuroids and polychaetes were characteristic of the slope fauna (Wlodarska-Kowalczuk *et al.* 2004). The location of the shelf stations within a canyon was believed to contribute to the high faunal biomass recorded (Wlodarska-Kowalczuk *et al.* 2004).

### 1.5.8 Yermak Plateau

A single giant boxcorer (0.25 m$^2$) was collected at each of the two stations on the Yermak Plateau between water depths of 550 and 900 m, and all samples were washed through a 500 μm mesh sieve (Kröncke 1994). Polychaetes were the dominant taxon on the plateau, with suspension feeders and deposit feeders having unusually similar abundances (Kröncke 1994). On the western slope, the benthic boundary layer is well developed and the benthic fauna is characterised by suspension feeders (Rutgers van der Loeff *et al.* 2002). The sediments of the Yermak Plateau exhibit relatively high concentrations of chloroplastic pigments (Soltwedel *et al.* 2000) and it was suggested that the presence of many species with low abundance and biomass indicates the food available can sustain a community of small short-lived species (Kröncke 1994).

### 1.5.9 Overview of Nordic Seas Fauna

In two recent reviews on the Arctic benthos, both Klages *et al.* (Klages *et al.* 2003) and Piepenburg (Piepenburg 2005) discussed the current understanding of the environmental and biological processes that determine the flow of carbon within the region. Availability of food certainly appears to be the most important factor for determining benthic community structure and function (Klages *et al.* 2003). On the shelves and upper slope,
echinoderms, and in particular ophiuroids are abundant the benthic community and play a significant role in benthic carbon remineralisation (Piepenburg 2000). Evidence from a number of authors indicate that benthic carbon remineralisation rates on the Arctic shelves are comparable with temperate locations (Glud et al. 1998; Rysgaard et al. 1998; Kostka et al. 1999); suggesting water temperatures close to freezing do not limit benthic activity (Klages et al. 2003).

Diversity of the benthic fauna on the shallower shelved seas of the Arctic is comparable to similar depths in the North Sea (55°N) and Java Sea (7°S) (Kendall and Aschan 1993; Kendall 1996). However, diversity within the deep Nordic Seas appears to be lower than temperate North Atlantic locations (Dahl et al. 1976; Wlodarska-Kowalczuk et al. 2004). The Arctic benthos has few endemic species, with the majority of the fauna having quite a high faunistic similarity to the North Atlantic assemblage (Piepenburg 2005). Low endemism is believed to be a strong indicator of the young age of the Arctic and that there has been little isolation of the Arctic fauna (Dunton 1992). Low endemism in the Arctic fauna is in contrast to the fauna of the Antarctic, where isolation south of the Antarctic convergence has led to high endemism (White 1984). Information on the natural history of the Arctic benthic fauna (including reproduction, life cycles, growth, population dynamics, activity and feeding) is limited, particularly within the deep sea (Dayton 1990; Piepenburg et al. 1995).
2 Material and methods

2.1 Sampling Locations

2.1.1 Study Sites

Sampling took place during two cruises onboard the RRS *James Clark Ross* to the Nordic Seas region in the summer of 2002 and 2005. During the RRS *James Clark Ross* cruise 75 between 14 June and 11 July 2002 four stations located along the Norwegian continental margin were selected for sampling at a depth of 1400 m (Figure 2.1). Sample collection and station details are summarised in Table 2.1. Seasonal ice cover at the Yermak Plateau prevented the collection of samples from 1400 m water depth and instead samples were obtained from the shallower depth of ~900 m. Samples obtained during the JCR75 cruise were collected by my supervisor Dr David Hughes and co-workers. A detailed description of the benthic sampling strategy during the JCR75 cruise in the summer of 2002 is provided in Section 2.2.1.
Figure 2.1 Stations sampled in 2002 during the JCR75 cruise are marked with a black circle (•). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.
Table 2.1 List of samples collected during the 2002 JCR75 cruise. Station key: VP = Vøring Plateau; BIF = Bear Island Fan; SM = Svalbard Margin; YP = Yermak Plateau. Sampling gear key: NBC = NIOZ boxcorer; BHC = bed hop camera; MC = multiple corer.

<table>
<thead>
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<th>Longitude</th>
<th>Latitude</th>
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During the RRS James Clark Ross 127 cruise between 29th August and 22nd September 2005 a further eleven stations were selected for sampling along two bathymetric transects that terminated at the same location within the deep Lofoten Basin, Norwegian Sea. The initial plan was to sample at 1000 m on Bear Island Fan and on the northern slope of the Vøring Plateau. Additional samples would have been collected at each location that was 500 m deeper than the previous station till both transects terminated at the deepest point in the Lofoten Basin at ~3300 m (Figure 2.2). However, poor weather conditions limited sampling opportunities during the cruise and resulted in only six of the planned eleven stations being sampled. Samples were collected from 1000, 1500 and 3000 m depth across Bear Island Fan, at 1500 and 3000 m across the Vøring Plateau and at 3300 m in the
Lofoten Basin. A summary of sample collection and stations details is provided in Table 2.2. A detailed description of the benthic sampling strategy during the JCR127 cruise in the summer of 2002 is provided in Section 2.2.2.

Figure 2.2 Stations sampled in the summer of 2005 during the JCR127 cruise are marked with a black circle (•). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.
Table 2.2 List of samples collected during the 2005 JCR127 cruise. Station key: VP = Vøring Plateau; BIF = Bear Island Fan; LB = Lofoten Basin. Sampling gear key: NBC = NIOZ boxcorer; MGC = megacorer.

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<td>68° 37.54’N</td>
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2.1.2 Summary of sampling locations

Lofoten Basin (LB): The Lofoten Basin is one of the four main deep basins present within the Nordic Seas region and reaches a maximum water depth of ~3300 m. As the Norwegian Atlantic Current flows north, there is a substantial deepening of the Atlantic Water as it flows north over the Lofoten Basin (Orvik 2004). Within the basin, there is a smaller cyclonic circulation pattern, in addition to the general cyclonic gyre circulation in the Nordic Seas (Poulain et al. 1996).

Vøring Plateau (VP): The Vøring Plateau is a marginal plateau located on the Norwegian continental margin between water depths of 1200 – 1600 m (Laberg et al. 2005). Surface water flow over the plateau is dominated from the south by the Norwegian Atlantic Current, an extension of the North Atlantic Current (Hansen and Østerhus 2000). The outer
plateau, descending steeply into the Lofoten Basin, is separated from the inner continental slope by the Vøring Plateau Escarpment (Rumohr et al. 2001). Bottom water currents prevail from the west and contrasting depositional environments exist north and south of the escarpment (Jensen et al. 1992). The 2002 Vøring Plateau station, located to the south of the escarpment, is influenced by a relatively low sedimentation rate of mainly pelagic organic matter (Romero-Wetzel and Gerlach 1991).

**Bear Island Fan (BIF):** Bear Island Fan is a gently-sloping depositional wedge of silty clay sediment located on the slope west of the Barents Sea Shelf (Bowles et al. 2003). Surface water flow is dominated by the northward flowing Norwegian Atlantic Current that splits into two branches at Bear Island Fan; forming the West Spitsbergen Current that continues north along the Norwegian continental margin and the North Cape Current that flows east into the Barents Sea (Olsen et al. 2003). The deep currents are normally weak (mean 10 cm s\(^{-1}\)) and predominately flow north along the slope, but are characterised by frequent reversals in flow direction (McPhee et al. 1998).

**Svalbard Margin (SM):** The station was located within the marginal ice zone, below the base of a canyon on a gently angled slope to the west of Spitsbergen (Wlodarska-Kowalczuk et al. 2005). The West Spitsbergen Current, steered by local bathymetry, continues to flow northwards along the margin towards the Fram Strait (Rutgers van der Loeff et al. 2002). The colder Norwegian Sea Deep Water occupying a depth range of 800 to 2000 m influences the station (Schlichtholz and Houssais 1999).

**Yermak Plateau (YP):** The Yermak Plateau lies between a depth of 650 and 900 m to the north of the mean summer sea ice extent (Howe et al. In Press). A sill separating the Yermak Plateau from the Svalbard Margin splits the West Spitsbergen Current into two
branches; one branch deflected east forms the North Spitsbergen Current and the remaining
deep layers of the West Spitsbergen Current follow the western slope of the Yermak
Plateau (YP) (Soltwedel et al. 2000). On the western slope, there is the formation of a
benthic nepheloid layer linked to the deeper layers of the West Spitsbergen Current
(Rutgers van der Loeff et al. 2002). The aim was to sample at a depth of 1400 m but sea
ice conditions resulted in this area being inaccessible and instead samples were collected
from a shallower water depth of approximately 900 m on the western crest of the plateau.

2.2 Benthic Sampling

2.2.1 Choice of sampling gear

Quantitative samples of deep-sea benthic fauna in soft sediments are normally obtained
through the deployment of corers. In order to obtain quantitative undisturbed samples of
the benthic fauna certain features from a corer are required (Blomqvist 1991):

1. Permit unimpeded flow through the core tubes to prevent formation of a bow wave.
2. Work on a supporting frame to allow settlement on sea floor before tubes penetrate
   sediment.
3. The coring operation should execute slowly, through a hydraulic damper.
4. Size of corer should be in relation to the size of the vessel and its facilities.

Box corers like the USNEL box corer and NIOZ box corer have become the standard gear
for sampling deep-sea benthic fauna (Gage and Tyler 1991) (Figure 2.3). Box corers
typically obtain a relatively undisturbed sediment sample covering an area of 0.25 m²
(50cm x 50cm) but the area sampled is dependent on design. This sample is large enough
to provide a significant number of organisms for estimates of population densities and to
successfully sample the larger members of the benthic fauna. Box corers normally have a
square detachable open-ended box core that is attached to a weighted column and mounted
on a supporting frame. When a successful core has been collected the sample will retain
the overlying water and an undisturbed sediment surface. However, due to the size of the
box corers there is the requirement for a suitably large research vessel for deployment.

Another means of obtaining quantitative samples of the benthic fauna is with the
hydraulically dampened SMBA multiple corer (Barnett et al. 1984) (Figure 2.13). Based
on the principle of the hydraulic damper design of Craib’s corer (Craib 1965), the SMBA
multiple corer can obtain virtually undisturbed sediment samples using a series of small
diameter cores (Barnett et al. 1984). The SMBA multiple corer consists of a supporting
framework for an array of up to 8 core tubes that are lowered slowly into the sediment by
the hydraulic damper. Each core has a diameter of 6 cm and samples an area of 28.3 cm².
The successful sampling of deposited phytodetritus from the deep-sea floor has highlighted
the ability of the multiple corer to obtain undisturbed sediment samples (Gooday 1988).
The mega corer (Figure 2.3c) is based on the hydraulically dampened design of the SMBA
multiple corer, but supports an array of either 8 or 12 core tubes that are 10 cm in diameter
with each core sampling an area of 78.5 cm² and penetrating a maximum sediment depth of
30 cm.

Figure 2.3 Benthic sampling gear: (a) NIOZ box corer (photograph: M. Shields), (b)
SMBA multiple core (Photograph: J. Gage), (c) mega corer (photograph: M. Shields).
Samples collected with the box corer can lead to serious underestimation of meiofaunal and macrofaunal density in the deep sea (Bett et al. 1994; Bett 2000b; Bett and Gage 2000; Hughes and Gage 2004). Bett et al. (1994) highlighted that the apparent density of meiofauna can differ by around 50% when samples obtained with the USNEL box corer were compared with SMBA multiple corer samples. A similar study on macrofauna revealed that the box corer macrofaunal abundance estimates were 48 to 68% of the corresponding mega corer estimates (Bett and Gage 2000). Differences in abundance estimates were associated with the bow wave created by the sampling action of the box corer that washes away smaller bodied fauna present in the upper sediment layers. However, a single drop of the box corer will sample a much larger area than either a single drop of the multiple or mega corer. Due to the larger area sampled a box corer is more likely to obtain samples of the larger bodied macrofauna and megafauna than the multiple or mega corer.

The limitations of both the box corer and hydraulically dampened multiple corer were considered when deciding on the sampling gear best suited for obtaining quantitative samples of the benthic fauna. For the quantitative analysis of the macrofaunal community during the JCR75 cruise in 2002 the multiple corer was preferred to the box corer, due to the abundance underestimation associated with the box corer. The box corer did however provide samples for quantitative analysis of the larger macrofauna and megafauna. During the JCR127 cruise in 2005, the mega corer was the sampling gear available for quantitative sampling and like the multiple corer is hydraulically dampened but samples a larger surface area.

2.2.2 JCR 75 Cruise (2002) benthic sampling

Sampling effort was focused on obtaining samples of the macrofaunal community at each station of the four stations along the latitudinal transect (Figure 2.1##). The macrofaunal
community was defined as macrofauna *sensu stricto* (this included all metazoans excluding Nematoda, Copepoda and Ostracoda normally considered to be part of the meiofauna and Porifera normally considered part of the megafauna). All samples obtained during the JCR 75 cruise in the summer of 2002 were collected by my supervisor Dr David Hughes and co-workers.

Samples of the macrofaunal community were obtained with the square NIOZ box corer and spare cores from SMBA multiple corer drops (Barnett *et al.* 1984). There were no dedicated drops of the multiple corer for biological sampling and spare cores remaining from those collected for geochemical analysis were retained for biological data. Therefore, the total number of cores available from each multiple corer drop for biological data varied from 2 - 8 cores and therefore total area sampled varied at each station (Table 2.1). All cores retained from each multiple corer for biological analysis were pooled to create a single sample. The multiple corer holds up to eight cores and each individual core has a diameter of 6 cm and samples an area of 28.3 cm$^2$, penetrating down to a maximum sediment depth of 30 cm. The NIOZ boxcorer (square core 50 x 50 cm) samples an area of 0.25 m$^2$ and penetrates sediment down to a maximum depth of 50 cm. In total there were three drops of the multiple corer and three drops of the box corer at each of the stations, with the exception of only two drops of the box corer at the Vøring Plateau. A list of all samples collected with the box corer and multiple corer are provided in Table 2.1.

Once samples were collected and onboard the JCR, the upper 10 cm of sediment from each of the corers was fixed in a 4% buffered formaldehyde solution and stained with Rose Bengal. On return to the laboratory, multiple corer samples were washed with tap water through a stack of 250 and 500 μm mesh sieves, and the boxcorer samples through a stack of 1 and 2 mm sieves. A mesh size of 500 μm and above has generally been the preferential sieve size in previous deep Nordic Seas studies. However a stack of 250 and 500 μm mesh sieves was selected for multiple corer samples in order to retain the smaller...
bodied macrofauna due to the higher sampling efficiency of smaller fauna associated with the hydraulically dampened multiple corer. All material retained on each sieve was sorted under a dissecting microscope (Wild M5). Boxcorer samples were sorted by my supervisor Dr David Hughes and individuals were identified to Phylum or Class level or, in the case of Polychaeta to Family and counted. All macrofauna \textit{sensu stricto} from multiple corer samples were identified to Species level or to Genus when a species name could not be assigned, and were counted. Only polychaete heads were counted as an individual animal.

Aggregated material for each taxon was blotted on filter paper and weighed on a top loading balance (Sartorius BP615, $d = 0.1 \text{ mg}$). Only macrofauna retained on sieve mesh size of $500 \mu m$ and greater were weighed for wet-weight biomass as fauna retained on sieve sizes smaller than $500 \mu m$ add little to biomass estimates within the deep sea (Gage \textit{et al.} 2002). For a list of the taxonomic keys employed for the identification of individuals, please see Taxonomic References. All animals and sediment were preserved in 70\% ethanol and 4\% propylene glycol mix and stored for future reference.

2.2.3 \textit{JCR127 (2005) benthic sampling}

The macrofaunal community at each station was sampled with the hydraulically dampened megacorer. The megacorer holds up to eight cores and each core has a diameter of 10 cm, samples an area of $78.5 \text{ cm}^2$ and penetrates down to a maximum sediment depth of 30 cm. At each station, four cores from each of the three megacorer drops were retained for macrofaunal community analysis. Once onboard, the position of each core retained for community analysis on the megacorer frame was noted. Core positions is not relevant to the results presented within this thesis, however, core position data could prove useful for future studies on spatial diversity patterns and so was noted. Cores were sliced at 0-2, 2-5, 5-10, 10-15 and 15-20 cm sediment depth horizons and fixed in a 4\% buffered
formaldehyde solution. After at least 48 hours, the sediment was then washed with filtered sea water through a 250 μm mesh sieve. The residue retained on the sieve was then washed into self seal poly bags with 70% ethanol and 4% propylene glycol mix and labelled accordingly. All self seal poly bag samples that represented a single core were stored within a larger polythene bag and then all larger poly bags that represented a single station were stored together in a 10 litre plastic tub.

Once back in the laboratory, the samples were stained with Rose Bengal prior to sample sorting. Sediment was then rewashed with tap water through a nest of 250 and 500 μm mesh sieves. All material retained on each sieve was sorted under a dissecting microscope (Wild M5) for macrofauna sensu stricto (this included all metazoans excluding Nematoda, Copepoda and Ostracoda normally considered to be part of the meiofauna). Individuals were identified to Phylum or Class level or, in the case of Polychaeta to Family and counted. Only polychaete heads were counted as an individual animal. Aggregated material for each taxon was blotted on filter paper and weighed on a top loading balance (Sartorius BP615, d = 0.1 mg). Only the macrofauna retained on sieve mesh size of 500 μm and greater was weighed for wet-weight biomass as fauna retained on sieve sizes smaller than 500 μm add little to biomass estimates within the deep-sea (Gage et al. 2002). All animals and sediment were preserved in 70% ethanol and 4% propylene glycol mix and stored for future reference. For a list of the taxonomic keys employed for the identification of individuals, please see Taxonomic References.

2.2.4 Polychaete functional groups and macrofaunal bioturbation potential

The polychaete fauna were classified according to feeding guilds at each station. Feeding guilds were defined as surface deposit feeders, sub-surface deposit feeders, suspension feeders, carnivores and interface feeders (Fauchald and Jumars 1979; Dauer et al. 1981; Dauer 1983; Gaston 1987). Interface feeders can switch between surface deposit feeding
and suspension feeding depending on the environmental conditions most favourable for each feeding mode (Dauer et al. 1981; Dauer 1983).

Macrofaunal bioturbation potential was estimated using the Bioturbation Potential Index ($BP_i$), and calculated using Equation 2.1 (Solan et al. 2004). The classification of fauna for the Bioturbation Potential Index (Solan et al. 2004) with regards to mobility and sediment reworking mode are presented within Table 2.3.

$$BP_i = \bar{B}_i^{0.5} \times M_i \times R_i$$

**Equation 2.1** Bioturbation Potential Index ($BP_i$) (Solan et al. 2004). $\bar{B}_i$ = mean body size (biomass in grams); $M_i$ = Mobility, scored on a categorical scale reflecting activity of animal:

1 = in a fixed tube or body structure,
2 = limited movement or sessile,
3 = slow movement through sediment,
4 = free movement through a burrow system;

$R_i$ = sediment reworking, scored on a categorical scale:
1 = epifauna,
2 = surficial modifiers,
3 = head-down/head-up feeders,
4 = biodiffusors,
5 = regenerators.

Population Bioturbation Potential ($BP_p$) was then calculated by multiplying the Bioturbation Potential Index, ($BP_i$) by mean taxonomic group abundance (Equation 2.2). Community Bioturbation Potential ($BP_c$) can then be calculated by summing the Population Bioturbation Potential ($BP_p$) for each taxonomic group in a sample.
Equation 2.2 Population Bioturbation Potential ($BP_p$). $BP_i = $ Bioturbation Potential Index; $A_i = $ mean taxonomic group abundance (Solan et al. 2004).

Table 2.3 Categorical scales for mobility ($M_i$) and sediment reworking mode ($R_i$) allocated for the macrofauna.

Mobility, $M_i$:
1 = fixed tube or body structure;
2 = limited movement, sessile, but not in a tube;
3 = slow movement through sediment;
4 = free movement through a burrow system.

Reworking mode, $R_i$:
1 = epifauna that bioturbate at sediment water interface;
2 = surficial modifiers, activity limited to <1-2 cm;
3 = head-down/head-up deposit feeders;
4 = biodiffusors, random diffusive transport of particles over short distances;
5 = regenerators, transport of sediment at depth to surface.

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<th>Reworking Mode, $R_i$</th>
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3 The functional ecology and bioturbation potential of the macrofaunal community along a latitudinal transect at the Norwegian Sea continental margin

3.1 Introduction

At the continental margins the biomass and abundance of the benthic fauna decreases with depth and often food supply becomes the limiting factor (Rowe 1983; Gage and Tyler 1991; Rex et al. 2006). Continental margins are recognised as globally important areas for the cycling of organic matter and are often associated with an increased flux of organic matter to the sediments (Walsh et al. 1991). However, information on benthic community structure and organic matter flux to the sediments along slope of continental margins is limited (Schaff et al. 1992; Aller et al. 2002). In the Nordic Seas region, the availability of food appears to be the main factor influencing benthic community structure, including species composition and standing stock across the whole size spectrum of the benthic community (bacteria to megafauna) (Klages et al. 2003). Furthermore, the strength of pelagic-benthic coupling varies between the ice-free Atlantic Domain and ice-covered Polar Domain (Wassmann et al. 1996). Therefore, the Norwegian Sea continental margin, with lack of major topographic boundaries is an ideal location for testing the response of the benthic community to contrasting fluxes of organic matter (Piepenburg et al. 2001).

Along the Greenland Sea continental margin detailed studies of the benthic community have taken place in three regions between 68°N and 82°N (Schnack 1998; Piepenburg et al. 2001). The aim of these studies was to determine how community patterns along the margin are influenced by pelagic-benthic coupling and seabed
properties. However, no similar study has previously taken place along the Norwegian Sea continental margin, where benthic community structure could be influenced by contrasting fluxes in organic matter in regions influenced by ice-free water and those areas influenced by seasonal ice coverage. Although sampling has previously taken place at the Vøring Plateau (Romero-Wetzel and Gerlach 1991; Jensen et al. 1992), Svalbard Margin (Weslawski et al. 2003; Wlodarska-Kowalczyk et al. 2004) and Yermak Plateau (Kröncke 1994) it is difficult to draw comparisons due to differences in sampling methods employed and by the limited replication in some studies. Furthermore, there is a wide time interval between samples collected from the Vøring Plateau (1985-1988) and more recently from the Svalbard Margin (1999-2001). Therefore, in order to consider patterns in benthic community structure at a number of locations covering a large geographical area sampling should take place during a single study and employ standardised methods.

Each of the above locations along the Norwegian continental margin is influenced by contrasting fluxes of organic matter to the sediment. Throughout the region, surface productivity and the flux of organic matter to the sediments shows increasing interannual variability with increasing latitude (Wassmann et al. 1996). The macrofaunal community at the Vøring Plateau is likely influenced by highly seasonal fluxes of fresh organic matter in the form of chlorophyll rich copepod faeces (Graf 1989; Graf 1992). At Bear Island Fan, the flux of organic matter is largely supplied via the lateral advection of organic matter by the North Atlantic Current and supplemented during ‘winter outburst’ of dense bottom water from the Barents Sea (Honjo et al. 1988). Located within the marginal ice zone to the north and west of Svalbard, are the Yermak Plateau and Svalbard Margin and although both locations are supplied with organic matter via lateral advection from the south, the strong pelagic-benthic coupling associated with ice edge processes will provide a high quality food source for the benthic community (Ramseier et al. 2001; Piepenburg 2005).
Different life history strategies of the benthic community may benefit from the contrasting fluxes of organic matter occurring throughout the Nordic Seas region. A larger mean body size, correlated with a longer lifespan can provide benthic fauna with a buffer against environmental unpredictability (Peters 1986). Furthermore, deposit feeders with a larger mean body size can process a greater volume of sediment (Cammen 1980) and have a longer gut residence time that could increase total digestive capacity (Mayer et al. 1995).

When food supply is limited and arrives as an episodic pulse of labile organic matter then the rapid subduction and sub-surface storage (‘caching’) of organic matter by some deep-sea deposit feeders can prove a successful strategy (Jumars et al. 1990). Such behaviour has previously been observed on the Voring Plateau (Graf 1989) and taxa known to adopt a ‘caching’ strategy include sipunculan worms *Nephasoma* sp. (Graf 1989), maldanid polychaetes (Levin et al. 1997) and echiurans (Ohta 1984). The steady, slow sedimentation of refractory organic matter is said to be favoured by sub-surface deposit feeders (Rice and Rhoads). In the deep basin of the Skagerrak, sediments receiving a large quantity of refractory organic matter were characterised by small, deep-burrowing sub-surface deposit-feeding polychaetes (Rosenberg 1995; Dauwe et al. 1998). In contrast, an input of large quantities of high quality organic matter at the German Bight was associated with a benthic community characterised by interface and suspension feeders (Dauwe et al. 1998).

In this chapter, the benthic macrofauna along the Norwegian Sea continental margin is characterised with respect to abundance, biomass, community size structure, taxonomic and functional group composition and bioturbation potential. Samples were collected during a single cruise and employing a standardised method. Stations were selected along a latitudinal transect for contrasting inputs of organic matter to test general ecological hypotheses on the relative influence of food quality, seasonality, interannual variability and other factors influencing macrofaunal community structure. With this in
mind, the following hypotheses were erected to determine the influence of contrasting fluxes of organic matter on benthic community structure:

1. All stations, irrespective of organic flux, will have the same proportion of large bodied macrofauna.

2. Species with a food ‘caching’ strategy will be equally abundant at each of the four sampling stations.

3. The macrofaunal community at all sampling stations will be characterised by surface deposit feeders irrespective of periodicity of nutrient flux.
3.2 Material and Methods

3.2.1 Benthic Sampling

Data for this chapter is provided by the samples collected with the multiple corer and box corer during the JCR75 cruise in the summer of 2002. Information on the samples obtained at each station is provided within the material and methods chapter. A summary of environmental data and samples collected at each station is provided in Table 3.1 and the location of each station is provided in Figure 3.1.

Figure 3.1 Stations sampled in 2002 during the JCR75 cruise are marked with a black circle (•). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.
Table 3.1 Summary of environmental and sampling data for each station. Bottom water temperature and salinity (F. Cottier, pers. comm.), sediment grain size (J. Howe, pers. comm.), sediment \( C_{\text{org}} \) content and Chl-\( a \) profiles (T. Brand, pers. comm.), \( ^{210}\text{Pb} \) mixed layer depths (T. Shimmield, pers. comm.).

<table>
<thead>
<tr>
<th>Station Designation</th>
<th>Vøring Plateau</th>
<th>Bear Island Fan</th>
<th>Svalbard Margin</th>
<th>Yermak Plateau</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nominal position</td>
<td>67° 13.0’ N</td>
<td>73° 39.6’ N</td>
<td>78° 58.4’ N</td>
<td>80° 45.0’ N</td>
</tr>
<tr>
<td>Water depth (m)</td>
<td>1390 - 1437</td>
<td>1440 - 1445</td>
<td>1380 - 1385</td>
<td>880 - 930</td>
</tr>
<tr>
<td>Bottom water temperature (°C)</td>
<td>-0.9</td>
<td>-0.9</td>
<td>-0.7</td>
<td>-0.5</td>
</tr>
<tr>
<td>Bottom water salinity (psu)</td>
<td>34.9</td>
<td>34.9</td>
<td>34.9</td>
<td>34.9</td>
</tr>
<tr>
<td>Sediment composition (%), 0-10 cm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Sand</td>
<td>4.0</td>
<td>10.1</td>
<td>11.2</td>
<td>3.7</td>
</tr>
<tr>
<td>- Silt</td>
<td>74.0</td>
<td>60.7</td>
<td>64.2</td>
<td>65.7</td>
</tr>
<tr>
<td>- Clay</td>
<td>22.0</td>
<td>29.2</td>
<td>24.6</td>
<td>30.6</td>
</tr>
<tr>
<td>Sediment mean grain size (μm), 0-10cm</td>
<td>15.1</td>
<td>24.4</td>
<td>28.4</td>
<td>15.5</td>
</tr>
<tr>
<td>( C_{\text{org}} ) inventory, 0 – 10 cm (mg cm(^{-2}))</td>
<td>46.5</td>
<td>35.8</td>
<td>76.1</td>
<td>62.2</td>
</tr>
<tr>
<td>Chl-( a ) inventory, 0 – 10 cm (µg cm(^{-2}))</td>
<td>0.40</td>
<td>0.03</td>
<td>0.12</td>
<td>0.09</td>
</tr>
<tr>
<td>Mixed layer depths, ( ^{210}\text{Pb} ) (cm)</td>
<td>~2-3</td>
<td>~8-10</td>
<td>~8-10</td>
<td>~8</td>
</tr>
<tr>
<td>Multiple corer drops</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Number of cores retained</td>
<td>21</td>
<td>14</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>Multiple cores, total area analysed (cm(^2))</td>
<td>593.7</td>
<td>395.8</td>
<td>452.3</td>
<td>452.3</td>
</tr>
<tr>
<td>Boxcorer drops</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Boxcorer, total area analysed (cm(^2))</td>
<td>5000</td>
<td>7500</td>
<td>7500</td>
<td>7500</td>
</tr>
<tr>
<td>Seabed photographs</td>
<td>50</td>
<td>25</td>
<td>25</td>
<td>25</td>
</tr>
</tbody>
</table>

3.2.2 Statistical Analysis

All data obtained on macrofaunal abundance and biomass from each multiple corer and NIOZ boxcorer sample was standardised to 1 m\(^2\) for each drop and station means calculated for macrofaunal density and biomass. Statistical tests: Anderson-Darling normality test, Levene’s equal variance test, one-way analysis of variance and Fisher’s pairwise comparison were carried out using Minitab\textsuperscript{®} version 14 computer statistical software. The one-way analysis of variance has a number of assumptions that have to be
considered and are discussed in detail by Underwood (1997). Firstly, the independence of data within and among samples is essential, with the non-independence of data causing a number of problems for the interpretation of the analysis (Hurlbert 1984). Secondly, the heterogeneity of variance within the samples must be equal because “samples from populations with different variances but with the same mean can differ in more ways than samples from populations that have the same variances” (Underwood 1997). Thirdly, the construction of the one-way ANOVA is based on data being normally distributed.

All data had equal variances but not all data were normally distributed. However, the outcome of the analysis of variance is not affected by non-normality (Underwood 1997). Data on mean individual body size were log$_{10}$ transformed due to unequal variances in the sample data. Dendrogram representations for group average clustering of Bray-Curtis similarities were produced using PRIMER® version 6 software package of the Plymouth Marine Laboratory.

There was an unbalanced sampling design due to unequal multiple corer sample sizes at each station. Unequal sample sizes within a group do not cause any computational difficulties with the one-way ANOVA but can influence the interpretation of results (Quinn and Keough 2002). Firstly, unequal samples sizes will result in macrofaunal abundance and biomass means for each station being calculated with different levels of precision that can make interpretation difficult (Underwood 1997). Secondly, the robustness of the one-way ANOVA to violations of assumptions becomes less with unequal sample sizes, particularly homogeneity of variances, and can result in a Type I error (Quinn and Keough 2002). Thirdly, it can be difficult to estimate group effects based on $F$-ratio tests due to multipliers of components of the mean squares not being the same due to variation in sample size (Underwood 1997). However, unequal samples sizes are only a worry for testing null hypotheses with fixed effects when the analysis produces a result ($p$-value) that is close to the critical level (Quinn and Keough 2002). If the results of
the one-way ANOVA are either far from significant or highly significant then confidence can be placed in the conclusions drawn from the analysis.

3.2.3 Seabed Photographs

Seabed photographs were taken at each station using the Proudman Oceanographic Laboratory (POL) bed-hop camera system, which consists of a 35 mm still camera and a strobe in pressure housings mounted on a frame. The camera was loaded with colour transparency film (36 exposures) and the system was deployed vertically by cable. A photograph is taken each time a suspended drop-weight makes contact with the seabed. Each image gives an oblique view of approximately 2.5 m² of seabed. Photographs were examined under a dissecting microscope for evidence of epifauna and biological activity (pits, mounds or other lebensspuren). The sea bed photographs provided supplementary information for each station, particularly for visual evidence of biological activity but did not provide quantitative data for analysis of the benthic community.

3.3 Results

3.3.1 Station Descriptions

Sample collection and environmental data for each station are given in Table 3.1. Bottom water salinity showed little variation between stations and temperature ranged from -0.9 °C at the Voring Plateau and Bear Island Fan to -0.5 °C at the Yermak Plateau. Organic carbon and Chl-a content of the upper sediment layers varied between stations with no latitudinal relationship observed (Table 2.1). There was limited evidence of biological traces associated with burrowing megafauna from seabed photographs or boxcorer
samples. Example photographs taken by the bed-hop camera system of the seabed at each station are provided in Figure 3.2.

**Vøring Plateau (VP):** Ophiuroids, the most abundant epifauna, were observed frequently in seabed photographs, often forming dense populations. The sediment surface generally appeared to be smooth but with evidence of pits and mounds associated with the burrowing activity of benthic fauna.

**Bear Island Fan (BIF):** There was no evidence of sediment structures formed by the presence of burrowing megafauna. Small granular lumps observed at the sediment surface were amphipod tubes constructed from sediment and sponge spicules.

**Svalbard Margin (SM):** Sediment was poorly-sorted homogenous mud, brown in colour with a mean grain size indicating a medium to very coarse silt (Howe et al. In Press). There was evidence of epifauna, with ophiuroids the most abundant, but little evidence of mounds associated with burrowing megafauna.

**Yermak Plateau (YP):** The upper sediment layers were finely-laminated brown to greenish grey mud, consisting mainly of a fine to coarse silt (Howe et al. In Press). The sediment surface appeared smooth with numerous pits and mounds created by the burrowing activity of benthic fauna, with few epifauna observed in photographs.
Figure 3.2 Seabed photographs taken with the bed-hop camera system at each station. (a) Vøring Plateau, (b) Bear Island Fan, (c) Svalbard Margin, (d) Yermak Plateau. Field of view (width x depth) approximately 120 x 150 cm.
3.3.2 Total Macrofauna: Standing Stock

Total macrofaunal abundance (Figure 3.3) and biomass (Figure 3.5) for each station was estimated from both the multiple corer and boxcorer samples. Macrofaunal abundance (250-500 µm) was significantly different between stations ($F_{3,8}=15.85$, $P=0.001$), but no relationship with latitude was observed. Both the Vøring Plateau and Svalbard Margin had significantly greater macrofaunal abundance than either Bear Island Fan or the Yermak Plateau (Table 3.2). There was no significant difference in macrofaunal abundance (250-500 µm) between the Vøring Plateau and Svalbard Margin. However, macrofaunal abundance at Svalbard Margin was significantly greater than the Vøring Plateau, when only >500 µm or >1 mm sieve fractions were compared. The abundance of larger macrofauna (>1 mm) appeared to increase with latitude between the Vøring Plateau and Svalbard Margin stations (Figure 3.3) and there was a significant difference in abundance between all stations ($F_{3,7}=30.76$, $P<0.001$) (Table 3.2). Svalbard Margin had significantly the greatest abundance of larger macrofauna (>1 mm) and there was no significant difference in abundance between the Vøring and Yermak Plateaus. The relative abundance of macrofauna >500 µm at each of the stations against Chl-$a$ and $C_{org}$ inventory is provided in Figure 3.4 (a) and (b). The abundance of larger bodied macrofauna (>1 mm and >2 mm) against Chl-$a$ and $C_{org}$ inventory is provided in Figure 3.4 (c) and (d). The abundance of the larger bodied macrofauna does not appear to show any clear relationships with Chl-$a$ or $C_{org}$ inventory.
Figure 3.3 Numerical abundance of macrofauna from each station sampled with the multiple corer (250-500 µm and >500 µm) and boxcorer (>1 mm). Error bars represent confidence intervals (95%). Station key: VP = Vøring Plateau, BIF = Bear Island Fan, SM = Svalbard Margin, YP = Yermak Plateau.

Table 3.2 Confidence intervals (95%) for macrofaunal abundance Fisher’s pairwise comparisons of least significant difference one-way ANOVA post hoc test, columns subtracted from rows. If confidence intervals do not contain zero then there is a significant difference between stations. Confidence intervals highlighted in grey are multiple corer data (250-500 µm) and white are boxcorer data (>1mm). Significant differences are highlighted with an asterix (*).
Figure 3.4 Relative abundance of macrofauna >500 µm (%) against (a) Chl-α inventory and (b) C_{org} inventory. Abundance of macrofauna >1mm and >2mm against (c) Chl-α inventory and (d) C_{org} inventory.

Macrofaunal biomass estimated from multiple corer samples (>500 µm) varied between 2.82 (±0.33 95% C.I.) and 16.61 (±5.71 95% C.I.) g m^{-2} along the latitudinal transect. Macrofaunal biomass (>500 µm) increased from the Voring Plateau to the Svalbard Margin and decreased at the Yermak Plateau along the transect (Figure 3.5). There was a significant difference in macrofaunal biomass (>500 µm) between stations (F_{3,8} = 14.85, P = 0.001), with Svalbard Margin having significantly the greatest biomass (Table 3.3). The Voring Plateau macrofaunal biomass (>500 µm) was not significantly different from either Bear Island Fan or Yermak Plateau, even though macrofaunal biomass at Bear Island Fan was significantly greater than the Yermak Plateau.
Figure 3.5 Wet-weight biomass of macrofauna at each station sampled with the multiple corer (>500 µm) and boxcorer (>1 mm) and Yermak Plateau minus large echiuran (>1 mm – echiuran). Errors bars represent confidence interval (95%) and the confidence interval (95%) for YP >1 mm of ±27.2 is not shown. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.

Table 3.3 Confidence intervals (95%) for macrofaunal biomass Fisher’s pairwise comparisons of least significant difference one-way ANOVA post hoc test, columns subtracted from rows. If confidence intervals do not contain zero then there is a significant difference between stations. Confidence intervals highlighted in grey are multiple corer data (>500 µm) and white are boxcorer data (>1 mm). Significant differences are highlighted with an asterix (*).
The Yermak Plateau was the only station where boxcorer macrofaunal biomass (>1 mm) was greater than multiple corer macrofaunal biomass (>500 μm; Figure 3.5). In one of the boxcorer samples from the Yermak Plateau, a large echiuran *Hamingia arctica* weighing over 10 g wet-weight was recovered. Normally an individual this large would be counted as a member of the megafauna. However, smaller individuals of *H. arctica* were recovered in the samples from the Yermak Plateau, and these individuals would be considered macrofauna. Then again, even if this large individual echiuran was removed from analysis, the boxcorer biomass (>1 mm – echiuran) remained greater than the multiple corer samples (>500 μm) at the Yermak Plateau (Figure 3.5). This difference between the sampling gears at the Yermak Plateau suggests there is a significant component of the benthic community not represented in the multiple corer samples.

Boxcorer macrofaunal biomass (>1 mm) varied significantly between stations ($F_{3,7} = 13.76$, $P = 0.003$), with the Vøring Plateau having significantly the lowest macrofaunal biomass (Table 3.3). Svalbard Margin had significantly the greatest biomass and there was no significant difference between Bear Island Fan and the Yermak Plateau. Mean individual biomass of the larger members of the macrofaunal community retained on the 1 mm sieve and above showed no significant difference between stations ($F_{3,7} = 4.21$, $P = 0.054$) (Figure 3.6). However, the abundance and biomass of macrofauna >1 mm (Figure 3.3, 3.5) did indicate a significant difference in the abundance of larger macrofauna between stations, with Svalbard Margin having significantly the greatest number of larger individuals (>1 mm). Macrofaunal community biomass (>500 μm and >1 mm) does not appear to relate directly to Chl-α and $C_{org}$ inventory (Figure 3.7).
Figure 3.6 Mean individual biomass (g) of the macrofauna at each station sampled with the multiple corer (>500 µm) and boxcorer (>1 mm). Errors bars represent confidence intervals (95%). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.

Figure 3.7 Macrofaunal biomass ( >500 µm and >1 mm) against (a) Chl-α inventory and (b) C_{org} inventory.
Chapter 3

3.3.3 Taxonomic Composition

The relative taxonomic composition of abundance (Figure 3.8) and biomass (Figure 3.9) of major macrofaunal groups was analysed for both multiple corer and boxcorer samples. With regard to the relative abundance of the macrofaunal community, polychaetes were the best represented group, contributing over 50% of total macrofaunal abundance in both multiple corer and boxcorer samples at each of the stations (Figure 3.8). Bear Island Fan was the only station with a polychaete abundance significantly lower than the other stations ($F_{3,8} = 7.52, P = 0.01$). The pattern of relative abundance of the macrofaunal groups estimated from the multiple corer samples (250-500 μm) was similar at each of the stations. The crustaceans accounted for over 15% of relative macrofaunal abundance in all multiple corer samples (250-500 μm) and had the second highest relative abundance. In the boxcorer samples, the sipunculans contributed the second highest relative abundance of larger macrofauna (>1 mm) at each station, with the exception of the Vøring Plateau, where echinoderms were the second best represented macrofaunal group.

In contrast to relative macrofaunal abundance, relative structure of macrofaunal group biomass varied between stations and the sampling gear employed (Figure 3.9). Macrofaunal biomass, instead of abundance, gives a more accurate indication of the benthic standing stock representing each macrofaunal group at each station. At the Vøring Plateau, there was little difference in relative biomass of the multiple corer samples (>500 μm) and boxcorer samples (>1 mm). However, at Bear Island Fan, crustaceans, mainly ampeliscid amphidods, represented >40% of biomass in the multiple corer samples (>500 μm), and accounted for >50% in the boxcorer samples (>1 mm). Molluscs and polychaetes between them represented almost 80% of biomass in the multiple corer samples from the Svalbard Margin. However, in the boxcorer samples from the Svalbard Margin, polychaetes alone accounted for about 60% of relative biomass. At the Yermak Plateau, macrofaunal biomass was predominately characterised by polychaetes, accounting for
>70% of total biomass in both the multiple corer and the boxcorer samples when the large individual echiuran was removed from analysis. Otherwise, echiurans represented almost 80% of biomass in the boxcorer samples from the Yermak Plateau. There was no significant difference in total polychaete biomass (>500 μm) between stations even though the relative percentage of biomass accounted for by polychaetes varied in the multiple corer samples from each station ($F_{3,8}=1.17$, $P=0.381$).

![Relative abundance of macrofaunal groups sampled with the multiple corer (mc) and boxcorer (bc). Station key: VP= Voring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.](image)

**Figure 3.8** Relative abundance of macrofaunal groups sampled with the multiple corer (mc) and boxcorer (bc). Station key: VP= Voring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.
Figure 3.9 Relative biomass of macrofaunal groups sampled with the multiple corer (mc) and boxcorer (bc). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau. *YP= Yermak Plateau minus large individual echiuran.

3.3.4 Macrofauna Feeding Types

The relative abundance of the macrofaunal community feeding types follows a similar pattern at each station. Surface deposit feeders represented >50% of macrofaunal feeding types relative abundance at all stations (Figure 3.10). Sub-surface deposit feeders contributed to >15% of abundance only at the Vøring Plateau. The boxcorer samples from the Bear Island Fan were the only samples in which suspension feeders represented >20% of relative abundance. At the Vøring Plateau, Svalbard Margin and Yermak Plateau the relative biomass of the macrofauna feeding types showed similar patterns to relative abundance, with surface deposit feeders contributing to >50% of the relative biomass (Figure 3.11). However, at the Bear Island Fan, suspension feeders contributed to a greater proportion of relative biomass than observed at any other stations, >60% of biomass in the boxcorer samples and about 40% in multiple corer samples. The higher representation of
suspension feeders at Bear Island Fan was due to the abundance of the tube building amphipod *Haploops setosa*.

**Figure 3.10** Relative abundance of macrofauna feeding types sampled with the multiple corer (mc) and boxcorer (bc). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.

**Figure 3.11** Relative biomass of macrofauna feeding types sampled with the multiple corer (mc) and boxcorer (bc). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.
3.3.5 Polychaete Functional Ecology

Polychaetes were the most abundant taxon, and a list of all polychaete families recorded in boxcorer and multiple corer samples from each station is presented in Table 3.6. Families that contributed to >5% of relative polychaete abundance are listed in Table 3.4. Capitellidae, Cirratulidae, Paraonidae and Spionidae each contributed to >5% of total polychaete abundance at each station. However, a lower number of polychaete families represented >5% of relative polychaete biomass at each station (Table 3.4). A single polychaete family represented >50% of relative polychaete biomass at each station, capitellids at the Vøring Plateau, lumbrinerids at Bear Island Fan, maldanids at Svalbard Margin and cirratulids at the Yermak Plateau.

Table 3.4 Relative abundance of Polychaeta families that contribute >5% of abundance of the total at each station, estimated from the multiple corer samples (250-500 µm).

<table>
<thead>
<tr>
<th>Vøring Plateau Family</th>
<th>Bear Island Fan Family</th>
<th>Svalbard Margin Family</th>
<th>Yermak Plateau Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capitellidae</td>
<td>Paraonidae</td>
<td>Paraonidae</td>
<td>Cirratulidae</td>
</tr>
<tr>
<td>24.9</td>
<td>37.7</td>
<td>28.4</td>
<td>37.6</td>
</tr>
<tr>
<td>Paraonidae</td>
<td>Cirratulidae</td>
<td>Ampharetidae</td>
<td>Paraonidae</td>
</tr>
<tr>
<td>19.7</td>
<td>28.2</td>
<td>13.8</td>
<td>20.4</td>
</tr>
<tr>
<td>Spionidae</td>
<td>Capitellidae</td>
<td>Maldanidae</td>
<td>Spionidae</td>
</tr>
<tr>
<td>14.0</td>
<td>10.7</td>
<td>12.2</td>
<td>14.6</td>
</tr>
<tr>
<td>Cirratulidae</td>
<td>Spionidae</td>
<td>Spionidae</td>
<td>Capitellidae</td>
</tr>
<tr>
<td>13.9</td>
<td>10.4</td>
<td>11.2</td>
<td>6.7</td>
</tr>
<tr>
<td>Sabellidae</td>
<td>Oweniidae</td>
<td>Capitellidae</td>
<td>Ampharetidae</td>
</tr>
<tr>
<td>13.5</td>
<td>10.1</td>
<td>7.5</td>
<td>5.8</td>
</tr>
<tr>
<td>Ampharetidae</td>
<td></td>
<td>Cirratulidae</td>
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</tr>
<tr>
<td>5.1</td>
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<td>Terebellidae</td>
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</tr>
<tr>
<td></td>
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<td>5.3</td>
<td></td>
</tr>
</tbody>
</table>

Table 3.5 Relative biomass of Polychaeta families that contribute >5% of biomass of the Polychaeta at each station, estimated from the multiple corer samples (>500 µm).

<table>
<thead>
<tr>
<th>Vøring Plateau Family</th>
<th>Bear Island Fan Family</th>
<th>Svalbard Margin Family</th>
<th>Yermak Plateau Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capitellidae</td>
<td>Lumbrineridae</td>
<td>Maldanidae</td>
<td>Cirratulidae</td>
</tr>
<tr>
<td>52.5</td>
<td>83.8</td>
<td>64.9</td>
<td>63.3</td>
</tr>
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<td>Amphinomidae</td>
<td>Cirratulidae</td>
<td>Ampharetidae</td>
<td>Amphinomidae</td>
</tr>
<tr>
<td>11.2</td>
<td>6.4</td>
<td>14.4</td>
<td>11.3</td>
</tr>
<tr>
<td>Cirratulidae</td>
<td></td>
<td>Paraonidae</td>
<td>Capitellidae</td>
</tr>
<tr>
<td>9.3</td>
<td></td>
<td>7.5</td>
<td>11.1</td>
</tr>
<tr>
<td>Paraonidae</td>
<td></td>
<td></td>
<td>Paraonidae</td>
</tr>
<tr>
<td>8.3</td>
<td></td>
<td></td>
<td>6.3</td>
</tr>
<tr>
<td>Ampharetidae</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
Table 3.6 Polyochaeta families recorded (*) in boxcorer and multiple corer samples from each station.

<table>
<thead>
<tr>
<th>Polychaeta Family</th>
<th>Vøring Plateau</th>
<th>Bear Island Fan</th>
<th>Svalbard Margin</th>
<th>Yermak Plateau</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrocirridae</td>
<td>*</td>
<td></td>
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</tr>
<tr>
<td>Ampharetidae</td>
<td>*</td>
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<td></td>
</tr>
<tr>
<td>Amphinomidae</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capitellidae</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cirratulidae</td>
<td>*</td>
<td></td>
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<tr>
<td>Dorvilleidae</td>
<td>*</td>
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<td></td>
</tr>
<tr>
<td>Flabelligeridae</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lumbrineridae</td>
<td>*</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maldanidae</td>
<td>*</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nephtyidae</td>
<td>*</td>
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<td>*</td>
<td></td>
</tr>
<tr>
<td>Opheliidae</td>
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<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oweniidae</td>
<td>*</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paraonidae</td>
<td>*</td>
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<td></td>
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<tr>
<td>Phyllocdocidae</td>
<td>*</td>
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<tr>
<td>Poecilochaetidae</td>
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<tr>
<td>Polynoidae</td>
<td>*</td>
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<tr>
<td>Sabellidae</td>
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<tr>
<td>Scalibregmatidae</td>
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</tr>
<tr>
<td>Sigalionidae</td>
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<tr>
<td>Sphaerodoridae</td>
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<td>Spionidae</td>
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<tr>
<td>Syllidae</td>
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<tr>
<td>Terebellidae</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Trichobranchidae</td>
<td>*</td>
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</table>

In general, the polychaete community was numerically dominated by deposit feeders, particularly surface deposit feeders. At Bear Island Fan, Svalbard Margin and Yermak Plateau surface deposit feeders contributed to >60% of polychaete feeding type abundance in both multiple corer (250-500 µm) and boxcorer samples (>1 mm) (Figure 3.12). The Vøring Plateau was the only station where sub-surface deposit feeders represented >20% of polychaete abundance.

Sub-surface deposit feeders represented a significantly greater proportion of polychaete feeding type biomass at the Vøring Plateau (Figure 3.13). There was an increased representation of carnivores in boxcorer samples when the sampling gears were
compared at each station. A large lumbrinerid polychaete was recovered in a single multiple corer sample resulting in sub-surface deposit feeders representing over 80% of polychaete feeding type biomass at Bear Island Fan. When this individual was removed from analysis then surface deposit feeders accounted for >80% of feeding type biomass at Bear Island Fan. At the Yermak Plateau, surface deposit feeders accounted for about 80% of multiple corer feeding type biomass but only about 20% of boxcorer samples. Sub-surface deposit feeders accounted for about 50% of feeding type biomass in the boxcorer samples at the Yermak Plateau. This dissimilarity in relative biomass at the Yermak Plateau may be a result of differences in sampling gear efficiency and sieve size employed for each sampling gear.

**Figure 3.12** Relative abundance of Polychaeta feeding types sampled with the multiple corer (mc) and boxcorer (bc). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.
Figure 3.13 Relative biomass of Polychaeta feeding types sampled with the multiple corer (mc) and boxcorer (bc). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, *BIF= Bear Island Fan excluding large lumbrinerid, SM= Svalbard Margin, YP= Yermak Plateau.

3.3.6 Macrofauna Bioturbation Potential

The classification of fauna for the Bioturbation Potential Index (Solan et al. 2004) with regards to mobility and sediment reworking mode are presented within Table 2.3. The values for bioturbation potential of the macrofaunal community estimated from multiple corer samples (>500 µm) and boxcorer samples (>1 mm) is presented in Figure 3.14. The relative bioturbation potential of each of the macrofaunal sediment reworking modes is presented in Figure 3.15. Head-up/head-down feeders and surficial modifiers account for the majority of the bioturbation potential at each station. The multiple corer samples from the Vøring Plateau were the only samples in which head-up/head-down feeders contributed to >50% of community bioturbation potential. Biodiffusors did not dominate the relative bioturbation potential at any of the stations, with the most significant percentage of ~30% of bioturbation potential occurring in multiple corer samples from the Svalbard Margin. The presence of echiurans at the Yermak Plateau resulted in regenerators contributing
>10% of community bioturbation potential. This was the only station where mounds and pits normally associated with the activities of burrowing megafauna were observed in seabed photographs.

**Figure 3.14** Bioturbation potential \( (BP_c) \) of the macrofaunal community at each station sampled with the multiple corer (>500 μm) and boxcorer (>1 mm). Error bars represent confidence intervals (95%). Station key: VP = Vøring Plateau, BIF = Bear Island Fan, SM = Svalbard Margin, YP = Yermak Plateau. Community bioturbation potential, \( BP_c \), is given in arbitrary units and does not provide a direct measure.

To investigate similarities in community bioturbation potential between stations, multivariate analysis was applied to the bioturbation potential of the macrofaunal sediment reworking modes. Dendrogram representations for group average clustering of Bray-Curtis similarities; based on untransformed data for the bioturbation potential of macrofaunal sediment reworking modes is shown in Figure 3.16. Between all stations similarity was >25% in the bioturbation potential of sediment reworking modes. There was no clustering according to stations and clustering of samples does not appear to be influenced by the choice of sampling gear.
Figure 3.15 Relative bioturbation potential of the macrofaunal community sampled with the multiple corer (mc) and boxcorer (bc). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, *BIF= Bear Island Fan excluding large lumbrinerid, SM= Svalbard Margin, YP= Yermak Plateau.

Figure 3.16 Dendrogram representation for group average clustering of Bray-Curtis similarities for the bioturbation potential of macrofaunal sediment reworking modes based on untransformed data. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau. MC or BC refers to the sampling gear (i.e. MC= multiple corer and BC= boxcorer). 1427a or 880b refers to water depth and sample (i.e. 1427 refers to a water depth and a or b refers to samples number in collection order).
3.4 Discussion

3.4.1 Overview of hypotheses

The results that relate to the findings for each hypothesis will be discussed in detail within the discussion section. An overview of the findings related to each hypothesis is presented below:

1. The hypothesis that all stations, irrespective of organic flux will have the same proportion of large bodied macrofauna can be rejected.
2. The hypothesis that taxa adopting a ‘caching strategy will be equally abundant at each of the four sampling stations can be rejected.
3. The hypothesis that all sampling stations will be characterised by the surface deposit feeders can be rejected.

3.4.2 Macrofaunal Community

Macrofaunal abundance estimates were compared with previous studies in the region. When both the 250-500 and >500 $\mu$m sieve fractions were considered, then macrofaunal abundance estimates were greater than previous studies (Table 3.7). It was expected that abundance estimated from the 250-500 $\mu$m sieve fraction would be greater than previous studies due to a larger mesh size of 500 $\mu$m or 1 mm having previously been employed. This lower abundance in previous studies may be an artefact of under-sampling by the boxcorer as discussed earlier, although it is important to note that the sampling efficiency of the macrofaunal community by both the multiple corer and boxcorer is not compared directly in this thesis. It is difficult to draw direct comparisons between studies when there is a significant length of time between the studies; nonetheless, macrofaunal biomass estimates were comparable with previous studies (Table 3.7). This suggests that mean individual biomass of the macrofauna is lower in this study due to the reported
higher abundances. However, it is more likely a larger proportion of smaller members of the macrofaunal community were sampled in the present study, particularly in the 250 µm sieve fraction and these smaller individuals would add very little to macrofaunal community biomass estimates (Gage et al. 2002).

Differences between studies may be a result of local scale variation in community patterns at each location on the Norwegian continental margin. Data presented in this thesis is based on replicated samples from a single station at each sampling location. Previous macrofaunal abundance estimates at similar depths on the Yermak Plateau and Svalbard Margin have been based on only a single sample from one station from each sampling location (Kröncke 1998; Wlodarska-Kowalczuk et al. 2004). Therefore, direct comparisons between studies can not be drawn due to the small area sampled in each study and it is difficult to determine if the samples collected are completely representative of the macrofaunal community at each sampling location. In order to obtain detailed information on the macrofaunal community at each location would require replicated sampling at number of stations. However, the time required for such a detailed study is seldom available during planned multidisciplinary research cruises that focus sampling in the deep sea. This then requires a decision on whether to sample a number of stations without replication or sample fewer stations with replication. It was decided that sampling fewer stations with replication was the best strategy for work presented in this thesis. The discussion of the macrofaunal community at each sampling location in this thesis is based on only a single station and is therefore not fully representative of that sampling location.

When comparing the relative abundance of the macrofaunal groups from boxcorer and multiple corer samples the polychaetes had similar relative abundance estimates from both sampling gear at each station (Figure 3.8). However, the relative abundance of crustaceans is higher in the multiple corer samples (250-500 µm) than in boxcorer samples (>1 mm) from each station, suggesting the majority of the crustacean community is less
than 1mm in body size. With the exception of the Vøring Plateau, the opposite trend was observed with regards to the sipunculans, with boxcorer samples having a higher relative abundance. However, biomass provides a better indication of benthic community standing stock than abundance. When relative biomass of the macrofaunal community was considered similar patterns were not observed between stations. In the boxcorer samples (>1 mm) from the Svalbard Margin, molluscs represented <10% of total biomass but almost 40% of biomass in the multiple corer samples, highlighting how differences in sampling gear and sieve mesh size can potentially influence results. When total macrofaunal biomass was considered, only the boxcorer samples (>1 mm) from the Yermak Plateau were greater than the multiple corer (250-500 µm). This suggests that the multiple corer may not provide a sample that is completely representative of the macrofaunal community at the Yermak Plateau and therefore choice of sampling gear at this station should be considered in future studies.

Table 3.7 Abundance and biomass data from this study compared with previous work at similar depths in the region. a (Romero-Wetzel & Gerlach, 1991); b (Wlodarska-Kowalczuk et al., 2004); c (Kröncke, 1998).

<table>
<thead>
<tr>
<th>Location</th>
<th>Vøring Plateau</th>
<th>Svalbard Margin</th>
<th>Yermak Plateau</th>
</tr>
</thead>
<tbody>
<tr>
<td>250-500 µm abundance (ind. m⁻²)</td>
<td>6253 (+1069)</td>
<td>6702 (+660)</td>
<td>4611 (+363)</td>
</tr>
<tr>
<td>&gt;500 µm abundance (ind. m⁻²)</td>
<td>3365 (+385)</td>
<td>4908 (+565)</td>
<td>2860 (+429)</td>
</tr>
<tr>
<td>&gt;500 µm biomass (g m⁻²)</td>
<td>5.27 (+1.27)</td>
<td>16.61 (+5.71)</td>
<td>2.82 (+0.33)</td>
</tr>
<tr>
<td>Previous number of stations</td>
<td>17ᵃ</td>
<td>1ᵇ</td>
<td>1ᶜ</td>
</tr>
<tr>
<td>Previous depth range (m)</td>
<td>1244-1450ᵃ</td>
<td>1545ᵇ</td>
<td>888ᶜ</td>
</tr>
<tr>
<td>Previous studies abundance (ind. m⁻²)</td>
<td>619 (+175ᵃ)</td>
<td>1500ᵇ</td>
<td>1200ᶜ</td>
</tr>
<tr>
<td>Previous studies biomass (g m⁻²)</td>
<td>4.1 (+1.27ᵃ)</td>
<td>11.5ᵇ</td>
<td>2.97ᶜ</td>
</tr>
</tbody>
</table>

Polychaetes represented the largest proportion of relative macrofaunal abundance at each station, similar to previous findings at the Vøring Plateau (Romero-Wetzel and Gerlach 1991), Svalbard Margin (Wlodarska-Kowalczuk et al. 2004) and Yermak Plateau (Kröncke 1998). Unlike relative macrofaunal abundance, the major taxonomic groups that represented the largest proportion of total biomass varied at each of the stations and
between sampling gear employed. At the Vøring Plateau, the ophiuroid species *Ophiocten gracilis* was responsible for echinoderms contributing significantly to relative macrofaunal biomass. The area surrounding the station at the Vøring Plateau was sampled extensively with a USNEL boxcorer between 1985 and 1986, and relative macrofaunal community biomass was reported to be dominated by the sipunculan *Nephasoma* sp., the ophiuroid *Ophiocten gracilis* and the capitellid polychaete, *Notomastus latericeus* (Romero-Wetzel and Gerlach 1991). These three species contributed significantly to the overall biomass of the macrofaunal community at the Vøring Plateau station. Although Romero-Wetzel and Gerlach (1991) recovered large individual entroponeusts, *Stereobalanus canadensis*, in more than 50% of their samples, only a single individual was recovered in one of the boxcorer samples from the present study and none in any of the multiple corer samples.

On the Svalbard Margin, at a slightly greater water depth of 1545 m than the present study station, Wlodarska-Kowalczuk *et al.* (2004) reported that polychaetes and bivalves contributing significantly to the macrofaunal community. Paraonids, similar to this study, were the most abundant polychaete family, with *Aricidea* sp. representing 16.8% of total macrofaunal abundance (Wlodarska-Kowalczuk *et al.* 2004). The most abundant species reported by Wlodarska-Kowalczuk *et al.* (2004) was the bivalve *Thyasira dunbari*, however, data on biomass of individual species was not presented. At the Svalbard Margin station sampled within the present study, molluscs and in particular, bivalves represented a significant proportion of benthic standing stock. This station had significantly the greatest biomass of macrofauna and is influenced by high primary production and high sedimentation of organic matter associated with absence of summer ice coverage (von Bodungen *et al.* 1995). Marginal ice zones have previously been reported to be areas of high benthic standing stock (Grebmeier and Barry 1991). One clear difference in the polychaete community between the studies was the lower abundance of the lumbrinerid polychaete family in multiple corer samples from this study. Wlodarska-
Kowalczuk et al. (2004) reported the lumbrinerid *Lumbrineris* sp. as the second most abundant polychaete, representing 9.1% of total abundance. Lumbrinerids are generally considered sub-surface deposit feeders (Petch 1986), with a body size larger than the majority of other polychaete families found at this station. In this present study maldanids represented the most significant proportion of polychaete community biomass, representing >60%, despite only representing 12.2% of relative abundance.

At the most northerly station, the Yermak Plateau, Kröncke (1998) described a benthic community in which polychaetes accounted for the largest proportion of macrofaunal abundance. Cirratulid polychaetes contributed significantly to macrofaunal abundance at her station (8.3%) (Kröncke 1998) but did not represent anywhere near the 37.6% of total polychaete abundance observed in the present study. The most abundant polychaete reported by Kröncke (1998) was a spionid, *Spiophanes kröyeri*, and spionids did contribute significantly to polychaete abundance in this present study. A notable difference between the studies was that no echiurans were recovered or reported in the previous study at the Yermak Plateau, although Kröncke (1998) did only obtain a single sample from her station. In the present study polychaetes represented >70% of macrofaunal biomass in the multiple corer (>500 µm) and boxcorer samples (>1 mm), when the large individual echiuran was not included in analysis. Representing >60% of this polychaete biomass were cirratulids, *Chaetozone* sp. However, Kröncke (1998) did not record any *Chaetozone* species in her samples from the Yermak Plateau. In fact a sabellid *Euchone analis* represented >20% of macrofaunal biomass at Kröncke’s (1998) Yermak Plateau station, while in the present study sabellids did not even contribute to >5% of polychaete biomass or abundance.

The presence of the tube-building amphipod, *Haploops setosa*, at Bear Island Fan was responsible for crustaceans contributing significantly to the total community biomass of the multiple and boxcorer samples. This amphipod is either a suspension or sediment
feeder (Mills 1971) and may benefit from the downslope transport of refractory organic matter across Bear Island Fan from the highly productive Barents Seas (Wassmann et al. 1996; Ritzarau et al. 2001). Furthermore, this amphipod was responsible for suspension feeders representing the highest proportion of macrofaunal feeding types at Bear Island Fan. Sponges and zoanthids also contributed to the biomass of suspension feeders at Bear Island Fan. The deep currents of Bear Island Fan are normally weak (mean 10 cm s\(^{-1}\)) but can reach velocities of 30-50 cm s\(^{-1}\) highlighting the Bear Island Fan as an energetic area (McPhee et al. 1998). These strong water velocities indicate a high potential for the resuspension of sediment and organic matter that would benefit suspension feeders, particularly as this mode of feeding is dependent on flow rate (Miller et al. 1992).

At the Vøring Plateau, Svalbard Margin and Yermak Plateau stations, surface deposit feeders represented the largest proportion of the macrofaunal abundance, a pattern more typical of deep-sea benthic communities (Gage and Tyler 1991). An increase in the relative proportion of surface deposit feeding polychaetes at the North Carolina continental margin was associated with increased organic matter input to the sediments (Schaff et al. 1992). However, the polychaete component of the Vøring Plateau community, unlike other stations, was characterised by an increase in the relative abundance and biomass of sub-surface deposit feeders. Patterns in the relative structure of the polychaete community are different from other locations in the northeast Atlantic when stations at similar water depths are compared such as at the Hatton-Rockall Basin (Hughes and Gage 2004) and Goban Spur (Flach et al. 2002). Carnivorous families characterised the polychaete community at a depth of 1100 m on the Hatton-Rockall Basin, situated off the north west coast of Scotland (Hughes and Gage 2004). Macrofaunal abundance, estimated at 9709 ind m\(^{-2}\) (±2264) on the Hatton-Rockall Basin was slightly greater than abundances observed within the Nordic Seas region.
Located further south in the northeast Atlantic is the Goban Spur, and macrofaunal abundances at this location are similar to those of the Nordic Seas region (Flach et al. 2002). The abundance of deposit feeders at all stations across the Goban Spur was generally lower than the ~80% in the present study (Flach et al. 1998). Suspension feeders were the most abundant feeding type of the benthic community at the Goban Spur, particularly between depths of 1000 and 1500 m (Flach et al. 1998; Heip et al. 2001). Flow velocities at 1470 m depth on the Goban Spur can reach ~35 cm s\(^{-1}\) and it was at this location that the highest abundance of suspension feeders was recorded (Flach et al. 1998). An increase in abundance of suspension feeders in the adjacent Whittard Canyon was believed to indicate an increase in the lateral transport of organic matter (Duineveld et al. 2001). At the Fram Strait, located within the Nordic Seas region, an increase in abundance of suspension feeders was also linked to increased lateral transport and resuspension of organic matter (Rutgers van der Loeff et al. 2002).

3.4.3 Body Size

The hypothesis that each station, irrespective of organic flux will have the same proportion of large bodied macrofauna can be rejected. Mean individual biomass of the macrofauna (>1 mm) from the boxcorer samples was not significantly different between stations (Figure 3.6). However, this common method of determining body size is based on dividing total biomass by total abundance but is misleading when influenced by rare large individuals (Kaariainen and Bett 2006). Kaariainen and Bett (2006) suggest it is important when considering mean individual biomass that the underlying size structure of the benthic community is considered. This potential issue is highlighted clearly at the Yermak Plateau when mean individual biomass of the macrofauna is compared between multiple corer (>500 µm) and boxcorer samples (>1 mm) (Figure 3.6).
Only larger individual animals would have been retained on the 1 mm sieve and these individuals are representative of only a small proportion of macrofaunal community abundance but can contribute significantly to total biomass (Gage et al. 2002). Despite no significant difference in mean individual biomass between the stations (>1 mm) the abundance and biomass of macrofauna >1 mm varied significantly between stations. Svalbard Margin had significantly the greatest abundance (>1 mm) and a significantly greater biomass than both the Vøring and Yermak Plateau communities (>1 mm). The Yermak Plateau was the other station expected to be best represented by larger macrofauna. Although the macrofaunal community at the Yermak Plateau has previously been reported to be of low abundance and small body size (Kröncke 1998) this was the only station with evidence of burrowing megafauna with a large body size that would provide a buffer against environmental unpredictability (Peters 1986).

The lowest representation of larger bodied macrofauna occurred at the Vøring Plateau and this station is supported by a relatively low sedimentation rate of mainly pelagic organic matter input (Romero-Wetzel and Gerlach 1991). When the food source is of low nutritional value then it would be beneficial for deposit feeders to have a larger body size to allow for the processing of greater volumes of sediment (Jumars et al. 1990). This may explain why Bear Island Fan, potentially supported by the advective input of low nutritional value refractory organic matter (Wassmann et al. 1996; Ritzarau et al. 2001) had a greater representation of larger individuals than the Vøring Plateau.

3.4.4 Occurrence of ‘caching’

The hypothesis that species with a food ‘caching’ strategy will be equally abundant at each of the sampling stations can be rejected. At the Vøring Plateau, the previously reported rapid subduction of organic matter at a rate > 1 cm day⁻¹ following the episodic input of copepod faeces was associated with the sipunculan, *Nephasoma* sp. (Graf 1989). At the
Vøring Plateau station, *Nephasoma* abundance was estimated at about 400 individuals m$^{-2}$, slightly less than the 500 individuals m$^{-2}$ estimate of Romero-Wetzel (1987). There are up to 11,000 capillary burrows m$^{-2}$ associated with *Nephasoma* at the Vøring Plateau, and with an introvert length of about 6 mm, and each individual having a network of about 10 vertical burrows, the *Nephasoma* community could potentially have 100% coverage of the sediment surface when feeding (Romero-Wetzel 1987). The abundance of *Nephasoma* at the Vøring Plateau was significantly greater than at the other stations; however, *Nephasoma* and the associated burrow structures were observed at each station.

The large echiuran recovered at the Yermak Plateau would consume a far greater volume of sediment than any of the deposit feeding members of the macrofaunal community recovered from the Yermak Plateau. At the Svalbard Margin, maldanid polychaetes and sipunculans, previously reported in the literature to adopt a ‘caching’ strategy, accounted for a significant proportion of the macrofauna from the multiple corer and boxcorer samples. At Bear Island Fan, sipunculans previously reported to adopt a ‘caching’ strategy were recorded but did not contribute to significant proportion of the benthic community. However, if there had been more intense sampling at a number of stations on the Bear Island Fan then species known to adopt a ‘caching’ strategy may have contributed to an overall significant component of the benthic community at this location.

### 3.4.5 Feeding groups

The hypothesis that the macrofaunal community at all sampling stations will be characterised by the same feeding group irrespective of the periodicity of nutrient flux can be rejected. Surface deposit feeders were the most abundant polychaete and macrofaunal community feeding type at Bear Island Fan and a similar pattern was observed at the Svalbard Margin and Yermak Plateau, two stations strongly influenced by the episodic input of organic matter. However, the polychaete community of the Vøring Plateau was
characterised by sub-surface deposit feeding polychaetes, an area where organic matter input can also occur episodically (Graf 1989; 1992) from mainly pelagic sources (Romero-Wetzel and Gerlach 1991). Further analysis of macrofaunal community dissimilarity between stations revealed two members of the community with a significantly greater abundance or biomass at the Vøring Plateau than at the other stations, the sipunculan, *Nephasoma* sp. and the ophiuroid, *Ophiocten gracilis*.

Individual species that contribute to a large proportion of total macrofaunal biomass are likely to consume or redistribute a large quantity of available organic matter that reaches the sea bed. At the Vøring Plateau, *O. gracilis* accounted for a significant component of relative biomass and, in the deep sea, ophiuroids are generalist feeders (Gage and Tyler 1991), with no dietary specialisations comparable to those of the polychaetes. The presence of ophiuroids on soft sediment can lower the abundance of polychaetes and sedentary surface deposit feeders in the upper few centimetres of the sediment column (Ambrose 1993). The occurrence of *O. gracilis* at the Vøring Plateau may explain the lower relative abundance and biomass of surface deposit feeders but does not explain the increased density and biomass of sub-surface deposit feeders, since *O. gracilis* would not redistribute organic matter deep down the sediment column to the benefit of sub-surface deposit feeders. Rapid subduction of organic matter deep down the sediment column at the Vøring Plateau was previously associated with the sipunculan, *Nephasoma* sp. (Graf 1989). At the North Carolina continental margin, a high abundance of sub-surface deposit feeders was associated with tube-building maldanid polychaetes redistributing fresh organic matter down the sediment column (Levin *et al.* 1997).

### 3.4.6 Bioturbation potential

Macrofaunal community bioturbation potential at Bear Island Fan was characterised by surficial modifiers. $^{210}$Pb profiles indicated a maximum sediment mixing depth of between
8-10 cm at Bear Island Fan, Svalbard Margin and Yermak Plateau, while the Vøring Plateau had the shallowest mixing depth of 2-3 cm (T. Shimmield, pers. comm.). This was surprising because head-up/head-down feeders were characteristic of the bioturbation potential of the macrofaunal community at the Vøring Plateau, and sediment mixing depth greater than 2-3 cm was expected. In addition, there was no evidence of intense sediment mixing at either the Vøring Plateau or Bear Island Fan from the $^{210}\text{Pb}$ profiles (T. Shimmield, pers. comm.).

### 3.5 Summary and Conclusions

With regard to the hypotheses proposed within the introduction the following conclusions can be drawn:

1. **Body size:** There was no significant difference in the mean individual biomass of fauna at each station. However, the Svalbard Margin, located within the marginal ice zone had significantly the greatest abundance of larger individuals (>1 mm). There was evidence of the presence of burrowing megafauna only at the Yermak Plateau. The significantly lowest proportion of larger macrofauna occurred at the Vøring Plateau and not Bear Island Fan. Therefore, the hypothesis that all stations, irrespective of organic flux will have the same proportion of large bodied macrofauna can be rejected.

2. **Occurrence of ‘caching’:** Taxa previously reported to adopt a ‘caching’ strategy of organic matter formed a significant component of the benthic community at the Vøring Plateau, Svalbard Margin and Yermak Plateau. Therefore, the hypothesis can be rejected that taxa adopting a ‘caching strategy will be equally abundant at each of the four sampling stations.

3. **Feeding mode:** Sub-surface deposit feeding polychaetes only contributed to a significant component of the polychaete community at the Vøring Plateau. Surface
deposit feeders were characteristic of the polychaete community at the other three stations. The hypothesis that all sampling areas will be characterised by surface deposit feeders can be rejected.

The rejection of all hypotheses presented within the chapter indicates that macrofaunal community structure along the Norwegian continental margin may be influenced by contrasting fluxes of organic matter. Information on the pulsed input of organic matter at each station sampled on the Vøring Plateau, Svalbard Margin and Yermak Plateau is based on historical data. Patterns in community structure will not solely be influenced by the flux of organic matter to the sea bed but also by variation in other environmental factors including sediment heterogeneity and flow velocity. Salinity and water temperature were fairly consistent at each of the stations; therefore, observed variations in community patterns between the stations may be independent of salinity and water temperature. At Bear Island Fan, the lateral advection of organic matter associated with increased flow velocities appears to influence the benthic standing stock of suspension feeders. Differences in the macrofaunal community at the Yermak Plateau may be influenced by the shallower water depth of this station, as the bathymetric distribution of individual species can be influenced by changes in hydrostatic pressure. Individual species that are known to adopt the sub-surface storage of organic matter accounted for a significant component of the macrofaunal community in areas where the flux of organic matter occurs episodically. There were no patterns in mean individual biomass of the macrofauna that could be associated with contrasting fluxes of organic matter. However, adopting the methods of Kaariainen and Bett (2006) for a more detailed analysis of individual body size for the macrofaunal community in future studies may reveal patterns that relate to organic matter input. Data from four stations was presented within this chapter, and it is therefore difficult to provide a larger regional overview based on a small sample size. However,
future studies on benthic community structure in relation to organic flux within the Nordic Seas region should assist in providing data that can be combined for a larger regional overview.
4 Biodiversity patterns of the macrofaunal community along the Norwegian Sea continental margin

4.1 Introduction

Within the deep sea, high diversity of the benthos on the local scale is now well established (Hessler and Jumars 1974; Grassle and Maciolek 1992; Snelgrove and Smith 2002). There have been a number of hypotheses put forward suggesting why there are potentially so many species occurring within the deep sea. Generally, hypotheses fall into two broad categories of equilibrium (relatively unchanging environment) and non-equilibrium hypotheses (reviewed by Snelgrove and Smith 2002). As yet, none of the hypotheses provide a unified theory explaining diversity patterns in one of the largest and possibly most species-rich biotopes on Earth (Grassle and Maciolek 1992; Snelgrove and Smith 2002).

The abyssal plains cover a huge area of the ocean basins and environmental conditions are relatively stable at the sea floor. However, in contrast to the abyssal plains, the continental margins experience extreme environmental changes along a depth gradient and, at mid-slope, species diversity appears to reach its maximum within the deep sea (Carney et al. 1993). Species patterns at the continental margins are influenced by recognised gradients in abiotic factors with increasing depth; including a reduction in light penetration, increasing hydrostatic pressure, decreasing temperature and often the presence of oxygen minimum zones (Carney 2005). In addition, a reduction in the availability of food with depth is an important factor that influences the benthic fauna. Many of the studies on diversity patterns at the continental margins have focused on variation in patterns along depth gradients; see Carney (2005) for review.
In contrast, a limited number of studies have focused on species diversity at similar depths along-slope of continental margins (Schaff et al. 1992; Schnack 1998). At the North Carolina continental margin, Western Atlantic, variation in species richness and community structure along-slope was linked with changes in the quantity of food available (Schaff et al. 1992). In both marine and terrestrial environments, there is a unimodal relationship between species richness and food supply (Figure 3.1) (Rosenzweig and Abramsky 1993; Waide et al. 1999; Levin et al. 2001). The influence of food supply and productivity on diversity within the deep sea was reviewed in detail by Levin et al. (2001). Essentially, diversity will be low when food levels are low because resources would not be sufficient to support viable populations of many species. Then, as food supply increases, diversity would increase because the number of viable populations of individual species that can be supported within the community increases.

**Figure 4.1** Patterns of diversity change along a food input gradient in the deep sea and the biotic interactions hypothesized to be responsible for generating diversity patterns. Adapted from Levin et al. (Levin et al. 2001).
A decline in diversity has been associated with high food levels (Figure 4.1) (Levin et al. 2001). It is not clear why diversity would decrease at high food levels, but it may be caused by decreased sediment heterogeneity, resulting in an increase in dominance by a few species (Rosenzweig and Abramsky 1993) and/or an increase in physiological stress associated with sulphide toxicity or a reduction in sediment oxygen concentrations (Sanders 1969; Schaff et al. 1992). In the terrestrial environment, there is often a direct link between species richness and net productivity (van Rensburg et al. 2002) and productivity is one of the many factors that can influence a poleward decline in species richness (Begon et al. 2006). Therefore, along-slope variation in species richness and community structure on continental margins could be influenced by contrasting fluxes of organic matter to the sea floor.

Within the deep sea of the northern hemisphere a poleward decline in species richness has previously been described for molluscs, isopods, cumaceans, nematodes and foraminiferans (Rex et al. 1993; Boucher and Lambshead 1995; Rex et al. 1997; Culver and Buzas 2000; Lambshead et al. 2002; Gage et al. 2004). However, several taxa do not support this poleward trend, including polychaetes and nematodes (Kendall and Aschan 1993; Dauvin et al. 1994; Lambshead et al. 2000; Lambshead et al. 2001). The environmental factors that influence diversity patterns are not homogenous throughout the Arctic and result in the contrasting diversity patterns previously observed within the region. Few studies on latitudinal gradients in species diversity have extended sampling into the Arctic because of operational difficulties associated with permanent ice coverage. However, recently a poleward decline in nematode and macrofaunal diversity was observed within the Arctic (Renaud et al. 2006), and possibly reflected primary production (Gosselin et al. 1997). Within the Arctic, permanent ice coverage strongly influences primary production and the flux of organic matter to the sediment (von Bodungen et al. 1995). The availability of food in the region has been reported to correlate with

Compared with the rest of the North Atlantic, the high latitude Nordic Seas region generally has a lower diversity (Rex et al. 1993; Rex et al. 1997). Low diversity within the region is believed to have been influenced by recent Quaternary glaciations (Dahl 1972; Svavarsson et al. 1993). Certainly, on the time scales of $10^3$-$10^4$ years, variation in deep-sea diversity appears to be coherent with glaciation cycles (Cronin and Raymo 1997). More recently, the benthic community of the Norwegian Basin may have been affected by massive sediment flows (~1700 km$^3$ of sediment) of the second Storegga Slide that occurred 6,000-8,000 years ago (Bugge et al. 1988). Biogeographical isolation may have limited recolonisation and maintained low diversity within the region. The absence of some North Atlantic genera of isopods in the deep Norwegian Sea does suggest isolation from the rest of the Atlantic (Svavarsson et al. 1993). Low diversity in the Norwegian Sea is likely a result of the region being the terminal point of a long colonisation route from the south (Sepkoki and Rex 1974; Rex et al. 1997).

The majority of studies on deep-sea macrofaunal diversity within the North Atlantic have taken place between 50°N and 65°N (Rowe et al. 1991; Gage et al. 2000; Narayanaswamy et al. 2003). At higher latitudes, diversity studies have predominately focused on a limited number of macrofaunal taxa, most notably gastropods, bivalves, isopods, cumaceans and polychaetes (Svavarsson et al. 1990; Rex et al. 1993; Dauvin et al. 1994; Rex et al. 1997; Gage et al. 2004). However, the macrofaunal community has been quantitatively sampled at different locations within the deep Nordic Seas, although only a few studies have analysed diversity patterns. Sampling has previously taken place at the Voring Plateau (Romero-Wetzel and Gerlach 1991), Svalbard Margin (Wlodarska-Kowalczuk et al. 2004), Yermak Plateau (Kröncke 1998), Greenland Margin (Schnack 1998) and the Greenland and Norwegian Basins (Dahl et al. 1976). However, direct
comparisons between previous studies are difficult to draw because of differences in sampling techniques and the personnel that identified the fauna. The identification of fauna to species level often depends on the experience and expertise of the individuals involved in the study. Studies of macrofaunal communities with a polychaete component generally have a higher species number and abundance when personnel were either polychaete specialists or focused on the polychaete component of the community (Knox 1977). Comparisons between previous studies are even more difficult to determine given the increasing evidence that many apparently cosmopolitan species within the marine realm are in fact complexes of sibling species (Knowlton 1993).

When measuring diversity there are two independent factors that should be considered: species richness (the number of species) and species evenness (the number of individuals for each species) (Magurran 1988). It is essential that the measure of diversity is distinguished from either ‘inventory diversity’ (the diversity within a specific area) or ‘differentiation diversity’ (turnover of species between areas) (Whittaker 1972). Furthermore, diversity can be measured on varying spatial scales as first described by Whittaker (Whittaker 1965) and later reviewed by Gray (Gray 2000). Those four scales of species richness are point species richness, sample species richness, large area species richness and biogeographical province species richness. Two other types of diversity, habitat species richness and assemblage species richness are not a measure of scale but instead of the habitat and assemblage (Gray 2000). Four common measures of diversity within the marine realm are listed below:

1. Sample species richness. This is a measure of diversity within a single sample.
2. Alpha or within-habitat diversity. Provides a measure of diversity within a single habitat or sampling location.
3. Beta or between-habitat diversity. Allows the measure of species turnover between sampling locations, habitats and/or community boundaries.
4. **Gamma diversity.** A measure of diversity on a regional scale covering a larger area than alpha diversity.

*Alpha diversity:* A decrease in diversity with increasing latitude in the deep North Atlantic was associated with low species richness in the Norwegian Sea (Gray 1994; Rex *et al.* 1997). However, information on diversity patterns within the Nordic Seas region is limited (Svavarsson *et al.* 1993). The distribution of species along the Norwegian continental margin is unlikely to be limited by geographical barriers. Therefore, diversity patterns along the Norwegian continental margin could be related to contrasting inputs of organic matter associated with ice-free and ice-covered regions (Figure 4.2).

*Beta diversity:* In coastal waters, some species of deposit feeders will feed on lipid-rich sea-ice algae in preference to planktonic diatoms, when both food sources are available (McMahon *et al.* 2006). Furthermore, some deep-sea fauna can selectively feed on particles depending on their size (Wheatcroft 1992) and age (Smith *et al.* 1993). The composition of species at stations located within the marginal ice zone should contain species that preferentially feed on organic matter associated with ice edge processes.

Within this chapter, alpha and beta diversity of the macrofaunal community will be discussed within the context of the Nordic Sea region and the following hypotheses tested:

1. Diversity, including species richness and evenness, will not vary between stations and be independent of ice cover.

2. Species composition will not vary between stations and be independent of ice coverage.

Hypothesis 1 will be discussed in the context of alpha diversity and hypothesis 2 will be discussed in the context of beta diversity.
Figure 4.2 Average Arctic ice cover and ice drift patterns in winter (upper panel) and summer (lower panel) are basically influenced by the distribution of high and low pressure over the Arctic region. Interannual variability is significant. Taken from Wassman et al. (2006).
4.2 Methods

4.2.1 Study Sites

Three multiple corer samples were obtained from each of the four continental margin stations located along a latitudinal transect that were selected for sampling at a depth of 1400 m during the RRS James Clark Ross cruise 75 between 14 June and 11 July 2002 (Figure 4.3). Pack ice prevented the collection of samples from 1400 m at the Yermak Plateau and instead, samples were collected from a depth of 900 m. Sample collection and station details are summarised in Table 4.1. Additional information on the study sites is provided in the materials and methods chapter. Samples were collected by my supervisor Dr David Hughes and co-workers.

Figure 4.3 Stations are marked with a black circle (•). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.
Table 4.1 Summary of environmental and sampling data for each station. Bottom water temperature and salinity (F. Cottier, pers. comm.), sediment grain size (J. Howe, pers. comm.), sediment C\textsubscript{org} content and Chl\textsubscript{a} profiles (T. Brand, pers. comm), 210Pb mixed layer depths (T. Shimmield, pers. comm.).

<table>
<thead>
<tr>
<th>Station Designation</th>
<th>Vøring Plateau</th>
<th>Bear Island Fan</th>
<th>Svalbard Margin</th>
<th>Yermak Plateau</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nominal position</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>VP 67° 13.0' N</td>
<td>73° 39.6' N</td>
<td>78° 58.4' N</td>
<td>80° 45.0' N</td>
</tr>
<tr>
<td></td>
<td>06° 05.6' E</td>
<td>13° 47.0' E</td>
<td>06° 42.5' E</td>
<td>07° 38.7' E</td>
</tr>
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<td>1440 - 1445</td>
<td>1380 - 1385</td>
<td>880 - 930</td>
</tr>
<tr>
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<td>-0.9</td>
<td>-0.7</td>
<td>-0.5</td>
</tr>
<tr>
<td>temperature (°C)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Bottom water</td>
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<td>34.9</td>
<td>34.9</td>
<td>34.9</td>
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<td></td>
<td></td>
</tr>
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<td>- Sand</td>
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<td>10.1</td>
<td>11.2</td>
<td>3.7</td>
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<tr>
<td>- Silt</td>
<td>74.0</td>
<td>60.7</td>
<td>64.2</td>
<td>65.7</td>
</tr>
<tr>
<td>- Clay</td>
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<td>29.2</td>
<td>24.6</td>
<td>30.6</td>
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<td>28.4</td>
<td>15.5</td>
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<td>C\textsubscript{org} inventory, 0 – 10 cm (mg cm\textsuperscript{-2})</td>
<td>46.5</td>
<td>35.8</td>
<td>76.1</td>
<td>62.2</td>
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<tr>
<td>Chl-a inventory, 0 – 10 cm (µg cm\textsuperscript{-2})</td>
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<td>0.03</td>
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<td>0.09</td>
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<td>Mixed layer depths, 210Pb (cm)</td>
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<td>Multiple corer drops</td>
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<td>3</td>
<td>3</td>
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<tr>
<td>Number of cores retained</td>
<td>21</td>
<td>14</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>Multiple cores, total area analysed (cm\textsuperscript{2})</td>
<td>593.7</td>
<td>395.8</td>
<td>452.3</td>
<td>452.3</td>
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<tr>
<td>Total number of individuals</td>
<td>336</td>
<td>128</td>
<td>274</td>
<td>191</td>
</tr>
</tbody>
</table>

4.2.2 Analysis of Species Diversity

Alpha diversity, or within habitat diversity was estimated with six univariate analyses of untransformed data using “DIVERSE” in Primer® version 6. The six univariate analyses selected to measure diversity were Shannon’s diversity ($H'$), Pielou’s evenness ($J'$), Hurlbert’s rarefaction index, E($S_n$), Simpson’s index ($D$), Fisher’s logarithmic series model ($\alpha$) and Chao 1.
• Shannon’s diversity \((H')\) assumes that all individuals are randomly sampled from an infinite population and all species are represented in the samples. Shannon’s diversity \((H')\) was estimated as:

\[
H' = -\sum p_i \cdot \log_e p_i
\]

Where \(p_i\) = the relative abundance of the \(i\)th species.

• Pielou’s evenness \((J')\), is the ratio of the observed diversity to the maximum diversity, giving an indication of the distribution of individuals among species, and was estimated as:

\[
J' = \frac{H'}{\log S}
\]

Where \(S\) = total number of species observed at the station.

• Hurlbert’s modification of Sanders rarefaction index, \(E(S_n)\), (Hurlbert 1971) gives an indication of the number of species expected in a sample of \(n\) individuals and was calculated for 20 individuals, \(E(S_{20})\) and 100 individual, \(E(S_{100})\).

• Fisher’s logarithmic series model \((\alpha)\) describes the relationship between the number of species and the number of individuals of each species from the population (Fisher et al. 1943).

• Simpson’s index \((D)\) is weighted towards the abundance of the most common species rather than providing a measure of species richness and was estimated as:

\[
D = 1 - \sum \left(\frac{n_i \cdot (n_i - 1)}{N \cdot (N - 1)}\right)
\]

Where \(n_i\) = the number of individuals in the \(i\)th species and \(N\) = the total number of individuals.

• Chao 1 is an estimator of the absolute number of species in an assemblage and is based on the number of rare species in a sample (Chao 1984)

\[
S_{\text{Chao 1}} = S_{\text{obs}} + \frac{F_1^2}{2F_2}
\]

Where \(S_{\text{obs}}\) = number of species in a sample

\(F_1\) = the number of observed species represented by a single individual

and \(F_2\) = the number of species represented by two individuals.
The histograms for each of the above univariate indexes were produced using Sigmaplot® version 10. Differences in the univariate analysis between each station were evaluated using a two-tailed non-parametric Mann-Whitney \( U \)-test in Minitab® version 14. To measure distributional patterns in diversity, both species counts per unit area and Hurlbert’s rarefaction index were calculated in Primer® version 6 and plotted in Sigmaplot® version 10. A cumulative species dominance curve was produced to visualise differences in species dominance between stations.

Beta diversity or between-habitat diversity was estimated with a Kulczynski (1927) presence/absence similarity index based on pooled data. This index calculates the similarity between stations based on the presence and absence of shared and unique species. Primer® version 6 was used to produce dendrogram representations and MDS ordination of Kulczynski’s index for group average clustering of Bray-Curtis similarities. In addition, dendrogram representations and MDS ordination for group average clustering of Bray-Curtis similarities were produced for presence and absence of species to limit the influence of dominant species in the analysis (Clarke and Warwick 2001). Canoco for Windows was used to produce the canonical correspondence analysis.

4.3 Results

4.3.1 Species Abundance

For information on macrofaunal abundance, please see Chapter 2. In total, 135 nominal species were recorded along the latitudinal transect at the Norwegian continental margin (Table 4.2). The majority of specimens were identified to a known genus and almost 50% of species recorded were polychaetes. Polychaetes, crustaceans and molluscs were the most species-rich groups.
Table 4.2 List of species and number of individuals recovered at each station.

<table>
<thead>
<tr>
<th>Major taxa</th>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Voring Plateau</th>
<th>Bear Island Fan</th>
<th>Svalbard Margin</th>
<th>Yermak Plateau</th>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet E</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet F</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet B</td>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ischnosoma</td>
<td>bispinosum</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tanaidae</td>
<td>indet A</td>
<td>3</td>
<td>6</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet B</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet C</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet D</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet E</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet F</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet A</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>indet B</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sphyraphus</td>
<td>anomalous</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Total number of species sampled: 29 31 31 21 23 18 39 43 39 30 28 15
Total number of individuals sampled: 100 134 102 45 47 36 76 95 103 85 84 22
Number of cores retained: 7 8 6 4 5 5 5 5 6 7 7 2
Total area sampled (cm²): 197.89 226.16 169.62 113.08 141.35 141.35 141.35 141.35 169.62 197.89 197.89 56.54
Table 4.3 The number of individuals and nominal species recorded at each station and for all stations combined.

<table>
<thead>
<tr>
<th></th>
<th>Vøring Plateau</th>
<th>Bear Island Fan</th>
<th>Svalbard Margin</th>
<th>Yermak Plateau</th>
<th>All Stations Combined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of individuals</td>
<td>336</td>
<td>128</td>
<td>274</td>
<td>191</td>
<td>929</td>
</tr>
<tr>
<td>Number of nominal species</td>
<td>52</td>
<td>43</td>
<td>75</td>
<td>45</td>
<td>135</td>
</tr>
</tbody>
</table>

4.3.2 Alpha Diversity

Values for a number of univariate measures of alpha diversity were measured for each of the multiple corer samples. Species richness was expressed in two ways: (1) as the number of species present per unit area sampled (cm$^2$), a plot is presented for species density for each station, (Figure 4.4); and (2) numerical species richness, given as the number of species in a sample of a specified number of individuals, Hurlbert’s rarefaction, $E(S_n)$, (Figure 4.5). Hurlbert’s rarefaction provides a method for comparing numerical species richness when there are different abundances at each station. The number of new species discovered increased more rapidly at the Svalbard Margin with increasing area sampled than at any of the other stations (Figure 4.4). Similarly, as the number of individuals sampled increased, the number of new species discovered showed the greatest increase at the Svalbard Margin (Figure 4.5). This indicates that the Svalbard Margin has the highest species richness with little difference in species richness between the other stations. It should be noted that the rarefaction curves (Figure 4.5) appear not to have reached an asymptote at any of the stations. Therefore it is unlikely that all species have been sampled at each station. Increasing the number of individuals sampled would increase the likelihood of the rarefaction curve for each station reaching an asymptote.
Figure 4.4 Number of species per area sampled.

Figure 4.5 Rarefaction curves for pooled sample data at each station.
Mann-Whitney U-tests (95% confidence interval) revealed no statistical difference between the stations in the $J'$, $H'$, $E(S_{20})$, $D$ and $\alpha$ univariate measures of diversity (Figure 4.6). However, the measures of diversity were significantly different between some of the stations for a Mann-Whitney U-test confidence interval of 91.9% (Table 4.4). Svalbard Margin had a significantly greater diversity than both the Bear Island Fan and Yermak Plateau for each of the measures of diversity. The dominance of individual species was lowest at the Svalbard Margin, with little difference in species dominance between the other stations (Figure 4.7). There was no significant difference between stations in the distribution of individuals among species from analysis with Pielou’s evenness (Figure 4.6(b)). The paraonid polychaete *Aricia abranchiata* was the most abundant species at each station. Table 4.5 lists the five most abundance species at each station and the relative proportion of total macrofaunal abundance.

**Table 4.4** Mann-Whitney U-test results for each measure of diversity at the 91.9% confidence interval. Significant results are highlighted with *. VP = Vøring Plateau, BIF = Bear Island Fan, SM = Svalbard Margin, YP = Yermak Plateau.

<table>
<thead>
<tr>
<th>Stations</th>
<th>Shannon's, $H'$</th>
<th>Pielou's, $J$</th>
<th>Rarefaction, $E(S_{20})$</th>
<th>Simpson’s, $1 - \lambda$</th>
<th>Fisher’s, $\alpha$</th>
</tr>
</thead>
<tbody>
<tr>
<td>VP – BIF</td>
<td>0.219, 0.450*</td>
<td>-0.0243, 0.0043</td>
<td>-0.236, 0.762</td>
<td>0.0107, 0.0257*</td>
<td>-5.149, 0.833</td>
</tr>
<tr>
<td>VP – SM</td>
<td>-0.500, -0.280*</td>
<td>-0.0525, -0.0125*</td>
<td>-2.974, -1.494*</td>
<td>-0.0322, -0.0146*</td>
<td>-19.493, -7.706*</td>
</tr>
<tr>
<td>VP – YP</td>
<td>-0.070, 0.382</td>
<td>-0.0971, -0.0108*</td>
<td>-1.530, -0.207*</td>
<td>-0.0269, 0.0007</td>
<td>-19.493, -7.706*</td>
</tr>
<tr>
<td>BIF – SM</td>
<td>-0.922, -0.527*</td>
<td>-0.0446, -0.0004*</td>
<td>-3.460, -1.535*</td>
<td>-0.0548, -0.0284*</td>
<td>-17.822, -5.064*</td>
</tr>
<tr>
<td>BIF – YP</td>
<td>-0.492, 0.135</td>
<td>-0.0892, 0.0013</td>
<td>-2.015, -0.0495</td>
<td>-0.0131, 3.096</td>
<td>-2.11, 17.44*</td>
</tr>
<tr>
<td>SM - YP</td>
<td>0.239, 0.854*</td>
<td>-0.0724, 0.0295</td>
<td>0.241, 2.490*</td>
<td>-0.0092, 0.0298</td>
<td>2.11, 17.44*</td>
</tr>
</tbody>
</table>
Figure 4.6  Alpha diversity statistics versus station. (a) Shannon’s diversity $H'$; (b) Pielou’s $J$; (c) Hurlbert rarefaction index for 20 individuals $E(S_{20})$; (d) Simpson’s diversity, as $1-\lambda$; (e) Chao 1; (f) Fisher’s logarithmic series model $\alpha$. The error bars represent 95% confidence intervals. VP= Voring Plateau, BIF= Bear Island Fan, SM= Svalbard Margin, YP= Yermak Plateau.
Figure 4.7 Ranked species cumulative dominance.

Table 4.5 The relative abundance of the five most abundant species at each station. All species are polychaetes unless (C) crustacean, (E) echinoderm, (N) nemerteans.

<table>
<thead>
<tr>
<th></th>
<th>Voring Plateau %</th>
<th>Bear Island Fan Species</th>
<th>Svalbard Margin Species</th>
<th>Yermak Plateau Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aricidea abranchiata</td>
<td>12.2</td>
<td>Aricidea abranchiata</td>
<td>Aricidea abranchiata</td>
<td>Aricidea abranchiata</td>
</tr>
<tr>
<td>Notomastus sp.A</td>
<td>11.6</td>
<td>Tanaid sp. C (C)</td>
<td>Minuspio cirrifera</td>
<td>Aphelochaeta sp.A</td>
</tr>
<tr>
<td>Sabellid sp.A</td>
<td>8.3</td>
<td>Haploops setosa (C)</td>
<td>Sabellid sp.D</td>
<td>Chaetozone setosa</td>
</tr>
<tr>
<td>Nephasoma abyssorum</td>
<td>7.1</td>
<td>Chaetozone sp.B</td>
<td>Ilyarachna sp.C (C)</td>
<td>Ilyarachna sp.B (C)</td>
</tr>
<tr>
<td>Minuspio cirrifera</td>
<td>6.6</td>
<td>Ophiura sp.A (E)</td>
<td>Nemertea sp.A (N)</td>
<td>Chaetozone sp.B</td>
</tr>
</tbody>
</table>
4.3.3 Beta Diversity

The degree of change in species composition between stations was analysed using multivariate statistics. Analysis of the presence and absence of each species revealed that the fauna at each station appeared to be distinct, with the exception of a single Bear Island Fan sample (BIF_927) grouped with the Vøring Plateau samples and a single Vøring Plateau sample (VP_869) group with the Svalbard Margin samples (Figure 4.8 and 4.9). Similarity in the overall species presence and absence at each station was low at just over 20%. A stress factor of 0.13 for the non-metric multi-dimensional scaling indicates a potentially useful 2-dimensional ordination space, and suggests that each station differs from the other locations in species composition (Figure 4.9).

Figure 4.8 Dendrogram of Bray-Curtis similarities of presence and absence of species in each sample.
Finally, Beta diversity was also expressed as a turnover of species between the stations, and analysed using a Kulczynski presence and absence similarity index. The dendrogram representation (Figure 4.10) revealed the two southern stations (VP and BIF) clustered separately from the two northern stations (SM and YP) with about 30% similarity between all stations. The numerical abundance of different species categories was calculated using the method of Glover et al. (2001) to assess the significance of the geographical clustering of species composition (Figure 4.11). Although about 20% of abundance at each station was accounted for by species that were unique to that station, the majority of community abundance was composed of species that were found at all stations. Bear Island Fan was the only station in which species that occurred at all stations (4 stations) accounted for about 50% of abundance. A list of species occurring at all stations is provided in Table 4.2.

**Figure 4.9** nMDS of Bray-Curtis similarities of presence and absence of species in each sample.
Figure 4.10 Dendrogram of Bray-Curtis similarities of Kulczynski presence and absence of species at each station.

Figure 4.11 Percentage abundance contribution histograms indicating the composition of fauna at each station. 4 stations = occurred at every station; 3 stations = occur at any three stations; 2-stations widespread = occur at any two stations; 2-stations regional = occur only at the two southern stations (VP and BIF) or two northern stations (SM and YP); 1 station = only occurring at one station. Stations: Vøring Plateau (VP), Bear Island Fan (BIF), Svalbard Margin (SM), Yermak Plateau (YP), all stations combined (AS).
Results from the canonical correspondence analysis of the 20 most abundant species are presented in Figure 4.12. The majority of the species are clustered in the middle of the canonical correspondence analysis (Figure 4.12), with a few individual species clustered with the Yermak and Vøring Plateau stations. None of the environmental factors measured accounted for the variability of the 20 most abundant species at each of the stations. One
group of species, including *Nemertea* indet. D, *Ilyarachna* indet. C and *Sabellidae* indet. B appear to be closely related to the temperature vector and another group appear to be closely related to the Chl-a vector.

**Table 4.6** Results from the canonical correspondence analysis (CCA) for the 20 most abundant species.

<table>
<thead>
<tr>
<th>Axes</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCA</td>
<td>0.59</td>
<td>0.46</td>
<td>0.43</td>
<td>0</td>
</tr>
<tr>
<td>Species-environment correlation</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

### 4.4 Discussion

#### 4.4.1 Overview of Hypotheses

The results that relate to the findings for each hypothesis will be discussed in detail within this discussion section. An overview of the findings related to each hypothesis is presented below:

1. The hypothesis that diversity, including species richness and evenness, will not vary between stations can be rejected.

2. The hypothesis that species composition will not vary between stations and is independent of ice coverage can be rejected.

#### 4.4.2 Rarefaction Issues

Within deep-sea studies, one of the most widely employed measures of species richness is Hurlbert’s rarefaction, $E(S_n)$. This standard rarefaction is based on estimating the numbers of species, $S$, found in a sample of $n$ individuals, $E(S_n)$. When considering species richness patterns it is important to consider the scale of the study. This study, along a latitudinal
transect covers a large spatial scale but species richness is specific to the samples from each station and so covers a much smaller spatial scale (Gray 2000). Therefore, Hurlbert’s rarefaction will provide sample species richness between each station sampled along the latitudinal transect but not of large scale species diversity patterns.

Hurlbert’s rarefaction is sensitive to both evenness and richness (Gage and May 1993) and often is employed by marine biologists to estimate the numbers of species in a sample of a fixed number of individuals, for example in Figure 4.6(c) for 20 individuals, E(S_{20}). Species evenness is consistent between the stations at the 95% confidence interval (Figure 4.6(b)) and is therefore unlikely to influence the results of the rarefaction analysis. However, it should be noted that at the 91.9% confidence interval, species evenness is significantly different between VP – SM, VP – YP and BIF – SM (Table 4.4). A confidence interval of 91.9% and not 95% for species evenness and the other measures of diversity (Table 3.4) is a small sampling size effect.

The reliance of rarefaction, E(S_n), on the number of individuals in a sample and therefore in a community of a fixed number of individuals, E(S_{20}), is dependent upon the number of species and relative abundance of each species (May 1993). This potential issue is described clearly by Levin et al. (2001): “a boxcore may yield 10,000 individuals from a continental shelf habitat, but fewer than 100 at greater bathyal depths. Normalizing the two samples to 100 individuals effectively compares the number of species at 9 cm$^2$ on the shelf to 900 cm$^2$ in the deep sea”. Rarefaction assumes a random distribution between the number of species and the number of individuals. The issues associated with rarefaction analysis are now well documented and can be addressed by other diversity analyses that can corroborate results. The number of species per sample area is one such useful analysis (Figure 4.4). Understanding between-habitat diversity along the sampling transect can be supported by the rarefaction analysis, but only when used in conjunction with other indices that measure beta diversity (Levin et al. 2001).
Typically, macrofaunal samples yield 24-56 species per hundred individuals sampled from deep-sea sediments (Snelgrove and Smith 2002). The accumulation of species at each of the four stations did fall within this range (Figure 4.5). However, once the accumulation of species is greater than 100 individuals at the Voring Plateau, Bear Island Fan and Yermak Plateau, species accumulation rate was less than that of Snelgrove and Smith (2002). It was only at the Svalbard Margin that the accumulation of species continued to fall within the range of 24-56 species per hundred individuals (Snelgrove and Smith 2002). This indicates that species richness in the deep Nordic Seas may be lower than in other deep-sea locations, however, to confirm this would require a greater sampling effort within the deep Nordic Seas region.

4.4.3 Alpha Diversity

The hypothesis that diversity, including species richness and evenness, will be equal throughout the Nordic Seas region and independent of ice cover can be rejected. Alpha diversity was analysed with univariate measures to determine (1) species richness and (2) species evenness of each station. Univariate analyses of species richness and evenness revealed no significant difference in diversity between any of the stations at the 95% confidence interval. However, at 91.9% confidence interval both Shannon’s diversity and the rarefaction analysis are significantly greater at Svalbard Margin than at the other stations (Figure 4.6). A higher species richness at Svalbard Margin is supported by Hurlbert’s rarefaction curve (Figure 4.5) and the species accumulation curve (Figure 4.4) that both indicate a higher species richness at the Svalbard Margin. However, overall diversity of the macrofaunal community showed little variation among the other stations. Svalbard Margin, with the highest species richness (Figures 4.5), had a significantly greater macrofaunal abundance than Bear Island Fan or the Yermak Plateau, see Chapter 2. Potentially, a greater abundance of individuals can influence the outcome of rarefaction
analysis, but the higher accumulation of species per sample area at Svalbard Margin (Figure 4.4) supports the findings from the rarefaction curve (Figures 4.5). The higher species richness at the Svalbard Margin may be due to the closer proximity of the station to the more productive coastal waters of the Kongsfjord and therefore a greater supply of organic matter that can support more species within a population.

A limited number of studies have investigated alpha and beta diversity within the deep waters of the Nordic Seas region. To compare results with previous studies it was essential to Analyse alpha diversity using the same univariate indices as employed previously. When it comes to Shannon’s diversity index, $H'$, the convention in marine studies according to Gage et al. (Gage et al. 2000) is to calculate diversity using log$_2$. However, Shannon’s, $H'$, was calculated using log$_e$ to allow for comparison with a previous study at the Svalbard Margin. Wlodarska-Kowalczuk et al. (Wlodarska-Kowalczuk et al. 2004) sampled along a depth transect that extended from the coastal waters of Svalbard down the continental margin to a maximum depth of 3000 m. One of their stations was located at a water depth (1500 m) slightly deeper than the station (1400 m) in the present study. When Shannon’s, $H'$, is compared between the studies, the values (Shannon’s $H'$ = 3.3 to 3.5) are broadly similar to those of Wlodarska-Kowalczuk et al. (Wlodarska-Kowalczuk et al. 2004) (Shannon’s $H'$ = ~2.5 to 2.8). A similar trend was observed when Pielou’s evenness index was compared (0.91 to 0.92, this study; and ~0.78 to 0.83, Wlodarska-Kowalczuk et al. (Wlodarska-Kowalczuk et al. 2004)). The diversity index of Wlodarska-Kowalczuk et al. (Wlodarska-Kowalczuk et al. 2004) was obtained from two 0.1 m$^2$ subcores taken from a single 0.25 m$^2$ box core sample collected from 1545 m water depth. In the present study, a smaller area of 0.045 m$^2$ was sampled, and therefore it could be expected that fewer species would have been recorded in the present study.
It is difficult to determine if the difference in the diversity indices between the studies is significant because diversity indices are dependent upon a complex combination of sieve size, sampling gear, size of area sampled and size distribution of the organisms (Warwick and Clarke 1996). Sampling differences do exist between the studies, most notably in sampling gear and sieve size employed and therefore it is difficult to draw direct comparisons between the univariate diversity indices. Differences in the sampling gear can directly influences the size of the sample collected, for example the boxcorer provides a much larger sample than the multiple corer. In addition variation in sample size can influence data on the distribution of species and which in turn can influence the identification of diversity patterns. Small samples sizes and variation in sample size can influence the presence of rare species at each station. Therefore the Chao 1 estimate of the total size of the species pool (Figure 4.6 (e)), determined by the presence of rare species, will be influenced by sample size. In the majority of deep-sea studies of the benthic fauna there are normally only a few replicates which can make it difficult to draw broad scale regional conclusions on diversity patterns. However, it is possible to conclude if there are differences in diversity patterns at each individual station sampled. Compared with stations previously sampled in the permanently ice-covered deep Arctic Ocean (Shannon’s $H’ = 0.82$ to 1.36; Pielou’s $J = 0.71$ to 0.97) (Renaud et al. 2006), alpha diversity of the Nordic Seas stations does appear to be higher, even after consideration of potential influences on the diversity indices as highlighted by Warwick and Clark (1996). However, despite the difficulties associated with comparing measures of diversity between studies it is possible to compare the species recorded between studies.

At the Vøring Plateau, six species of polychaetes were present in >50% of the 17 samples analysed by Romero-Wetzel and Gerlach (1991). Of those six species, \textit{Paramphinome jeffreysii}, \textit{Aricidea abranchiata}, \textit{Chaetozone setosa} and \textit{Myriochele fragilis} were recorded in the present study. Furthermore, \textit{Notomastus latericeus} was one of the
species recorded by Romero-Wetzel and Gerlach (Romero-Wetzel and Gerlach 1991) and a *Notomastus* species was recorded in the present study, although it was not confirmed as *N. latericeus*. The bivalve *Malletia obtusa* was recovered in 94% of the samples recovered by Romero-Wetzel and Gerlach (Romero-Wetzel and Gerlach 1991), but this species was not recorded in the present study at the Vøring Plateau, with the most abundant bivalve being *Yoldiella* indet A. In the present study, the isopod *Desmosoma lineare* was recorded in each of the replicate samples from the Vøring Plateau station. Evidence suggests there are similarities in the species composition of the present study with previous studies at the Vøring Plateau, despite differences in the sampling methods employed.

Unlike similarities at the Vøring Plateau, the species composition of the present study compared with that of the previous study of Wloderśka-Kowalczuk on the Svalbard Margin appears to be different (Weslawski *et al.* 2003; Wlodarska-Kowalczuk *et al.* 2004). In the present study, the paraonid polychaete *Aricidea abranchiata* was one of the most abundant species recorded at Svalbard Margin. However, no specimens of *Aricidea abranchiata* were reported at 1545 m on the Svalbard Margin in the previous study (Weslawski *et al.* 2003). However, *Aricidea cerruti* was reported at depths >1500 m on the Svalbard Margin by Weslawksi *et al.* (2003) from the same samples analysed by Wlodarska-Kowalczuk (2004). There are similarities (in the generic level of individual species identified) between the studies, but often there are few similarities in the allocated species name to specimens. This difference between the studies is almost certainly a result of differences in the personnel identifying specimens. Typically studies of macrofaunal communities with a polychaete component generally have a higher species number and abundance when personnel were either polychaete specialists or focused on the polychaete component of the community (Knox 1977).
4.4.4 Latitudinal Patterns in Diversity

One of the most widely recognised global diversity patterns, is the poleward decline in species richness linked to environmental gradients in predation, productivity, nutrient supply, climate and the area covered by each latitudinal zone, see Begon et al. (2006). In the deep sea, it was once believed that benthic communities were unaffected by environmental gradients that can cause large-scale diversity patterns at the surface. However, it is now known that the abundance and species composition of animals living at the deep-sea floor can be influenced by interannual variability in surface environmental conditions (Ruhl and Smith Jr. 2004). In the marine environment of the northern hemisphere, a poleward decline in species richness has been reported for some taxa, including bivalves, isopods, cumaceans, nematodes and foraminiferans (Svavarsson et al. 1990; Rex et al. 1993; Dauvin et al. 1994; Rex et al. 1997; Gage et al. 2004). However, for other taxa including polychaetes and nematodes, no such decline in species richness with increasing latitude has been observed (Kendall and Aschan 1993; Dauvin et al. 1994; Lambshead et al. 2000; Lambshead et al. 2001). Each of the studies above has looked at sample species richness and therefore does not provide an overview of beta or gamma diversity. In addition previous observed diversity patterns were focused mainly in the northeast Atlantic and so are not representative of the Arctic but of the individual stations sampled.

This poleward decline in species richness within the marine environment does appear more pronounced in the northern hemisphere than in the southern hemisphere (Rex et al. 1993; Rex et al. 1997; Gage 2004; Gage et al. 2004). In the southern hemisphere, there is no obvious poleward decline in diversity because of the high diversity of many taxa in the Antarctic (Clarke 1992). Despite limited sampling in the deep waters of the Antarctic, there does appear to be high diversity and high endemism within the region (Gage et al. 2004; Brandt et al. 2007). In contrast, low diversity and low endemism has
been reported in the much younger Arctic (Dayton et al. 1994). Furthermore, Quaternary glaciations within the Northern Atlantic potentially destroyed the deep-water fauna via low bottom-water oxygen concentrations and the shallow-water fauna via the direct impact of glaciers (Svavarsson et al. 1993; Wlodarska-Kowalczuk et al. 2004).

Species richness along the latitudinal transect did not decrease with increasing latitude and was actually highest at the Svalbard Margin, the second most northerly station. It should be noted that in order to observe any patterns in diversity that can be directly related to latitude requires samples that cover a larger latitudinal gradient than presented within this thesis. Differences in diversity between stations are more likely representative of local scale variations in the environmental conditions including sediment heterogeneity, productivity and food supply, bottom-water oxygen concentrations, deep-sea currents and disturbance events (Levin et al. 2001). The differences in diversity between the Svalbard Margin and Yermak Plateau stations may be due to differences in mean sediment grain size and sediment heterogeneity and the location of the Yermak Plateau in shallower water. On the northwest Atlantic slope, where sediment grain size was more varied then more species were found to coexist (Etter and Grassle 1992). A poleward decline in the species richness of some deep-sea taxa has previously been reported by Rex et al. (1993). Direct comparisons cannot be drawn between findings presented in this thesis and those of Rex et al. (1993). Samples from the present study are smaller in size, fewer in number, located within a single biogeographical province and testing different hypotheses, therefore creating potential problems for comparisons between the studies (Hurlbert 1971).

Sediment characteristics are known to influence benthic community structure and composition (Gray 1981). The majority of organisms living in the deep sea are deposit feeders (Gage and Tyler 1991) and are capable of selectively feeding on particles dependent on size (Wheatcroft 1992) and age (Smith et al. 1993). This biological selective particle mixing can alter sediment heterogeneity creating biological structures that are
more persistent than in shallower waters and may contribute to niche diversification (Jumars 1976; Jumars and Gallagher 1983). Furthermore, species diversity on the northwest Atlantic slope has been shown to correlate with the heterogeneity of sediment grain size over varying spatial scales (Etter and Grassle 1992). Food supply for the benthic community can further influence community structure and composition. On the western Atlantic slope, variation in species diversity and community structure was linked to the quantity of food supply (Schaff et al. 1992). At high levels of food supply, diversity may decrease and this is potentially linked to physiological stress associated with sulphide toxicity and/or a reduction in oxygen concentrations (Sanders 1969; Schaff et al. 1992).

For example on the Oman Margin, Arabian Sea, the macrofaunal community located within the oxygen minimum zone had a low diversity and high dominance (Levin et al. 2000). The influence of the hydrodynamic regime within the deep sea may influence species richness of the benthic community and disturbance events associated with ocean currents and/or sediment flows may also act to alter benthic community structure and composition (Gage 1997).

4.4.5 Beta diversity or species turnover

The hypothesis that species composition and turnover is independent of ice cover can not be rejected. Beta diversity was measured as species turnover between stations and analysed using the following approaches: (1) similarity in species composition in terms of the presence/absence of species (Figure 4.8, 4.9, 4.10), (2) determining the percentage contribution of ‘1 station’, ‘2 stations - regional’, ‘2 stations - widespread’, ‘3 stations’ and ‘4 stations’ species (Figure 4.11).

Analysis of the similarity in presence and absence of species from individual samples revealed that samples tended to cluster by station (Figure 4.8). The samples
generally clustered into two groups, those influenced by the episodic input of organic matter (VP, SM and YP) and those supported by a continual input of refractory organic matter (BIF), see Chapter 2. Variation in the sample size area and the small size of some samples will influence the low similarity in species composition observed between individual samples from a single station. A single Bear Island Fan sample (BIF_927) was clustered with the Vøring Plateau stations, but it should be noted that the small area sampled (113.1 cm$^2$) may not have provided a representative sample of the macrofaunal community. However, when the presence and absence of species is considered for samples pooled for each station a clear clustering of the two southern stations (Vøring Plateau and Bear Island Fan) and the two northern stations (Svalbard Margin and Yermak Plateau) is observed (Figure 4.10). About 40% of the macrofaunal abundance is represented by species that occur at all stations, although differences in the composition of species found between the north and south exist (Figure 4.11).

Evidence does suggest a relatively high species turnover between stations and that a north/south divide in species composition of the macrofaunal community does exist. Species turnover between stations can be influenced by a number of factors including sea-ice coverage. Wlodarska-Kowalczyk et al. (2004) reported that the species pool of the benthic community decreases with depth and is highest in the coastal waters of Kongsfjord. In the present study, about 20% of macrofaunal abundance at all the stations consisted of species that were unique to only a single station (Figure 4.11). The presence of unique species and variation in species composition will be influenced by environmental conditions on the local scale and sample size. Increasing samples size at each station would very likely result in a reduction of the relative macrofaunal abundance of unique species.

The two northern stations, located within the marginal ice zone to the west and north of Svalbard, will certainly be influenced by ice edge processes that stimulate the rapid episodic flux of particles to the sea bed (Sakshaug and Skjodal 1989; Niebauer 1991;
Andreassen et al. 1996; Peinert et al. 2001). If species composition is influenced by ice edge processes associated with the marginal ice zone, then the quantity and quality of organic matter input to the sediments must be considered. Svalbard Margin with the highest species richness had the highest content of organic carbon in the sediments (Table 4.1). Results from the canonical correspondence analysis suggest that none of the environmental variables measure account for the differences in the distribution of the 20 most abundant species (Figure 4.12). However, this does not consider the presence of rare species that may be dependent on specific environmental variables, i.e. ice cover and may explain the higher similarity between the two northern and two southern stations in terms of presence and absence of species.

Organic matter flux and associated food levels in the sediment can influence benthic diversity (Figure 4.1) (Levin et al. 2001). An interaction between productivity and diversity within the deep sea was reported off the coast of North Carolina (Schaff et al. 1992). Diversity was reduced and biomass elevated in an area with high organic matter input and slightly reduced oxygen concentrations when compared with adjacent areas at a similar depth with environmental conditions that were more typical of the deep sea (Schaff et al. 1992). A similar pattern was also observed for Foraminifera at the same location (Gooday et al. 2001). Associated with the site with reduced diversity were high sedimentation rates (>0.5 cm yr\(^{-1}\)) and high fluxes of labile carbon (Schaff et al. 1992). The benthic community of the ice-free region of the Nordic Seas is supported by the continual steady input of low quantities of refractory organic matter (Ritzarau et al. 2001). Therefore, low species richness and low diversity within the ice-free region is unlikely to be associated with high food input to the sediments.

On the Arctic shelf, it appears that benthic community patterns are not only influenced by the food availability but also disturbance levels (Dayton 1990; Grebmeier and Barry 1991). Disturbance levels are generally high in shelf seas located in marginal ice
zones due to physical disturbances (ice gouging, variable salinities, high turbidity and variable ice coverage) and biological disturbances (associated with the burrowing and feeding activities of the benthic fauna) (Piepenburg 2005). The distribution and composition of the benthic community on a regional scale appears to be primarily regulated by patterns in the quantity and quality of food availability (Graf 1992). Marginal ice zones are areas of known high benthic standing stock (Grebmeier and Barry 1991; Piepenburg 2000) influenced by the ice edge process that stimulate the pulsed sedimentation of organic matter to the sediments (Sakshaug and Skjodal 1989; Schewe and Soltwedel 2003). It does seem likely that differences in the diversity and structure of the benthic community between the two northern and southern stations is influenced by ice edge processes. Despite the data not providing enough evidence to reject the null hypothesis of no effect of seasonal ice cover on benthic diversity there were differences in the species composition between the northern stations, influenced by seasonal ice cover, and the southern stations. Species only recorded at the southern stations included Ophiocten gracilis, Acanthotrocus mirabilis, Harpina abyssi, Desmosoma lineare and Chaetozone sp A. While species only recorded at the northern stations included Ampharetinae sp A, Pseudoclymene sp A, Sabellid sp B, Prionospio indet A and Ilyarachna sp C.

4.5 Summary

Patterns in macrofaunal community diversity along the Norwegian continental margin appear to be influenced by ice cover. A significant difference in the diversity of the macrofaunal community does exist, with the Svalbard Margin station located within the marginal ice zone having the highest observed diversity. However, it is difficult to determine if any broad-scale patterns in diversity exist within the Nordic Seas due to the
limited number of stations sampled and small sample sizes. Species turnover between stations revealed a difference in the composition of the species between the northern and southern stations sampled. This difference in species turnover suggests that the distribution of species within the deep Nordic Seas could be influenced by ice cover and ice edge process. It is likely the species present at the Svalbard Margin and Yermak Plateau stations are adapted to the episodic pulse of high quality organic matter associated with ice edge processes. Organic matter flux in marginal ice zones can vary over relatively small spatial scales (kms) (Tamelander et al. 2005), and the influence of this on local scale diversity patterns needs to be determined. With regard to alpha and beta diversity the following conclusions can be drawn:

1. **Alpha diversity:** Svalbard Margin, located within the marginal ice zone had significantly the greatest diversity. However, macrofaunal diversity at the Yermak Plateau was comparable to both the Vøring Plateau and Bear Island Fan, two stations located in ice-free water. The flux of organic matter to the sea floor can vary on spatial scales of tens of kilometres within the marginal ice zone (Tamelander et al. 2005) and may influence local scale patterns in species richness and diversity. Therefore, in order to determine the influence of ice edge processes, and associated local scale fluctuations in the episodic flux of organic matter on benthic community structure would require a sampling programme covering a much smaller spatial gradient than presented within this thesis.

2. **Beta Diversity:** Species composition and abundance of the macrofaunal community varied at each station. About 40% of individuals recorded at all stations consisted of species that could be found at all stations. Species turnover between the stations indicated that species composition at the two northern stations was different from the two southern stations. Differences in species composition between the north and south are likely to be influenced by variation in the strength of pelagic-benthic
coupling and the quality and quantity of organic matter associated with ice-covered and ice-free regions. Differences in similarity between the two northern stations, Svalbard Margin and Yermak Plateau may be related to differences in sampling depth and spatial scale variations in organic matter flux associated with ice edge processes.
5 Patterns in macrofaunal community structure along two 
bathymetric transects located at the Norwegian Sea
continental margin

5.1 Introduction

Within the deep sea, the availability of organic matter is often the major factor that limits 
the standing stock of the benthic community dependent upon the flux of surface produced 
material (Rowe 1983; Galéron et al. 2000). The reported zonation of faunal assemblages 
across continental margins is influenced by a combination of environmental factors other 
than just the availability of food (Carney 2005). As water depth increases, some specific 
environmental factors have a greater influence on the benthic community, in particular the 
availability of food, flow velocity, sea bed topography and sedimentation rate (Flach 
2002). However, the benthos is a complex ecosystem and the influence of the majority of 
these environmental factors on the benthic community are coupled either directly or 
indirectly (Flach 2002) and determined by the spatial scale (Gage and Tyler 1991).

Recently in the literature, global bathymetric trends in standing stock and body size 
of deep-sea benthic communities revealed the abundance of larger animals to be lower and 
to decrease more rapidly with depth than smaller bodied animals (Rex et al. 2006). This 
work updated the classic review of Rowe (1983), that first described the rapid decrease in 
macrofaunal abundance and biomass with increasing water depth. In order to determine 
global bathymetric patterns in the benthic fauna Rex et al. (2006) compiled a database of 
2310 estimates of standing stock from 128 studies. The sampling methods employed varied 
between studies and differences in the sample gear and sieve mesh size can influence 
estimates of benthic standing stock (Bett et al. 1994; Bett and Gage 2000; Gage et al.
2002; Hughes and Gage 2004). However, despite differences in the sampling methods having a significant independent effect on the analysis of some studies, any effects associated with the different sampling methods were found to be secondary to depth (Rex et al. 2006).

Although benthic standing stock declines with increasing depth on a global scale (Rowe 1983; Rex et al. 2006) similar patterns may not be observed on smaller scales. Apparent bathymetric patterns on a regional or local scale could be influenced by factors including sediment grain size, flow velocity and food availability and, any significant independent effects may not necessarily be subordinate to depth. Following a depth transect across the continental margin off Scotland, macrofaunal abundance and biomass at a station just below the shelf (~400 m) was comparable with that at the deepest stations (~2000 m) (Gage et al. 2000). This reduced abundance and biomass on the upper slope was associated with coarse sediments and a local hydrodynamic regime of strong flow velocity (Gage et al. 2000). When this station was excluded from analysis, then bathymetric patterns in macrofaunal abundance and biomass fitted easily within the range of bathymetric patterns plotted by Rowe (1983).

There have been a limited number of studies describing trends in the macrofaunal community both across and along the Nordic Seas continental margin. Most notably a decline in macrofaunal abundance and biomass with depth was described from the shelf to the deep sea at the Svalbard Margin (Weslawski et al. 2003; Wlodarska-Kowalczuk et al. 2004) and Greenland Margin (Schnack 1998). Across the Svalbard Margin, zonation of the benthic community with depth resulted in three distinct assemblages on the shelf, slope and rise (Wlodarska-Kowalczuk et al. 2004). While on the Greenland shelf, similarities in benthic community structure between two bathymetric transects at 74°N and 79°N decreased with depth, highlighting how bathymetric community patterns can vary within a single region (Schnack 1998). Both studies at the Svalbard Margin and Greenland Margin
were located within the marginal ice zone where the benthic fauna is potentially influenced by local scale variations in organic matter flux associated with ice-edge processes (Tamelander et al. 2005).

Flow velocity and the associated lateral advection of organic matter can strongly influence benthic community structure and functional ecology at continental margins (Flach et al. 1998; Rutgers van der Loeff et al. 2002). On a local scale, variation in organic matter flux can potentially influence benthic fauna abundance, the bathymetric range of individual species and the functional ecology of the benthic community (Probert et al. 1996; Nodder et al. 2003). In the Faeroe-Shetland Channel, located in the ice-free zone of the Nordic Seas, the zonation of polychaete species downslope appeared to be determined by water temperature rather than depth (Narayanaswamy et al. 2005). Surprisingly, polychaete community biomass actually increased with depth, contradicting global patterns (Narayanaswamy et al. 2005). On the shelf and upper slope polychaetes accounted for 20-40% of total biomass and became more dominant with depth, contributing to 60-80% of total biomass on the lower slope and channel (Bett 2000a). However, when the whole macrofaunal community was considered no clear patterns in abundance and biomass could be associated with depth (Bett 2000a).

In this chapter, the benthic macrofauna across the Norwegian continental margin is characterised with respect to abundance, biomass, community size-structure, taxonomic and functional group composition and bioturbation potential. Samples were collected during a single cruise and employing a standardised method. Stations were selected along two bathymetric transects that terminated at the same oceanic basin station. Each bathymetric transect was selected for contrasting fluxes of organic matter to determine trends in macrofaunal community structure across the continental margin within a single oceanic basin. With this in mind, the following hypotheses were erected with regard to bathymetric trends in the macrofaunal community:
1. There is no change in macrofaunal abundance with increasing water depth.
2. There is no change in macrofaunal biomass with increasing water depth.
3. There is no difference between the response of larger (>500 µm) and smaller macrofauna (250-500 µm) with water depth.
4. The abundance of sub-surface deposit feeders does not vary with water depth.
5. The abundance of head-up/head-down feeders does not vary with water depth.

5.2 Methods

5.2.1 Benthic Sampling

Data for this chapter is provided by the samples collected with the mega corer during the JCR127 cruise in the summer of 2005. Information on the samples obtained at each station is provided within the material and methods chapter. A summary of environmental data and samples collected at each station is provided in Table 5.1. The location of each sampling station is provided in Figure 5.1. The initial plan was to sample five stations at 500 m depth interval along two transect across the Bear Island Fan and Vøring Plateau, with both transects terminating at the same station in the Lofoten Basin. However, poor weather conditions hampered sampling and only three stations on Bear Island Fan, two on the Vøring Plateau and the Lofoten Basin could be sampled.
Figure 5.1 Stations sampled in the summer of 2005 during the JCR127 cruise are marked with a black circle (•). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.

Table 5.1 Summary of environmental and sampling data for each station. Bottom water temperature and salinity (F. Cottier, pers. comm.). Data on sediment grain size, sediment $C_{\text{org}}$, Chl-$\alpha$ profiles and $^{210}$Pb mixed layer depths was not available at the time of printing. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.

<table>
<thead>
<tr>
<th>Station Designation</th>
<th>BIF-1</th>
<th>BIF-2</th>
<th>BIF-5</th>
<th>LB</th>
<th>VP-5</th>
<th>VP-2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nominal position</td>
<td>73° 57.47'N 15° 34.97'E</td>
<td>73° 40.20'N 13° 47.64'E</td>
<td>71° 37.96'N 06° 23.71'E</td>
<td>70° 03.11'N 03° 59.96'E</td>
<td>68° 35.69'N 04° 35.69'E</td>
<td>68° 02.02'N 05° 13.64'E</td>
</tr>
<tr>
<td>Water depth (m)</td>
<td>969-970</td>
<td>1456-1457</td>
<td>2964-2968</td>
<td>3211</td>
<td>2918-2924</td>
<td>1418-1424</td>
</tr>
<tr>
<td>Bottom water</td>
<td>-0.9</td>
<td>-0.9</td>
<td>-0.8</td>
<td>-0.8</td>
<td>-0.8</td>
<td>-0.9</td>
</tr>
<tr>
<td>temperature (°C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bottom water</td>
<td>34.9</td>
<td>34.9</td>
<td>34.9</td>
<td>34.9</td>
<td>34.9</td>
<td>34.9</td>
</tr>
<tr>
<td>salinity (psu)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megacorer drops</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>No. of cores</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>Mega cores, total</td>
<td>942.5</td>
<td>942.5</td>
<td>942.5</td>
<td>942.5</td>
<td>942.5</td>
<td>942.5</td>
</tr>
<tr>
<td>area analysed (cm$^2$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
5.2.2 Statistical Analysis

Megacorer samples were standardised to 1 m² and station means calculated for macrofaunal density and biomass. Statistical tests for Anderson-Darling normality test, Levene’s equal variance test, one-way analysis of variance and Fisher’s pairwise comparison were carried out using Minitab® version 14 computer statistical software. All data had equal variances, were normally distributed and therefore data transformation was not required prior to the one-way analysis of variance (Underwood 1997). Dendrogram representations for group average clustering of Bray-Curtis similarities were produced using PRIMER® version 6 software package of the Plymouth Marine Laboratory.

5.3 Results

5.3.1 Initial sample observations

Bear Island Fan-1 (BIF-1): The sediment was very compact and individual mega-cores only managed to penetrate to a sediment depth less than 10 cm when all eight core heads were attached to the frame. When the number of megacorer heads was reduced to four, then penetration of the sediment column was closer to 20 cm depth. Small stones and many ophiuroids were observed on the surface of each core.

Bear Island Fan-2 (BIF-2): Amphipod tubes could be observed in the majority of the cores collected from this location. A large glass sponge was recovered in sample MGC1179. There was no visual evidence of burrows at the sediment surface.

Bear Island Fan-5 (BIF-5): A dense layer of coccolithophores at a sediment depth of about 19 cm were observed in each of the cores from this station. At the sediment surface there was no visual evidence of the presence of burrows, tubes or epifauna.
**Lofoten Basin (LB):** At the sediment surface there was no visual evidence of the presence of burrows, tubes or epifauna.

**Vøring Plateau-5 (VP-5):** Fine burrows were observed below the sediment surface at this station. There was no visual evidence at the sediment surface of burrows, tubes or epifauna.

**Vøring Plateau-2 (VP-2):** Small, fine burrows were observed down to a sediment horizon depth greater than 30 cm. There was visual evidence of epifauna, mainly ophiuroids.

**Individual core abundance and biomass:**

Macrofaunal abundance and biomass estimated for each of the twelve cores at each station (three drops of four cores) is presented in Figures 5.2 and 5.3. Macrofaunal abundance estimated for each core is fairly evenly distributed at each station. Macrofaunal biomass estimated for each core is again fairly evenly distributed at each station with the exception of one core at the Lofoten Basin. The Lofoten Basin core had an estimated biomass >40 g m$^{-2}$, due to the presence of a large individual holothurion. The presence of a large holothurian highlights how rarer larger bodied fauna can have a significant influence on macrofaunal community biomass estimates.
Figure 5.2 Macrofaunal abundance estimated for each core (three drops of four cores) at each station. Station key: BIF = Bear Island Fan, LB = Lofoten Basin, VP = Vøring Plateau.

Figure 5.3 Macrofaunal biomass estimated for each core (three drops of four cores) at each station. Station key: BIF = Bear Island Fan, LB = Lofoten Basin, VP = Vøring Plateau.
5.3.2 Total Macrofauna: Abundance and Biomass

Total macrofaunal abundance (Figure 5.4) and biomass (Figure 5.5) was estimated for each station. Macrofaunal abundance and biomass declined with increasing water depth. Interestingly, the biomass of the macrofaunal community appeared to increase very slightly on the bathyal plain away from the base of the continental margin at a depth of ~3000 m (Bear Island Fan-3000 and Vøring Plateau-3000) to the deepest point in the Lofoten basin at a depth of ~3300 m. Macrofaunal abundance (250-500 μm) varied significantly between stations ($F_{5,12} = 13.64$, $P < 0.001$) (Table 5.2). The shallowest station, Bear Island Fan-1, had significantly greater macrofaunal abundance than any of the other stations. Both the Vøring Plateau-2 and Bear Island Fan-2 stations at a depth of ~1500 m had a significantly greater abundance than the three deepest stations. There was no significant difference in macrofaunal abundance between the deep continental margin stations at Bear Island Fan-5, Vøring Plateau-5 and the Lofoten Basin.

<table>
<thead>
<tr>
<th>Stations</th>
<th>Abundance (ind. m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIF1 (970 m)</td>
<td>2000</td>
</tr>
<tr>
<td>BIF2 (1457 m)</td>
<td>4000</td>
</tr>
<tr>
<td>BIF5 (2966 m)</td>
<td>6000</td>
</tr>
<tr>
<td>LB (3211 m)</td>
<td>8000</td>
</tr>
<tr>
<td>VP5 (2921 m)</td>
<td>10000</td>
</tr>
<tr>
<td>VP2 (1422 m)</td>
<td>12000</td>
</tr>
</tbody>
</table>

Figure 5.4 Numerical abundance of macrofauna from each station sampled with the megacorer (250-500 μm and >500 μm). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin. Error bars represent 95% confidence intervals.
Table 5.2 Confidence intervals (95%) for macrofaunal abundance from pairwise comparisons, columns subtracted from rows. Significant differences are highlighted with an asterix (*).

<table>
<thead>
<tr>
<th>Stations</th>
<th>BIF-1 (970 m)</th>
<th>BIF-2 (1457 m)</th>
<th>BIF-5 (2966 m)</th>
<th>LB (3211 m)</th>
<th>VP-5 (2921 m)</th>
<th>VP-2 (1422 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIF-1 (970 m)</td>
<td>(-3165, -62)*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIF-2 (1457 m)</td>
<td></td>
<td>(-3291, -1230)*</td>
<td>(-5946, -2291)*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIF-5 (2966 m)</td>
<td></td>
<td>(-4556, -1453)*</td>
<td>(-5394, -688)*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LB (3211 m)</td>
<td>(-3066, -1658)*</td>
<td>(-1658, 2103)</td>
<td>(-5394, -168)*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VP-5 (2921 m)</td>
<td>(-6169, -1658)*</td>
<td>(-4556, -1453)*</td>
<td>(-5394, -168)*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VP-2 (1422 m)</td>
<td>(-3271, -1658)*</td>
<td>(-1658, 2103)</td>
<td>(-5394, -168)*</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 5.5 Wet-weight biomass of the macrofaunal community at each station sampled with the megacorer (>500 μm). Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin. Error bars represent 95% confidence intervals.
Table 5.3 Confidence intervals (95%) for macrofaunal biomass pairwise comparisons, columns subtracted from rows. Significant differences are highlighted with *.

<table>
<thead>
<tr>
<th>Stations</th>
<th>BIF-1 (970 m)</th>
<th>BIF-2 (1457 m)</th>
<th>BIF-5 (2966 m)</th>
<th>LB (3211 m)</th>
<th>VP-5 (2921 m)</th>
<th>VP-2 (1422 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIF-1 (970 m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIF-2 (1457 m)</td>
<td>(-14.61, -2.55)*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIF-5 (2966 m)</td>
<td>(-21.32, -12.65)</td>
<td>(-9.17)*</td>
<td>(-0.59)*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LB (3211 m)</td>
<td>(-17.76, -5.70)*</td>
<td>(-9.18, 2.88)</td>
<td>(-2.55, 9.51)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VP-5 (2921 m)</td>
<td>(-21.04, -12.446)</td>
<td>(-12.446, -0.40)*</td>
<td>(-6.23, 2.75)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VP-2 (1422 m)</td>
<td>(-12.23, -0.17)*</td>
<td>(-3.65, 2.97)</td>
<td>(-0.51, 14.83)*</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Macrofaunal biomass varied significantly between stations ($F_{5,12} = 8.87, P = 0.001$), with Bear Island Fan-1 having a significantly greater biomass than all other stations (Table 5.3). Biomass at Bear Island Fan-2 and Vøring Plateau-2 was significantly greater than the three deepest stations and there was no significant difference in total biomass between the three deepest stations. The majority of the macrofaunal community in terms of both biomass and abundance occurred within the upper 2 cm of the sediment column at each station (Figure 5.6). A greater biomass of macrofauna occurred below 2 cm at the three upper slope stations than at the three deepest stations. Some larger members of the benthic community may not have been sampled by the megacorer, similar to observations associated with multiple corer samples from the Yermak Plateau in Chapter 2. There was no evidence of mounds or burrows associated with megafauna in any samples collected from each of the stations.
Figure 5.6 The distribution of macrofaunal abundance and biomass within the sediment column at each station. Error bars represent 95% confidence intervals. 95% confidence interval for macrofaunal biomass at 0-2 cm sediment depth for Bear Island Fan-1 of ±12.20 is not shown.
5.3.3 Taxonomic Composition

The relative taxonomic composition of the macrofaunal community for abundance (Figure 5.7) and biomass (Figure 5.8) was analysed. Travelling downslope from Bear Island Fan-1 to the Lofoten Basin the relative abundance of polychaetes appeared to increase with depth. Polychaetes represented over 30% of the total macrofaunal community at each station and were the most abundant component of the macrofaunal community from the study. There were significant differences in polychaete abundance between the stations ($F_{5,12} = 6.2$, $P = 0.005$), with a relative increase in polychaete abundance with depth between Bear Island Fan-1 and the Lofoten Basin. There was little difference in the relative abundance of the polychaetes at the Vøring Plateau-2 and Vøring Plateau-5 stations. As depth increased, the relative abundance of molluscs appeared to increase while the relative abundance of echinoderms and sipunculans decreased. There was no obvious pattern in the overall relative abundance of crustaceans with increasing depth.

With regards to the relative biomass of the macrofaunal community, the echinoderms accounted for >40% of community biomass at all stations with the exception of Bear Island Fan-2. At Bear Island Fan-1 and the Vøring Plateau-2, ophiuroids accounted for the majority of echinoderm biomass, while at the deeper stations the holothurians were responsible. At Bear Island Fan-2, the crustaceans accounted for >30% of total biomass, largely due to the presence of the tube building amphipod, *Haploops setosa*. Polychaetes accounted for less than 30% of community biomass at all stations, with the exception of Bear Island Fan-2, even though they were the most abundant major faunal group. The biomass of the polychaete community varied significantly between the stations ($F_{5,12} = 8.98$, $P = 0.001$), with both Bear Island Fan-1 and -2 stations having a significantly greater biomass than the three deepest stations. There was no significant difference in the biomass of the polychaete community between the other four stations. It was only at Bear Island
Fan-1 that sipunculans represented over 5% of total community biomass, and the relative biomass of the sipunculans appeared to decrease with increasing water depth.

<table>
<thead>
<tr>
<th>Stations</th>
<th>Polychaeta</th>
<th>Mollusca</th>
<th>Echinodermata</th>
<th>Crustacea</th>
<th>Sipuncula</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIF1 (970 m)</td>
<td>0%</td>
<td>20%</td>
<td>40%</td>
<td>60%</td>
<td>80%</td>
<td>100%</td>
</tr>
<tr>
<td>BIF2 (1457 m)</td>
<td>0%</td>
<td>20%</td>
<td>40%</td>
<td>60%</td>
<td>80%</td>
<td>100%</td>
</tr>
<tr>
<td>BIF5 (2966 m)</td>
<td>0%</td>
<td>20%</td>
<td>40%</td>
<td>60%</td>
<td>80%</td>
<td>100%</td>
</tr>
<tr>
<td>LB (3211 m)</td>
<td>0%</td>
<td>20%</td>
<td>40%</td>
<td>60%</td>
<td>80%</td>
<td>100%</td>
</tr>
<tr>
<td>VP5 (2921 m)</td>
<td>0%</td>
<td>20%</td>
<td>40%</td>
<td>60%</td>
<td>80%</td>
<td>100%</td>
</tr>
<tr>
<td>VP2 (1422 m)</td>
<td>0%</td>
<td>20%</td>
<td>40%</td>
<td>60%</td>
<td>80%</td>
<td>100%</td>
</tr>
</tbody>
</table>

**Figure 5.7** Relative abundance of macrofaunal groups sampled with the megacorer. Station key: VP = Vøring Plateau, BIF = Bear Island Fan, LB = Lofoten Basin.

**Figure 5.8** Relative biomass of macrofaunal groups sampled with the megacorer. Station key: VP = Vøring Plateau, BIF = Bear Island Fan, LB = Lofoten Basin.
5.3.4 Macrofaunal Feeding Types

With the exception of Vøring Plateau-5, >60% of relative abundance of the macrofauna was represented by surface deposit feeders at each station (Figure 5.9). At the Vøring Plateau-5 and Lofoten Basin stations interface feeders represented >30% of relative abundance. Surface deposit feeders represented >70% of macrofaunal biomass at all stations with the exception of Bear Island Fan-2 where suspension feeders represented >40% of biomass (Figure 5.10).

![Figure 5.9 Relative abundance of macrofaunal feeding types. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.](image-url)
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5.3.5 Polychaete Functional Ecology

Polychaetes were the most abundant taxon, and the polychaete families that accounted for >5% of polychaete abundance are given in Table 5.4. At the three shallowest stations, Cirratulidae, Sabellidae and Paraonidae were the only families that accounted for more than 5% of total polychaete abundance at each of the stations. Sabellidae and Ampharetidae were the only families that accounted for more than 5% of polychaete abundance at the three deepest stations. Only at the Vøring Plateau-5 did a single polychaete family account for more than 50% of polychaete abundance, with Sabellidae representing 70.1%. At the two upper Bear Island Fan stations, BIF-1 and BIF-2, Terebellididae represented >30% of polychaete community biomass (Table 5.5). Two different polychaete families represented >60% of total polychaete biomass at each of the stations. A list of polychaete families recovered at each of the stations is presented in Table 5.6.

Figure 5.10 Relative biomass of macrofaunal feeding types. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.
Table 5.4 Relative abundance of Polychaeta families that contribute >5% of abundance of the Polychaeta at each station.

<table>
<thead>
<tr>
<th>Bear Island Fan-1</th>
<th>Bear Island Fan-2</th>
<th>Bear Island Fan-5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family</td>
<td>%</td>
<td>Family</td>
</tr>
<tr>
<td>Cirratulidae</td>
<td>38.9</td>
<td>Paraonidae</td>
</tr>
<tr>
<td>Terebellidae</td>
<td>23.9</td>
<td>Spionidae</td>
</tr>
<tr>
<td>Spionidae</td>
<td>7.3</td>
<td>Spionidae</td>
</tr>
<tr>
<td>Amphinomidae</td>
<td>5.1</td>
<td>Cirratulidae</td>
</tr>
<tr>
<td>Paraonidae</td>
<td>5.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vøring Plateau-2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Family</td>
<td>%</td>
<td>Family</td>
</tr>
<tr>
<td>Paraonidae</td>
<td>25.2</td>
<td>Sabellida</td>
</tr>
<tr>
<td>Sabellida</td>
<td>21.1</td>
<td>Ampharetida</td>
</tr>
<tr>
<td>Sigalionidae</td>
<td>13.1</td>
<td>Cirratulidae</td>
</tr>
<tr>
<td>Spionidae</td>
<td>12.4</td>
<td>Oweniida</td>
</tr>
<tr>
<td>Capitellidae</td>
<td>7.4</td>
<td></td>
</tr>
<tr>
<td>Cirratulidae</td>
<td>7.4</td>
<td></td>
</tr>
<tr>
<td>Acrocirridae</td>
<td>5.7</td>
<td></td>
</tr>
</tbody>
</table>

Table 5.5 Relative biomass of Polychaeta families that contribute >5% of abundance of the Polychaeta at each station.

<table>
<thead>
<tr>
<th>Bear Island Fan-1</th>
<th>Bear Island Fan-2</th>
<th>Bear Island Fan-5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family</td>
<td>%</td>
<td>Family</td>
</tr>
<tr>
<td>Terebellidae</td>
<td>34.7</td>
<td>Terebellidae</td>
</tr>
<tr>
<td>Onuphidae</td>
<td>27.7</td>
<td>Amphinomidae</td>
</tr>
<tr>
<td>Capitellidae</td>
<td>15.2</td>
<td>Capitellidae</td>
</tr>
<tr>
<td>Cirratulidae</td>
<td>7.0</td>
<td>Ampharetida</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sphaerodoridae</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Vøring Plateau-2</th>
<th>Vøring Plateau-5</th>
<th>Lofoten Basin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family</td>
<td>%</td>
<td>Family</td>
</tr>
<tr>
<td>Capitellidae</td>
<td>45.0</td>
<td>Lumbrinerida</td>
</tr>
<tr>
<td>Polynoidae</td>
<td>23.5</td>
<td>Oweniida</td>
</tr>
<tr>
<td>Amphinomidae</td>
<td>6.2</td>
<td>Opheliida</td>
</tr>
<tr>
<td>Paraonidae</td>
<td>5.6</td>
<td>Ampharetida</td>
</tr>
<tr>
<td>Cirratulidae</td>
<td>5.1</td>
<td></td>
</tr>
</tbody>
</table>
With regard to the relative abundance of the polychaete feeding modes, deposit feeders were generally the best represented feeding mode (Figure 5.11). There appeared to be a decline in the relative abundance of surface deposit feeders with increasing depth while the relative abundance of interface feeders appeared to increase with increasing depth. An increase in interface feeders with depth was largely due to the presence of the Sabellidae subfamily, Fabriciinae. This subfamily are poor filter feeders when compared with other Sabellidae subfamilies, due to the simple construction of their tentacular crown with only few radioli (Lewis 1968; Fauchald and Jumars 1979). In addition, Fabriciinae are believed to have adopted a secondary feeding mode of selective surface feeding and capable of limited movement on the sediment surface (Lewis 1968; Fauchald and Jumars 1979). Therefore, the Fabriciinae are considered as interface feeders.
Deposit feeders represented the largest proportion of macrofaunal biomass at each of the stations (Figure 5.12). At Bear Island Fan-5, Vøring Plateau-2 and the Lofoten Basin sub-surface deposit feeders accounted for about 50% of polychaete biomass, even though sub-surface deposit feeders represented less than 10% of total polychaete abundance. Interface feeders represented less than 10% of polychaete biomass at all stations, despite interface feeders contributing significantly to polychaete abundance at some of the stations. This indicated the presence of a few larger bodied sub-surface deposit feeders and numerous smaller bodied interface feeders. Larger bodied sub-surface deposit feeders were represented by capitellids at the Lofoten Basin and opheliids at Bear Island Fan-5, while the smaller bodied interface feeders were represented by sabellids and spionids at the Lofoten Basin and only sabellids at Bear Island Fan-5. In general, carnivores accounted for a larger proportion of polychaete biomass than polychaete abundance. Carnivores are generally larger and obtained less frequently within smaller sample sizes and therefore abundance estimates based solely on mega corer samples may not be reliable.

![Figure 5.11](image-url)  
*Figure 5.11* Relative abundance of Polychaeta feeding types sampled with the megacorer. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.
Figure 5.12 Relative biomass of Polychaeta feeding types sampled with the megacorer. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.

5.3.6 Bioturbation Potential

The classification of fauna for the Bioturbation Potential Index (Solan et al. 2004) with regards to mobility and sediment reworking mode is presented within Table 2.3. The bioturbation potential of the macrofaunal community is presented in Figure 5.13. No clear trends were observed in the predominant sediment reworking mode with increasing water depth. The presence of small bodied echiurans at Bear Island Fan-5 resulted in this station being the only one with regenerators accounting for >10% of community bioturbation potential. Surficial modifiers, such as cirratulids and paraonids contributed to >10% of bioturbation potential at all the stations and Bear Island Fan-2 was the only station where they represented greater than 50%. Head-up/head-down deposit feeders were not present in any of the samples collected at either Bear Island Fan-5 or Vøring Plateau-5, two stations located at 3000 m at the base of the continental margin. At Bear Island Fan-2 biodiffusors, such as protobranchid bivalves represented a greater proportion of bioturbation potential.
than any of the other stations, while suspension feeders represented a greater proportion of bioturbation potential at Vøring Plateau-5 than at any other station.

To compare the community bioturbation potential at each station multivariate analysis was applied to the bioturbation potential of the macrofaunal sediment reworking modes. A dendrogram representation for group average clustering of Bray-Curtis similarities, based on untransformed data, is shown in Figure 5.13. There was about 20% similarity between all the stations and with two Vøring Plateau-5 stations forming a distinct cluster from all the other stations. Bear Island Fan-5 and the Lofoten Basins stations along with a single Vøring Plateau-5 formed a distinct cluster from the shallower stations. The shallowest samples from Bear Island Fan-1 formed distinct cluster from the other continental margin stations at Bear Island Fan-2 and Vøring Plateau-2. A stress factor of 0.06 from the non metric multidimensional scaling indicates a good ordination with no real prospect of misleading interpretation, Figure 5.15 (Clarke and Warwick 2001). This indicated that the sediment reworking modes responsible for bioturbation on the upper slope of the continental margin are different from those stations at the base of the slope. Figure 5.15 also indicates that there was greater spatial variation in the bioturbation potential of sediment reworking modes at the three deepest stations, influenced by local scale variation in epifauna, surficial modifiers and biodiffusors.
Figure 5.13 Relative bioturbation potential of each sediment reworking mode of the macrofaunal community. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.

Figure 5.14 Dendrogram representation for group average clustering of Bray-Curtis similarities for the bioturbation potential of the macrofaunal sediment reworking modes based on untransformed data. Station key: VP= Vøring Plateau, BIF= Bear Island Fan, LB= Lofoten Basin.
Figure 5.15 Multi-dimensional scaling for group average clustering of Bray-Curtis similarities for the bioturbation potential of the macrofaunal sediment reworking modes based on untransformed data. Station key: VP = Vøring Plateau, BIF = Bear Island Fan, LB = Lofoten Basin.

Figure 5.16 Relative biomass of each sediment reworking mode of the macrofaunal community. Station key: VP = Vøring Plateau, BIF = Bear Island Fan, LB = Lofoten Basin.
In the deep sea, individual macrofauna generally have a smaller body size than their counterparts living in shallower seas (Kaariainen and Bett 2006). If there are clear differences in the relative biomass represented by the fauna of each of the sediment reworking modes then the specific sediment reworking modes with the greatest biomass could potentially have the greatest influence on bioturbation. The relative biomass of the sediment reworking modes at each station was calculated and presented in Figure 5.13. The most striking difference between the biomass and the bioturbation potential of sediment reworking modes is the increased representation by the epifauna in community biomass. This was evident at almost all stations, with the epifauna representing over 50% of biomass of the sediment reworking modes at all stations with the exception of Bear Island Fan-2. At Bear Island Fan-2, surficial modifiers and epifauna represented >70% of biomass.

5.4 Discussion

5.4.1 Overview of hypotheses

A summary of the findings for each hypothesis is provided below:

1. The hypothesis that there is no change in macrofaunal abundance with increasing water depth can be rejected.

2. The hypothesis that there is no change in macrofaunal biomass with increasing water depth can be rejected.

3. The hypothesis that there is no difference between the response of larger (>500 µm) and smaller macrofauna (250-500 µm) with water depth can be rejected.

4. The hypothesis that the abundance of sub-surface deposit feeders does not vary with water depth can be accepted.
5. The hypothesis that the bioturbation potential of head-up/head-down feeders does not vary with water depth can be accepted.

Detailed discussions on each hypothesis will be provided within the subsections of this discussion.

5.4.2 *Macrofaunal Community*

Macrofaunal abundance appears to be greater in this study than previous studies within the Nordic Seas (Table 5.7). It is difficult to draw direct comparisons due to differences in the sampling gear and sorting methods employed that can influence macrofaunal community abundance estimates. The boxcorer has been the preferential choice of sampling gear in the region and may under-sample the benthic fauna when compared with hydraulically dampened devices (Bett *et al.* 1994; Bett and Gage 2000; Hughes and Gage 2004). In addition, a sieve size of 500 µm has generally been employed in previous studies, but employing a smaller sieve size would retain more animals and increase abundance estimates. Sieve size is an important consideration for any deep-sea benthic community study particularly due to the generally smaller size of macrofauna in the deep-sea than in shallower waters (Gage and Tyler 1991; Gage *et al.* 2002). The time scale between the present study and previous studies is more than a decade and macrofaunal abundance may have altered during the intervening period between studies. The most recent of the previous studies was by Thomsen *et al.* (1995) at the Bear Island Fan, based on samples collected in 1991 and 14 years prior to sampling for this study. However, any differences observed between studies are more likely to be artefacts associated with differences in the sampling methods employed.
Table 5.7 Macrofaunal abundance and biomass (± 95% C.I.) from previous studies in the region and the present study. a (Romero-Wetzel & Gerlach, 1991), b (Thomsen et al. 1995), c (Dahl et al., 1976).

<table>
<thead>
<tr>
<th>Location</th>
<th>Voring Plateau</th>
<th>Bear Island Fan</th>
<th>Lofoten Basin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of stations</td>
<td>17</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Depth range (m)</td>
<td>1200-1500(^a)</td>
<td>1330-1350(^b)</td>
<td>2957-3213(^c)</td>
</tr>
<tr>
<td>Previous abundance (ind. m(^{-2}))</td>
<td>619 (±174)(^a)</td>
<td>741 (±294)(^b)</td>
<td>291 (±122)(^b)</td>
</tr>
<tr>
<td>Previous biomass (g m(^{-2}))</td>
<td>4.1 (±1.25)(^a)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&gt;250 µm abundance (ind. m(^{-2}))</td>
<td>5457 (±422)(^a)</td>
<td>5563 (±170)</td>
<td>3334 (±748)</td>
</tr>
<tr>
<td>&gt;500 µm abundance (ind. m(^{-2}))</td>
<td>3694 (±130)</td>
<td>4257 (±315)</td>
<td>2081 (±402)</td>
</tr>
<tr>
<td>Biomass (g m(^{-2}))</td>
<td>10.73 (±3.02)</td>
<td>8.36 (±4.40)</td>
<td>5.2 (±6.19)</td>
</tr>
</tbody>
</table>

*Bear Island Fan:* The polychaete community at Bear Island Fan-2 was characterised by the families Paraonidae, Spionidae and Cirratulidae, with all three families combined accounting for >75% of total polychaete abundance at the station. Thomsen et al. (1995) sampled three stations at similar depths but located further north than the sampling station Bear Island Fan-2. Polychaetes primarily dominated the relative abundance of the macrofaunal community, although the structure of the community was not discussed in detail. Photographs of the sea bed did reveal a high abundance of polychaete tubes, mainly associated with Myriochele sp. belonging to the Family Oweniidae, and the tubes showed alignment with the direction of flow (Thomsen et al. 1995). Differences between the studies are almost certainly due to different sampling locations. Thomsen et al. (1995) also reported the presence of the epifaunal ophiuroid, Ophiocten sp. in sea bed photographs. At the shallower Bear Island Fan-1 station, a high abundance and biomass of ophiuroids from the megacorer samples were reported. Bear Island Fan-2 was the only station at which echinoderms accounted for <40% of macrofaunal biomass. The amphipod Haploops setosa and its associated tubes were characteristic of the benthic community at Bear Island Fan-2 and were not observed at any of the other stations or reported by Thomsen et al. (1995). However, in Figure 3 of Thomsen et al. (1995) there is a tube similar in structure and appearance to those observed and associated with Haploops setosa at the Bear Island Fan-2 station (Figure 5.17).
Figure 5.17 (a) Figure 3 from Thomsen et al. (1995), bottom photograph revealing high densities of polychaete tubes (mainly Oweniidae, *Myriochele* sp.), the tube structure associated with the amphipod, *Haploops setosa* is circled and is aligned with flow direction. (b) Photograph of a mega-core (diameter of core is 10 cm) with sample from the Bear Island Fan-2. A tube associated with *Haploops setosa* can be observed in the centre of the core.

**Vøring Plateau:** The sampling station, Vøring Plateau-2, was located to the north of most stations previously sampled by Romero-Wetzel and Gerlach (1991). Macrofaunal abundance of about 5456 (± 422, (95% C.I.)) individuals m\(^{-2}\) is much greater than previous studies on the plateau (Table 5.7), and the macrofaunal abundance was still much greater when only the >500 μm fraction was considered (3694 ± 130 (95% C.I.) individual m\(^{-2}\)). However, macrofaunal biomass of 10.73 (± 3.02 (95% C.I.)) g m\(^{-2}\) is similar to the previous highest biomass estimates from the Vøring Plateau. The significantly greater abundance estimates are possibly an artefact of differences in the sampling gear and sorting methods employed in each of the studies. The polychaete community at the Vøring Plateau-2 study site was characterised by 7 families that each accounted for >5% of total polychaete abundance. There are similarities in the families represented at the Vøring Plateau-2 station and those previously recorded. In particular, paraonids were the most abundant polychaete family recorded at the station, and were previously reported to be one
of the most abundant families on the Vøring Plateau in a station located further south and discussed in Chapter 2.

Echinoderms accounted for the largest proportion of community biomass at Vøring Plateau-2 due to the presence of the ophiuroid *Ophiocten gracilis*. This station, unlike the previous sampling location, is located on the edge of the plateau where it descends steeply down into the Lofoten Basin. However, the Vøring Plateau-2 was the only station where community biomass greater than 1 g m\(^{-2}\) wet weight was recorded at a sediment depth greater than 10 cm due to the presence of the capitellid polychaete, *Notomastus* sp. Although *Notomastus* at the Vøring Plateau-2 did not contribute to a similarly high relative abundance, as previously reported in Chapter 2, these individuals were generally the largest polychaetes recorded at the station. Another noticeable difference is the low abundance of the sipunculan *Nephasoma* sp. at the Vøring Plateau-2 compared with the previous work on the plateau (Romero-Wetzel and Gerlach 1991). *Nephasoma* at the Vøring Plateau-2 reached abundances of about 100 individuals m\(^{-2}\), this is considerably lower than the 400 individuals m\(^{-2}\) at the station located further south on the plateau and reported in Chapter 2 and the 500 individuals m\(^{-2}\) estimated by Romero-Wetzel (1987).

*Lofoten Basin:* Two stations within the Lofoten Basin were previously sampled in 1975 by Dahl *et al.* (1976) using an array of sampling techniques, including the Reineck boxcorer, baited trap, epibenthic sled and beam trawl. In addition, a further nine stations were sampled in the Greenland, Norwegian and Spitsbergen Basins. Dahl *et al.* (1976) reported relatively low densities of macrofauna estimated from boxcorer samples in the Lofoten Basin (Table 5.7). A relatively high abundance of small bivalves were obtained from sled samples collected from the Lofoten Basin station at ~3000 m, when compared with abundance of bivalves in the other basins of the region (Dahl *et al.* 1976). This high abundance of small bivalves was believed to be potentially linked to the close proximity of
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the station to the rich Norwegian coastal shelf and steep continental margin (Dahl et al. 1976). It was at this same location that small-sized polychaetes were reported to be best represented within the deep basins of the region. In the present study, small bivalves contributed to a relatively high proportion of macrofaunal abundance at the three deepest stations. Furthermore, small Sabellidae polychaetes accounted for greater than 70% of relative polychaete abundance at the Vøring Plateau-5 station located at the base of a steep slope.

5.4.3 Bathymetric Trends

The hypotheses that there is no change in macrofaunal abundance and biomass with increasing water depth could both be rejected. Macrofaunal abundance based on 250-500 and >500 µm sieve fractions (Figure 5.18) and macrofaunal biomass (Figure 5.19) decreased with increasing water depth. The bathymetric trends of macrofaunal abundance of both 250-500 and 500 µm sieves sizes analysed with an analysis of covariance revealed the 250-500 µm regression slope to be significantly higher and less steep than the >500 µm regression slope (F_{1,33} = 13.24, p <0.0001). Therefore the third hypothesis that there is no difference between the response of larger (>500 µm) and smaller macrofauna (250-500 µm) with water depth can be rejected. The 250-500 µm regression intercept was expected to be higher than the >500 µm due to more individuals being obtained on the smaller sieve mesh size. However, this significant difference in the response of body size of macrofauna with depth indicates that the macrofaunal community at the Norwegian Sea continental margin becomes more dominated by smaller individuals with increasing water depth.
**Figure 5.18** Relationship of macrofaunal abundance (>250 μm and >500 μm) to depth. World-wide mean pattern is included for comparison. Regression equations available in Table 4.9.

**Figure 5.19** Relationship of macrofaunal biomass (>500 μm) to depth. World-wide mean pattern is included for comparison. Regression equations available in Table 4.9.
Recently in the literature, Rex et al. (2006) described global bathymetric trends of benthic community standing stock and body size. Meiofaunal, macrofaunal and megafaunal abundance and biomass were found to decrease with increasing water depth (Figure 5.18 and 5.19). In addition, the benthic community becomes more dominated by smaller individuals with increasing depth. Analysis of bathymetric trends in macrofaunal abundance within the deep Norwegian Sea revealed macrofaunal abundance was greater than the global mean calculated by Rex et al. (2006) (Figure 5.18). There are differences in the sampling gear and sorting methods employed between studies analysed by Rex et al. (2006) that could potentially influence macrofaunal abundance estimates as previously described. However, no significant independent effects of sieve size and sampling gear on global macrofaunal abundance and biomass were revealed, and effects were generally subordinate to depth (Rex et al. 2006).

Macrofaunal biomass was converted from wet weight to organic carbon content with commonly employed conversion factors (Rowe 1983). Bathymetric patterns of macrofaunal biomass within the Norwegian Sea revealed a regression line almost identical to the global patterns described by Rex et al. (2006) (Figure 5.19). This is in contrast to the macrofaunal abundance regression for the bathymetric transect being higher than the global mean (Table 5.8). Differences in the regressions of macrofaunal abundance and biomass within Norwegian Sea, when compared with global patterns, suggest macrofauna may be more abundant within the region but with a body size generally smaller than the global mean. This assumption would be based on dividing total biomass by total abundance providing mean individual biomass for the macrofauna community. If the macrofauna are generally smaller then the choice of sampling gear and sieve size could have a significant influence on results presented for macrofaunal community studies within the Nordic Sea. The previously reported under sampling of macrofauna associated with the boxcorer could be heightened by the smaller bodied macrofauna described in the present
study. In addition, the selection of a sieve size of 500 µm or more would not quantitatively sample a significant component of the macrofaunal community, in particular the smaller bodied polychaete interface feeders.

It is important to note that the presence of rare large individuals in samples can potentially skew mean individual biomass results based on dividing total biomass by total abundance and provide an overestimate of mean individual biomass (Kaariainen and Bett 2006). Only one rare large individual was recovered in the samples obtained for the present study, a holothurian in one of the Lofoten Basin samples. The lack of rare large individuals may be due to the small area sampled by an individual mega core (10 cm diameter). If the box corer had been the preferential choice of sampling gear then the increased sampling area (50 x 50 cm) would have increased the likelihood of sampling rare large individuals. However, macrofaunal community biomass data at each station has not been influenced by the presence of rare large individuals with the exception of the Lofoten Basin. Therefore, the reported smaller body size of macrofauna within the present study when compared with global patterns has not been influenced be rare large individuals.

Other studies have investigated bathymetric trends within the region and one such study was located north of the sampling transects at the Svalbard Margin (Wlodarska-Kowalczuk et al. 2004). Compared with the transects across Bear Island Fan and Vøring Plateau, the abundance of macrofauna was lower and biomass was generally comparable on the Svalbard Margin. Wlodarska-Kowalczuk et al. (2004) calculated the log of biomass versus depth across the Svalbard Margin and the slope of their regression (-0.0013) was considerably higher than the slope for this study (-0.00044) and the global mean (-0.00045) of Rex et al. (2006). The study of Wlodarska-Kowalczuk et al. (2004) included stations located in the Kongsfjord at a significantly shallower water depth than in the present study. The Kongsfjord stations had a high biomass that influenced the faster decline in macrofaunal biomass with depth across the Svalbard Margin. The location of the
Kongsfjord stations within a canyon and the potential associated channelling of organic matter was believed to influence the biomass of the benthic fauna and therefore influenced the observed bathymetric trends (Vetter and Dayton 1998; Wlodarska-Kowalczuk et al. 2004).

**Table 5.8** Regression analyses for macrofaunal abundance (ind. m\(^{-2}\)) and biomass (g C\(_{\text{org}}\) m\(^{-2}\)) against depth. World-wide mean regression analyses are also presented (Rex et al. 2006).

<table>
<thead>
<tr>
<th>Regression</th>
<th>Equations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Norwegian Sea abundance (250-500 μm)</td>
<td>(y = 4.01 - 0.00018x)</td>
</tr>
<tr>
<td>Norwegian Sea abundance (&gt;500 μm)</td>
<td>(y = 3.97 - 0.00023x)</td>
</tr>
<tr>
<td>Global mean abundance</td>
<td>(y = 3.547 - 0.00028x)</td>
</tr>
<tr>
<td>Norwegian Sea biomass (&gt;500 μm)</td>
<td>(y = 0.213 - 0.00044x)</td>
</tr>
<tr>
<td>Global mean biomass</td>
<td>(y = 0.219 - 0.00045x)</td>
</tr>
</tbody>
</table>

### 5.4.4 Polychaete Feeding Modes

It was hypothesised that the abundance of sub-surface deposit feeders would not vary with increasing water depth. The relative abundance of sub-surface deposit feeders appeared not to be influenced by depth and therefore the hypothesis was accepted. This was in contrast to previously reported increases in abundance of sub-surface deposit feeders with increasing water depth (Rosenberg 1995; Flach et al. 1998). Sub-surface deposit feeders are believed to favour a steady, slow sedimentation of refractory organic matter (Rice and Rhoads 1989). Therefore, we might expect the three stations where sub-surface deposit feeders accounted for about 50% of polychaete community biomass to be supplied by a steady slow sedimentation of refractory organic matter.

Across both Bear Island Fan and the Vøring Plateau margin, the relative abundance of surface deposit feeders decreased with increasing water depth. A high representation of
surface deposit feeding polychaetes within deep southern polar seas was linked to a higher availability of organic matter (Maurer and Williams 1988). In contrast to surface deposit feeders, the relative abundance of interface feeders increased with increasing water depth. However, any suspension feeding associated with interface feeders will be restricted to the sediment-water interface due to the small body size of individuals, particularly the sabellid subfamily Fabriciinae. An increase in the abundance of interface and suspension feeders has previously been linked to strong flow velocities and the resuspension of sediment (Duineveld et al. 2001; Rutgers van der Loeff et al. 2002). At the Vøring Plateau-5, the relative abundance of interface feeders was greater than at similar depths on the Bear Island Fan. This higher relative abundance of interface feeders and higher biomass of suspension feeders at the Vøring Plateau-5 may be directly related to higher flow velocities and/or the increased resuspension of sediment.

The relative biomass of interface feeders did not increase with increasing depth even though abundance did, indicating that small bodied interface feeders are more prevalent at deeper locations. A high abundance of interface feeders on the continental shelf and upper slope of western New Zealand may have reflected the high input of terrigenous sediment and episodic upwelling believed to favour opportunistic species (Probert et al. 2001). Bottom water currents appear to be steered by local bathymetry at the Vøring Plateau (Fohrmann et al. 2001) and high accumulation rates of sediment occur on the northern edge of the plateau (Rumohr et al. 2001). However, chloroplastic pigment equivalents and organic carbon content of the sediment do not indicate an increase in organic matter availability with increasing water depth (Ritzarau et al. 2001).
5.4.5 Bioturbation Potential

The hypothesis that the bioturbation potential of head-up/head-down deposit feeders does not vary with water depth can be accepted. Head-up/head-down deposit feeders were not observed at either Bear Island Fan-5 or Vøring Plateau-5 at the base of the continental margin but were present at the deepest station located in the Lofoten Basin (predominately capitellids). Therefore the bioturbation potential of head-up/head-down deposit feeders does not vary directly with depth but is influence by a combination of environmental factors. Within the deep sea, the redistribution of organic matter down the sedimentary column has been associated with head-up/head-down deposit feeders (Levin et al. 1997; Witte et al. 2003a). The relative biomass of head-up/head-down deposit feeders appeared to show little variation between stations where individuals were recorded.

Results from the multivariate analysis suggest a difference in the bioturbation potential of the macrofaunal community at the three deepest and three shallowest stations at the Norwegian Sea continental margin (Figure 5.14). Contrasts in the bioturbation by the macrofaunal community of a continental margin location and an abyssal plain location have previously been reported (Aberle and Witte 2003; Witte et al. 2003a; Witte et al. 2003b). The relative bioturbation potential of biodiffusors at the Bear Island Fan-5 and Vøring Plateau-5 stations was greater than at the Lofoten Basin. The biodiffusors at both stations were represented mainly by small bivalves that occurred in the upper 2 cm of the sediment.

Surficial modifiers at Bear Island Fan-2 and the epifauna at all other stations could be responsible for a significant proportion of sediment mixing. However, epifauna would not be responsible for the redistribution of organic matter deep down the sedimentary column and would more likely account for sediment surface traces. A sediment mixing depth of 6 cm has previously been recorded in the deep basins of the Norwegian Sea from chloroplastic pigment equivalents (Ritzarau et al. 2001) and is comparable to the world-
wide mean of 9.8 ± 4.5 cm (Boudreau 1998). A sediment mixing depth of 9 cm on the 
Vøring Plateau was previously linked to the head-up deposit feeding sipunculan worm, *Nephasoma* sp. (Graf 1989). It is possible that a lower reported sediment mixing depth 
within the deep basins may be associated with a low abundance of head-up/head-down 
deposit feeders.

Similarity in macrofaunal community bioturbation potential at comparable depths 
between both transects decreased with increasing water depth (Figure 5.14 and 5.15). 
There was higher similarity in bioturbation potential of the macrofaunal community 
between Bear Island Fan-2 and Vøring Plateau-2 than between Bear Island Fan-5 and 
Vøring Plateau-5 even though the distance between the two deeper stations was less. A 
similar pattern was observed along two bathymetric transects at 74°N and 79°N on the East 
Greenland continental margin (Schnack 1998). Polychaete community structure at the East 
Greenland continental margin along both transects was similar in composition on the shelf 
and decreased in similarity with increasing water depth (Schnack 1998). Probert *et al.* 
(1996), reported a higher similarity in polychaete communities from stations sampled on 
the crest of the Chatham Rise, southwest Pacific than between those stations occurring on 
the slopes. A decrease in similarity in community patterns with increasing depth can be a 
result of variation in food supply, flow velocity, topography and sedimentation rates (Flach 
2002).

### 5.5 Summary

With regard to the hypotheses proposed in the introduction the following conclusions can 
be drawn:

1. *Standing stock and body size:* Macrofaunal abundance and biomass declined with 
   increasing depth across the Norwegian continental margin. In addition, the
dominance of smaller macrofauna (>250 μm) increased with increasing water depth. Macrofaunal abundance was greater than the global mean at comparable depths, even though biomass was similar. This suggests the macrofaunal community body size within the Nordic Seas is generally smaller than the global mean, although data could be skewed by the presence of rare large bodied individuals (Kaariainen and Bett 2006).

2. **Polychaete feeding modes:** The relative abundance of interface feeders appeared to increase with increasing water depth across the margin. No trends were observed in the relative abundance of sub-surface deposit feeders across the margin, although they did contribute to almost 50% of biomass at two of the three deepest stations. However, patterns in polychaete feeding modes did not follow similar patterns as observed previously at the Goban Spur (Flach et al. 1998). Therefore, the hypothesis of an increase in relative abundance of sub-surface deposit feeding polychaetes with depth can be rejected.

3. **Bioturbation potential:** Head-up/head-down deposit feeders did not contribute to community bioturbation potential at the two lower slope stations. However, at the steepest station and on the upper slope head-up/head-down deposit feeders contributed to a significant proportion of community bioturbation potential. Head-down deposit feeders have previously been associated with the rapid subduction of fresh organic matter deep-down the sedimentary column (Levin et al. 1997).

4. **Bathymetric patterns:** There were no clear patterns in the functional ecology of the macrofaunal community that could be associated with increasing water depth. Similarities in the bioturbation potential of the macrofaunal community along both transects did decrease with depth even though the distance between stations located at similar depths became shorter with increasing water depth. Potentially flow velocity plays a significant role in determining benthic community structure across
the Norwegian Sea continental margin as suggested by the high biomass of suspension feeders at the Bear Island Fan-2 station. Previously reported high abundances of suspension feeders at continental margins has been linked to favourable flow velocities (Flach et al. 1998; Duineveld et al. 2001; Rutgers van der Loeff et al. 2002).
6 The response of the macrofaunal community within the deep Norwegian Sea to an artificial pulse of $^{13}$C labelled diatoms

6.1 Introduction

Data presented within this chapter is from a pilot study to determine what members of the macrofaunal community respond to an artificial pulse of $^{13}$C enriched organic matter at different locations within the Nordic Seas. This pilot study would provide important natural history data on the members of the macrofaunal community responding to organic matter and influencing the incorporation of organic carbon within the sedimentary column. It is important to consider any variation in community response to an episodic pulse of organic matter could have a significant influence on sediment geochemistry. In addition, the response of the macrofaunal community from the continental margin was compared with the bathyal plain to determine if any contrasts in community response exist.

In the late 1980s, advancement in analytical technology combined with an improved understanding of the factors that cause isotope fractionation increased the potential applications of the stable isotope analysis of ecological systems (Grey 2006; West et al. 2006). Ecological studies that analysed the natural abundance ratios of stable isotopes have tended to focus on carbon ($\delta^{13}$C), nitrogen ($\delta^{15}$N), hydrogen ($\delta^2$H), oxygen ($\delta^{18}$O) and sulphur ($\delta^{34}$S). Ratios of these isotopes can provide a useful tool to trace “the movement of nutrients, compounds, particles and organisms across landscapes and between components of the biosphere and reconstruct aspects of dietary, ecological and environmental histories” (West et al. 2006). Measuring the natural abundances of stable carbon isotopes ($\delta^{13}$C) can be a powerful tool for studying the dietary organisation of a whole ecosystem (Gearing 1991). On occasion, the interpretation of marine food webs from natural abundance ratios
of stable carbon isotopes can be misleading and there can be a requirement for the analysis of the ratio of multiple stable isotopes for some food web studies (Matson and Brinson 1990; Fry et al. 1995; Peterson 1999).

The majority of ecological system studies have focused on the natural abundance ratios of stable isotopes; however, there is also the possibility of employing stable isotopes as tracers to determine how communities are structured and how they function. In nature, approximately 98.89% of all carbon is $^{12}\text{C}$, and 1.11% is $^{13}\text{C}$ with the ratio of the two stable isotopes varying slightly because of isotope fractionation (Boutton 1991). Photosynthesis and respiration lead to the fractionation of organic carbon, producing an end-product enriched in isotopically lighter $^{12}\text{C}$ (Burdige 2006). Benthic fauna have low $^{13}\text{C}$ levels, but artificially enriching the $^{13}\text{C}$ content of the food supply can provide important information on the fauna responding to the food supply enriched in $^{13}\text{C}$. Any organism that consumes organic particles enriched in $^{13}\text{C}$ would then have elevated levels of $\delta^{13}\text{C}$ compared with background levels occurring naturally. Therefore, artificial enrichment of organic particles with the stable carbon isotope $^{13}\text{C}$ can provide a useful tracer for studying the function and response of ecological communities.

Within the deep-sea environment, one potentially useful application of $^{13}\text{C}$ enriched organic matter is to act as a tracer to determine the short term fate and incorporation of fresh organic matter within the benthos. Arrival of organic matter to the deep-sea floor can occur both episodically and seasonally (Honjo 1982; Lampitt 1985; Rice and Rhoads 1989; Hecker 1990; Graf 1992; Gooday 2002). This vertical flux of organic matter to the sea floor is the main process connecting plankton and benthic fauna within the global carbon cycle (Wassmann et al. 1996). Input can occur as a pulse of organic matter, potentially influencing the activity and feeding strategies of benthic organisms (Gooday and Turley 1990; Jumars et al. 1990; Smith 1994). Previous studies have successfully employed $^{13}\text{C}$ enriched organic matter to determine the response of the benthic community to an artificial

Recently in the literature, contrasts have been drawn between continental margin and abyssal plain environments with respect to the rapid burial of fresh organic matter (Aberle and Witte 2003; Witte et al. 2003a; Witte et al. 2003b). The abyssal site was located in the Porcupine Abyssal Plain (4850 m), Atlantic Ocean, while the continental margin station was in fact a deep fjord, Sognefjord (1285 m) on the west coast of Norway. Macrufaunal abundance and biomass in Sognefjord fell within the regression range for the Goban Spur continental margin, NE Atlantic (Flach and Heip 1996). For this reason, Witte et al. (2003a) believed the benthic community of Sognefjord was comparable with continental margin communities and therefore would provide a comparable response of a continental margin community to a pulse of organic matter.

A benthic lander was deployed at both locations for in-situ artificial pulse experiments employing $^{13}$C enriched organic matter. Results from the Porcupine Abyssal Plain revealed that the penetration of the $^{13}$C labelled organic matter rarely occurred below 2 cm sediment depth (Aberle and Witte 2003). Initial processing of the tracer was linked to benthic macrofauna, despite the macrofauna only accounting for <5% of the benthic community biomass (Witte et al. 2003b). Enriched $\delta^{13}$C signatures varied between higher taxa and families, suggesting abyssal benthic communities cannot be considered as one functional group and surface deposit feeders had higher $\delta^{13}$C signatures than other feeding modes. Within 2.5 days of tracer input, a significant increase in abyssal sediment community oxygen consumption occurred (Witte et al. 2003b). The increase in oxygen consumption was linked to the microbial community that accounted for approximately 95% of total benthic biomass. Only 14% of the labelled organic matter was processed within 23 days and it was suggested that a large pulse of organic matter could sustain
elevated levels of benthic activity for a period of several months (Witte et al. 2003b). However, the quality of the food would deteriorate with time and the level of benthic activity could not be sustained at the initially increased levels of activity immediately after a pulse of fresh phytodetritus.

In contrast, almost 50% of macrofaunal biomass in the Sognefjord occurred below 5 cm sediment depth, and abundance was dominated by polychaetes, accounting for 65% of abundance (Witte et al. 2003a). After a period of only 1.5 days, 81% of the macrofaunal community had ingested the $^{13}$C-labelled organic matter and after just 3 days all macrofauna (including deep-dwelling taxa) had elevated levels of $\delta^{13}$C. Rapid subduction of the $^{13}$C enriched organic matter down to sediment depths of 5-10 cm occurred within just 3 days. Maldanid and opheliid polychaetes were believed to be responsible for the rapid subduction of organic matter and a similar rapid subduction of organic matter has previously been observed on the Voring Plateau, Norwegian Sea (Graf 1989) and on the North Carolina continental margin off Cape Hatteras (Levin et al. 1997). The sediment mixing depth of 5-10 cm at Sognefjord (Witte et al. 2003a) was considerably greater than the 2 cm sediment mixing depth at the Porcupine Abyssal Plain (Aberle and Witte 2003). Although there was a similar rapid response to a fresh input of organic matter at both sites, it appeared that the lower sediment mixing depth at the Porcupine Abyssal Plain may have been associated with the low abundance of deep-dwelling polychaetes (Aberle and Witte 2003).

In the deep Norwegian Sea the rapid subduction of organic matter at a rate $> 1$ cm d$^{-1}$ was reported following the pulsed input of copepod faeces in late May 1986 (Graf 1989). Enriched in Chl-a, the copepod faeces were believed to be a high quality food source for some members of the benthic community (Bathman et al. 1987). Rapid subduction of the Chl-a rich copepod faeces was linked to the presence of a sipunculan worm, Nephasoma sp. (Graf 1989) and believed to be a strategy for sub-surface storage of
food (Jumars et al. 1990). Within only a few days after the arrival of the copepod faeces sediment concentrations of Chl-a increased from 0 to 3.3 µg cm$^{-2}$, but sediment community oxygen consumption demonstrated little response (Graf 1992). However, only 4 weeks later, in late June 1986, sediment community oxygen consumption doubled following the arrival of a second much larger pulse of organic matter (Graf 1992). Sediment community oxygen consumption from the intertidal zone to the deep sea does not appear to have any relation with benthic faunal biomass (Moodley et al. 2005). However, the mixing and processing of fresh organic matter does appear to be directly related to the presence of benthic fauna (Blair et al. 1996; Levin et al. 1997; Levin et al. 1999; Moodley et al. 2002; Aberle and Witte 2003; Witte et al. 2003a; Witte et al. 2003b; Moodley et al. 2005).

Consequently, the mixing and final deposition of organic matter arriving at the sea floor is strongly influenced by the feeding and locomotion activities of the benthic community. Surface deposit-feeders appear to out-compete other feeding modes for organic matter in the time immediately following a fresh pulse (Levin et al. 1999; Aberle and Witte 2003). High sediment mixing depths of 5-10 cm at the continental margin have been linked to the presence of deep-dwelling fauna (Witte et al. 2003a). In contrast, a sediment mixing depth of only 2 cm at an abyssal plain location was linked to a lack of deep-burrowing fauna at the station sampled (Aberle and Witte 2003; Witte et al. 2003b). At the Vøring Plateau, Norwegian Sea, the rapid subduction of organic matter was linked to the presence of the head-up/head-down deposit feeding sipunculan, *Nephasoma* sp. (Graf 1989). In other continental margin locations, $^{13}$C tracer experiments have reported elevated ratios of $\delta^{13}$C in other classic head-up/head-down deposit feeders (Levin et al. 1997; Witte et al. 2003a). Therefore, individual members of the benthic community, rather than the community as a whole, are likely to be responsible for the redistribution of organic matter down the sedimentary column (Ohta 1984; Graf 1989; Levin et al. 1997). Levin et
al. (1997) suggested the redistribution of organic matter could potentially influence the following benthic community characteristics:

a) The temporal and spatial distribution of sub-surface deposit feeders.
b) The abundance, biomass and vertical range of the infauna.
c) The composition of infaunal feeding groups and foraging strategies.
d) The distribution of microbial metabolic processes in time and space.

Within the Nordic Seas region, there has been little work to determine the response of individual members of the benthic community to the fresh input of organic matter. With this in mind the following hypotheses were proposed to investigate the response of the benthic community to an artificial pulse of $^{13}$C enriched organic matter within the deep waters of the Nordic Seas region:

1. There is no difference in $^{13}$C enrichment between deep burrowing species living on the continental margin and those from the bathyal plain.

2. All feeding groups will take up the 13C enriched material at the same rate.

### 6.2 Methods

#### 6.2.1 Experiment Overview

The experiment was designed to provide a preliminary analysis on the response of the macrofaunal community to an artificial pulse of organic matter and involved the culture and labelling of diatoms with $^{13}$C for the experiment. The pilot study was conducted during the JCR 127 cruise in the summer of 2005 and involved shipboard experiments.
6.2.2 Diatom Culture

Initially the following diatom species were selected for $^{13}$C enrichment: *Thalassiosira anguste-lineata*, *T. antarctica*, *T. gravida* and *T. latimarginata*. All of these species had previously been recorded in deep-sea sediments within the Nordic Seas region (Hasle 1976; Kohly 1998). *Thalassiosira* species of diatoms are heavily silicified and are therefore less likely to suffer from silica dissolution when sinking through the mixing layer. However, at the time of culture, none of the diatom species listed above formed part of the algal collection of the Culture Collection of Algae and Protozoa (CCAP) based at SAMS. This led to the selection of another species of *Thalassiosira* diatom, *T. rotula*. It has previously been suggested that *T. rotula* is a subspecies of *T. gravida*, one of the species initially selected for culture (Hasle 1976). Both species are bipolar diatoms and the distribution patterns of *T. gravida* (70 to 35°N and 77 to 33°S) and *T. rotula* (60°N to 43°S) support the assumption of a single species (Hasle 1976). Furthermore, $^{13}$C enriched *T. rotula* had been successfully used to measure the rapid burial of organic matter within the region at Sognefjord, western Norway (Witte et al. 2003a) and further south at the Porcupine Abyssal Plain, Atlantic Ocean (Aberle and Witte 2003).

The culture was grown from CCAP *Thalassiosira rotula* 1085/13 strain and training on the culture and $^{13}$C enrichment of diatoms was provided by CCAP staff. *T. rotula* was cultured in four 10 litre carboys under constant temperature laboratory conditions. Firstly, the carboy screw lids were set up in the standard method as shown in Figure 6.1. A 20 μm filter was attached to the inlet tubing to be connected to the air supply for the culture. Then for each carboy, an artificial seawater recipe was prepared with standard f/2 medium with added silicate (Table 5.1). The source of $^{13}$C for the artificial seawater was provided by adding $^{13}$C enriched sodium bicarbonate, NaH$^{13}$CO$_3$ ($^{13}$C, 99%) from Cambridge Isotope Laboratories.
Table 6.1 Artificial seawater salts per 10 litres of Milli-Q water (D. Pond, British Antarctic Survey, pers. comm.).

<table>
<thead>
<tr>
<th>Artificial seawater:</th>
<th>(g per 10 litres Millie-Q water)</th>
<th>Hydrated Salts</th>
<th>(g per 10 litres Millie-Q water)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Anhydrous salts</strong></td>
<td></td>
<td><strong>MgCl₂.6H₂O</strong></td>
<td>93.95</td>
</tr>
<tr>
<td>Nail</td>
<td>207.58</td>
<td>CaCl₂.2H₂O</td>
<td>13.16</td>
</tr>
<tr>
<td>Na₂SO₄</td>
<td>34.77</td>
<td>SrCl₂.6H₂O</td>
<td>0.214</td>
</tr>
<tr>
<td>ACL</td>
<td>5.87</td>
<td>NaHCO₃</td>
<td>1.70</td>
</tr>
<tr>
<td>Kerr</td>
<td>0.845</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H₂BO₃</td>
<td>0.225</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nave</td>
<td>0.027</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Once the artificial seawater with standard f/2 medium plus silicate had been prepared, 10 litres was added to each carboy along with a magnetic stirrer. All ends of tubing not inside the carboy were then wrapped in aluminium foil to prepare for autoclaving. The carboy was then autoclaved at 121°C for 15 minutes and once autoclaving was complete, the carboy lid was screwed loosely on to allow the medium to cool, then once cool the lid was tightened.

The carboy was then transferred to the constant temperate control room and subjected to constant light. Within the room, an aeration system was set up and connected
to the carboy, as shown in Figure 6.2. Air was then pumped through an aeration bottle containing 1.5 litres of 2M KOH to generate CO$_2$ free air. To prevent KOH travelling back into the air pump a safety bottle was set up as shown in Figure 5.2. The carboy was allowed to equilibrate to the room temperature of 16°C for a period of 24 hours. The Milli-Q water used for the artificial sea water recipe contained $^{12}$CO$_2$, so during the 24 hour equilibrating period CO$_2$ free air was bubbled through the carboy to scrub the system of $^{12}$CO$_2$. Air entering the carboy was sterilised by passing through the 20 μm hydrophobic filter attached to the inlet tubing of the carboy as shown in Figure 6.2.

![Figure 6.2](image_url) The air supply and carboy setup for the production of CO$_2$ free air. Arrows indicate airflow direction.

After the 24-hour equilibrating period, the carboy was inoculated with 500 ml of $T. \textit{rotula}$ starter culture grown in standard f/2 medium with added silicate. Inoculation was achieved by carefully and quickly unscrewing the lid and pouring the starter culture into the medium. Each of the four cultures were produced one after the other to allow the inoculation of the following carboys with 1 litre of culture from the previous carboy, so carboy 4 was inoculated with 3, 3 with 2, and 2 with 1. Inoculation between carboys was achieved by connecting tubing C of the new carboy with tubing C of the previous carboy.
Then clips A and C of the previous carboy were opened, then switch 2, switch 1 and then the air pump was switched on (Figure 6.2). This allowed 1 litre of culture from the previous carboy to be siphoned into the new carboy. After 1 litre of culture had been siphoned, the clip on tube A was closed and the clip on the tubing connecting A and C directly was opened to clear all culture from the tubing. Once the culture was cleared from tubing, the air supply was first turned off and then all clips and switches closed. Inoculating the new carboy with 1 litre of culture from the previous carboy would allow for a higher $^{13}$C content of the starter *T. rotula* culture.

After inoculation, the magnetic stirrer was switched on and set to spin at a low enough velocity so as not to destroy the *T. rotula* cells but to allow for mixing within the carboy. Mixing within the carboy could be achieved on a lower spinning velocity when a larger magnet was used. It was essential that the spinning velocity was set to the slowest velocity that produced mixing, because a high velocity would increase the probability of damage to the diatom cells and potentially inhibit the growth of the culture. Each day during culture growth, CO$_2$ free air was bubbled through the carboy for a period of 2 hours to prevent the culture becoming anoxic. To avoid any spillage of KOH and a build-up of air pressure within the system, tube clips A and B and switches 1 and 2 had to be opened prior to turning on air supply. After 2 hours, the air supply was turned off and clips and switches were closed in reverse order, but only once air had stopped bubbling through the system. When there was no longer any air bubbling through the system, then all clips remained closed to prevent any $^{12}$CO$_2$ rich air entering the system. There was a maximum of two carboy cultures growing within the constant temperature room at any time. After inoculation, the additional carboy was attached to switch 2 and set up exactly as described previously. Cultures were grown until reasonably dense, and this resulted in a culture time of 24 days for carboy 1, 27 days for carboy 2 and 20 days for carboy 3. The culture in carboy 4 crashed.
Prior to harvesting the culture, the magnetic stirrer was switched off for a 24 hour period to allow the culture to settle. After the settling period, the carboy was then transferred to the laboratory and the supernatant was siphoned through a 20 μm plankton net. The concentrated culture remaining in the carboy was then washed through the plankton net using filtered seawater. Culture collected in the plankton net was then dispensed into centrifuge bottles and centrifuged at 2000 rpm for 15 minutes. A diatom paste then remained at the bottom of each centrifuge bottle and this was dispensed into a single centrifuge bottle that was again centrifuged at 2000 rpm for 15 minutes. Diatom paste was then frozen immediately in liquid nitrogen and stored at -80°C until ready for freeze-drying.

After freeze-drying for 24 hours the centrifuge bottle containing the sample was labelled according to the carboy batch, wrapped in silver foil and stored at -20°C until required for the tracer experiments. A total of 0.67 g of freeze-dried 49% $^{13}$C enriched $T. rotula$ was produced from the three successful carboy cultures. The equivalent of 1 g C m$^{-2}$ was to be added to each incubation, a similar quantity as employed successfully in previous studies (Aberle and Witte 2003; Witte et al. 2003a; Witte et al. 2003b).

6.2.3  Tracer Experiment

Shipboard tracer experiments using the $^{13}$C enriched $T. rotula$ were carried out during the JCR127 cruise between the 29th August and 22nd September 2005. Four stations were selected for the tracer experiments, two continental margin stations (Bear Island Fan-2 and Vøring Plateau-2) and two abyssal plain stations (Lofoten Basin and Vøring Plateau-5). In total four cores were obtained at each station, two cores from each of two megacorer drops, with only undisturbed cores that penetrated to a sediment depth of about 20 cm
selected. At each station two cores would provide background $^{13}$C data for the macrofauna and the other two cores were enriched with *T. rotula*.

Experiments were set up in the temperature controlled cold room of the RRS *James Clark Ross* to allow maintenance of temperature at *in-situ* levels for each station. Prior to the cruise, it was decided that 1 g C m$^{-2}$ would be added to each experimental core. This quantity of carbon input had provided successful results in previous $^{13}$C enrichment studies within the deep sea. In order to provide 1 g C m$^{-2}$ for each megacore with an area of 0.00785m$^2$, 0.075g of the freeze dried *T. rotula* (Carbon: 10.49%, Nitrogen: 2.71%) was required.

Once the megacorer was onboard deck, the cores for the tracer experiment were selected and immediately transferred to the temperature control room and covered in black plastic to create a dark environment. Both background and experimental cores were then left for a period of four hours to settle. During the settlement period, about 15 ml of water was removed from each core to be mixed with the freeze-dried *T. rotula* pre-weighed for that core. After the four hour settlement period, the rehydrated *T. rotula* was then added to the two enrichment cores and all four cores were continually aerated and left for a period of 36 hours.

At the end of the 36 hour incubation period, cores were sliced at 0-1, 1-2, 2-3, 3-5, and 5-10 cm sediment horizons. Samples from the Vøring Plateau-2 had additional sediment horizons sliced at 10-15 and 15-20 cm depths because of the presence of deep fine burrows. All sediment horizons were washed as soon as possible with filtered seawater through a 250 µm mesh sieve and each fraction was frozen at -25ºC for sorting later at Dunstaffnage Marine Laboratory. Two separate sets of sieves, extruders and slicers were used during this process, one set for background cores and the other for the enriched cores to prevent contamination of background cores with enriched levels of $^{13}$C.
6.2.4 Sample preparation for analysis

Once back in the laboratory, the frozen samples were slowly defrosted within a fridge to minimise any potential tissue damage to the macrofauna from the defrosting process. All macrofauna were sorted under a light microscope and identified to the lowest taxonomic level possible. Two sets of sorting dishes and forceps were employed, again to prevent cross-contamination between background and enriched samples. Each individual macrofaunal organism was rinsed with Milli-Q water, placed into an individually labelled 1.5 ml Eppendorf tube, stored at -20°C and later freeze dried.

Before samples could be weighed, it was required to decarbonise specimens with a carbonate shell or skeleton to remove all inorganic carbon from the specimen. Decarbonising specimens with a carbonate shell or skeleton would remove all inorganic carbon from analysis. This was achieved by adding HCl (1M) drop wise until there was no more visible development of CO$_2$, and the volume of HCl required depended largely on the individual macrofauna. Acidified samples were then freeze dried and were not washed with Milli-Q water to prevent the loss of dissolved organic matter. Samples were then weighed out into cleaned 6 x 4 mm tin capsules using a micro balance (Mettle Toledo UMX2, max = 2.1 g, d = 0.1 µg). The use of a standard of known carbon content allows for the calculation of the carbon isotope ratios of individual macrofauna. The carbon isotope ratios of individual macrofauna were expressed as $\delta^{13}$C signatures and calculated using the following equation ‰:

$$\delta^{13}C (‰) = \left[ \frac{(\text{C}^{13}/\text{C}^{12})_{\text{sample}}}{(\text{C}^{13}/\text{C}^{12})_{\text{standard}}} - 1 \right] \times 1000$$

The standard, acetonilide (71.1% C), was weighed so that the specific weight of the standard at the highest and lowest weights measured would bracket the carbon content of the specimens to be analysed for $\delta^{13}$C signatures. This is a method that has previously been employed for the successful analysis of deep-sea macrofaunal samples with a low biomass.
Samples were sent to the Scottish Crop Research Institute and analysed for carbon abundance ratios using their Europe Scientific ANCA-NT 20-20 Stable Isotope Analyser with ANCA-NT Solid/Liquid Preparation Module (Europe Scientific Ltd., Crewe, UK). The analytical precision (SD, \( n = 5 \)) was 0.2 ‰ for C, estimated from standards analysed along with the samples. The working standards were 1 mg leonine, prepared by freeze drying 50 µl of a 20 mg/ml stock solution into tin cups, and calibrated against ‘Europe flour’ and IAEA standards N1 and N2 (Scrimgeour and Robinson 2003).

### 6.3 Results

#### 6.3.1 Isotopic signatures

Analysis of stable carbon isotope signatures was hindered by the low biomass of some of the individual macrofauna retained in the samples from each station (Table 6.2). All the specimens analysed from the Lofoten Basin and Vøring Plateau-5 had less than 20 µg of carbon, resulting in the data for these stations being potentially unreliable. In addition, only two individuals were obtained in background cores from the Vøring Plateau-5 samples and none in the experimental \(^{13}\)C enriched cores. At the two upper slope stations, some of the individuals had a carbon content greater than 20 µg while others did not. For the analysis of \(\delta^{13}\)C of the macrofaunal community it was decided that individuals with a carbon content less than 20 µg would be excluded, and a list of individuals included can be found in Table 6.2.
Table 6.2 Isotopic signatures of individual macrofaunal organisms from background (0 days) and enrichment experiments (1.5 days) and their vertical position within the sediment column (0 to 10 cm) from each station (a) Bear Island Fan-2, (b) Bear Island Fan-5, (c) Vøring Plateau-2, (d) Vøring Plateau-5. Values highlighted in grey represent individuals with a carbon content less than 20 μg.

(a) Bear Island Fan-2, 1456 m.

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(b) Bear Island Fan-5, 2964 m.

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<td>Crustacea</td>
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(c) Vøring Plateau-2, 1418 m.

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(d) Vøring Plateau-5, 2918 m.

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</tr>
<tr>
<td>Terebellidae</td>
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Natural isotopic signatures of the macrofauna in background sediment samples from Bear Island Fan-2 and the Vøring Plateau-2 all showed negative values (Figure 6.3 and 6.4). After 1.5 days, the macrofaunal community did have a higher δ¹³C signature than background levels, although this is not necessarily conclusive evidence of enrichment (Figure 6.3 and 6.4). However, there is clear evidence of enrichment of the ophiuroids from the Vøring Plateau-2, with a δ¹³C signature of 15.30 ± 5.84 ‰ after only 1.5 days. At Bear Island Fan-2, two of the amphipods recovered from the enrichment experiment had a positive δ¹³C signature while the other seven individuals had a negative value. This suggests that approximately one-third of the amphipods in the sample had consumed the δ¹³C labelled diatoms after only 1.5 days following the artificial pulse. All other macrofauna recovered from the δ¹³C enrichment experiment had negative δ¹³C signature but appeared to show evidence of having consumed some labelled diatoms.
Figure 6.3 Background and experimental δ13C signatures of the macrofauna taxa at the Vøring Plateau-2.

Figure 6.4 Background and experimental δ13C signatures of the macrofauna taxa at the Bear Island Fan-2.


6.4 Discussion

A summary of the findings for each hypothesis is provided below:

1. The hypothesis that there is no evidence in 13C enrichment between deep burrowing species living on the continental margin and those from the bathyal plain could neither be rejected or accepted. The lack of specimens from the bathyal plain stations prevented this hypothesis from being addressed.

2. The hypothesis that all feeding groups should take up labelled diatoms at the same rate can be rejected. Positive δ\textsuperscript{13}C signatures for only the surface feeding ophiuroids at the Vøring Plateau-2 station resulted in rejection of this hypothesis.

The main point for discussion in this chapter is the large number of specimens that did not provide reliable results. In total 102 individuals were analysed and only 41 of those individuals had a carbon content greater than 20 μg that provided reliable δ\textsuperscript{13}C signatures. This issue was related to the smaller body size of the fauna within the region as discussed in Chapters 2 and 4. Before individual macrofauna were weighed and prepared for stable isotope ratio analysis it was noted that some individuals may not provide a biomass high enough to provide reliable δ\textsuperscript{13}C signatures. Therefore, there were two possible choices to address this problem; one was to pool individuals of the same taxa to obtain a higher biomass for samples or to analyse individuals only by weighing out standards that would bracket the carbon content of the specimens to be analysed.

The number of individuals available for analysis from the two deepest stations was extremely low and resulted in the pooling of specimens not being a viable option for these stations. Furthermore, one of the aims of the experiment was to determine the response of individual macrofauna and this information would have been lost if animals were pooled. Therefore, the decision was made to analyse only individual specimens and attempt to bracket the carbon content of those individuals with the standard acetanilide. In addition,
the number of individuals that could be analysed for $\delta^{13}C$ signatures from all the stations was low and therefore the number of individuals for separate taxa would have been considerably reduced if specimens were pooled. If the number of cores available for the stable isotope experiment had been higher then it would have been possible to pool specimens to achieve an optimal biomass for analysis. However, poor weather conditions and the demand for cores during the tight cruise schedule resulted in no more cores being available for the stable isotope experiment. It was observed that the number of individual macrofauna recovered in individual cores for the stable isotope experiment was lower than in the cores retained for analysis of the macrofaunal community. The macrofauna from the stable isotope experiments were not fixed with buffered formaldehyde before sieving and it is therefore more likely that individuals were lost or damaged during sieving. Furthermore, these same samples were not stained with Rose Bengal and due to the small body size of the macrofauna some of the individuals may have been missed during the sorting process.

There is evidence that the enrichment experiment was to some extent successful and could achieve what the experiment was initially designed to achieve, i.e. the identification of the animals responding initially to the enrichment. This is confirmed by the positive $\delta^{13}C$ signatures of the ophiuroids at the Vøring Plateau-2 station and of some of the amphipods at Bear Island Fan-2. Other macrofauna from Vøring Plateau-2 and Bear Island Fan-2 do appear to have ingested small quantities of the $^{13}C$ enriched organic matter, even though their $\delta^{13}C$ values were still negative. It may be argued that 36 hours was not a long enough time period to allow the macrofaunal community to fully respond and ingest the $^{13}C$ enriched organic matter. However, individual macrofauna have previously shown evidence of $^{13}C$ enrichment only 24 hours after an artificial pulse of $^{13}C$ enriched organic matter at 850 m water depth on the North Carolina margin (Levin et al. 1997). Surface deposit feeders represented the group with highest initial enrichment and
sub-surface deposit feeders and carnivores displayed levels of enrichment within a period of 14 months at the same station (Levin et al. 1999).

The main difference between this study and the previous work is that the experiments for this chapter were carried out within the laboratory and not *in-situ*. It was planned to compare laboratory based enrichment experiments with *in-situ* experiments. However, the Elinor chamber of the SAMS lander failed to recover any sediment during the cruise. Recovering cores for incubations from the deep sea can potentially have an effect on the benthic fauna, particularly during the transport of cores through the water column. Some organisms are strongly influenced by the pressure decrease through the water column while others are more sensitive to temperature changes (Childress *et al.* 1978). A rapid change in water temperature could potentially kill the specimens. However, this is not a major issue within polar seas and would be of more concern in the tropics where the animals could experience an increase in temperature greater than 10°C during transport to the surface.

Another factor that could potentially influence the behaviour or even survival of the recovered deep-sea organisms is the change in pressure. Only 6 of 427 specimens of scavenging amphipods survived decompression from between 1920 and 4420 m in the Arabian Sea (Treude *et al.* 2002). The animals were recovered in thermally insulated containers that maintained temperature at in-situ deep-sea conditions and prevented the animals experiencing the temperature increase from 1.2°C in the deep-sea to 26°C at the surface. Nonetheless, the general increase in $\delta^{13}$C signatures of the macrofauna in the enrichment experiments of the two upper slope stations does suggest that at least some members of the macrofaunal community had survived decompression from about 1500 m water depth. In addition, during sample sorting, members of the macrofaunal community were observed alive following decompression.
The seasonal timing of the experiment could have a potential influence on the response of the benthic fauna. At the Vøring Plateau, there are two seasonal pulses of organic matter input to the sea bed. The first occurs in late May, consisting of copepod faeces rich in Chl-\(\alpha\) while the second occurs about a month later and is induced by summer sedimentation (Graf 1992). These experiments were carried out in late August and early September and followed the two seasonal pulses. It is likely that the deep-sea benthic communities are opportunistic feeders taking advantage of any organic matter arriving at the sea bed. However, it is known that organic matter can arrive seasonally and episodically to the deep sea. Potentially it could be expected that deep-sea benthic communities show signs of biorhythmic and/or seasonal behaviour patterns that are linked to the seasonal input of organic matter. In shallow water the polychaete orders Eunicida and Phyllodocida exhibits a highly developed biorhythmic capability (Olive et al. 2005). Laboratory based experiments on the polychaete \textit{Nereis virens}, belonging to the Order Phyllodocida, have revealed the animal has a period of feeding cessation during the autumn when there was a supply of food (Last and Olive 2004). This period of cessation was linked to an interval timer or seasonal endogenous oscillator that would allow for gamete maturation and potentially maximizes the fitness of the animal (Last and Olive 2004). With the supply of particulate organic matter arriving seasonally and episodically, particularly at the marginal ice zones then we may expect to find some deep-sea macrofauna adopting a similar strategy to maximise fitness.

6.5 Summary

The smaller body size of the macrofauna within region, compared to global patterns as discussed in Chapter 6, resulted in the majority of the individuals being too small to provide reliable \(\delta^{13}\)C signatures. If individual specimens had been pooled to achieve a higher
biomass for analysis then it is likely there would have been a larger number of reliable δ\textsuperscript{13}C signatures. Despite the small number of samples this pilot study of the macrofaunal community response to an artificial pulse of organic matter has provided useful information that should be considered for future studies. There are improvements that can be made to the experiment for future work within the Nordic Seas region. The first and most obvious is to increase the sample size so the number of individuals available for analysis can be pooled to achieve a higher biomass that should provide reliable δ\textsuperscript{13}C signatures. The second would be for the experiment to be carried out over different lengths of time to determine if the response of the benthic community alters as time passes following the artificial pulse. Furthermore, it would be of value to determine if the response of the benthic community to an artificial pulse is always consistent no matter what season the experiment is carried out. This could provide valuable information on potential seasonal and/or biorhythmic patterns within the benthic community. Lastly, it would be ideal for the experiments to be carried out in-situ; however, this is not always a possibility. This could form part of a latitudinal isobathic study that would allow for the control of pressure on the behaviour of the fauna. If the experiments must be run in the laboratory then all measures should be taken to minimize the potential stress on the benthic fauna during transport to the surface.
7 Distribution of Sipunculans belonging to the Genus Nephasoma within the Nordic Seas region

7.1 Introduction

The aim of this chapter is to highlight the potential ecological and biogeochemical importance of the sipunculan belonging to the genus *Nephasoma* within the Nordic Seas. Sipunculans have often been overlooked in previous ecological studies within the Nordic Seas (Kedra and Murina 2007). However, the presence of species belonging to the genus *Nephasoma* within the Nordic Seas region could have significant ecological and geochemical consequences for the region that are almost always overlooked and rarely considered. This chapter aims to highlight the potential ecological and geochemical importance of the genus *Nephasoma* within the Nordic Seas region.

Sipuncula is currently recognised as a phylum consisting of about 150 exclusively marine species. They are unsegmented, vermiform, marine coelomates closely related to annelids and molluscs, with a long and complicated systematic history recently described in detail by Schulze *et al.* (Schulze *et al.* 2005). Sipunculans have two body regions, the posterior trunk and the anterior introvert. The shape of the trunk can vary from a slender cylinder to almost a sphere and ranges in length between 3 to >400 mm, although a more typical length is 15-30 mm (Cutler 1994). The introvert is the retractable narrow anterior part of the sipunculan and can vary in length from one-fourth to ten times the trunk length (Cutler 1994). Sipunculans can be found at all depths within the oceans and are predominately deposit feeders living in soft sediments, although some species may seek shelter in mollusc shells, foraminiferan tests or coral (Cutler 1968; Murina 1984).
On the Vøring Plateau, the previously reported rapid subduction of organic matter at rate $> 1$ cm day$^{-1}$ following the episodic input of copepod faeces was associated with the sipunculan, *Nephasoma* sp. (Graf 1989). The abundance of *Nephasoma* was estimated at about 500 individuals m$^{-2}$ and the animals inhabited deep narrow burrows less than 1 mm in diameter, extending to sediment depths greater than 50 cm (Figure 7.1) (Romero-Wetzel 1987). There are up to 11,000 capillary burrows m$^{-2}$ associated with *Nephasoma* on the Vøring Plateau, and with an introvert length of about 6 mm, and each individual having a network of about 20 vertical burrows, then *Nephasoma* could potentially have 100% coverage of the sediment surface when feeding (Romero-Wetzel 1987). Similar deep burrow structures have been reported in deep sea sediments from other locations (Thomson and Wilson 1980; Weaver and Schultheiss 1983), and Romero-Wetzel (1987) believed the burrows to be similar in structure to the trace fossil genus *Trichichnus*. Potentially the deep network of burrows associated with *Nephasoma* could have a significant impact on sediment geochemistry throughout the Nordic Seas region and could be an important feature of the region that is often overlooked. However, specimens of *Nephasoma* previously obtained from the Vøring Plateau have only been identified to genus. Therefore the species responsible for the burrow network and the geographical distribution of that species remains unknown. This chapter aims to identify the species of *Nephasoma* responsible for the burrow networks that can extend to sediment depths greater than 50 cm.

The majority of macrofaunal community studies within the Nordic Seas region have overlooked the need to identify sipunculans to species level, often only identifying to phylum level. A recent synopsis of the composition and distribution of the Sipuncula in Svalbard waters noted that sipunculans were often neglected in benthic ecosystem studies (Kedra and Murina 2007). This led to Kedra and Murina (2007) producing a useful identification key for the Sipuncula species of Svalbard waters with the aim of increasing the number of sipunculans identified to species level in future studies.
There are six species of *Nephasoma* occurring within the deep waters of the Nordic Seas region (Table 7.1) (Cutler 1994). However, prior to the present thesis it was unknown which *Nephasoma* species was responsible for the dense network of capillary burrows on the Vøring Plateau. Furthermore, there is limited information on the geographical distribution of *Nephasoma* species and associated burrow structures within the region. With this in mind, it was decided to identify the species of *Nephasoma* responsible for the deep burrow network and rapid subduction of organic matter on the Vøring Plateau and determine their geographical distribution within the region.
Table 7.1 List of *Nephasoma* species and subspecies present within the Nordic Seas region and their recorded depth ranges (Cutler 1994; Kedra and Murina 2007).

<table>
<thead>
<tr>
<th>Species of <em>Nephasoma</em></th>
<th>World Ocean 40 - 60°N</th>
<th>North Atlantic &gt;60°N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>min. (m)</td>
<td>max. (m)</td>
</tr>
<tr>
<td><em>N. abyssorum</em> (Koren &amp; Danielssen, 1875)</td>
<td>10</td>
<td>4800</td>
</tr>
<tr>
<td><em>N. capilleforme</em> (Murina, 1973)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>N. diaphanes diaphanes</em> (Gerould, 1913)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>N. diaphanes corrugatum</em> (Gutter &amp; Gutter, 1986)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>N. eremite</em> (Sars, 1851)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>N. lilljeborgi</em> (Koren &amp; Danielssen, 1880)</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

7.2 Methods

As described in Chapter 2, samples of the macrofaunal community were obtained during the James Clark Ross cruises 75 and 127. Information on the sampling techniques and sorting methods of the macrofaunal community is provided in the previous chapters within the thesis. All sipunculans obtained were identified to species level. Identification of sipunculans to species level can be a difficult task because it is internal features which often help to distinguish between individual species. Therefore, in order to allocate a species name to a specimen this requires the careful dissection of a specimen only a few mm in length and less than 1 mm in diameter. Additional specimens of sipunculans were kindly provided by Professor Graf (University of Rostock), Dr Rumohr (University of Rostock) and Dr Marina Romero-Wetzel (previously the University of Kiel). The specimens provided by Graf, Rumohr and Romero-Wetzel were from the previous studies on the Vøring Plateau that associated the dense burrow network and rapid subduction of organic matter with *Nephasoma* (Romero-Wetzel 1987).
7.3 Results

Sipunculans were recovered at seven of the ten stations sampled throughout the region during both JCR cruises. The highest abundance of *Nephasoma* was recorded at the Vøring Plateau station sampled during JCR 75 cruise in the summer of 2002, estimated at ~400 individuals m\(^{-2}\) (Figure 7.2). A list of *Nephasoma* species recovered during the JCR75 and JCR127 cruise is provided in Tables 7.2 and 7.3 respectively. In total, there were three species of *Nephasoma* identified from all the sipunculan specimens. Those species were *Nephasoma abyssorum*, *N. diaphanes* and *N. lilljeborgi*. The most widespread of the three *Nephasoma* species recovered during both cruises was *N. lilljeborgi*. *Nephasoma abyssorum* was only recovered between a depth of 1380 and 1418 m on the Vøring Plateau. It could not be confirmed if the single *N. diaphanes* specimen recovered from Bear Island Fan-2 during JCR75 cruise was either *N. diaphanes diaphanes* or *N. diaphanes corrugatum*. The majority of the sipunculans were retained in the 500 µm, and *N. lilljeborgi* (~10 mm in length) was larger than *N. abyssorum* (>2 mm in length).
Table 7.2 List of *Nephasoma* species and the number of individuals recovered in the multiple corer samples (250-500 µm) collected during the JCR75 cruise in the summer of 2002. Values in ( ) for each of the multiple core drops represent the number of individuals that were retained in the 500 µm sieve fraction only.

<table>
<thead>
<tr>
<th><em>Nephasoma</em> species</th>
<th>Vøring Plateau</th>
<th>Bear Island Fan</th>
<th>Svalbard Margin</th>
<th>Yermak Plateau</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MC869</td>
<td>MC870</td>
<td>MC871</td>
<td>MC893</td>
</tr>
<tr>
<td><em>N. abyssorum</em></td>
<td>9 (8)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>N. diaphanes</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>N. lilljeborgi</em></td>
<td>2 (1)</td>
<td>1 (1)</td>
<td>1 (1)</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Area sampled (cm²)</td>
<td>197.89</td>
<td>226.16</td>
<td>169.62</td>
<td>197.89</td>
</tr>
<tr>
<td>Water depth (m)</td>
<td>1390</td>
<td>1390</td>
<td>1390</td>
<td>188 (7)</td>
</tr>
</tbody>
</table>

Table 7.3 List of *Nephasoma* species and the number of individuals recovered in megacorer samples (200-500 µm) collected during the JCR127 cruise in the summer of 2005. Values in ( ) for each of the multiple core drops represent the number of individuals that were retained in the 500 µm sieve fraction only.

<table>
<thead>
<tr>
<th><em>Nephasoma</em> species</th>
<th>Vøring Plateau-2</th>
<th>Bear Island Fan-2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MGC1188</td>
<td>MGC1189</td>
</tr>
<tr>
<td><em>N. abyssorum</em></td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td><em>N. diaphanes</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>N. lilljeborgi</em></td>
<td>-</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Area sampled (cm²)</td>
<td>314.2</td>
<td>314.2</td>
</tr>
<tr>
<td>Water depth (m)</td>
<td>1423</td>
<td>1418</td>
</tr>
</tbody>
</table>
Figure 7.2 Mean abundance and standard deviation of *Nephasoma* species *N. abyssorum*, *N. lilljeborgi*, and *N. diaphanes* at each of the stations.

For the first time the species of *Nephasoma* associated with the dense network of burrows described by Romero-Wetzel (1987) was identified as *N. lilljeborgi*. The fine capillary burrows associated with *N. lilljeborgi* were observed at all four stations during the JCR 75 cruise and at Bear Island Fan-2 and Vøring Plateau-2 during the JCR 127 cruise. Images of the capillary burrows at different sediment depth horizons from a single mega core collected at the Vøring Plateau are shown in Figure 7.6.

The geographical locations of the *N. lilljeborgi*, *N. abyssorum* and *N. diaphanes* specimens are shown in Figure 7.3. Data on the depth range of *N. lilljeborgi* presented by Kedra and Murina (2007) can be updated to between 1380 and 2553 m for the Nordic Seas region, although it has been reported to occur at depths of 40 m in the North Atlantic >60°N (Cutler 1994). *Nephasoma lilljeborgi* can also be associated with the rapid subduction of organic matter previously described on the Vøring Plateau (Graf 1989). However, there was no positive δ$^{13}$C enrichment of sipunculans during the 36 hour tracer experiment discussed in Chapter 5.
Figure 7.3 Location of *N. lilljeborgi*, *N. abyssorum* and *N. diaphanes* specimens within the Nordic Seas region. Blue circles (●) are stations where *N. lilljeborgi* was recorded; black circles (●) are stations where *N. abyssorum* was recorded and red circles (●) are the locations of *N. diaphanes*. 
Figure 7.4 Photographs of different sediment depth horizons from a single mega core tube recovered from the Vøring Plateau during the JCR 75 cruise. The fine burrows can be observed down sediment depths of at least 21 cm and highlighted with arrows. *N. lilljeborgi* (N) are present in the upper sediment depth horizons. Images were provided by Mr Peter Lamont (Scottish Association for Marine Science).
7.4 Discussion

Sipunculans belonging to the genus *Nephasoma* were recovered at 70% of the stations that were sampled during the JCR 75 and 127 cruise for this PhD thesis. The *Nephasoma* sp. responsible for the previously reported dense network of burrows at the Vøring Plateau was identified to species level for the first time within this thesis. Specimens collected during the JCR 75 and 127 cruises indicated that the species responsible for the burrow network was *Nephasoma lilljeborgi*. The specimens provided by Graf, Rumohr and Romero-Wetzel confirmed that the species associated with the dense network of burrows on the Vøring Plateau was N. *lilljeborgi*. Results of the geographical distribution of *N. lilljeborgi* suggest that the network of deep burrows associated with the species could actually be quite a common feature throughout the Nordic Seas region, particularly on the continental margins. Although deep burrows similar in structure were observed at all stations where *N. lilljeborgi* were recorded (Tables 7.2 and 7.3), it was only on the Vøring Plateau that burrows occurred in a similar high density as first reported by Romero-Wetzel (1987). *N. lilljeborgi* burrows appear to be built by the displacement of sediment laterally (Romero-Wetzel 1987), most likely via crack propagation (Dorgan et al. 2005; Dorgan et al. 2007). Crack propagation involves an alternating ‘anchor’ system of burrowing that serves as a wedge to extend the crack-shaped burrow (Dorgan et al. 2005). The force required to propagate cracks through the sediment is relatively small (Johnson et al. 2002; Boudreau et al. 2005) and the formation of burrows via crack propagation is an ideal method to conserve energy, particularly within the food limited environment of the deepsea. This conservation of energy is of particular importance due to the dense network of burrows associated with *N. lilljeborgi* and that burrows can often extend to sediment depths of 50 cm.

Despite the dense network of burrows that occurred on the Vøring Plateau, $^{210}$Pb profiles indicate a maximum mixing depth of 2-3 cm with no evidence of intense sediment
mixing (T. Shimmield, pers. comm). The burrows were recorded down to sediment depths of 30 cm in the present study at the Vøring Plateau and the low sediment mixing depths associated with $^{210}$Pb profiles was surprising. However, Graf (1989) reported a sediment mixing depth of 9 cm based on Chl-a profiles that were associated with *Nephasoma*. It seems likely that *N. lilljeborgi* can be classed as both a conveyor-belt and reverse conveyor-belt feeder. Certainly, this selective feeding at the surface and transport of Chl-a particles to sediment depths of 9 cm is typical of a head-up deposit feeder responsible for reverse conveyor-belt mixing (Rhoads 1974; Graf 1989). Head-up deposit feeders typically ingest sediment at the sediment-water interface and defecate at depth within the sediment column. However, Graf (unpublished) also discovered that *Nephasoma* transported a tracer (luminophores) to sediment depths of 4 cm and then back to the sediment-water interface within a period of 10 days. This non-local transport is more typical of what can be described as conveyor-belt mixing (Rhoads 1974), and may explain the discrepancies in the $^{210}$Pb mixing depths of Shimmield (pers. comm.) and the Chl-a mixing depth of Graf (1989). The sipunculans could be expected to selectively feed and transport particles that are rich in Chl-a (Wheatcroft 1992; Smith et al. 1993). Particle tracers, including $^{210}$Pb, tend to be retained in the surficial mixed layer by conveyor belt mixers (Robbins 1986) and so could expect a lower mixing depth for the $^{210}$Pb profiles when *N. lilljeborgi* occur in high densities. In addition, the formation of the burrow network via crack propagation is unlikely to result in the downward non-selective transport of particles down the sedimentary column.

Potentially the geochemistry of the sediment column could be altered by the dense network of burrows at locations where they occur throughout the region (Romero-Wetzel 1987). The burrows can extend deep down the sedimentary column and in particular, pore water chemistry could be altered by the movement of *N. lilljeborgi* within the burrow network drawing overlying water into the burrows via capillary action (Romero-Wetzel
Movement within the burrow would result in regular flushing that would allow for an exchange between pore water and bottom water across the burrow surface. Furthermore, the dense network of burrows would increase the available surface area for this exchange (Aller 2001). The sediment immediately adjacent to burrows can have an increased bacterial population and activity in relation to background levels of the sediment (Aller 1988). A combination of rapid subduction of Chl-a rich particles and an increase in bacterial population adjacent to the burrows could help support sub-surface deposit feeders and in particular the capitellid, *Notomastus* sp. at the Vøring Plateau. At the North Carolina continental margin, a high abundance of sub-surface deposit feeders was associated with tube-building maldanid polychaetes redistributing fresh organic matter down the sediment column (Levin et al. 1997).

The ability of individual members of the macrofaunal community to redistribute the availability of resources, by alteration of their physical environment led Jones et al. (1994) to coin the phrase ‘ecosystem engineers’. It is proposed that *N. lilljeborgi* at the Vøring Plateau and other locations within the Nordic Seas regions are potential ecosystem engineers. Ecosystem engineers can modify sediment geochemistry via bioirrigation, particle redistribution and alteration of sediment spatial heterogeneity (Meysman et al. 2006). If overlying water is drawn into the burrow network then *Nephasoma* could be classed as a gallery-diffusor (Francois et al. 2001; Gerino et al. 2003) in addition to being a head-up feeder. Gallery-diffusors build a network of burrows, are responsible for biodiffusion in the upper sediment layers and the advective transport of particles deep down the burrow network.

Results from the $^{13}$C enrichment experiments presented in Chapter 6 suggested that *Nephasoma* may have consumed small quantities of the enriched organic matter following an artificial pulse. Possible factors that could have influenced the limited uptake by some members of the benthic fauna were discussed in detail in the previous chapter. However,
the $^{13}$C enriched diatoms employed in the tracer experiment may not be a favoured food source for the Nephasoma. The rapid subduction associated with Nephasoma occurred following a pulse of copepod faecal pellets rich in Chl-$a$. Similar mixing depths were not observed following the summer sedimentation about one month later. Graf (1989) believed the copepod faecal pellets, enriched in Chl-$a$, provided a high quality food source for N. lilljeborgi. During a spring phytoplankton bloom in the Baltic Sea, copepod faecal pellets were found to have high levels of Chl-$a$ but with low levels of phaeopigments indicating the presence of undigested phytoplankton cells (Bathman and Liebezeit 1986). Scanning electron microscopy confirmed that faecal pellets did indeed contain abundant intact diatom cells. Therefore, faecal pellets would provide a concentrated supply of diatom cells for N. lilljeborgi.

The summer sedimentation was a much higher flux of particulate organic carbon but lower Chl-$a$ concentration than the pulse of copepod faecal pellets; suggesting Nephasoma selectively feed on the higher quality copepod faecal pellets in preference to organic matter associated with the summer sedimentation and mainly consisting of phytodetritus (Graf 1989). However, sediment community oxygen consumption increased following the summer sedimentation event indicating a response by the benthic community (Graf 1989). Within the Nordic Seas region, copepods are believed to influence the quality and quantity of organic matter arriving at the sea bed (Wassmann et al. 1996). Therefore, future tracer studies should possibly consider testing the response of the benthic community to both $^{13}$C enriched phytodetritus and copepod faecal pellets to determine which component of the benthic community responds to each food source.

N. lilljeborgi could be expected to have physiological adaptations for gas exchange that permit the worm to burrow deep down the sedimentary column. It was suggested by Ruppert and Rice (1995) that sipunculans potentially fall within three functional
physiological categories depending on the body region or regions used for gas exchange. Those categories are:

1. **Tentacle breathers.** Numerous tentacles are extended into the water and well-developed contractile vessels transport dissolved gases between the tentacular and coelomic cavities.

2. **Tentacle and introvert breathers.** The elongated and thin walled introvert is extended into the water along with the tentacles. Contractile vessels are normally simple unbranched tubes.

3. **Integumentary breathers.** Usually have small tentacles and often the contractile vessels are weakly developed. Integumentary specialisations allow dissolved gas exchange across the entire body surface.

*Nephasoma lilljeborgi* is likely to belong to the integumentary breathers and have behavioural specialisations that allow for the transport and storage of organic matter deep down the sediment column. This sub-surface storage of organic matter is a useful technique employed by some members of the benthic community, particularly when organic matter arrives episodically (Rhoads 1974).

The previously reported deep burrow networks and rapid subduction of organic matter on the Vøring Plateau can now be associated with the sipunculan, *N. lilljeborgi*. Work carried out for this thesis has increased knowledge of the geographical distribution of *N. lilljeborgi* and associated burrow structures within the Nordic Seas region. This species is of Arctic/boreal origin and appears to be endemic to the cold deep waters of the Nordic Seas region (Cutler 1994). If this is the case then the deep burrow network associated with *N. lilljeborgi* should only occur within the deep waters of the Nordic Seas region. *N. lilljeborgi* and the associated burrow networks could significantly influence benthic community structure. In addition it is unknown what impact *N. lilljeborgi* has on sediment geochemistry, in particular pore water chemistry and this needs to be addressed.
Additional sampling is required throughout the region to confirm the geographical distribution of *N. lilljeorgi* and the potential contribution of the species to organic carbon cycling within the region. It is important that future studies on the macrofaunal community within the region identify the sipunculans to species level. If specimens are only identified to genus then there is the possibility to misinterpret the ecological and geochemical importance of the specimens obtained. The possibility of misinterpretation is highlighted by the presence of six species of the genus *Nephasoma* occurring within the Nordic Seas region but only one of those species, *N. lilljeorgi*, being responsible for a deep burrow network and rapid subduction of organic matter.
8 Discussion

8.1 Overview of findings

Results presented within this thesis indicate that previous macrofaunal community studies within the Nordic Seas region may have underestimated macrofaunal abundance. Underestimation of macrofaunal abundance most likely occurred as a result of the sampling strategy employed and the smaller body size of the Nordic Seas macrofauna reported within this thesis, when compared to global patterns (Rex et al. 2006). A smaller body size of macrofauna can influence the estimation of macrofaunal abundance and is particularly influenced by the selection of sampling gear and sieve size and this will be discussed in detail later within this chapter. The highest proportion of larger bodied macrofauna along the Norwegian continental margin occurred at the Svalbard Margin station located within the marginal ice zone. There was higher similarity in the species composition of the macrofaunal community at the two stations located within the marginal ice zone. This difference in species composition indicated that ice cover is one of a combination of environmental factors that influence the distribution of species along the Norwegian continental margin. The influence of a changing climate and receding ice edge is expected to result in a system switch from sea-ice algae-benthos to phytoplankton-zooplankton of the marginal ice zones (Carrol and Carrol 2003). If the expected switch does occur then deep-sea benthic species distribution patterns within the Nordic Seas will be influenced and ultimately alter in relation to a switch in supply of organic matter to the sea bed.

Deposit feeders were generally characteristic of the macrofaunal community at all the stations sampled throughout the Nordic Seas. However, the relative abundance of
interface feeders unexpectedly increased with depth across the Bear Island Fan and Vøring Plateau. The $^{13}$C enrichment of the continental margin macrofaunal community indicates that the macrofauna can respond to the episodic arrival of organic matter within 36 hours. Species known to adopt the sub-surface storage of organic matter were present at stations influenced by the episodic input of organic matter. In this thesis the sipunculan, *Nephasoma lilljeborgi* for the first time was associated with the previously reported rapid subduction of organic matter (Graf 1989) and deep burrow networks on the Vøring Plateau (Romero-Wetzel 1987). In addition, the deep burrows associated with *N. lilljeborgi* are a feature that not only occur on the Vøring Plateau but throughout the Nordic Seas. These burrow networks could have a significant influence on the sediment geochemistry of the region, in particular pore water chemistry (Romero-Wetzel 1987). With six different species of *Nephasoma* occurring in the deep Nordic Sea it is therefore essential that future macrofaunal community studies identify sipunculans to species level.

### 8.2 Macrofaunal community

#### 8.2.1 Nordic Seas region

Few of the previous studies on the macrofaunal community of the Nordic Seas region have focused on community patterns over such a large geographical area as presented within this thesis. In the late 1970s, Dahl *et al.* (1976) investigated macrofaunal community patterns in each of the four deep basins. This was the first quantitative study that sampled the deep benthic community over a large geographical area within the region. Extensive sampling has also taken place on the East Greenland slope, between 68° and 81°N (Schnack 1998; Piepenburg *et al.* 2001). Results presented within this thesis are the first to focus on macrofaunal community patterns over a similarly large area on the continental slope of the eastern Atlantic Domain. Furthermore, with the exception of work carried out
in the Faeroe-Shetland Channel (Narayanaswamy et al. 2003; Narayanaswamy et al. 2005), none of the previous studies have obtained macrofaunal community samples with the hydraulically dampened megacorer. This difference in sampling gear may help explain lower macrofaunal abundance estimated in previous studies. The boxcorer commonly employed in previous macrofaunal community studies can potentially under-sample both the macrofaunal (Bett and Gage 2000; Hughes and Gage 2004) and meiofaunal community (Bett et al. 1994), when compared to samples obtained with the multiple corer.

The multiple corer samples a smaller area than the boxcorer but is unlikely to underestimate macrofaunal abundance. The smaller area sampled by the multiple corer could lower the possibility of sampling rarer species or larger bodied macrofauna when compared to the boxcorer. However, the sampling of rarer species will be dependent on the body size of that species and the sampling gear selected. For example, the sampling of smaller rarer species that are likely to be washed away by a bow wave is more likely to be successful when the hydraulically dampened multiple corer is employed in preference to the boxcorer.

A significantly greater macrofaunal biomass and abundance of larger macrofauna (>500 µm & >1 mm) at the Svalbard Margin may be explained by the location of the station within the marginal ice zone to the west of Svalbard. The seasonally receding ice edge can induce prolonged diatom blooms (Rey and Loeng 1985; Smith and Nelson 1985), resulting in the strongly pulsed sedimentation of organic matter (Honjo 1990; Hebbeln and Wefer 1991) that provides a potential food source for the benthos (Schewe and Soltwedel 2003). Marginal ices zones in shelf seas are areas of known high benthic standing stock (Grebmeier and Barry 1991; Piepenburg 2000).

The Yermak Plateau station located within the marginal ice zone actually had significantly the lowest mean individual biomass (>500 µm) from the multiple corer samples. Mean individual biomass increased significantly at the Yermak Plateau station
when the boxcorer samples were considered (>1 mm) and this was due to the presence of rare large-bodied echiurans of the species *Hamingia arctica*. This highlights how results for mean individual biomass can be skewed by the presence of a few large-bodied individuals within a sample collection (Kaariainen and Bett 2006). Sampling macrofaunal community abundance has different properties to sampling community biomass. In benthic samples the majority of the community biomass will be from the large animals obtained in the samples. A larger body size and longer life span would provide benthic fauna with a buffer against the unpredictable seasonal input of organic matter associated with ice edge processes (Peters 1986). The large body of *H. arctica* would provide the animal with a buffer against the unpredictable seasonal input of organic matter associated with ice edge processes. The lack of the presence of *H. arctica* in the Yermak Plateau multiple corer samples highlights that sampling macrofaunal community abundance has different properties to sampling community biomass. Macrofaunal community biomass estimates will be predominately influenced by the large animals collected in the samples and will be relative to the sample size. Therefore, when sampling for larger members of the macrofaunal community then the boxcorer should be choice of sampling gear due to the larger sample size.

Macrofaunal abundance estimates are generally higher in this study than previous studies at similar depths in the region. While macrofaunal community biomass was comparable with previous studies that apparently had lower estimates of macrofaunal abundance when compared with the present study. It can be difficult to draw direct comparisons between studies when there are differences in the sampling gear, sorting methods and personnel employed to process samples. The previous Nordic Seas studies that employed the boxcorer and a larger sieve size may have resulted in the underestimation of macrofaunal abundance. However, comparable macrofaunal
community biomass estimates indicates that samples obtained with the multiple corer are in general not undersampling the larger macrofauna.

To confirm if any changes in macrofaunal abundance and biomass within the region would require replicated seasonal and annual sampling at fixed stations over a number of years and employing standardised methods. If both macrofaunal abundance and biomass findings were to hold true, then it would indicate that mean individual biomass of the macrofaunal community has decreased within the region. There are limitations associated with mean individual biomass, but it would be possible to investigate patterns in body size employing the methods described by Kaariainen and Bett (2006). Furthermore, the Hausgarten observatory of the Alfred Wegener Institute (Schewe and Soltwedel 2003), located between water depths of 1000 and 5000 m at 79°N to the west of Spitsbergen and comprising of 15 stations could provide a useful time-series data set for such an analysis.

8.2.2 Macrofaunal community structure

The relative abundance of the macrofaunal community at each of the stations both along and across the Norwegian Sea continental margin was largely represented by deposit feeders and in particular surface deposit feeders. Deposit feeders are typically the most abundant feeding type observed within deep-sea benthic communities (Gage and Tyler 1991). However, the importance of considering the relative biomass of the benthic community in addition to abundance was highlighted within this thesis. When relative biomass of the macrofaunal feeding types was considered, the community was shown not to be dominated by deposit feeders at each of the stations as indicated by the relative abundance. Suspension feeders contributed significantly to relative community biomass at Bear Island Fan (Chapter 3), Bear Island Fan-2 and the Voring Plateau-5 (Chapter 5) despite the relative abundance of the macrofaunal community indicating the dominance of
deposit feeders. Macrofaunal community biomass can provide a clearer indication of the benthic standing stock at each station and the presence of a high biomass of suspension feeders highlights the potential influence of water flow on benthic community structure at these locations (Miller et al. 1992). When the relative abundance and biomass of the macrofaunal community are considered this can provide a far more informative description of the community structure than abundance alone. This is further highlighted when polychaetes, the most abundant member of the macrofauna are considered. Generally polychaetes represented >60% of macrofaunal abundance but did not represent anywhere near a similarly high relative biomass at each of the stations.

8.2.3 Comparisons with global patterns

A decline in macrofaunal abundance and biomass with increasing water depth across the Norwegian continental margin was observed. In addition, the relative abundance of smaller sized macrofauna (250-500 µm) increased with increasing water depth. This observation was similar to the findings of Rex et al. (2006), who described global patterns of an increase in the relative abundance of smaller metazoans with increasing water depth. Macrofaunal abundance within the Nordic Seas region was higher than the global mean, while biomass was comparable (Rex et al. 2006). Therefore, mean individual biomass of the macrofauna within the Nordic Seas region is lower than global patterns. A smaller body size associated with the Nordic Seas macrofaunal community could have important consequences for any future sampling strategies in the region. Ideally a hydraulically dampened corer and sieve size smaller than 500 µm should be the selected for future deep Nordic Seas studies.

In the deep basins of the Arctic Ocean, meiofauna appear to have shifted towards a smaller body size compared with meiofauna sampled from similar depths in the Atlantic
Ocean (Schewe and Soltwedel 2003). Any shift towards a smaller body size or dwarfism within the central Arctic is most likely linked to an extremely limited food supply (Thiel 1975). The deep Arctic Ocean is extremely oligotrophic and the input of organic matter from surface derived sources is generally low and very patchy (Soltwedel and Schewe 1998). Often a large quantity of the organic matter produced in the upper water column or sea ice is either consumed by zooplankton or recycled within the microbial loop, resulting in limited availability of food for the benthic fauna (Grebmeier and Barry 1991).

### 8.3 Species richness and diversity

Results presented within this thesis support previous findings of lower species richness in the deep Nordic Seas, when comparisons are drawn with other deep-sea locations (Snelgrove and Smith 2002). However, measure of diversity can be influenced by sample size, sampling a larger area will increase the likelihood of sampling rarer species. It is possibly that diversity measures based on the multiple corer samples may have been underestimated due the small area sampled. It is difficult to draw direct comparisons between studies in the region when there are differences in sampling and sorting methods employed that can influence diversity indices (Warwick and Clarke 1996).

There were no latitudinal patterns in diversity observed but there was a north/south divide in species composition of the benthic fauna at the continental margin. Multivariate analysis of species composition suggested a higher similarity between the two northern stations, the Yermak Plateau and Svalbard Margin, than between the northern and southern stations. A higher similarity in the species composition of the macrofaunal community was also observed between the two southern stations, Bear Island Fan and the Vøring Plateau. It is important to note that this difference in species composition is based on a low number of sampling stations and may not be representative of the whole Nordic Seas regions.
However, what can be concluded is that there were clear differences in the species composition between the two northern and two southern stations.

Both the Svalbard Margin and Yermak Plateau stations were located within the marginal ice zone and are therefore potentially influenced by the associated ice edge processes. Climate induced changes at the two northern stations could lead to a switch from a sea-ice algae-benthos system to a phytoplankton-zooplankton system (Carrol and Carrol 2003). A continued northward retreat in the marginal ice zone could lead to the species composition of the two northern stations increasing in similarity with the two southern stations. Deep-sea species composition of the benthic community at an abyssal station in the Pacific Ocean has previously been observed to fluctuate in relation to surface climate variability and primary production (Ruhl and Smith Jr. 2004). However, confirmation of any such change within the Nordic Seas would require the long term time-series monitoring of benthic communities, benthic-pelagic coupling and sea ice coverage over interannual, decadal or even longer time scales.

8.4 Benthic response to organic matter

8.4.1 Community overview

In this thesis, tracer experiments based on sediment cores collected from the Vøring Plateau and Bear Island Fan revealed that the macrofaunal community and in particular the ophiuroid *Ophiocten gracilis* can respond to and take up $^{13}$C enriched diatoms within 36 hours following an artificial pulse. *Ophiocten gracilis*, a bathyal species, has previously been reported to occur at the Kolbeinsey Ridge (Piepenburg and von Juterzenka 1994) and at the Vøring Plateau (Romero-Wetzel and Gerlach 1991), and is now considered a species that is present within Arctic waters (Piepenburg *et al.* 2001). On the Arctic shelves and upper continental margin slope, echinoderms and in particular ophiuroids contribute
significantly to carbon remineralisation (Piepenburg 2000). Species known to adopt the sub-surface storage of organic matter were recorded at locations influenced by the episodic flux of organic matter to the sea floor. The biogeographic boundaries of such species within the region could be influenced by changes in organic matter flux patterns to the sea floor, most notably if input switches to a continual steady flux of refractory organic matter. A change in the dominant sediment mixing modes of the benthic fauna could have a profound impact on sediment geochemistry within the region.

One species known to adopt the sub-surface storage of organic matter and previously reported in the region is the sipunculan *Nephasoma*. This genus was observed responding rapidly to a seasonal pulse of copepod faecal pellets on the Vøring Plateau and subducting the pellets deep down the sedimentary column within days (Graf 1989). Furthermore, the same species was reported to form a dense network of burrows extending deep down the sedimentary column to sediment depths greater than 50 cm (Romero-Wetzel 1987). However, there are 6 species of *Nephasoma* occurring in the deep waters of the Nordic Sea region but which of the species was responsible for the deep burrows and rapid subduction of organic matter was unknown. Following examination of the original specimens from the Vøring Plateau (Romero-Wetzel 1987; Graf 1989), the *Nephasoma* species was confirmed as *Nephasoma lilljeborgi*, a species believed to be endemic to the region (Cutler 1994; Kedra and Murina 2007). *N. lilljeborgi* and the associated fine burrows were recorded at each of the stations sampled along the Norwegian Sea continental margin during the JCR75 cruise in the summer of 2002. It was only at the Vøring Plateau that the burrows appeared to occur in similar high densities deep down the sedimentary column as first reported by Romero-Wetzel (1987).

The rapid subduction of the faecal pellets down the sedimentary column could provide a food source for sub-surface deposit feeders, most notably the capitellid *Notomastus* sp. at the Vøring Plateau. If *N. lilljeborgi* is an ecosystem engineer, any shift
in the biogeographic boundaries of the species could have a profound impact on sediment geochemistry and benthic community structure within the region. Although this species is unlikely to have a significant impact on sediment mixing depths (based on $^{210}$Pb profiles) the animal is capable of altering sediment heterogeneity and selectively feeding on particles rich in Chl-$\alpha$. Furthermore, movement within the burrow could draw down overlying water into the burrow network and potentially alter pore water chemistry (Romero-Wetzel 1987), although this has to be confirmed.

The availability of food has been shown to be the most important factor influencing community structure and function within the deep waters of the region (Klages et al. 2003; Piepenburg 2005). Although food availability can influence benthic standing stock, it is not the only environmental factor influencing community structure and function in the Nordic Seas region. Within this thesis, the influence of water flow velocity has been suggested to be one of the environmental factors that can influence macrofaunal community structure and function, particularly the relative biomass of suspension feeders. This was highlighted by the presence of the relatively large bodied suspension feeding amphipod *Haploops setosa* at the Bear Island Fan (Chapter 2) and Bear Island Fan-2 (Chapter 4) stations. High flow velocities at the Bear Island Fan had previously been reported, reaching velocities of 40 cm s$^{-1}$ (McPhee et al. 1998) and influencing the presence and orientation of suspension feeding polychaetes (Thomsen et al. 1995).

All members of the benthic community, including the mega-, macro- and meiofauna influence the incorporation of organic matter into the sea floor. Changes in the larger bodied mega and macrofaunal community could influence the meiofaunal community structure (Austen et al. 2003; Olafsson 2003). Meiofaunal abundance estimates in the deep waters of the Nordic Seas marginal ice zone appear to be influenced by the availability of phytodetrital food (Hoste et al. 2007). The response of the benthic community to potential long term changes in food supply remains unknown. Such a change
could be expected at the marginal ice zones if the system switches from sea-ice algae-benthos to phytoplankton-zooplankton (Carrol and Carrol 2003). Sea-ice algae can contribute significantly to primary production in polar seas (Legendre et al. 1992) and provide a high quality food source for some deposit feeders (McMahon et al. 2006). A decrease in sea ice algae production and subsequent increase in pelagic phytoplankton production could have a significant impact on the quantity and quality of organic matter available to the benthic fauna. Results presented within this thesis suggest a shift in species composition and community structure of the benthos could be expected if the marginal ice zone continues to retreat further north. Furthermore, any change in the flux of organic matter could have a significant influence on the functional ecology of the benthic community.

8.5 Future sampling recommendations

The smaller mean body size of the Nordic Seas macrofauna could influence the accuracy of quantitative studies, depending on the sample sorting and processing methods employed. First and foremost, the choice of sampling gear should be considered. Traditionally in the Nordic Seas region, the USNEL boxcorer, developed by Hessler and Jumars (1974), has been the standard gear employed for sampling the macrofaunal community. A higher macrofaunal abundance estimated from multiple corer samples in this study, along with a small mean body size suggests a device that collects undisturbed samples would be preferential. Therefore, the hydraulically dampened multiple- or megacorer is recommended as the preferential device for obtaining quantitative samples of the macrofaunal community. However, the boxcorer does provide a larger sample size and would be more likely to obtain a single sample with a larger representation of the macrofaunal community than the multiple- and megacorer. Therefore for sampling the
rarer larger members and rarer species of the macrofaunal community the boxcorer is recommended.

Another important consideration due to the small body size of the macrofauna is the selection of sieve mesh size. Within this study, 250 and 500 µm sieve mesh sizes were employed, when the majority of previous studies in the Nordic Seas have employed a 500 µm mesh size. A difference in mesh sizes may contribute to the higher macrofaunal abundance estimates presented within this thesis. A 250 µm mesh sieve has become accepted as the standard sieve size for sampling the lower size limit of the macrofaunal community (Bett and Gage 2000). Therefore, due to the small body size of the macrofauna in the Nordic Seas a mesh size of 250 µm is viewed as essential for any future quantitative studies of the whole macrofaunal community of the region. However if future research interests are focused on the larger size fractions of the community then a sieve size of 500 µm and samples collected with the boxcorer would be acceptable.
References


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**Taxonomic References**


