Mariene Biologie
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UNIVERSITEIT GENT
Faculteit Wetenschappen
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Spatial distribution and biodiversity patterns of the hyperbenthos along NE Atlantic continental margins

Ruimtelijke distributie en biodiversiteit van het hyperbenthos langsheen continentale randen in het noordoosten van de Atlantische Oceaan

Véronique Vanquickelberghe

Thesis submitted in partial fulfilment of the requirement for
the Degree of Doctor in Science (Biology)

Proefschrift voorgelegd tot het behalen van
de graad van Doctor in de Wetenschappen (Biologie)

Promotor: Prof. Dr. M. Vincx

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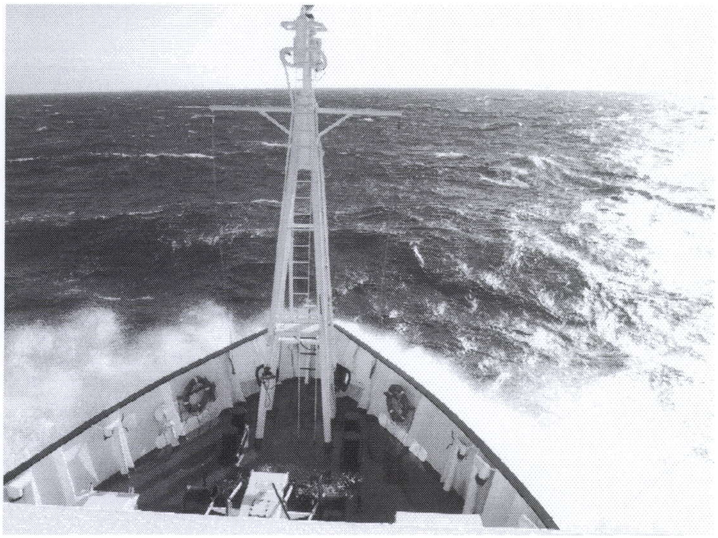

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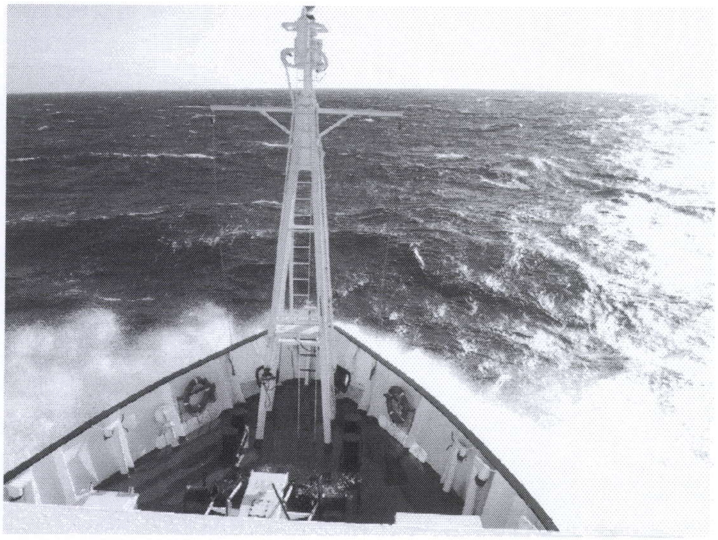

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Chapter 1

Introduction and objectives

1.1. State of the art

The **deep sea** is the part of the world's ocean below the continental shelves, covering almost two third of the earth's surface. Therefore, the deep-sea bottom can be seen as the most typical and extensive environment, harbouring typical life forms (Gage & Tyler, 1991). Exploration of the topography of the deep ocean started after World War II, when researchers began systematically to survey and chart the ocean bottom using new echo-sounding technologies. The deepc-sea bottom is not, as was widely believed, monotonously flat and featureless. Rather, parts of it are as uneven and as rugged as the familiar mountain topography on land.

Three large physiographic provinces can be distinguished, each having unique landform characteristics: continental margins, deep-ocean basins and mid-ocean ridges. The system of broad **mid-ocean ridges**, a continuous submarine mountain range, winds its way through all the oceans. They are separated from the drowned edges of the continents, the **continental margins**, by large intervening tracts of **deep-ocean basins**, the ocean floor that lies deeper than two kilometres below the sea level (Pinet, 1998).

From a biological point of view, our awareness of the existence of a **deep-sea fauna** is remarkably recent. It is more than a century since the Challenger expedition (1872-1876) recorded the presence of a deep-sea benthos throughout the oceans, refuting the concept that the great depths were devoid of life (Rex, 1981). The ever expanding knowledge of the physical nature and processes of the deep oceans has increasingly determined the approach and methodology adopted in the biological study of this unique habitat. Recently, mainly through the use of adequate sampling techniques, biological information of these habitats has become available.

High **species diversity** on continental margins, and in the deep sea in general, was first recorded by Sanders *et al.* (1965) and Hessler & Sanders (1967). This discovery was made possible by advances in sampling technology allowing collection of semi-quantitative and quantitative samples of smaller animals (macrofauna and meiofauna) living in deep-sea sediments (Gage & Tyler, 1991; Gooday *et al.*, 1998). Subsequent observations have confirmed that high species diversity in the deep sea, particularly the benthic macrofauna and meiofauna, is a global feature (Jumars, 1976; Hecker & Paul, 1979; Rowe *et al.*, 1982, Gage, 1996; Gooday *et al.*, 1998).

Due to intense observations, existing patterns in deep-sea density and diversity have been elucidated. Firstly, the density of all size categories of organisms gradually decreases with increasing distance from the continental shelf (Hessler & Sanders, 1967; Rex, 1981; Rex *et al.*, 1990). Secondly, the diversity within the deep sea is not evenly distributed amongst phyla, but polychaetes, crustaceans (Peracarida) and molluscs (Bivalvia) form the highest proportions of species in the macrofauna (Hessler & Sanders, 1967; Grassle & Maciolek, 1992). Finally, species diversity shows a parabolic distribution with depth, reaching a peak in the bathyal zone, before decreasing to the abyssal plain (Sibuet, 1977; Rex, 1981; Paterson *et al.*, 1985).

Another deep-sea research topic, the **zonation of fauna,** has been documented extensively (Carney *et al.*, 1983). Zones are described as regions of lesser faunal change bounded by regions of greater faunal change (Menzies *et al.*, 1973; Hecker, 1990; Gage & Tyler, 1991). Previous workers have focused either on general faunal zonation patterns (Le Danois, 1948; Rowe & Menzies, 1969; Haedrich *et al.*, 1975; Ohta, 1983) or on the zonation of specific taxa, *e.g.* fish (Day & Percy, 1968), gastropods (Rex, 1977), echinoderms (Gage, 1986), holothurians (Billett, 1991) and decapod crustaceans (Cartes & Sardà, 1993). These studies have shown, regardless of the taxon examined, that deep-sea fauna undergo a non-repeating sequential change with depth and most species have predictable and restricted depth ranges (Rowe & Menzies, 1969; Carney *et al.*, 1983; Gage & Tyler, 1991).

There are many logistic problems associated with identifying and measuring factors that may affect zonation and depth related distribution, and as a result, nearly all deep-sea studies were focussed on those factors that correlate with changes in the fauna (Howell *et al.*, 2002). These factors include temperature (Rowe & Menzies, 1969; Haedrich *et al.*, 1975), pressure (Siebenaller & Somero, 1978; Somero *et al.*, 1983; Young *et al.*, 1996), oxygen minimum (Gage, 1986; Rogers, 2000), sediment type (Day & Pearcy, 1968; Haedrich *et al.*, 1975), water mass structure (Tyler & Zibrowius, 1992), currents, topography and food supply (Rowe & Menzies, 1969; Hecker, 1990; Rice *et al.*, 1990; Cartes & Sardà, 1993), larval dispersal (Rowe & Menzies, 1969; Grassle *et al.*, 1979, Billett, 1991), competition, predation and trophic level (Rex, 1976; 1977; Haedrich *et al.*, 1980; Cartes & Sardà, 1993).

Identifying specific environmental variables that restrict the depth ranges of deep-sea species and their effects on an organism remains an unsolved problem. However, a more detailed knowledge of the vertical distribution of deep-sea species may help to indicate factors that affect species distribution and large-scale zonation (Young *et al.*, 1996).

Recently, continental margins and the adjacent abyssal plains have been the focus for a number of major scientific programs. The northeastern Atlantic Ocean has been the subject in a number of national (*e.g.* British, Dutch, French and German) programs, and in international ones, mainly funded by the European Union, which have influenced the development of modern themes in deep-sea biology (Levin & Gooday, 2003): *e.g.* the International Council for the Exploration of the Sea (ICES) (http://www.ices.dk); the Ocean Margin Exchange (OMEX) project (Huthnance *et al.*, 2001; Wollast & Chou, 2001); the GEOmound/ECOmound project (http://geomound.ucd.ie/) focusing on environmental controls on mound formation along the European margin; the project ACES (Atlantic Coral Ecosystem Study) studying the biology and ecology of deep-water coral ecosystems (http://www.pal.uni-erlangen.de/proj/aces/).

The Ocean Margin Exchange (OMEX) Programme was a large-scale multidisciplinary project bringing together scientists from 40 universities and institutes throughout Europe. This project supported by the European Commission in the framework of its Marine Science and Technology programme (MAST) aimed at gaining a better understanding of the physical, chemical and biological processes occurring at the ocean margins in order to quantify fluxes of energy and organic matter across this boundary. Recognising the environmental significance of shelf-edge exchange and its role in global biogeochemical cycling, this MAST initiative aimed to characterise the flux of carbon, nutrients and other trace elements between the coastal seas and the open ocean.

During OMEX I (1993-1996) investigations concentrated in the northeastern Atlantic Ocean on the Celtic Sea shelf edge which links a relatively broad continental shelf with the deep sea (Flach *et al.*, 1998; Heip *et al.*, 2001; van Weering *et al.*, 1998a). OMEX II (1997-2000) was designed to look at a contrasting system, the relatively narrow Iberian margin off the north-western Spanish and Portuguese coasts (van Weering *et al.*, 2002; Davies *et al.*, 2002). Designed to meet the priority objectives of the International Geosphere-Biosphere Program (IGBP), OMEX took into account the specific features of the European marine environments and settings, and capitalised on the expertise of the European oceanographic community within the MAST framework.

Recognising the importance of deep-sea research, this PhD research aims at giving an overview of the hyperbenthic fauna inhabiting the benthic boundary layer at two continental slope areas in the northeastern Atlantic Ocean, the Porcupine Seabight, west of Ireland and Meriadzek Terrace, west of France. This study, based on quantitative samples of hyperbenthic fauna, determines the bathymetric distribution and biodiversity of hyperbenthic taxa and species from the shelf break to bathyal depths and examines the depth-related distribution and abundance of species within their depth ranges. Patterns of the hyperbenthic distribution are discussed in terms of what is known about the ecology of the taxa and species sampled. The main objectives are described in more detail at the end of this chapter (see 1.5. Research objectives). The general aspects of the studied topographic unit and the studied fauna are described in the next paragraphs.

1.2. Definition of continental margins and slopes

Ocean margins are global scale features that mark the transition between the continental and oceanic crust. They are the product of predominantly vertical *(i.e.* subsidence and uplift) rather than horizontal movements and are the expression of sea-level changes throughout geological times (Henriet, pers. comm.). Ocean margins are the transitional zones between the oceans and continents where most of the sediments derived from the land are deposited (Wefer *et al.*, 2002). The effective processes here are influenced by a variety of steering mechanisms, from mountain building and climate on the land to tectonics and sea-level fluctuations at the margins of the seas. These areas are also of great importance for the global biogeochemical cycles because, although they only make up about 20 % of the ocean's surface, 50 % of the global marine production takes place here. The continental margins can be broadly divided into the **continental shelf** close to the coast (down to about 200 m on average), the adjacent and somewhat steeper **continental slope** (down to 3000 m) (Fig. 1.1), and the **continental rise** at the limit with the abyssal plains (Blondel, 2002). Two types of continental margins can be distinguished: active and passive ones.

1.2.1. Active and passive continental margins

Continental margins are of two types, depending on the tectonic condition: margins at the edges of **converging** tectonical plates, where one lithospheric plate has to dive below another one (*i.e.* subduction), are called convergent or **active margins**, while **passive continental margins** (Fig. 1.1) are created by **divergence** as a result of tensile stresses (Henriet, pers. comm.). Active margins are the sites of tectonic activity (*e.g.* earthquakes, volcanoes). Because of the mountainous terrain, most of the rivers are fairly short, and the continental shelf is narrow to non-existent, dropping off quickly into the depths of the subduction trench. A good example is the west coast of South America with the Andes Mountains. At passive continental margins there is no subduction taking place, so tectonic activity is minimal and the earth's weathering and erosional processes are winning. This leads to low-relief (flat) land extending both directions from the beach, long river systems, and the accumulation of thick piles of sedimentary debris on the relatively wide continental shelves. Passive margins are typical for the Atlantic Ocean. This latter type of continental margin is the study object of this PhD research.

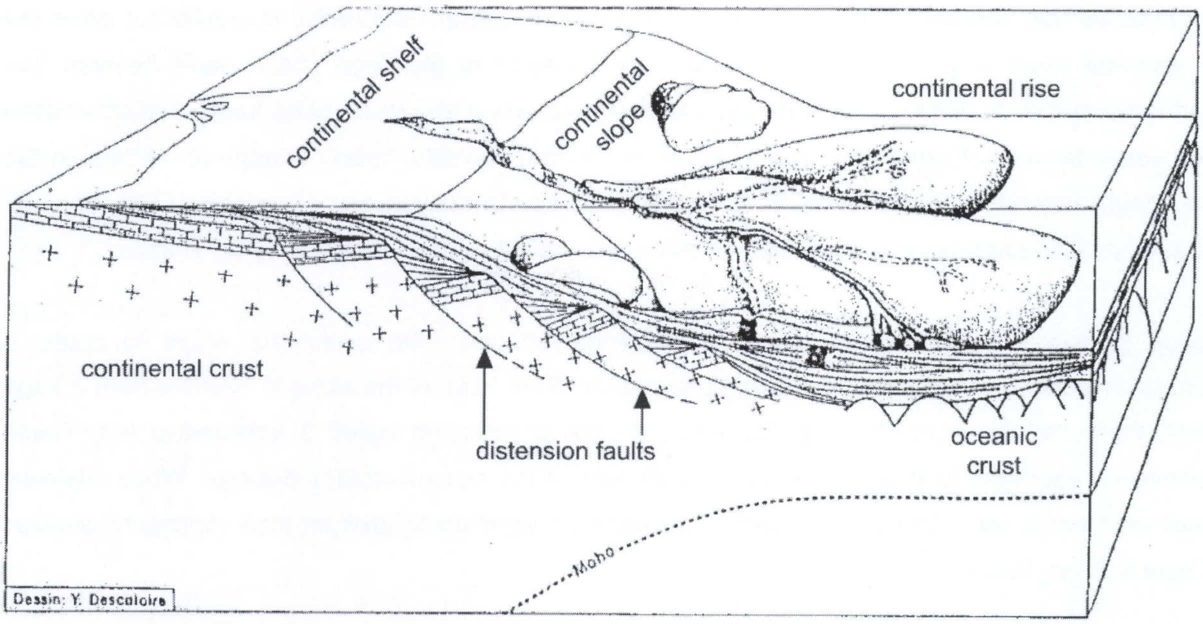


Fig.1.1 Illustration of the evolution of a passive continental margin with distension faults and sedimentation processes. The major margin structures are indicated: continental shelf, continental slope and continental rise. (modified after Henriet & De Batist, 2001)

1.2.2. Topography of the deep-sea floor

The topography of the deep-ocean floor is predominantly the result of a cooling history of the ocean crust (Henriet, pers.comm.). New lithosphere forms at a spreading center. As the new crust spreads laterally it cools, becomes denser and gradually subsides. As the oceanic crust ages and begins to spread laterally the deep-sea sediment layer thickens. Moreover, the topography of the floor of the deep ocean (Fig. 1.2) is a balance between this seafloor spreading and secondly sedimentation of inorganic and organic particles. Most places along the boundary of every continent are characterized by an area of shallow water, which may range from a few kilometres to more than 1000 kilometres in width. These areas, where the oceans cover a portion of the continental landmass, are called **continental shelves**. Averaging approximately 60 metres depth, these shelves slope gradually away from the shore at a rate of about twelve metres every kilometre, ending at the **shelf break**.
The deep sea is usually defined as beginning at the shelf break, because this physiographic feature coincides with the transition from the basically shallow water fauna of the shelf to the deep-sea fauna (Sanders *et al.*, 1965; Hessler, 1974; Merrett, 1989). In many parts of the ocean, the shelf break is situated at about 200 m depth, initiating the deep sea (Thistle, 2003).

The transition from the gently sloping continental shelf to the deep ocean basin is called the **continental slope** (Fig. 1.2). Here, the ocean depth increases rapidly, reaching several thousand metres within a few kilometres. The base of the continental slope is the boundary between the continental crust and the oceanic crust. The continental shelf and slope are often cut by deep **canyons** running perpendicular to the shoreline. These canyons are associated with powerful currents which scour the canyon out of the surrounding sediment. The gradient of the slope may be interrupted by terraces and submarine canyons. The latter appear irregular, fissure-like channels cut down the continental slope which may act as conduits for transport to the deep ocean basin beyond. The canyons were most active as such during glacial periods when sea levels were lower, and downslope processes far more intense than today. However, bottom currents, strong enough to resuspend the sediment, may occur from internal tides focussed along the canyon axis (Gardner, 1989). Their V-shaped profiles are probably the result of erosion by turbidity currents (Gage & Tyler, 1991).

Along passive margins, where sediments have moved down the continental slope to settle, a formation called a **continental rise** may be found, or, if the base of the slope is offshore from a large river, there may be a much larger formation of alluvial sediment called a **submarine fan**. These formations vary greatly in width and in the thickness of the accumulated sediments. While relatively gradual in slope, up to 25 degrees, continental rises are significantly steeper than continental shelves (Gage & Tyler, 1991).

By a depth of ca. 4000 metres the seabed has levelled off to give a wide expanse of relatively flat **abyssal plain** (Fig. 1.2), which extends gently from four kilometres to six kilometres depth. Abyssal plains are often undulating and quite featureless, or they may be interrupted by numerous flat-topped **guyots or seamounts**, which are inactive ocean-floor volcanoes that do not rise above sea level, and sometimes occur in chains (Epp & Smoot, 1989).

The abyssal plains do not extend across the oceans but are separated by the **mid-ocean ridge**. The ridge is the site of formation of new ocean crust and is a more or less continuous system occupying about 33 % of the area of the ocean floor. Mid-ocean ridges are usually about 2.5 km below sea level, but, with increasing distance from the ridge, depth increases to about five to six kilometres.

Trenches occur if the abyssal plain is bordered by an active margin, when the oceanic crust (the lithosphere) buckles and deepens by subduction beneath an adjacent continent.

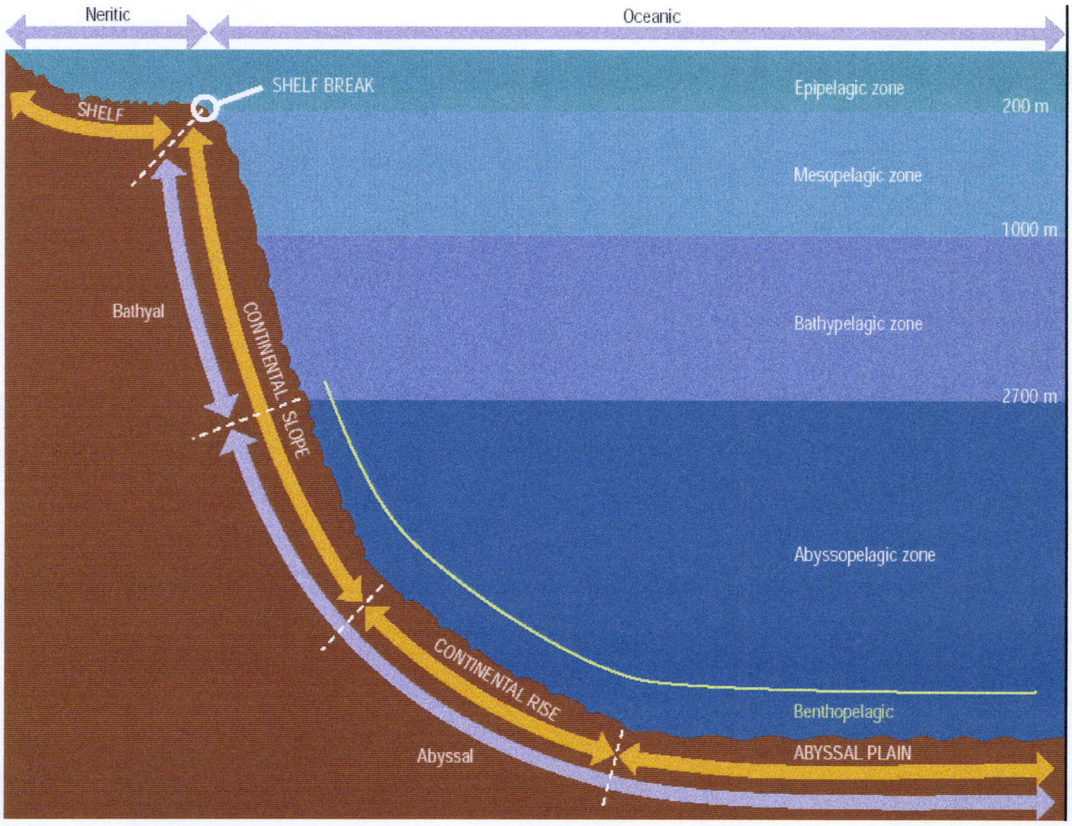


Figure 1.2 Schematic diagram showing the topography of the deep ocean (Angel, 1997).

The terms applied so far are geological (such as margin, ridge, continental slope, shelf *etc.*), whilst the ecological depth zones associated with them are also given in Fig. 1.2 and are described below (Table 1.1). A first and obvious division is the separation of the sea bottom, the **benthic province**, from the water column, the **pelagic province**. Because water depth and illumination directly and indirectly affect the distribution of organisms, both the benthic and the pelagic province are subdivided into smaller zones (Fig. 1.2 and Table 1.1). In addition the **neritic zone** is that part of the pelagic zone which extends from the high tide line to the ocean bottom less than 200 m deep, while water deeper than 200 m is referred to as the **oceanic zone** (Fig. 1.2).

Table 1.1 Characteristics of the different ecological depth zones in the oceans.

Pelagic Province			**Benthic Province**	
zone	depth	illumination	zone	depth
epipelagic	0-200 m	euphotic	littoral	intertidal
mesopelagic	200-1000 m	disphotic	sublittoral	0-200 m
bathypelagic	1000-2700 m	aphotic	bathyal	200-2700 m
abyssopelagic	2700-6000 m	aphotic	abyssal	2700-6000 m
hadalpelagic	> 6000 m	aphotic	hadal	> 6000 m

1.3. The northeastern Atlantic continental slope

Some specific aspects of the northeastern (NE) Atlantic continental slope will be described below because this is the topographical feature studied in this PhD work.

1.3.1. NE Atlantic area situated

The research presented here is concentrated on two continental slope areas in the NE Atlantic Ocean: Porcupine Seabight (Ireland) and Meriadzek Terrace (France) (Fig. 1.3). The NE Atlantic includes the European part of the Atlantic Ocean. The area is limited to the south by the 36°N parallel, to the west by the 42°W, to the north by the 62°N and to the east by the Atlantic coast of Europe up to the British Channel and further along the west coast of England and Scotland (Fig. 1.3). Porcupine Seabight is part of the Irish continental margin, while the Meriadzek Terrace belongs to the French margin, both situated in the NE Atlantic.

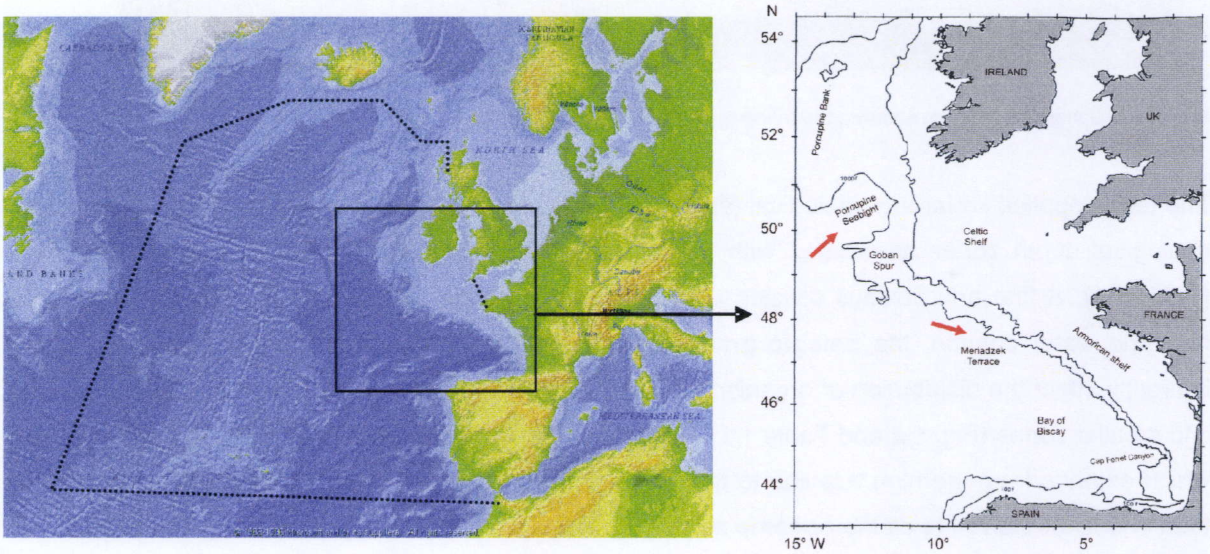


Figure 1.3 Map showing the NE Atlantic indicated by the dashed square. (modified after Encarta atlas) and a detailed map indicating the two study sites Porcupine Seabight and Meriadzek Terrace (red arrows) (modified after Pingree & Le Cann, 1990). The 100 feet (=30.48 m) and 1000 feet (=304.80 m) isobaths are indicated.

Topography of a section of this area (Fig. 1.4) shows some of the most prominent physiographic features of the deep ocean between 58°-42° N and 0°-18° W. The Rockall Plateau (RP), built up of almost completely submerged continental crust, is separated from the continental crust of northern Europe by the Rockall Trough (RT). Two seamounts, the flat-topped Anton Dohrn Seamount (ADS) and Hebridean Seamount (HS) lie on the continental rise of the eastern Rockall Trough. The latter basin opens into the deeper Porcupine Abyssal plain (PAP). The steep continental margin lying southwest of Ireland is broken by a large bight-like terrace, the **Porcupine Seabight** and further south by numerous canyons on the continental slope of the **Bay of Biscay**.

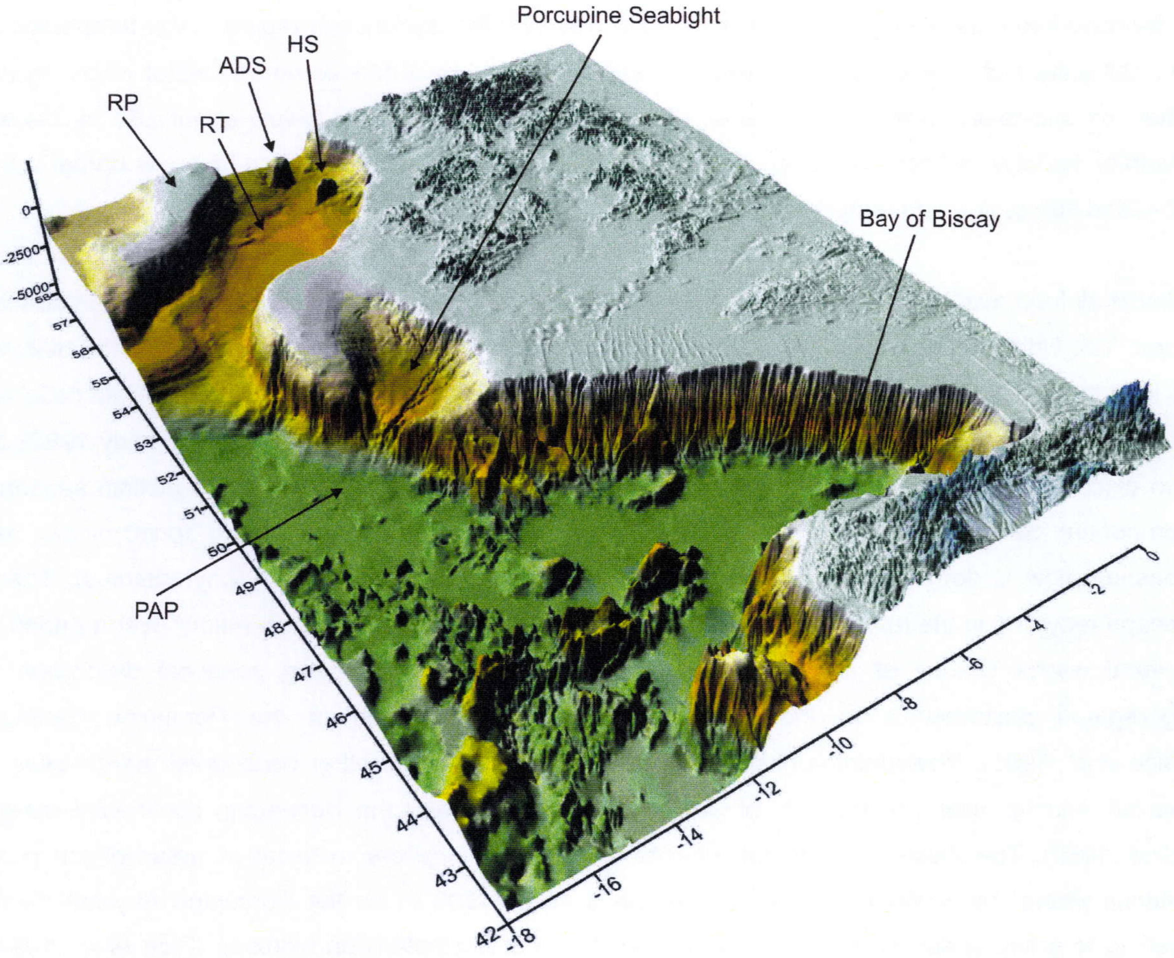


Figure 1.4 Topography of a section of the NE Atlantic based on GEBCO (General Bathymetric Chart of the Ocean, version 2003) bathymetry. The different abbreviations are explained in the text above.

1.3.2. NE Atlantic continental slope as a habitat

As mentioned before, the **continental slope** is the band of seabed that slopes steeply down from the edge of the continental shelf (the shelf break), at about 200 m depth, to the deep-ocean floor at between 1000 m and 2000 m depth. The **habitat** includes both the **seabed** and the **overlying water column**. Some background information on this area as a habitat is outlined below.

Hydrographically the habitat is dominated by the **slope current**. The axis of this current is at a depth of around 500 m. It flows poleward at speeds of about a knot, transporting warm North Atlantic Central Water (originating in the Bay of Biscay) over the Wyville-Thomson Ridge and through the Shetland sub-region into the Norwegian Sea. At a depth of 600 m in the Rockall sub-region, water temperatures are still quite high (circa 7°C) and there is a salinity maximum of Mediterranean water origin. In the Shetland sub-region water temperatures drop rapidly to less than 0°C below about 550 m, the sill depth of the Wyville-Thomson Ridge. Consequently the fauna living deeper than 550 m is boreal in the Shetland sub-region and temperate in the Rockall sub-region.

Almost all food available to the deep-sea benthos is derived from **primary production** in the euphotic zone. The North Atlantic has been an important area for the development of ideas about the delivery of food to the ocean floor (Gooday & Turley, 1990; Rice & Lambshead, 1994). The long-held notion of a uniform (non-seasonal) rain of fine particles was swept aside in the late 1970s and early 1980s by two discoveries. Firstly, it was found that the flux of settling particles may have a distinct seasonal component. Secondly, in areas of the North Atlantic which experiences a strong spring bloom, this seasonal flow is dominated by sinking aggregates of phytoplankton detritus (phytodetritus). These escape recycling in the mixed layer of the ocean and settle to the abyssal ocean floor over a period of several weeks (Turley *et al.*, 1995; Lampitt & Antia, 1997). This mass seasonal deposition of aggregated phytodetritus to the ocean floor was first revealed at the Porcupine Seabight (Rice *et al.*, 1991). Phytodetritus has been observed at a variety of other continental margin sites in the NE Atlantic, including the Bay of Biscay (Sibuet, 1985) and the Norwegian continental margin (Graf, 1989). The delivery of phytodetritus to the seafloor appears to occur in areas of the north Atlantic where the winter thermocline is relatively deep (>500 m on the Porcupine Abyssal Plain), leading to a strong spring bloom and an accumulation of phytoplankton biomass (Rice *et al.*, 1994). Thus, primary productivity in the region follows a seasonal fluctuation. It is low during the winter when day lengths are short and the upper water column is mixed to depths of several hundred meters. Between spring and early summer, as weather conditions moderate and day length and solar radiation increase, the upper few tens of meters of the water column become thermally stratified. Phytoplankton ceases to be either light- or nutrient-limited and some species, particularly diatoms, grow rapidly. A spring bloom develops rapidly using up all the available nutrients. The stratification inhibits replacement by vertical mixing, so the bloom collapses. Heavy deposition of phytodetritus usually follows the collapse of the bloom and stimulates a marked seasonal response in the seabed communities. In the post-bloom period the productivity remains at a relatively low level throughout the summer until autumnal storms begin to erode the stratification. When the early storms do not totally disrupt this stratification, there is a short-lived autumnal bloom before the onset of winter conditions. Pulses of phytodetritus and other forms of organic matter typically evoke a rapid response by the benthic community and serve to couple processes on the deep-sea floor and in the upper water column (**benthopelagic coupling**) (Gooday & Turley, 1990).

An important feature of the continental slope is the **shelf break**, *i.e.* the transition zone between the continental shelf and slope (Wefer *et al.*, 2002). Along the shelf break in the NE Atlantic there is a front between shelf (neritic) and oceanic waters. **Oceanic fronts** are sites of enhanced productivity because nutrients tend to be resupplied to the euphotic zone by upwelling. Another important process enhancing productivity at the shelf-break is the generation by tidal oscillations of internal wave packages (solitons) which break, under certain circumstances, vertically mixing the water (Wefer *et al.*, 2002). The shelf-break front marks a sharp change in the species composition. Offshore there is an increase in species richness in benthic and pelagic communities, and the mean size of phytoplankton generally becomes smaller (Gage & Tyler, 1991).
The high production of plankton at the shelf break makes it an important feeding ground for large schools of fish, flocks of oceanic birds and cetaceans. Several commercially exploited fish species spawn along the shelf break including mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*) (http://www.ukbap.org.uk).

Species richness, in both pelagic and benthic taxa, increases with depth (along the slope) reaching a maximum at 1000 to 2000 m, despite community biomass generally decreases by an order of magnitude from the shallowest depths (Gage & Tyler, 1991). However, the decline in benthic biomass is erratic and high concentrations of biomass occur especially where internal waves result in resuspension and a local increase in suspended material (Rex, 1981).
In recent times, deep-water communities along the continental margins have received increasing attention because of the interest in new fishing grounds and fisheries at bathyal depths (Hopper, 1994). The number of fish species caught rises to a maximum at a depth of 1000 m, and then declines slowly into deeper water. Mean body size and longevity tend to increase with depth, whereas fecundity declines. Consequently deeper-living species are more susceptible to over-exploitation (Lack *et al.*, 2003). Commercial fishing for orange roughy (*Hoplostethus atlanticus*) started only recently (1991) but stocks of this long-lived, slow-growing and low fecundity species have already fallen to near extinction levels (Lack *et al.*, 2003). Other species caught regularly include blue ling (*Molva dypterygia*), roundnose grenadier (*Coryphaenoides rupestris*) and a variety of deep-sea sharks (including *Centrophorus* spp, *Centroscymmus* spp and *Etmopterus* spp) (Basson *et al.*, 2002; Large *et al.*, 2004).

Deep-water coral banks are widespread along the NE Atlantic margin, at shelf breaks and on the upper continental slope. The majority of these coral banks, whose biodiversity is comparable to those of tropical coral reef settings, are constructed by the framework builder *Lophelia* and associated fauna (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Rogers, 1999). A wide variety of animals such as bryozoans, hydroids, sponges and other corals are attached to the coral framework. Several fish species, (e.g. redfish, cod, ling), crustaceans, molluscs, starfish, brittle stars and other animal taxa live in association with the corals.

1.3.3. Current factors affecting the habitat

Anthropogenic activities in the coastal areas and in the open sea will affect marine ecosystems in different ways. Around the NE Atlantic Ocean, the human population is concentrated in the coastal area. An increasing human population in this area has led to an increase in sewage discharge, in maritime transport, use of the sea for tourism and recreation and exploration of the natural resources in the sea. Over-fishing, eutrophication, dumping, direct discharges and spills of contaminants are all threats to the biodiversity in the ocean.

Many factors have been identified as possible influences on the quality of the continental shelf/slope habitat by the UK Biodiversity action plan (http://www.ukbap.org.uk). A short discussion of these threats and possible solutions is given below.

- Fishing activity has extended into deep water as stocks on the shelf have dwindled. Some trawling and lining has been conducted for demersal species to depths of 1000 to 2000 m. There is little regulation of this activity at present and some species have been driven to very low, nearly extinction stock levels. As an example of over-fishing, intensification of fishing in the southern Bay of Biscay has led to the virtual extinction of elasmobranches (e.g. rays, skates, sharks), which have a long reproduction time. Most of the commercial fish stocks are outside 'safe biological limits' in the Atlantic area (OSPAR, 2000), including cod, hake, sardine, etc. The International Council for the Exploration of the Sea (ICES, 1996) indicate that there is a need for a 40 % reduction in the fishing fleet to avoid over-fishing and match available fish resources.
- The input of contaminants and discarded materials from shipping traffic is becoming a real threat. This is being reduced but offshore monitoring is difficult. The offshore environmental impacts of aerial sources of contaminants are not known.
- The most recent potential threat is posed by the offshore oil exploration and associated activities, causing contamination and disturbance to the seabed and an increased risk of accidental oil spills from platforms and maritime transport. For example the accidental oil spill caused by the tanker 'Prestige' in 2002 had a major impact on seabirds, mammals, fishing and the marine life at the polluted seashore.

1.3.4. Current regulations for protection

In the NE Atlantic Ocean there is a large diversity of ecosystems. To protect ecologically valuable areas, all countries have established some form of Marine Protected Areas (MPA's). Most of the MPA's so far established are close to or adjacent to shores. However, many offshore areas are important spawning areas and nursery grounds that need protection, thus a considerable increase of offshore MPA's could be considered. The introduction of No-Fishing Zones (NFZ's) may be useful to protect some species of fish and ecosystems. International legislation and agreements have a major influence on the management measures (http://www.ukbap.org.uk; UK Biodiversity Action Plans, 1999). Some of the international agreements and regulations are outlined below.

- the UN Convention on the Law of the Sea (1982) which was ratified by the UK in 1997 and which provides a framework for the regulation of all ocean space. It sets out responsibilities of coastal nations for marine habitats and wildlife.
- the London (Dumping) Convention which is concerned with the protection of the marine environment from ship pollution, aircraft and man-made structures and resulting from normal operations (*i.e.* not from deliberate dumping). It covers a wide range of substances with some generally biodegradable or innocuous bulky substances specifically excluded. It includes a ban on incineration at sea.
- the International Convention for the Prevention of Pollution from Ships (MARPOL Convention) which covers pollution from shipping and includes provisions for identifying Particularly Sensitive Sea Areas and Special Areas, where stronger regulations to limit ship-based pollution apply.
- the Oslo and Paris Conventions (OSPAR) which aim to prevent pollution of the marine environment of the northeastern Atlantic from land-based sources, and from dumping from ships and aircraft. Unlike the previous two conventions, which are global, these are only regional but cover a wider range of sources.
- the EU Common Fisheries Policy which is aimed at the management of the fish stocks in the UK waters, along with those of other EU coastal states.
- the UN agreement on Straddling Stocks which tries to achieve the holistic management of migratory stocks.
- the International Whaling Commission (IWC) which has banned the commercial exploitation of whales. Not all nations agree with these measures, for example Norway continues to catch minke whales (*Balaenoptera acutorostrata*).
- the Bonn Convention which aims to improve the status of all threatened migratory species through national and international agreements between range states of particular groups of species, for example the Agreement on the Conservation of Small Cetaceans of the Baltic and North Sea (ASCOBANS).

Many other national and international requirements have an indirect effect on the quality of the oceans by regulating matters such as ship construction and other safety issues. All these actions rely on and are supported by major scientific research.

1.4. Hyperbenthos living in the benthic boundary layer

The **hyperbenthos**, the studied fauna in this PhD research, is a term applied to the association of small animals living in the water layer close to the seabed (Mees & Jones, 1997). The species composition of the hyperbenthos is distinctly different from that of other benthic and planktonic groupings, and includes **typical species**, **planktonic species** derived from their downward extensions and **endo- or epibenthic species** as they emerge into the water column (Mees & Jones, 1997). Besides this theoretical definition of hyperbenthos, a working definition of this fauna for this particular study is described in chapter 2 (2.2 Working definition for hyperbenthos).

In recent years, there have been considerable developments in hyperbenthic research in the tropics, in temperate to cold-water coastal and shelf regions, and in the deep sea. Unfortunately, there is little or no mutual acknowledgement of results partly due to differences in **terminology**. For example, 'hyperbenthos' and 'suprabenthos' are used mainly in temperate and northern areas, whereas 'demersal zooplankton' and 'benthopelagic plankton' are preferred to designate the same fauna in tropical areas and the deep sea respectively (Mees & Jones, 1997). **Sampling** these often highly mobile animals is not easily done as they are not collected efficiently by conventional benthic or pelagic samplers. A wide range of hyperbenthic sampling devices has been constructed and used with varying success. Typically, soft-bottom communities are sampled with sledges and hard substrata (including coral reefs) with traps. Problems with quantitative hyperbenthic sampling are discussed in chapter 2 (2.3.2. Problems with quantitative hyperbenthic sampling).

Despite the scattered knowledge on hyperbenthic communities, evidence of the **potential role** of this fauna in marine ecosystems has often been emphasized. Hyperbenthos plays an important role in marine food webs. Hyperbenthos as a food source for juvenile demersal fish species and adult shrimp species is well documented for shallow coastal areas and estuaries (*e.g.* Mauchline, 1980; Mees & Jones, 1997; Hostens & Mees, 1999; Beyst *et al.*, 1999; Oh *et al.*, 2001) and more recently for the deep sea as well (Mauchline, 1986; Cartes, 1998; Bjelland *et al.*, 2000). So a function in carbon flux to higher trophic levels is established. Hyperbenthic species are also believed to contribute to the conversion and recycling of organic matter as several species were indicated to feed on non-refractory detrital matter (Kost & Knight, 1975; Jansen, 1985; Fockedey & Mees, 1999). Particularly for the deep sea, scavenging amphipods and isopods might be of specific importance for the flux of organic matter to the sea floor (Thurston, 1979; Lampitt *et al.*, 1993; Kaïm-Malka, 1997). The swimming activities of the hyperbenthos may also contribute to the fragmentation of organic matter or marine snow in the water column, as was indicated for Euphausiacea (Dilling & Alldredge, 2000; Graham *et al.*, 2000). Disaggregation of marine snow alters the availability and size distribution of particles possibly leading to a change in the rate of particulate carbon utilization and overall microbial activity in the water column (Dilling & Alldredge, 2000). In addition, the motility and behaviour of the hyperbenthos at the water-sediment interface can cause bioresuspension and biodeposition, resulting in an increasing particle flux (Graf & Rosenberg, 1997).

The hyperbenthic fauna is an important component of the **benthic boundary layer (BBL)** fauna. In nearly all marine ecosystems investigated to date, there is a general increase in the biomass at the benthic boundary layer relative to the water column immediately above it. The benthic boundary layer is defined as the layer of water, often tens of metres thick, adjacent to the seabed and with homogeneous properties of temperature and salinity, which sometimes contains resuspended detrital particles (Turley, 2000). It is an environment of great complexity both from a physical (Gage & Tyler, 1991) and biological (Smith & Hinga, 1983) perspective, because it is the interface between pelagic and benthic environments, communities and processes (Wishner & Meise-Munns, 1984). Faunal biomass close to the bottom seems to be higher than biomass further away from the bottom (Wishner, 1980b, Smith, 1982). Measurements of ATP suggest that bacterial abundances are also elevated (Karl *et al.*, 1976). Data from nephelometers (Eittreim et al., 1976; Biscaye & Eittreim, 1977), sediment traps (Rowe & Gardner, 1979) and water samples (Baker & Feely, 1978; McCave, 1983) indicate that there is much sediment resuspension from the bottom into the BBL, and material transported downward from the upper ocean must also pass through the BBL before becoming available as food to benthic consumers or being deposited on the bottom as sediment. The increased concentrations of particles and greater biomass of organisms that may be utilizing and altering these particles suggest that the BBL is a zone of relatively intense biological activity within the deep sea. This is also supported by the elevated rates of zooplankton oxygen consumption and ammonium excretion (Smith, 1982). Thus, within the deep sea, the BBL can be distinguished from the remainder of the water column by its species composition, increased concentrations of particulate material and biologically active chemical substances, elevated biomasses of organisms from bacteria to fish, and elevated metabolic rates (Wishner & Gowing, 1987).

Besides this biological approach of defining the benthic boundary layer, this layer is also mathematically described by Thomsen (2002). Approaching the sea floor from above, the upper limit of the BBL is defined as the distance above bottom at which the mean flow velocity is $0.99\ u_\infty$, where u_∞ is the free-stream velocity. The BBL at continental margins is in the order of 5 to 50 m thick (Thomsen, 2002). More than the theoretical 10 % of the BBL thickness obeys what is known as the law of the wall:

$$\bar{u}(z) = \frac{u_*}{\kappa} \ln \frac{z}{z_0}$$

which is often used to describe the mean velocity profile in regions near the bed where the flow is fully turbulent and neutrally stable (*i.e.* not stratified) (Thomsen, 2002). Convention in BBL work is to use z as a distance (L) upward from the bottom, K is von Karman's constant (0.41, dimensionless), u_* is shear velocity (LT^{-1}) and z_0 is the roughness height. The z_0 of a natural sea floor is strongly affected by benthic organisms structuring the microtopography of the sediment surface.

The existence of specific BBL assemblages (mainly composed of crustaceans) at **continental slope environments** was already suggested by Marshall & Merrett (1977), Wishner (1980a, 1980b), Hargreaves (1984) and Gordon & Mauchline (1990). Moreover these deep-water communities have received increasing attention because of the interest in new fishing grounds and fisheries at bathyal depths (Hopper, 1994; Merrett & Haedrich, 1977). Despite of the growing effort to study these communities, the dynamics of the bathyal benthic boundary layer and its fauna is still far from being well understood.

For this PhD research the term BBL is used to describe the part of the water column sampled by the hyperbenthic sledge just above the ocean floor, *i.e.* 0-100 cm above the bottom.

1.5. This study: overview and objectives

1.5.1. Overview

Traditional marine biology has long been conditioned by what is most accessible. Our knowledge has perhaps been overly influenced by what can be learned from intertidal and shallow subtidal systems that represent only a very small portion of the total ocean bed and its biological populations (Gage, 2002). On the shore, easier access and greater visibility of biota, has provided a rich fund of knowledge compared to what we know about life in deeper waters. Here, direct observations might only be possible from hugely expensive manned submersible and deep-diving ROV's. Yet most of what we know of the rich biodiversity at the continental margins and beyond is still very largely based on what can be retrieved in trawls and grabs lowered to the bottom on hundreds or thousands of metres of wire rope. Deep-sea environments are likely to harbour high levels of natural biodiversity, and although there is a large (and growing) body of evidence both for and against hypothesis, the deep sea remains relatively poorly unexplored. This has meant that, despite more than a century of study, knowledge of the deep-sea benthos is still limited (Horton, 2003).

Ocean margins are the prime sites for marine biodiversity research since they offer an extraordinary range of environmental gradients and contrasts that will help unravel the highly complex relationship between the environment and biodiversity at all of its scales. Growing exploration of continental margins has indicated the existence of specialized benthic communities in association with a large variety of seafloor habitats at depths from 200 m up to 4000 m. These habitats are characterized by particular substrate features (from fine pelagic sediments up to *Lophelia* rubble), by specific topographic profiles (created by mounds, slopes, canyons), by biogeochemical gradients (due to seepage, oxygen minimum zones) and by differences in productivity in relation to latitudinal or bathymetric gradients. As these habitats are often fragmented in nature, their communities may be more sensitive to disturbance. There is a growing scale of intervention by man in the deep waters of the continental margins which poses a threat of disturbance to what is perceived as a pristine ecosystem. The main actual and potential threats to the margin system habitats and biodiversity in the NE Atlantic are the lack of sustainable regulation of fisheries, the pollution from maritime transport and the oil/gas prospecting. Therefore further attention should be given to particular continental margin ecosystems since growing exploitation pressure could soon lead to irreversible changes to these hotspots of biodiversity.

Despite recent advances in ocean margin research providing us with new insight and hypotheses as to the nature of geosphere and biosphere interactions, knowledge on hyperbenthic communities inhabiting this unique habitat along continental margins is still limited. One might expect clear diversity and community patterns of this BBL fauna with depth along continental slope areas. This PhD research aims at improving the knowledge on spatial distribution and biodiversity patterns of the hyperbenthic fauna along the continental slope by studying this fauna in two sites along the NE Atlantic Ocean: Porcupine Seabight and Meriadzek Terrace. These two transect represent a natural depth gradient along the European ocean margin and were selected for different reasons. The Porcupine Seabight is a bight-like terrace which interrupts the steep continental margin southwest of Ireland. The sampled transect in this area is characterized by the nearby mound provinces and associated deep-water coral reefs, which might able us to study possible influences of this habitat. Moreover, no hyperbenthic research was performed in this area before. The second transect is part of the continental slope of the Bay of Biscay and was studied before, but within a restricted depth range, which is extended by this research. Both transect, as part of the European ocean margin might provide new insights to across and along slope spatial distribution and biodiversity patterns of hyperbenthic fauna. Moreover, comparing these two unique sites to other studied sites in more northern and southern areas may create useful hypotheses on large scale phenomena.
An overview of the research objectives is given in the next paragraph.

An overview of recent literature reporting on the hyperbenthos (or on certain hyperbenthic taxa) of deep-sea areas (deeper than 200 m) is given in Table 1.2. Deep-sea communities have been described, both from a faunistic and community structure perspective (*e.g.* Elizalde *et al.*, 1991; Dauvin *et al.*, 1995; Sorbe, 1999; Cartes & Sorbe, 1995, 1996, 1997; Cartes, 1998).

Table 1.2. Overview of recent literature reporting on the ecology of hyperbenthos (or on hyperbenthic taxa) occurring at depth strata below 200 m. All studies applied sledges for sampling: BB: Brandt-sledge (Brandt & Barthel, 1995), BS: benthopelagic sampler attached to Agazzis trawl (see Sirenko *et al.*, 1996), MG: Macer-GIROQ sledge (Dauvin & Lorgeré, 1989), RP: Rothlisberg and Pearcy sledge (Rothlisberg & Pearcy, 1977), SH: Sanders and Hessler sledge (see Marquiegui & Sorbe, 1999), SS: Sorbe sledge (Sorbe, 1983), WH: Woods hole epibenthic sledge (Svavarsson *et al.*, 1990).

Source	Sledge	Mesh size	Depth range	Fauna
NE Atlantic - temperate waters				
Norwegian Sea and fjords				
Buhl-Jensen (1986)	RP	0.5 mm	147 - 550 m	Amphipoda
Fosså & Brattegard (1990)	RP	0.5 mm	32 - 1260 m	Mysidacea
Meriadzek Terrace (W Bay of Biscay)				
Vanquickelberghe (1999)	SS	1 mm	200-700 m	Hyperbenthos
Dewicke (2002)	SS	1 mm	200-700 m	Hyperbenthos
Cap Ferret area (SE Bay of Biscay)				
Elizalde *et al*. (1991)	MG	0.5 mm	346 - 1099 m	Mysidacea
Elizalde *et al.* (1993)	MG	0.5 mm	425 - 1043 m	Hyperbenthos
Dauvin & Sorbe (1995)	MG	0.5 mm	346 - 1099 m	Amphipoda
Dauvin *et al*. (1995)	MG	0.5 mm	346 - 3070 m	Hyperbenthos
Sorbe & Weber (1995)	SS	0.5 mm	392 - 717 m	Hyperbenthos
Sorbe (1999)	MG	0.5 mm	2400, 3000 m	Hyperbenthos
Capbreton canyon (SE Bay of Biscay)				
Marquiegui & Sorbe (1999)	SH	0.5 mm	1000 m	Hyperbenthos
Corbari & Sorbe (2001)	MG	0.5 mm	162 - 987 m	Hyperbenthos
Asturian Central Coast (S Bay of Biscay)				
Anadón (1993)	SH	0.5 mm	50 - 1347 m	Mysidacea
Portuguese continental margin (off Aveiro)				
Cunha *et al*. (1997)	SS	0.5 mm	21 - 299 m	Hyperbenthos
Catalan Sea (NW Mediterranean)				
Cartes & Sorbe (1995)	MG	0.5 mm	385 - 1859 m	Mysidacea
Cartes & Sorbe (1996)	MG	0.5 mm	389 - 1808 m	Cumacea
Cartes & Sorbe (1997)	MG	0.5 mm	389 - 1859 m	Cumacea
Cartes & Sorbe (1998)	MG	0.5 mm	355 - 1355 m	Mysidacea
Cartes & Sorbe (1999a)	MG	0.5 mm	389 - 1859 m	Amphipoda
Cartes & Sorbe (1999b)	MG	0.5 mm	391 - 1255 m	Peracarida
Cartes & Maynou (2001)	MG	0.5 mm	638 - 1256 m	Mysidacea
Cartes *et al*. (1994)	MG	0.5 mm	389 - 1859 m	Euphausiacea
Cartes (1998)	MG	0.5 mm	389 - 1859 m	Hyperbenthos
Cartes *et al*. (2004)	MG	0.5 mm	147 - 2266 m	Peracarida
SW Balearic Islands (SW Mediterranean)				
Cartes *et al*. (2003)	MG	0.5 mm	249 - 1622 m	Peracarida
Northern (sub)polar regions				
Laptev Sea (Siberian Arctic)				
Sirenko *et al.* (1996)	BS	0.4 mm	51- 3042 m	Hyperbenthos
Westwind Trough (off NE Greenland)				
Brandt (1995)	BB	0.3 mm	45 - 517 m	Peracarida
Off E Greenland				
Brandt (1997a, 1997b)	BB	0.3 mm	197- 2681 m	Peracarida
Kolbeinsey Ridge (off N Iceland)				
Brandt (1993), Brandt & Piepenburg (1994)	BB	0.3 mm	830 - 1100 m	Peracarida
Northern Seas				
Svavarsson *et al*. (1990)	WH and RP	0.5 mm	794 - 3709 m	Isopoda
Svavarsson *et al*. (1993)	WH and RP	0.5 mm	10 - 3970 m	Isopoda
Southern (sub)polar regions				
South Shetland Islands & Bransfield Strait (Antarctic Peninsula)				
San Vicente *et al*. (1997)	MG	0.5 mm	45 - 650 m	Hyperbenthos
Beagle Channel (Patagonia)				
Brandt *et al.* (1997)	BB	0.3 mm	40 - 665 m	Peracarida
This PhD research (Porcupine Seabight/Meriadzek Terrace)				
Vanquickelberghe (2005)	SS	1 mm	200 - 1250 m	Hyperbenthos Peracarida

1.5.2. Research objectives

The aim of this study is to characterise the hyperbenthic communities inhabiting continental margin areas in the NE Atlantic. In a first part an extensive study covering the complete hyperbenthos (on higher taxon level) in the two study areas, Porcupine Seabight (Ireland) and Meriadzek Terrace (France), is performed. A second part covers the detailed study of the main inhabitants of the studied benthic boundary layer (BBL): the peracarid crustaceans (on species level). This group of animals comprises the orders Mysidacea, Cumacea, Amphipoda, Isopoda and Tanaidacea. The study sites description and the methodology used are given in **chapter 2**.

For the first part (chapters 3 and 4) the study's approach is to assess the fauna of the hyperbenthal zone (i.e. the zone occupied by the hyperbenthos) as an ecological entity at the interface between the benthic and the pelagic realms. Thus, rather than to focus on one or two specific taxa, the entire hyperbenthic community is considered, i.e. all small animals swimming in the vicinity of the seabed.

In **chapter 3** the hyperbenthic fauna of the continental slope (between 200 and 1250 m water depth) at Porcupine Seabight, offshore southwest of Ireland is studied in order to characterise the BBL assemblages on the continental slope environment as suggested by Marshall & Merrett (1977), Wishner (1980a, 1980b), Hargreaves (1984) and Gordon & Mauchline (1990). Studying the **vertical or near-bottom distribution** (also referred to as stratified distribution) of the hyperbenthic fauna in the BBL in the first part of this chapter can provide more information on community structure patterns within the BBL: is this BBL layer one homogeneous water mass or are there smaller scale patterns within this one metre of water? Patterns of vertical distribution of the hyperbenthic fauna are discussed in terms of what is known of the ecology. The second part of this chapter determines the **horizontal or bathymetric distribution** (also referred to as across isobaths distribution) of the hyperbenthic fauna along the slope environment and examines the zonation and abundance of the different higher taxa within their depth ranges. Large-scale zonation will be analysed in view of the physical environment and the ecology of the hyperbenthic taxa.

Chapter 4 presents the investigations made on the hyperbenthic communities of the second study area Meriadzek Terrace and these results are compared with the data collected from a similar bathymetric transect at Porcupine Seabight (see chapter 3). The two slope areas in the NE Atlantic were sampled from 200 to 1250 m depth, following a standardised sampling strategy. Three important distribution patterns will be studied and discussed in order to find out what mechanisms are important for the structuring of the hyperbenthic communities: 1) **vertical or stratified distribution** of the hyperbenthos in the BBL, 2) **across isobaths or bathymetric distribution** and 3) **along isobaths or geographical distribution** of the hyperbenthic fauna. This near-bottom or hyperbenthic fauna, a link between the benthos and the water column, may quantitatively as well as qualitatively differ from the rest of the deep-sea plankton (pelagial) and may be important in biological interactions within the BBL. These animals, because of their proximity to the bottom, inhabit a more heterogeneous and possibly richer environment than deep plankton higher in the water column and may show a clear stratified distribution within the BBL. More niches may be available, and a specialized hyperbenthic fauna probably exists along with the regular deep-sea zooplankton (Wishner, 1980a). By comparing the data from both study sites by means of multivariate analysis, some specific questions can be addressed here: are the major hyperbenthic stratified and bathymetric or across isobaths distribution patterns similar for both slope areas and can they be explained by environmental variables sampled along the slope? Can comparison of the hyperbenthic community structure found in Porcupine Seabight and Meriadzek Terrace put forward some general trends in geographical distribution patterns (*i.e.* along isobaths distribution), depth related distribution patterns (*i.e.* across isobaths distribution) or stratified distribution patterns (*i.e.* lower BBL zone 0-50 cm versus upper BBL zone 50-100 cm) of hyperbenthic fauna? The results will be discussed in terms of taxa composition, hyperbenthic densities and environmental variables and in relation to other hyperbenthic community studies from the northeastern Atlantic described in literature.

Chapter 5 (second part of the thesis) emphasizes the depth related distribution of peracarid crustacean species along the two studied slope areas Porcupine Seabight and Meriadzek Terrace and how the species of the different taxa Amphipoda, Mysidacea, Cumacea, Isopoda and Tanaidacea behave along this bathymetric gradient. One might expect different strategies within the different taxa, *e.g.* occurrence in a preferred depth range. In addition to the distribution this chapter deals with the alpha and beta component of diversity of peracarid crustaceans along both continental slope areas. Alpha diversity is translated into diversity of the peracarid species associated with one station or one depth along the continental slope. Beta diversity is designated as the degree of species change along the depth gradient characteristic of the studied continental slopes. Are both spatial levels of diversity similar for the five major peracarid taxa, Amphipoda, Mysidacea, Isopoda, Cumacea and Tanaidacea on species level and how does the species turn-over (beta diversity) along the continental slope relates between the different taxa?

These interpretations will be discussed in terms of the ecology (*e.g.* feeding strategy) of the different species.

Chapter 2

Methodology

2.1. Characterisation of study sites

2.1.1. Area of interest

The two study sites, **Porcupine Seabight** (Ireland) and **Meriadzek Terrace** (France) are situated along the northeastern (NE) Atlantic continental margin between the Porcupine Bank and the Bay of Biscay (Fig. 2.1). More specifically this research concentrates on the upper and middle part of the continental slope in both study sites, between 200 and 1250 m of water depth (see 2.3. Sampling strategy). Both study sites are described below in more detail.

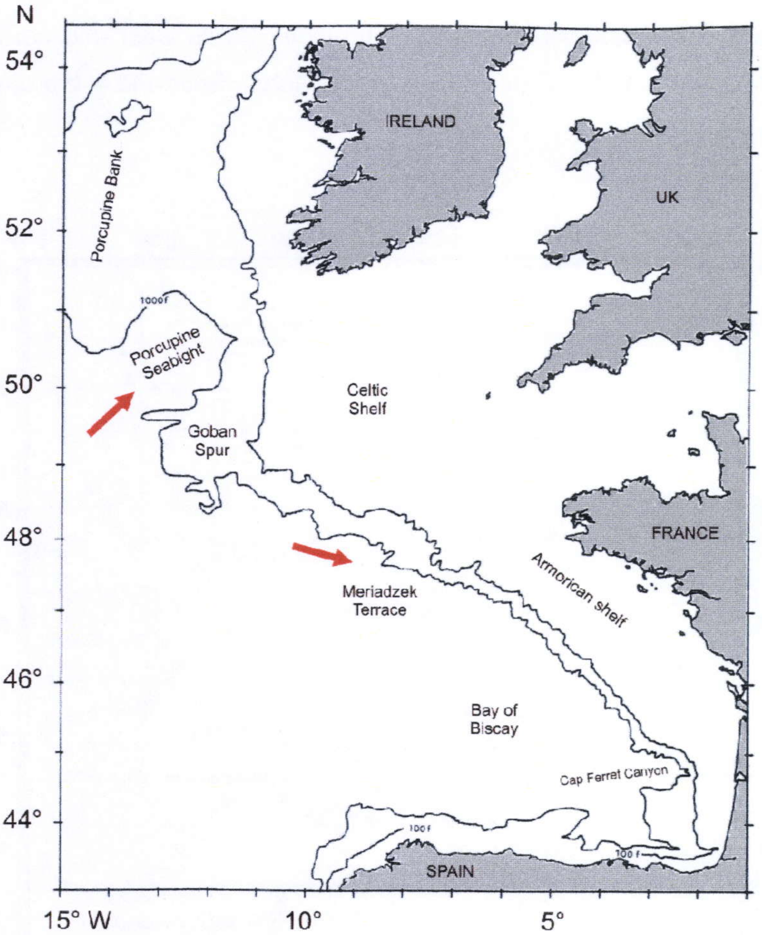


Figure 2.1 Part of the NE Atlantic continental margin between the Porcupine Bank and the Bay of Biscay, with the two study sites Porcupine Seabight and Meriadzek Terrace indicated (arrows) (modified after Pingree & Le Cann, 1990). The 100 feet (=30.48 m) and 1000 feet (=304.80 m) isobaths are indicated.

Generally, between the Goban Spur (northerly delimited by the Porcupine Seabight) and the northern Bay of Biscay (Fig. 2.1) from a depth of 150-4000 m, the NW European margin of the NE Atlantic Ocean is characterized by a relatively mature, mud/sand rich system with deeply incised canyons on the continental slope and submarine fans on the continental rise (Cunningham *et al.*, 2003). The upper part of the system (on the continental shelf) shows two sets of sand features: sand banks that are orthogonal to the shelf break and sand waves that are parallel to the shelf break. The latter comprise parallel sand dunes between water depths of 150-300 m and provide a sand source for the sediment transported via the canyon system to the abyssal plains. The middle part of the system is made up of a series of incised canyons with depths of 50-200 m and lengths of up to 2 km. The lower part of the system comprises a series of divergent, braided and meandering channels, which funnel major turbidity flows (Cunningham *et al.*, 2003).

2.1.2. Porcupine Seabight

The Porcupine Seabight is a bathymetric feature that forms an amphitheatre-shaped embayment in the NE Atlantic continental margin southwest of Ireland (Fig.2.2). It extends for about 230 km in the north-south direction, and is 100 km wide at most (Masson & Miles, 1986; Rice *et al.*, 1991; Huvenne *et al.*, 2002). The Porcupine Seabight is bounded on its west and north-west side by the Porcupine Bank, on its south and south-east side by the Goban Spur and to the east by the Irish Shelf (Moore, 1992) (Fig. 2.2).

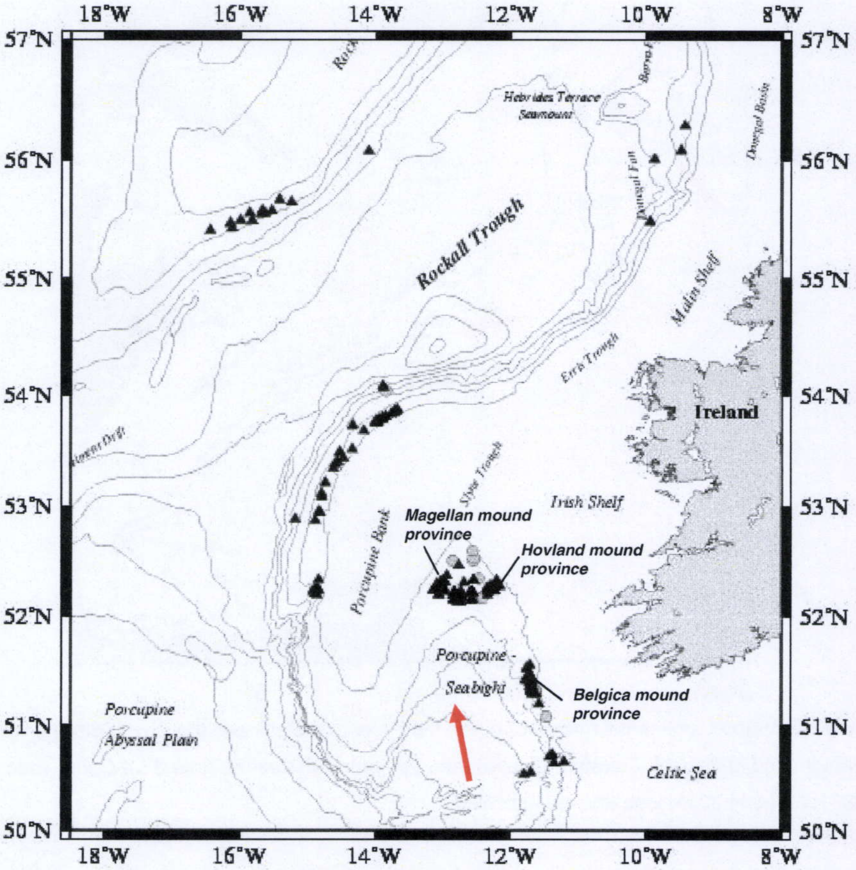


Figure 2.2 The study site Porcupine Seabight (arrow) situated along the NE Atlantic continental margin. The position of three important carbonate mound provinces, the Magellan mound province, the Hovland mound province and the Belgica mound province, are also indicated (http://geomound.ucd.ie/).

Its sides slope steadily from the edge of the Irish shelf at 200 m down to a depth of about 3000 m. At the mouth of the Seabight, the seabed slopes away more steeply to a depth of about 4000 m to join the Porcupine Abyssal Plain. The western slopes of the Porcupine Seabight are steeper than the eastern slopes. The eastern and northern slopes are the sites of important coral mounds (see 2.1.2.3.) like the Hovland mounds and the Belgica mounds (Huvenne *et al.*, 2002) (Fig. 2.2). On the eastern slope of the Seabight are a series of channels, knows as the Gollum Channel System, running roughly east-west through the Seabight.

2.1.2.1. Physical oceanography of the Porcupine Seabight

The physical oceanography of the Porcupine Seabight has been reported by Rice *et al.* (1991) and van Weering *et al.* (1998b), while a more extensive review of the currents and water masses in the area was published recently by White (2001). A short overview of the main points is given below.

Water mass structure

The description of the hydrographic conditions at the mouth of the Porcupine Seabight is based on potential temperature-salinity plots of CTD (Conductivity, Temperature, Depth) measurements (Hargreaves, 1984; Ellet *et al.*, 1986; Vangriesheim, 1985) (Fig. 2.3). An upper layer of Eastern North Atlantic Water (ENAW) was found to a depth of about 750 m where it overlies a core of Mediterranean Outflow Water (MOW), reaching down to about 1500 m, and marked by a salinity maximum and an oxygen minimum at a depth of about 950 m (Fig. 2.3). A fresher and more oxygen-rich layer of Labrador Sea Water (LSW), was located between 1500 and 1800 m. A small increase in salinity at about 1900 m indicates the influence of Norwegian Sea Water (NSW), while below this depth there are only small changes in temperature and salinity. A similar water column structure was found by Ellet *et al.* (1986) a little further north along the Porcupine Bank, and by White (2001) from a large number of CTD casts in the Porcupine Seabight. There is a permanent thermocline between 600 and 1400 m depth, with temperatures reducing from 10 to 4°C, while a seasonal thermocline forms at about 50 m depth (Rice *et al.,* 1991).

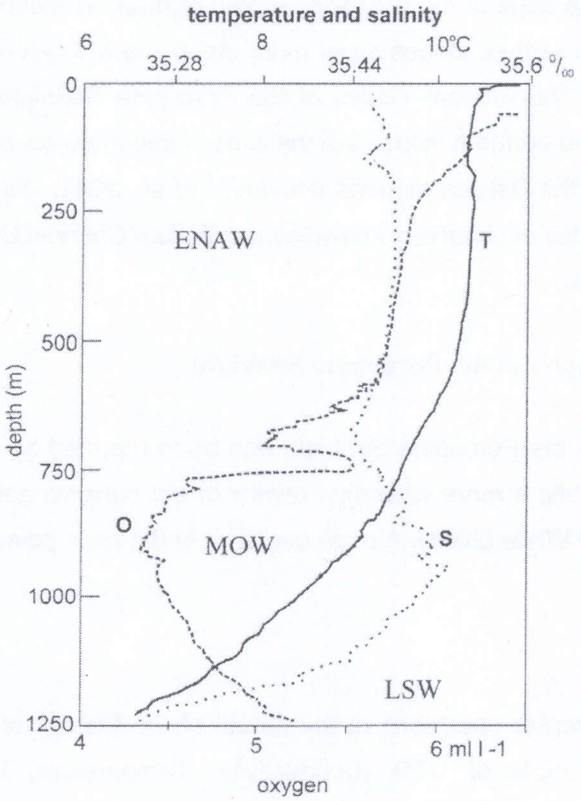


Figure 2.3 CTD (Conductivity, Temperature, Depth) profile in the Porcupine Seabight mouth showing the water mass characteristics between 0-1250 m water depth (Rice *et al.*, 1991). T= temperature; O= oxygen; S= salinity; ENAW= Eastern North Atlantic Water; MOW= Mediterranean Outflow Water; LSW= Labrador Sea Water.

Flow patterns and currents

A general northward current system, the **slope current**, is present along the NE Atlantic continental slope margin (Huthnance & Gould, 1989; Pingree & Le Cann, 1989, 1990; Huthnance *et al.*, 2001; Pingree *et al.*, 1999). This slope current is an eastern boundary current (Smith, 1989) comprising at the upper levels a relatively warm and saline shelf edge current (SEC) between depths of 150-400 m. Below this level the Mediterranean Outflow Water and deep ocean re-circulation boundary also flows poleward (Dickson *et al.*, 1985).

Based on historical and recently gathered current data of a few ECOmound (Environmental Controls on Mound formation along the European margin, European project; Henriet *et al.*, 1998) and ACES (Atlantic Coral Ecosystem Study; Freiwald *et al.*, 1999) moorings in the Rockall Trough and the Porcupine Seabight region, a map was produced with the mean current vectors between 200-1400 m depth (White, 2001) (Fig. 2.4). Nor interannual variability, nor seasonal variability was taken into account in this plot, due to different measurement periods. It is clearly imaged that the poleward (northward) flowing current has been recorded at all depth levels along the continental slope, in particular close to the seabed. The driving mechanism of the slope current is the poleward decline in sea-surface height, caused by the increase of water density with latitude. The rate of reduction in sea-surface height is greater over the deeper ocean than over the continental shelf, so that a difference in sea-surface height is generated across the continental margin, which becomes larger further to the north (Huthnance & Gould, 1989; Pingree & Le Cann, 1989; Huthnance *et al.*, 2001). Beside the baroclinic effect, friction also plays a role in the current pattern, which results in different characteristics in the slope flow at different locations along the Atlantic margin (Pingree & Le Cann, 1990). Friction slows down the effect of continuously increasing current speed further northwards along the slope due to the baroclinic effect (White, 2001).

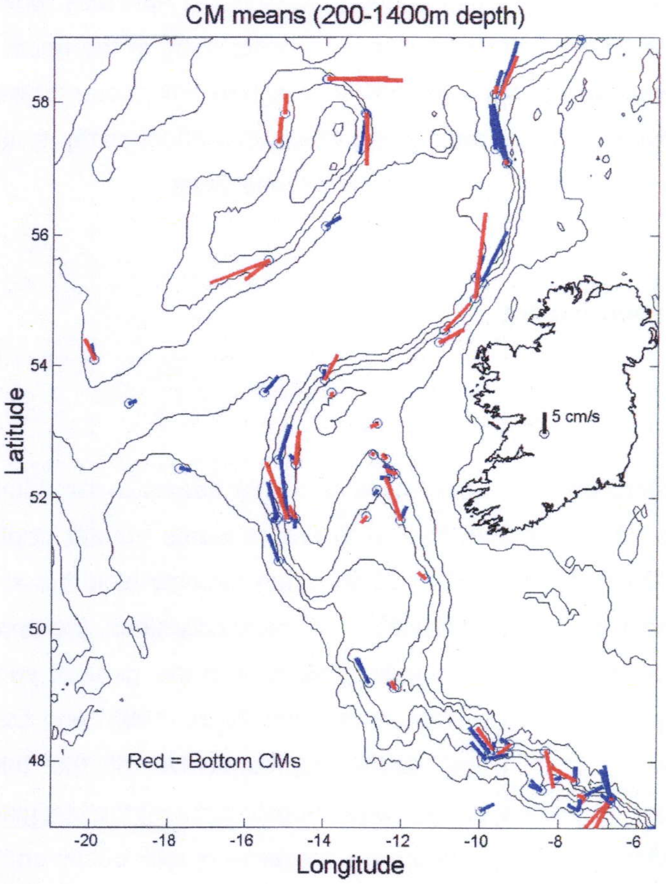


Figure 2.4 Mean current vectors of bottom and surface currents in the northern part of the NE Atlantic (White, 2001)

The existence of this general slope current has been confirmed by several sets of current measurements along the North West European continental shelf and slope (Pingree *et al.*, 1999). In general mean poleward currents of about 5 cm/s have been measured along the Celtic Sea slope (Pingree & Le Cann, 1990; Huthnance *et al.*, 2001). In the Porcupine Seabight, a mean poleward current is observed with a mean speed of 4 cm/s in the near-bottom current meters on the eastern flank (Pingree & Le Cann, 1990). At the northern end of the Porcupine Seabight, currents are relatively weaker (1-5 cm/s) with some evidence of a topographic steering of the mean flow, cyclonically (anticlockwise) along the slope to the Porcupine Seabight. In general, the stability of the current in Porcupine Seabight is stable to a large degree (White, 2001). The most stable currents are associated with the strongest speeds and generally the greatest mean flows. Overall, the northern Porcupine Seabight moorings adjacent to the Hovland mound province have the lowest current stability and speeds. This might be expected as it is located near the barrier of the relatively deep shelf between the Porcupine Bank and the Irish continental margin, which is a barrier to flows below about 350 m

(White, 2001). An important seasonal variation in the slope current regime (speed and direction) at certain locations was observed (Pingree & Le Cann, 1990; White, 2001; Huthnance *et al.*, 2001). South of the 53°N maximum poleward slope and shelf edge currents are found in winter (December-February) with strong flows west of the Porcupine Bank (>10 cm/s) and at the slope of the eastern Porcupine Seabight (Huthnance *et al.*, 2001, White, 2001). At the northern part of the Seabight the poleward flow is the strongest through the deeper portion of the Irish shelf in January/February. The flow first turns on-slope in February/March and than reverses in April/May. Mean monthly speeds are also weakest at this time. The reverse and significant weakening in the upper level currents are not apparent in the lower layer current measurements although minimum current were found in summer in the Porcupine region. Pingree & LeCann (1990) relate this effect partly to changes in large scale density/pressure forcing or a change in wind stress at these times.

2.1.2.2. Sedimentary environment

Sediment type

The present-day sedimentation in the Porcupine Seabight seems to be dominated by pelagic and hemipelagic depositions with sediments becoming finer towards greater depths (Rice *et al.*, 1991, Huvenne *et al.*, 2002). Between 500-900 m depth, often strongly bioturbated coccolith-foraminiferal marls were found, (Lampitt *et al.* 1986). However, in many occasions, the uppermost centimetres of cores sampled contained watery clayey sands. This is also the general succession described by Foubert (2002), and supported by observations of Coles *et al.* (1996) and De Mol *et al.* (2002): an upper layer of Holocene, foraminiferal sands, representative of the interglacial sedimentary environment, overlying several meters of silty clays deposited during the last glacial event.

In addition, ample evidence has been found for the presence of rock debris on the Porcupine seafloor, mainly of glacial origin (Kidd & Huggett, 1981). The same authors also report a large amount of clinker and coal residues dumped from steamships decennia ago. Surprisingly these residues can be, in some locations, even more abundant than ice-rafted debris or other materials transported by geological agents.

Nepheloid layers

Nepheloid layers are layers of suspended sediment in the water column. The sediment has been lifted into suspension by the mixing processes at the seabed, forming bottom or benthic nepheloid layers (BNL) or intermediate nepheloid layers (INL), layers detached from the seabed in mid water. In light attenuation profiles on the eastern flank of the Porcupine Bank, Rice *et al.* (1991) found indications of nepheloid layers at different depths. An intermediate nepheloid layer (INL) occurred between 700 and 800 m depth, while a bottom nepheloid layer (BNL) was encountered up till circa 50 m above the seabed (at 950 m). Similar INL and BML have been found on the western flank of the Porcupine Bank (Dickson & McCave, 1986), and on the Goban Spur (van Weering *et al.*, 2001). These nepheloid layers at Porcupine Seabight are thought to originate from the Porcupine Bank, where they are formed through the erosion of the seabed by internal waves and tides. They detach from the seabed and move off-slope along isopycnal surfaces until a depth of 700-800 m.

Sedimentation along the continental slope

The sedimentary processes along a continental margin often consist of an interplay between **downslope** and **alongslope sediment transport**. Depending on the sediment input and the strength of bottom currents, one of the processes will be rather dominant (Cremer *et al.*, 1993; Faugères *et al.*, 1999). In Porcupine Seabight, both processes are important (Huvenne *et al.*, 2002). The existence and strength of bottom currents, especially on the eastern slope of the Seabight illustrates alongslope sediment transport and has been discussed above. They severely influence the sedimentation. Evidence for the existence of 2 types of sediment drift, an elongated and a confined drift, on the eastern flank of the Porcupine Seabight (Belgica mound area) has been presented by Van Rooij *et al.*, 2003. The occurrence of the sandy top layer in the cores points to the reworking and the presence of a contourite or drift sedimentation in the interglacials, linked to a higher bottom current activity (Foubert, 2002; Van Rooij *et al.*, 2003). A similar situation has been found in the northern Rockall Trough, where several indications for sediment drifts and increased bottom currents during interglacials were described by Masson *et al.* (2002). Although there is no general relation between climate and drift development (Faugères *et al.*, 1999), both Rockall Trough and Porcupine Seabight are influenced by similar water masses and current systems, and may very well have known a similar development. In addition to the alongslope sediment transport, evidence for downslope transport between water depths of 500 to 3000 m, apart from channel and canyon systems, from the shelf into the Seabight has been pointed out by Lampitt *et al.* (1986). However, in deeper areas shells of upper-slope Foraminifera were encountered, indicating at least a limited amount of downslope transport (which may be linked to the presence of nepheloid layers). According to Rice *et al.* (1991), the main sediment supply zone is located on the shelves (Celtic and Irish shelf), while the input from the Porcupine Bank is much smaller. Therefore only on the eastern flank of the Seabight, channels and canyons are found. Some of these are partly buried, but on the steepest flanks (2-3°) a dendritic channel system was recognised by Brenot & Berthois (1962). It was named 'Gollum Channel', by Kenyon *et al.* (1978), who studied its lower stretches by means of sidescan sonar imagery. They found flat-floored, deeply cut channels (100 to 280 m deep), with a high-backscatter floor, indicating the presence of coarse material and hence of recent activity. However, submersible dives by Tudhope & Scoffin (1995) revealed soupy, biodetrital materials and oozes on the channel floors, and hence an as yet inactive channel. The upper parts of the Gollum Channel System seem to be more dynamic. Rippled sands indicate reversing currents, although the actual long-term sediment displacement is rather limited. Tudhope & Scoffin (1995) measured instantaneous currents of up to 50 cm/s, and report the occasional occurrence of *Lophelia* and *Madrepora* corals.

2.1.2.3. Carbonate mounds and coral banks in Porcupine Seabight

Carbonate mounds are found at several locations along the margin of the NE Atlantic between depths of 500-1000 m. These mounds consist of a sediment-filled framework composed of carbonate material, principally dead deep-water coral, live specimens of which are prevalent in the NE Atlantic (Freiwald, 2002). These mound structures have been associated with deep-water corals and occur in well-defined areas in the Porcupine Seabight. The coral banks in the Porcupine Basin reach spectacular sizes, up to 200 m height and 5 km length. They occur in three mound provinces, each with a different mound type displaying distinct morphological features (Henriet *et al.*, 1998; De Mol *et al.*, 2002).

- The **Hovland** mound province, in the central part of the Porcupine Seabight (Fig. 2.2), is characterized by high-relief surface mounds which have a dimension of one by five kilometres and a height up to 200 m.

- The **Magellan** mound province (Fig. 2.2) occurs north to northwest of the Hovland mound province and is characterized by buried mounds, somewhat smaller (up to 90 m) in a large variety of irregular shapes. These mounds have been reported in a site survey by the commercial survey ship RV "Svitzer Magellan", a few months before the Belgica cruise.

- The **Belgica** mound province is located on the south-eastern margin of the Porcupine Seabight between 51°10'N and 51°40'N (Fig 2.2), which is aligned roughly north-south. Large mounds, which display a well-exposed downslope side in the bathymetry but an almost entirely buried upslope side, characterize this province. These mound structures were called "Belgica mounds" after their discovery by the RV Belgica on high-resolution seismic profiles.

Subsequent sampling and recording of some video transects illustrated clearly the growth of the cold-water deep-sea coral species *Lophelia pertusa* (L.) and *Madrepora oculata* (L.) on these mound structures (Kenyon *et al.*, 1998). Further study showed that *L. pertusa* forms the main framework builder on (at least the upper part of) the mounds.

2.1.3. Meriadzek Terrace

The Meriadzek Terrace is a large relatively flat plateau at 2100-2300 m depth situated in the Bay of Biscay south-east of the Goban Spur (van Weering *et al.*, 2001) (Fig. 2.5). The (Eperon) Berthois Spur forms the connection between Meriadzek Terrace and the continental shelf and lies between 200 and 2000 m depth. Strictly spoken, sampling in this area was performed along the Berthois Spur, but the name Meriadzek Terrace is used in this research, because this is more frequently recognized in literature. Moreover, the name Meriadzek Terrace is often used in literature to describe the area comprising Berthois Spur and Meriadzek Terrace.

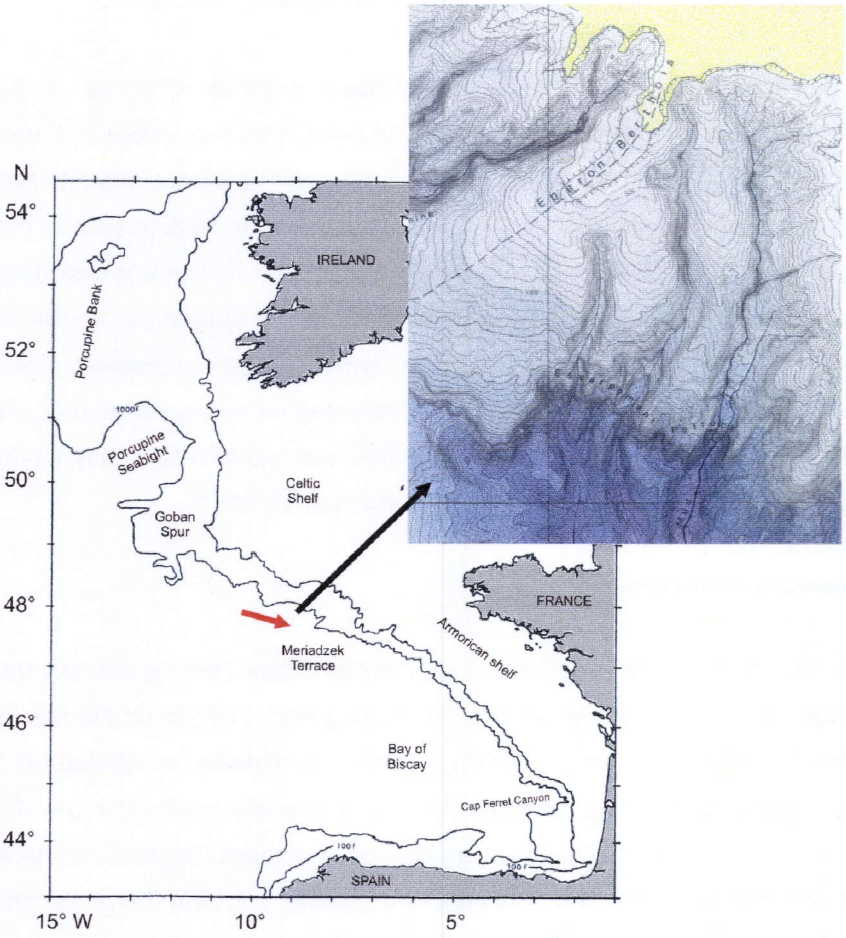


Figure 2.5 The study site Meriadzek Terrace situated along the NE Atlantic continental margin (red arrow) (modified after Pingree & Le Cann, 1990). The 100 feet (=30.48 m) and 1000 feet (=304.80 m) isobaths are indicated. A detailed map of the Eperon Berthois Spur area is shown.

The Berthois Spur and the Meriadzek Terrace spreads out into the Trevelyan Escapment forming a morphological boundary between the Celtic Margin and the Armorican Margin (Fig. 2.5), which splits the shelf supply between the Celtic Fan and the Armorican Fan (Zaragosi *et al.*, 2000). The Meriadzek Terrace is less intensively studied than Porcupine Seabight. Van Weering *et al.* (2001) investigated the benthic dynamics and the carbon fluxes on the NW European continental margin at Goban Spur and Meriadzek Terrace in the framework of the OMEX (Ocean Margin Exchange) project. An overview of observations on the hydrography and current regime in the Meriadzek Terrace area is given by Vangriesheim (1985). More observations resulting from a lander deployment on Meriadzek Terrace are reported by Vangriesheim & Khripounoff (1990). A short overview of the main points is given below.

2.1.3.1. Oceanography and hydrography

The Meriadzek Terrace is bathed by three main water masses, the North Atlantic Central Water (NACW) from the thermocline down to 800 m, the Mediterranean outflow water (MOW) from 800 m to 1200 m water depth, and the North Atlantic Deep Water (NADW) from 1200 m downwards with a contribution of oxygen-rich Labrador Sea Water (van Weering *et al.*, 2001).

The northerly and north-westerly directed, along-slope currents (Pingree & Le Cann, 1989; Pingree *et al.*, 1999) and internal waves and tides (Dickson & McCave, 1986, Huthnance *et al.*, 2001) are considered important to sediment transport and energy dissipation at the NE Atlantic margin. At Meriadzek Terrace currents show a strong semi-diurnal tidal pattern, with speeds in the same order as observed on Goban Spur (circa 5 cm/s on average). The residual current is directed to the north, often with a westerly component. At about 3000 m depth however, photographs provide evidence of high current speeds (Auffret & Sichler, 1981). Overall, a dynamic near-bed current regime at the upper slope was shown, with currents sufficiently high and directed off-slope, capable of resuspension and transport of particles in the benthic boundary layer (BBL), and maintaining a benthic nepheloid layer of variable extension and particle concentration (van Weering *et al.*, 2001).

2.1.3.2. Sedimentary environment

The variations in near-bed current conditions along the Meriadzek Terrace are reflected in the surface sediment grain size, with the median grain size decreasing from 100 µm on the shelf to below 10 µm on the lower slope (van Weering *et al.*, 1998b). Surface sediments on Meriadzek Terrace consist predominantly of hemipelagic ooze, comparable to lower slope sediments on Goban Spur (van Weering *et al.*, 2001). On the Berthois Spur, upslope of Meriadzek Terrace, terrigenous silty clay of Pleistocene age was found below a few centimetres of gravely relict sand (van Weering *et al.*, 2001). The Meriadzek Terrace is presently characterized by low terrigenous supply in contrast to the southern Bay of Biscay margin marked by high terrigenous input (Cremer *et al.*, 1992).

Compared to Goban Spur, the central Meriadzek Terrace appears to receive a markedly higher input of lithogenic material, $CaCO_3$ and organic carbon (van Weering *et al.*, 2001). These data suggest a trend of decreasing lithogenic fluxes along the northern Biscay margin from SE to NW. Taking into account the general northwestern current direction along the slope, the decreasing lithogenic flux seems to be related primarily to the increasing distance to continental sediment sources (van Weering *et al.*, 2001). The higher $CaCO_3$ flux is in accordance with the higher primary productivity at the shelf edge near Meriadzek Terrace (Joint *et al.*, 2001) and higher $CaCO_3$ production in the surface water (Wollast & Chou, 1998). The area is also known for the occurrence of coccolith blooms (Holligan *et al.*, 1983).

2.1.3.3. Utilization

Kenyon & Hunter (1985) conducted a long-range side-scan sonar survey in the area in order to determine a suitable route for the construction of the transatlantic fibre optic cable in this area. The few strips of smooth seafloor on the continental slope in the Bay of Biscay were recommended as potential routes for undersea cables by Belderson & Kenyon (1976). The Meriadzek Terrace is one of the largest of these strips of smooth floor. It can be divided into an Upper Meriadzek Terrace and a Lower Meriadzek Terrace. Both parts of the Terrace appear to be free from any relief features or other acoustic targets and have gradients less than 2 degrees.

2.2. Working definition for hyperbenthos

Due to the discussion on ecological terminology of the studied fauna (as described in chapter 1) a working definition for this PhD study is given below. As mentioned before, the **hyperbenthos** is defined as the association of small animals living in the water layer close to the seabed (Mees & Jones, 1997). The applied working definition for this study therefore categorizes the hyperbenthos as all animals caught with the hyperbenthic sledge modified after Sorbe (1983) (see 2.3. Sampling strategy), with a size range between 1 and 20 mm. Hyperbenthos can be divided into two main groups: the holohyperbenthos and merohyperbenthos (Fig. 2.6A). The **holohyperbenthos** consists of small animals that spend variable periods of their adult life in the hyperbenthal zone (Mees & Jones, 1997). Most abundant holohyperbenthic taxa are mysids, amphipods, isopods, copepods and chaetognaths (Fig. 2.6A). The term **merohyperbenthos** is applied for the early life history stages of species that subsequently recruit to the nekton, epibenthos and endobenthos communities (Mees & Hamerlynck, 1992). Caridean shrimps, brachyuran crabs, postlarval fish and polychaete larvae are most common. For this PhD research this division in holohyperbenthos and merohyperbenthos will not be applied due to the very small amount of merohyperbenthos sampled in the studied areas. Figure 2.6B shows the most abundant hyperbenthic species belonging to the peracarid crustaceans sampled in this PhD research.

As a general rule, all animals larger than approximately 20 mm and animals manifestly belonging to the endo- or epibenthos (attached organisms and animals being strictly buried in, or sitting onto the bottom) were considered as non-hyperbenthos. Most of these animals were rather occasionally caught and were removed from all analyses. For juvenile and adult polychaets it was more difficult to decide upon, as they are generally burrowing, but might spend some time swimming in the water column. Yet, they were poorly caught, except in few cases when the catch was slightly contaminated by touching a sand ripple or some mud from the bottom. These catches could be distinguished, as we experienced the presence of other endobenthic organisms. Therefore, it was decided to exclude all polychaetes (apart from larval stages).

Recently Sorbe (1999) mentioned that according to the definition of Brunel *et al.* (1978), suprabenthos components are bottom-dependent animals that perform daily or seasonal vertical migrations above the bottom and due to the unknown degree of sled biting into the sediment on deep-sea muddy bottoms, hyperbenthic samples may be contaminated by some infaunal elements from the uppermost layer of the substrate. Therefore, Sorbe (1999) suggests it is preferable to use a more neutral terminology referring to the natatory abilities of the near-bottom collected species. Such a terminology (BBL macrofauna) was used by Wildish *et al.* (1992) for Browns Bank community studies in the northwest Atlantic and by Dauvin *et al.* (1995) for the slope communities from the southern margin of the Cap-Ferret Canyon. Arguments for using the term hyperbenthos are given in Mees & Jones (1997) and this term will be used for this research.

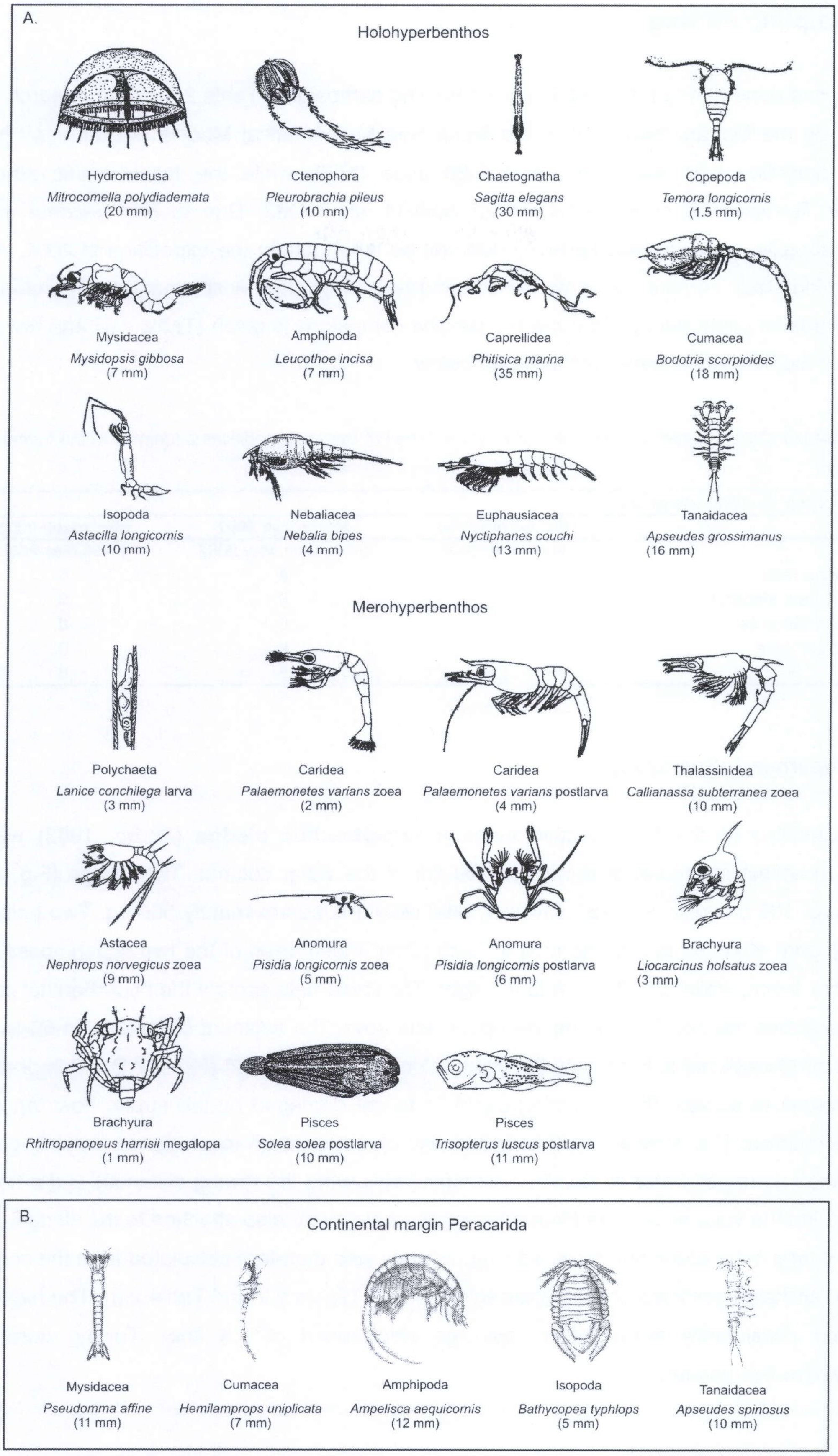


Figure 2.6 A) The major taxonomic groups belonging to the holohyperbenthos and merohyperbenthos, with illustrations of coastal species (after Dewicke, 2002) B) Illustration of abundant holohyperbenthic species belonging to the Peracarida studied in this PhD work.

2.3. Sampling strategy

Sampling was done during three RV Belgica sampling campaigns (Table 2.1). This research vessel is managed by the Management Unit of the North Sea Mathematical Models (MUMM). At Porcupine Seabight sampling was performed from 9-29 June 2000, while the hyperbenthic sampling at Meriadzek Terrace was conducted from 22 April-11 May 2002. Due to bad weather conditions sediment samples at Meriadzek Terrace could not be taken during the expedition in 2002. A second cruise to Meriadzek Terrace was organised from 11-18 May 2003. A summary of the number of the different samples taken during the three RV Belgica campaigns is given (Table 2.1) and the sampling strategy for the different samples is described below.

Table 2.1 Number of the different samples taken during the three RV Belgica expeditions performed in the framework of this PhD research.

Three RV Belgica sampling campaigns			
	Porcupine 2000	**Meriadzek 2002**	**Meriadzek 2003**
Date	9-29 June 2000	22 April-11 May 2002	11-18 May 2003
Hyperbenthic samples	8	8	0
Boxcore sediment samples	8	0	8
Boxcore water samples	8	0	0
Niskin water samples	4	8	0
SCTD	2	8	0

2.3.1. Hyperbenthic sampling

For the sampling of the hyperbenthic fauna a **hyperbenthic sledge** (Sorbe, 1983) was used, designed to collect the fauna of the lower 100 cm of the water column. The sledge (Fig. 2.7 A) is 301 cm long, 169 cm wide and 137 cm high; total weight is approximately 500 kg. Two pairs of nets (3 m long) were attached in a frame next to each other. Mesh sizes of the two superimposed nets to the left were 1 mm, while only 0.5 mm to the right. The lower nets sample the hyperbenthal zone from 0 to 50 cm above the sea floor, while the upper nets cover the adjacent stratum from 50 to 100 cm. The collector of each net is fixed onto the frame along an angle of 45° (Fig. 2.7 B). This prevents the collected fauna to escape (by swimming back) or to get damaged by the strong flow. An opening-closing mechanism (*i.e.* a roller blind) automatically operates when touching the bottom, preventing contamination by upper water strata. An odometer (registering the towing distance) and a flow meter (for calculating the volume of water filtered trough the nets) were also attached to the sledge, but were damaged during most of the sampling. Towing distance was therefore calculated from the coordinates of the start and stop positions of the hyperbenthic sledge (Table 2.2 and Table 2.3). The hyperbenthic sledge was consistently towed at an average ship speed of 1.5 knot. Towing duration was standardized to five minutes.

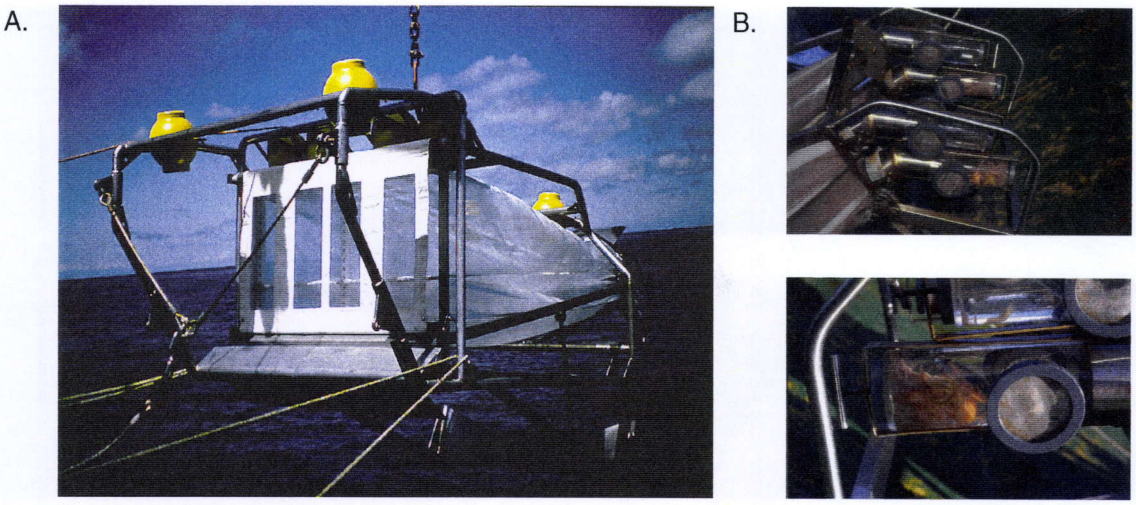


Figure 2.7 A) The hyperbenthic sledge (Sorbe, 1983) used to sample the hyperbenthic fauna during the expeditions. B) a detailed view of the collectors (filled with hyperbenthic fauna) attached at the end of each net on the backside of the hyperbenthic sledge.

In both sampling sites, Porcupine Seabight and Meriadzek Terrace, a **standardized sampling strategy** was followed. Eight sampling stations, between 200 and 1250 m water depth, were selected along the continental slope in the two areas, so a total of 16 stations over both sites were sampled. Between each station approximately 150 m difference in water depth existed, resulting in a bathymetric transect along both continental slope areas. The names of the stations are composed of the first letter of the study site (**P** for Porcupine Seabight samples and **M** for Meriadzek Terrace samples) together with the rounding off of the sampling depth in metres (200, 350, 500, 650, 800, 950, 1100 or 1250) (Table 2.2 and Table 2.3). At each station one hyperbenthic sample was taken with the hyperbenthic sledge described above. The hyperbenthic sampling was carried out during daytime and towing lasted five minutes at an average ship speed of 1.5 knot. Sampling was done parallel to the isobaths. An overview of the exact positions, exact depths and dates of the hyperbenthic samples is given for Porcupine Seabight (Fig. 2.8 and Table 2.2) and for Meriadzek Terrace (Fig. 2.9 and Table 2.3). The start position and the stop position are the positions of the hyperbenthic sledge at the beginning of sampling and after five minutes of trawling. For each station the distance trawled in metres is also indicated.

At each station four different net samples were collected, an upper (U) and lower (L) sample from the nets with 0.5 mm mesh size and an upper and lower sample from the 1 mm nets. The catches from the upper and lower 1 mm and 0.5 mm nets were rinsed separately over a 1 mm and 0.5 mm mesh size sieve respectively and preserved in a neutralised formaldehyde solution (7 % final concentration). For this PhD research only the samples (upper and lower) from the 1 mm nets were worked out and analysed. Also note that the terms upper slope, mid slope and lower slope in this research are used to describe the different community zones within this bathymetric transect of 200-1250 m depth, nevertheless this depth range only covers the upper part of the geographical continental slope.

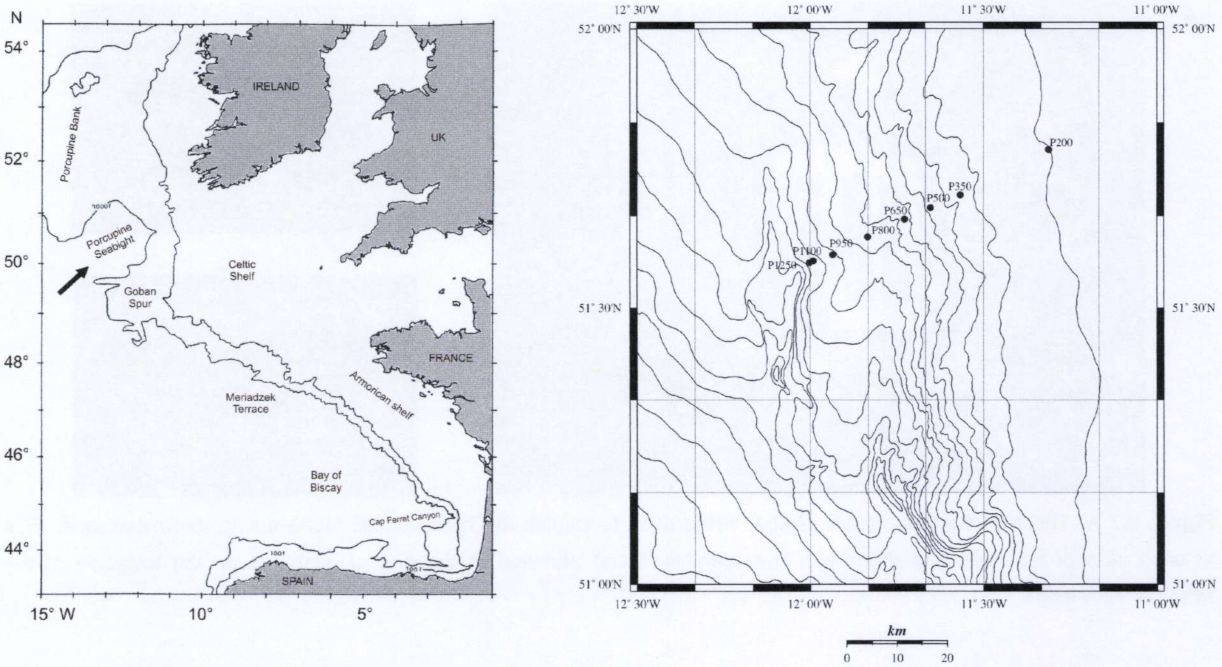


Figure 2.8 Porcupine Seabight situated (arrow) (map modified after Pingree & Le Cann, 1990) and a detailed map indicating the location of the eight sampled stations (P200-P1250) along the bathymetric transect on the Porcupine Seabight continental slope between 200 and 1250 m water depth. On the left map, the 100 feet (=30.48 m) and 1000 feet (=304.80 m) isobaths are indicated.

Table 2.2 Date, sampling coordinates, depth, trawling duration and distance trawled at the eight stations (P200-P1250) sampled at Porcupine Seabight. Start position= position when the sledge is on the bottom, starting to trawl; stop position= position after five minutes of trawling.

Porcupine Seabight 2000								
station	**date**	**start position N**	**start position W**	**stop position N**	**stop position W**	**depth (m)**	**trawling (min)**	**distance trawled (m)**
P200	24/06/2000	51° 47.15'	11° 18.78'	51° 47.20'	11° 18.57'	207	5	260
P350	25/06/2000	51° 42.28'	11° 33.98'	51° 42.42'	11° 33.89'	336	5	283
P500	24/06/2000	51° 40.92'	11° 39.19'	51° 41.02'	11° 39.14'	469	5	187
P650	25/06/2000	51° 39.64'	11° 43.69'	51° 39.76'	11° 43.58'	628	5	259
P800	24/06/2000	51° 37.75'	11° 50.04'	51° 37.85'	11° 49.90'	765	5	241
P950	25/06/2000	51° 35.79'	11° 56.10'	51° 35.90'	11° 56.07'	914	5	195
P1100	25/06/2000	51° 35.11'	11° 59.44'	51° 35.22'	11° 59.36'	1067	5	216
P1250	25/06/2000	51° 34.92'	12° 01.42'	51° 34.99'	12° 1.45'	1215	5	124

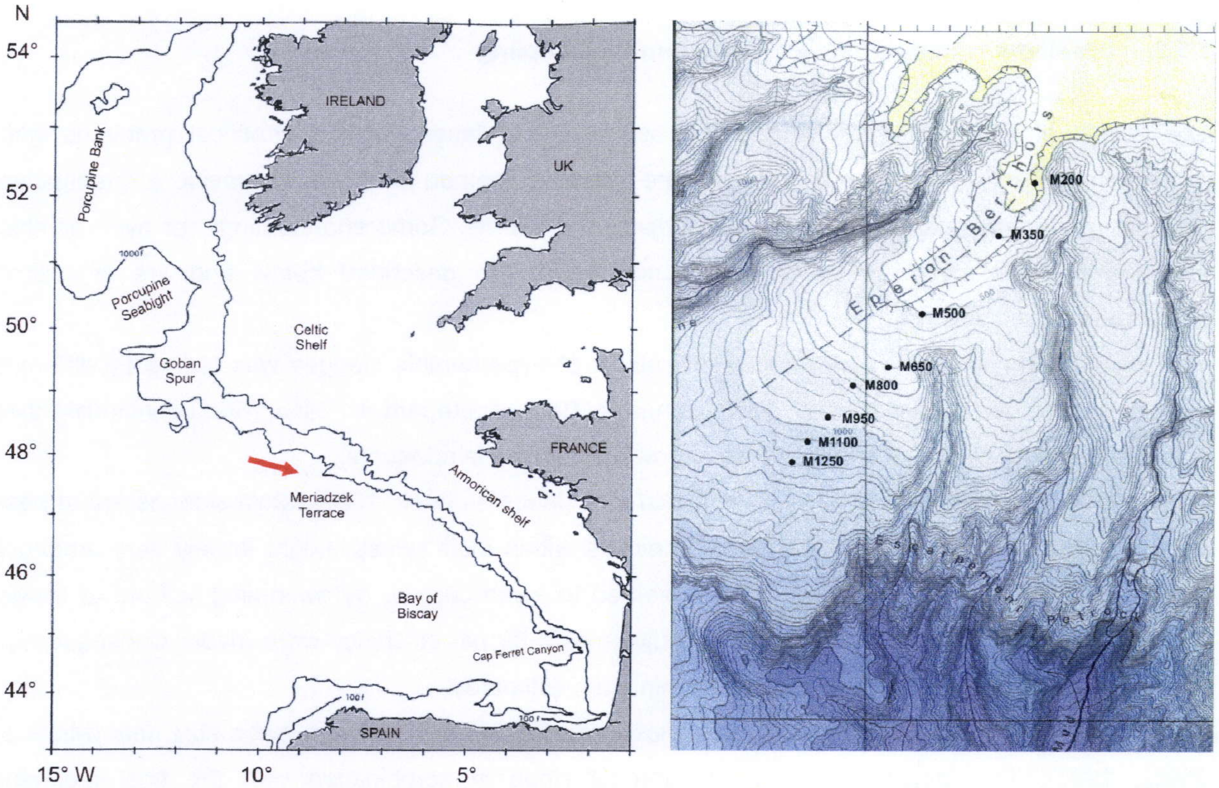


Figure 2.9 Meriadzek Terrace situated (arrow) (map modified after Pingree & Le Cann, 1990) and a detailed map indicating the location of the eight sampled stations (M200-M1250) along the bathymetric transect on the Berthois Spur continental slope between 200 and 1250 m water depth. On the left map, the 100 feet (=30.48 m) and 1000 feet (=304.80 m) isobaths are indicated.

Table 2.3 Date, sampling coordinates, depth, trawling duration and distance trawled at the eight stations (M200-M1250) sampled at Meriadzek Terrace. Start position= position when the sledge is on the bottom, starting to trawl; stop position= position after five minutes of trawling.

Meriadzek Terrace 2002								
station	**date**	**start position N**	**start position W**	**stop position N**	**stop position W**	**depth (m)**	**trawling (min)**	**distance trawled (m)**
M200	25/04/2002	47° 53.24'	7° 50.57'	47° 53.27'	7° 50.79'	227	5	284
M350	25/04/2002	47° 51.10'	7° 54.59'	47° 51.22'	7° 54.67'	352	5	241
M500	25/04/2002	47° 49.29'	7° 58.61'	47° 49.42'	7° 58.69'	494	5	258
M650	24/04/2002	47° 47.25'	8° 02.73'	47° 47.28'	8° 2.84'	678	5	152
M800	25/04/2002	47° 45.22'	8° 02.53'	47° 45.15'	8° 2.39'	795	5	212
M950	4/05/2002	47° 44.53'	8° 06.17'	47° 44.59'	8° 6.33'	953	5	225
M1100	5/05/2002	47° 42.10'	8° 09.19'	47° 42.03'	8° 9.07'	1110	5	203
M1250	5/05/2002	47° 41.01'	8° 12.54'	47° 40.93'	8° 12.43'	1215	5	199

2.3.2. Problems with quantitative hyperbenthic sampling

The choice of the studied fauna and the sampling site faces different practical problems with quantitative sampling. The use of an adequate sampling method is crucial to provide a quantitative data set to study spatial distribution and biodiversity patterns. Some shortcomings for hyperbenthic sampling are still important topics of discussion and are described below and are of critical importance.

No replicate sampling was performed. Replicability of hyperbenthic sledges was tested by different authors (Hesthagen & Gjermunsen, 1978; Schnack, 1978; Brattegard & Fosså, 1991) concluding that samples are highly representative as long as towing distance is adequate.

Catch efficiency of sledges remains largely unknown (Mees & Jones, 1997). Most sledges are at best semi-quantitative. The ability to capture all animals within their sweep, might largely vary amongst taxa. As an example, mysids have been observed to avoid capture by swimming in front of trawls (Lasenby & Sherman, 1991). Therefore, no adjustments for net efficiency were made. Consequently, all densities values should be considered as minimum estimates.

Standardized sampling for hyperbenthos is mostly carried out with 0.5 mm mesh size nets (Mees & Jones, 1997). The steepness of the continental slope in combination with the fine sediment composition in the study area the filter capacity of the 0.5 mm nets was strongly reduced. It was therefore decided on to only examine the samples derived from the 1 mm nets, being acceptable in such cases (Mees & Jones, 1997), although being aware of the underestimation of smaller individuals of certain hyperbenthic taxa (*e.g.* copepoda, ostracods).

2.3.3. Environmental samples

In addition to the hyperbenthic samples, following environmental variables were sampled at each station of Porcupine Seabight and Meriadzek Terrace. The oceanographic instruments used on board of the RV Belgica are managed by the Management Unit of the North Sea Mathematical Models (MUMM).

Sediment samples

At each station a large boxcore (Fig. 2.10) was lowered to sample the sediment. Dates, the exact coordinates and depth for each boxcore sample taken at Porcupine Seabight and Meriadzek Terrace are summarized (Table 2.4). A small subsample (using a core) of sediment was taken from the box and dried to perform grain fraction analysis in the laboratory. During the RV Belgica cruise at Porcupine Seabight the overlying water from the boxcore was sucked of to perform water analysis (see below).

Figure 2.10 Boxcore sampling during RV Belgica expedition.

Table 2.4 Geographic positions and depth of the boxcore samples taken at Porcupine Seabight and Meriadzek Terrace.

Porcupine Seabight 2000

station	date	position N	position W	depth (m)
P200	26/06/2000	51° 47.07'	11° 18.86'	207
P350	26/06/2000	51° 42.37'	11° 34.03'	337
P500	26/06/2000	51° 40.72'	11° 39.98'	494
P650	26/06/2000	51° 39.43'	11° 44.04'	628
P800	26/06/2000	51° 37.03'	11° 51.09'	765
P950	26/06/2000	51° 35.36'	11° 56.18'	914
P1100	26/06/2000	51° 34.05'	11° 59.97'	1067
P1250	26/06/2000	51° 33.30'	12° 1.88'	1215

Meriadzek Terrace 2003

station	date	position N	position W	depth (m)
M200	13/05/2003	47° 53.28'	7° 50.68'	228
M350	13/05/2003	47° 51.05'	7° 54.49'	347
M500	13/05/2003	47° 49.24'	7° 58.65'	491
M650	13/05/2003	47° 47.19'	8° 02.83'	676
M800	13/05/2003	47° 45.39'	8° 02.52'	778
M950	13/05/2003	47° 44.42'	8° 06.08'	953
M1100	13/05/2003	47° 41.97'	8° 08.33'	1110
M1250	13/05/2003	47° 40.85'	8° 12.79'	1280

The grain fraction analysis was performed with a Coulter LS 100 particle size analyser with a measure range of 2 µm to 850 µm. These grain fractions were calculated as percentages of volume (vol%). Fractions larger than 850 µm were sieved and calculated as percentages of weight (mass%). For the classification of the particle size the Wentworth scale (Buchanan, 1984) was used (Table 2.5). For each station the granulometric composition was determined. In addition the median grain size, percentage mud (*i.e.* sum of percentage silt and clay; <63 µm) and the sorting coefficient were calculated for each station, the latter being an index for the range of the grain size distribution present in a sample (Dyer, 1986). The sorting coefficient was calculated using the diameter values (in µm) at the 25th and 75th percentiles.

Table 2.5 Wentworth scale (Buchanan, 1984) used for the classification of the particle sizes of sediment samples.

Fraction	Size (µm)
Granule	>2000
Very coarse sand	850-2000
Coarse sand	1000-500
Medium sand	500-250
Fine sand	250-125
Very fine sand	125-63
Silt	63-4
Clay	<4

Water samples

Water from just above the bottom was sampled using the Niskin bottles (Fig. 2.11). During the RV Belgica cruise to Porcupine Seabight an older version of these Niskin bottles carousel was on board and could not take water samples deeper than 500 m due to technical failing. This problem was solved by sucking up the overlying water from the boxcore samples and performing the same analysis on this water. For Meriadzek Terrace this problem was not encountered and 8 Niskin water samples could be taken. The water samples were analysed for nutrients and pigments in the laboratory. Pigments (chlorophyll a) were analysed from the water by filtering the water over a GF/F filter. Pigments were extracted using 90 % aceton and analysed by the technique of high-pressure liquid chromatography (HPLC). Nutrient contents of the water was analysed using a segmented flow analyser device. The quantity (µg/litre water) of NO_2, NO_3, NH_4 en PO_4 was measured. Only the pigment data were useful, nutrients were non detectable in the water samples, probably due to technical failure during the sample processing.

Figure 2.11 Niskin- bottles for water sampling attached to a carousel which also contains the SCTD-probes for measuring different physico-chemical parameters.

Other environmental parameters

The SCTD-system allowed measurement of different physico-chemical parameters: salinity, temperature, concentration dissolved oxygen, turbidity and water density. This device, attached to the same carousel as the Niskin bottles (Fig. 2.11), was lowered into the water at a speed of 0.8 m per second and measured every parameter every 1 m it was lowered. This device was at our disposal during the cruise to Meriadzek Terrace, but SCTD data for Porcupine Seabight lack.

2.4. Sample processing

In view of the characteristics of the selection of the organisms, the study sites and the sampling method in combination with the time management of this research, some important choices concerning the sample processing were made. As mentioned before only the upper (U) and lower (L) net samples of the 1 mm nets were processed further for this research due to the reduced filter capacity of the 0.5 mm nets, keeping in mind an underestimation of smaller individuals of certain taxa (*e.g.* copepods, ostracods). Given the main aim of this research, studying the community structure of the total hyperbenthos and a detailed study of the Peracarida, only density measurements were performed; no biomasses were calculated and staging of the organisms was not performed. Moreover, identifying all peracarid crustaceans sampled (>250 species) was a very time-consuming work as no expertise for identifying this unique but difficult fauna was available at the UGent Marine Biology Laboratory. These well considered choices are acceptable in order to obtain a useful and detailed dataset for exploring the hyperbenthic community structure and biodiversity patterns in the unique habitat along the ocean margins. The sample processing is described in more detail below.

Both the upper and lower 1 mm net sample of each sampling station were processed separately in order to obtain information on the stratified distribution of the hyperbenthic fauna within the one metre water layer above the seafloor. After sorting out, all organisms were identified to higher taxon level (*e.g.* Phylum, Classis, Ordo) and counted. After identification, non-hyperbenthic representatives were removed from the dataset (see 2.2. Working definition for hyperbenthos). For this research these were juvenile or adult organisms belonging to the phyla Cnidaria, Echinodermata (mainly belonging to the Classis Ophiuroidea), Annelida (Classis Polychaeta), Brachiopoda and Mollusca. Also adult organisms of the Classis Pisces and Decapoda were caught in the hyperbenthic sledge, but were removed from the hyperbenthic dataset. Most of these non-hyperbenthic organisms were only occasionally caught in the hyperbenthic sledge. This selection resulted in a hyperbenthic dataset, with all organisms counted and identified on higher taxon level. After identification and counting of the hyperbenthic organisms on higher taxon level, densities were calculated. In this study densities are expressed as individuals per 100 m^2 (surface unit), since most fauna was restricted to the bottom (*i.e.* caught with the lower net of the hyperbenthic sledge). Densities were calculated based on the trawled distance and the width of the hyperbenthic sledge net (0.71 m). This **hyperbenthic taxa density dataset** was used for analysis in this PhD study (see Chapter 3 and 4) and is listed in appendix 1.

Furthermore all peracarid crustaceans (Amphipoda, Isopoda, Cumacea, Mysidacea and Tanaidacea), the most abundant group in the studied hyperbenthic fauna, were identified to species level (full species list in appendix 2) and densities were also calculated. This resulted in a **peracarid species density dataset** which was also further analysed in this study (see Chapter 5) and is listed in appendix 3. Identification of the Peracarida on species level was possible for the majority of the species. Some organisms could only be identified to genus or family level and were named as 'Genus-name species 1' or 'Family-name species 1', others as 'Genus-name aff. species-name' when the organisms showed great affinity to a certain species, but were another species. Table 2.6 lists the books with identification keys used for the identification of the Peracarida species.

Table 2.6 List of books used for identification of the Peracarida.

Title	Author
British marine Amphipoda: Gammaridae	Lincoln, R.J., 1979
The Amphipoda of the Mediterranean	Ruffo, S., 1982
The families and genera of marine gammaridean Amphipoda (except marine gammaroids)	Barnard, J.L. & Karaman, G.S., 1991
Faune de France n° 9 Amphipodes	Chevreux, E. & Fage, L., 1925
Faune de France 54 Cumacés	Fage, L., 1951
Synopses of the British Fauna n° 7 British Cumaceans	Jones, N.S., 1976
Synopses of the British Fauna n° 3 British Marine Isopods	Naylor, E., 1972
The British Mysidacea	Tattersall, W.M. & Tattersall, O.S., 1951
Synopses of the British Fauna n° 27 Tanaids	Holdich, D.M. & Jones, J.A., 1983
An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. 1. Amphipoda	Sars, G.O., 1895
Abyssal Crustacea	Barnard, J.L., Menzies, R.J. & Bacescu, M.C., 1962

2.5. Data analysis

Data analysis was performed on two datasets: the hyperbenthos taxa density dataset and the peracarid species density dataset. Both datasets were transformed prior to analysis in order to scale down the effect of abundant species (Field *et al.*, 1982; Clarke & Green, 1988). The hyperbenthos dataset was fourth root transformed while the peracarid dataset was square-root transformed.

In order to study the community structure of the hyperbenthos and the Peracarida, the transformed data were ordinated by non-metric Multi-Dimensional Scaling (MDS) (Kruskal, 1964) and cluster analysis (group-average linkage method; Bray-Curtis similarity coefficient) was performed. A measurement of goodness-of-fit test of the MDS ordination was given by the stress value. A low stress value (<0.2) indicated a good ordination with no real prospect of a misleading interpretation (Clarke, 1993). Ordination techniques are most accurate for interpretation of community composition in terms of species response to environmental gradients (Ter Braak & Prentice, 1988). One-way analysis of similarities (ANOSIM, Clarke, 1993) was subsequently applied to asses the significance of differences between groups of multivariate samples from different zones along the continental slope areas. The similarity percentages programme (SIMPER, Clarke, 1993) was applied to identify the species primarily providing the discrimination between the zones along the continental slopes. The distribution of environmental variables along the transects was analysed using correlation-based principal-component analysis (PCA) on normalised log(x+1) transformed values as described by Clarke (1993). The relationships between multivariate assemblage structure and combinations of environmental variables were analysed using the BIO-ENV procedure (Clarke & Ainsworth, 1993) to define suites of variables that best explain the hyperbenthic assemblage structure. Scatter plots of all pair wise combinations of environmental variables indicated that conversion to approximate normality using log(x+1) transformation was appropriate before multivariate analysis. The described analyses were performed by using the PRIMER v5.2.9 software package (Clarke & Gorley, 2001).

2.6. Calculating biodiversity

There are strong relationships between sampling scale and the processes that influence diversity (Huston, 1994). At small scales all species are presumed to interact with each other and to compete for similar limiting resources (Gray, 1997). This is called within-habitat diversity or **alpha diversity** (Fisher *et al.*, 1943; Whittaker, 1960, 1967). At slightly larger scales, habitat and/or community boundaries are crossed and sampling covers more than one habitat or community. This level is referred to as between-habitat diversity or **beta diversity** (Whittaker, 1960, 1975, 1977). At an even larger scale (regional scale) where evolutionary rather than ecological processes operate the patterns are defined as **gamma diversity** or landscape diversity (Whittaker, 1960; Cody, 1986). This idea can be easily adapted for this particular study by clearly defining the different levels (Whittaker, 1977). Alpha diversity in this study is translated into diversity associated with one station or one depth along the continental slope. Beta diversity is designated as the degree of species change along the depth gradient characteristic of the studied continental slopes. Gamma diversity is defined as the change in species in the similar habitat, the continental slope over broad geographic areas, the two sampling sites. Many indices have been proposed to calculate diversity (see Magurran, 1988). A fundamental drawback of many diversity indices is their sample-size dependence (Sanders, 1968), making comparison between studies difficult. Soetaert & Heip (1990) argued that this dependence is more pronounced in high diversity than in low diversity assemblages. Moreover indices more sensitive to rarer species require larger sample sizes to estimate diversity with reasonable precision than indices which put more weight on commoner species (Soetaert & Heip, 1990). For reasons of standardization some widely used indices were selected in the present study.

The diversity indices of Hill (Hill, 1973) were used to calculate diversity of both hyperbenthic higher taxa and peracarid species. N_0 or the number of higher taxa or species, N_1, the inverse natural logarithm of the Shannon-Wiener diversity index and N_∞ or N_{inf}, the reciprocal of the relative abundance of the most common higher taxa or species were calculated. The Kruskall-Wallis test was used to compare sample series.

Some other commonly used diversity indices were used to quantify alpha and beta diversity of the peracarid species dataset. To avoid incomparability of measurements resulting from different-sized samples, the density-independent index ES(n) was calculated. This Hurlbert's modification of Sanders' rarefaction curves (Hurlbert, 1971) was used to calculate diversity for a standardized sample size: ES(100) determines the expected number of species present in a sample of 100 individuals. Because ES(n) does not cover all information present in the community as it is not related to the way the individuals are divided among species (Soetaert & Heip, 1990), other diversity measures were considered as well: Pielou's evenness (J') (Pielou, 1975), Hill's N_0, N_1 and N_∞ (Hill, 1973), and the Shannon index of diversity (H', log base e). In addition average taxonomic diversity (Δ) and average taxonomic distinctness (Δ^*) (Warwick & Clarke, 1995) were calculated to describe the peracarid diversity. Equal step-lengths between each taxonomic level were assumed, setting the path length ω to 100 for two species connected at the highest (taxonomically coarsest) possible level as stated by Clarke and Warwick (1999). Nine taxonomic levels were used (species, genus, family, order, superorder, subclass, class, subphylum and phylum). In addition to the selected diversity indices, k-dominance curves were calculated in order to draw conclusions (Lambshead *et al.*, 1983). A k-dominance curve is obtained by plotting k-dominance as percentage cumulative abundance against k (species or taxon rank). An assemblage A is considered to be more diverse than assemblage B if the k-dominance curve for assemblage A is always below or touching the k-dominance curve of assemblage B. Platt *et al.* (1984) argued that diversity can only be unambiguously assessed when the k-dominance plots do not overlap. Diversity measurements were performed using the PRIMER v5.2.9 software package (Clarke & Gorley, 2001).

Chapter 3

Hyperbenthic communities at Porcupine Seabight (NE Atlantic)

3.1. Introduction and objectives

Research on **hyperbenthos**, also referred to as suprabenthos (Kaartvedt, 1989; Sorbe, 1989) and benthopelagic plankton (Marshall & Merrett, 1977; Wishner, 1980a, 1980b), started in the late 1950's when this faunal group was first recognised as a functional unit by Beyer (1958). Most studies were carried out over the last three decades, reporting mainly on temperate and cold-water environments ranging from shallow coastal to deep-sea areas (reviewed by Mees & Jones, 1997). Marine coastal hyperbenthic communities have been studied in the North Sea (Buhl-Jensen & Fosså, 1991; Hamerlynck & Mees, 1991; Beyst *et al.*, 1999), the English Channel (Dauvin *et al.*, 1994; Wang & Dauvin, 1994; Zouhiri & Dauvin, 1996), the Bay of Biscay (Sorbe, 1981a, 1981b, 1982, 1989; Cornet *et al.*, 1983) and the Portuguese margin (Cunha *et al.*, 1997). A few brackish water hyperbenthic communities have been investigated: in the Westerschelde, The Netherlands (Mees & Hamerlynck, 1992; Cattrijsse *et al.*, 1993; Mees *et al.*, 1993a, 1993b); in the Gironde, France (Sorbe, 1981a; Fockedey & Mees, 1999); in the Rias de Guipuzcoa, north of Spain (San Vicente *et al.*, 1993) and in two tidal channels of the Ria de Aveiro, NW of Portugal (Cunha *et al.*, 1999).

Deep-sea hyperbenthic communities have been described, both from a faunistic and community structure perspective (Elizalde *et al.*, 1991; Dauvin *et al.*, 1995; Sorbe, 1999; Cartes *et al.*, 2001a, 2001b; see also Table 1.2 in chapter 1). Deep-water communities have received increasing attention because of the interest in new fishing grounds and fisheries at bathyal depths (Hopper, 1994; Merrett & Haedrich, 1977). Despite of the growing effort to study these communities, the dynamics of the **bathyal benthic boundary layer** is still far from being well understood.

The **benthic boundary layer** (BBL) is the layer of water, often tens of metres thick, adjacent to the seabed and with homogeneous properties of temperature and salinity, which sometimes contains resuspended detrital particles (Turley, 2000). It is an environment of great complexity both from a physical (Gage & Tyler, 1991) and biological (Smith & Hinga, 1983) perspective. The existence of specific BBL assemblages (mainly composed of crustaceans) at continental slope environments was already suggested by Marshall & Merrett (1977), Wishner (1980a, 1980b), Hargreaves (1984) and Gordon & Mauchline (1990).

One of the most important biological characteristics of the BBL is the progressive increase of biomass near the bottom (from around 100 m above the sea bed) within this layer (Angel, 1990), in contrast to the general exponential decline of pelagic biomass with depth in the water column (Vinogradov & Tseitlin, 1983). Since the first qualitative data obtained on the BBL (Wishner, 1980b), the studies carried out on the composition and structure of this environment, both at bathyal and abyssal depths, have been relatively scarce (Hargreaves, 1984, 1985; Wiebe *et al.*, 1988; Angel, 1990). Benthopelagic organisms, inhabiting the near bottom environment, are a fundamental part of the BBL. These communities of organisms living above the seabed have been included in distinct concepts, such as suprabenthos (Brunel *et al.*, 1978), hypoplankton (Mauchline & Gordon, 1991) and hyperbenthos (Mees & Jones, 1997) resulting in a discussion on terminology.

From a biological viewpoint, the near-bottom layer lies between two principal oceanic biotopes: pelagial and benthal. Therefore, its animal population should be expected to be most diverse and consisting of various ecological groups. The **deep-sea BBL** is enriched in biomass and number of species, relative to the overlying water column (Wishner, 1980b; Angel, 1990; Cartes, 1998; Christiansen *et al.*, 1999). It is inhabited by pelagic species whose ranges are truncated by the seabed, by benthic species using this zone as a refuge, for dispersal and for locating their food and also by other species from a wide variety of taxonomic groups that seem to be specialized to the benthopelagic environment (Angel, 1990).

These studies are closely linked to benthopelagic coupling studies as reviewed by Angel (1984, 1990), Deuser (1986) and Fowler & Knauer (1986). Particulate matter reaching the seafloor primarily originates from the ocean's surface layers. As the particles sink, their concentration and composition are altered by aggregation, disaggregation, zooplankton grazing, decomposition and dissolution. Understanding these processes is complicated by horizontal advection and by the existence of nepheloid layers caused by resuspension of already deposited particles from the bottom (Thomsen & Graf, 1995). Once deposited in deep-sea environments, sedimented detritus decays rapidly (Lampitt, 1985; Thiel *et al.*, 1989; Rice *et al.*, 1986). For certain continental margin environments, benthic-pelagic coupling is tight and the benthic community responds rapidly to a pulse of natural organic matter.

In this chapter the hyperbenthic fauna of the continental slope (between 200 and 1250 m water depth) at Porcupine Seabight, offshore southwest of Ireland is studied in order to characterise the BBL assemblages on the continental slope environment as suggested by Marshall & Merrett (1977), Wishner (1980a, 1980b), Hargreaves (1984) and Gordon & Mauchline (1990). Studying the **vertical or near-bottom distribution** (also referred to as stratified distribution) of the hyperbenthic fauna in the BBL in the first part of this chapter can provide more information on community structure patterns within the BBL: is this BBL layer one homogeneous water mass or are there smaller scale patterns within this one metre of water? Patterns of vertical distribution of the hyperbenthic taxa are discussed in terms of what is known of their ecology. The second part of this chapter determines the **horizontal or bathymetric distribution** (also referred to as across isobaths distribution) of the hyperbenthic taxa along the slope environment and examines the zonation and abundance of the taxa within their depth ranges. Large-scale zonation will be analysed in view of the physical environment and the ecology of the hyperbenthic taxa. For detailed information of the study site Porcupine Seabight and the sampling strategy and methodology we refer to chapter 2.

3.2. Results

The results are based on the hyperbenthic fauna collected during the RV Belgica expedition in June 2000 at Porcupine Seabight (Ireland) (see chapter 2 for study site description and sampling strategy). Along the continental slope, eight stations, ranging from 200-1250 m of water depth were sampled with the hyperbenthic sledge and the boxcore.

3.2.1. Sedimentology

The granulometric results from the eight stations at the Porcupine Seabight (for details of methodology see chapter 2) are summarized (Fig. 3.1 and Table 3.1 and Table 3.2).

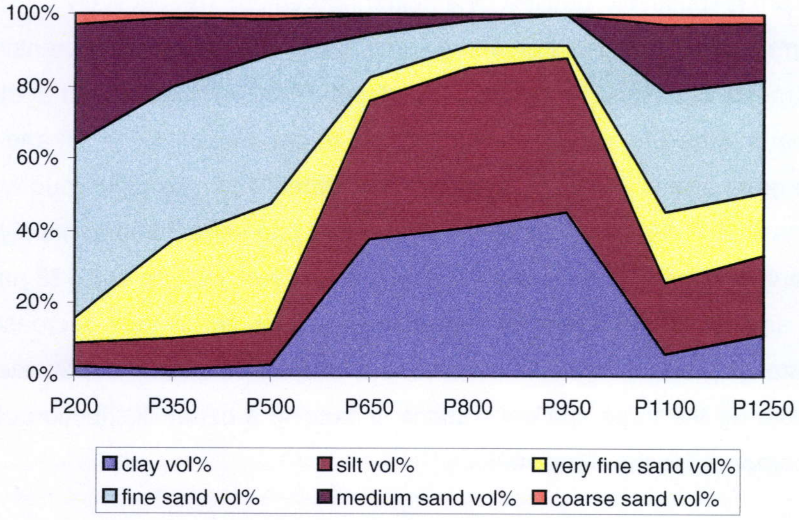


Figure 3.1 Relative sediment composition at the eight stations (P200-P1250) of the Porcupine Seabight continental slope.

Table 3.1 Sediment composition of the eight stations (P200-P1250) along the depth gradient at Porcupine Seabight.

station	clay vol%	silt vol%	very fine sand vol%	fine sand vol%	medium sand vol%	coarse sand vol%	mud=clay+silt vol%
P200	2,5	6,4	6,7	48,2	33,19	3,01	8,9
P350	1,5	8,7	27,3	42,6	18,77	1,13	10,2
P500	3	9,7	35	41,3	9,5	1,5	12,7
P650	37,9	38,4	6,6	11,53	5,34	0,23	76,3
P800	41,2	44,2	6,07	6,7	1,83	0	85,4
P950	45,5	42,7	3,44	8,264	0,096	0	88,2
P1100	6,2	19,6	19,8	33,2	18,45	2,75	25,8
P1250	11,5	22	17,4	31,3	15,43	2,37	33,5

Table 3.2 Median grain size (µm) and the sorting coefficient of the eight stations (P200-P1250) at Porcupine Seabight.

station	median (µm)	sorting coefficient
P200	215	0,44
P350	152	0,59
P500	129	0,50
P650	7	2,34
P800	6	1,70
P950	5	1,42
P1100	140	0,97
P1250	122	1,58

Stations P200, P350 and P500, at the upper part of the continental slope, are characterized by a relative high percentage (more than 40 %) of fine sand. At station P200 the median grain size is highest, 215 µm due to a high percentage (33 %) medium sand in combination with the high percentage fine sand. In the two deeper stations P350 and P500, the median grain size is smaller, 152 µm and 129 µm respectively, caused by a higher percentage (respectively 27 % and 35 %) of very fine sand in combination with the percentage fine sand. The trend of increasing percentages of fine-grained sediments continues till 950 m water depth (P950). The sediment at stations P650, P800 and P950 are characterized by very high percentages (more than 35 %) of silt and clay, resulting in a very low median grain size of 7 µm, 6 µm and 5 µm respectively indicating muddy sediment. Deeper than 950 m, at stations P1100 and P1250 an increase of coarser sediment, mainly of the percentage fine sand is observed, resulting in a higher median grain size of 140 µm and 122 µm respectively. The percentage clay and silt at these two deepest stations shows an obvious decrease compared to the three shallower stations, so no continuous increase of fine sediment with depth was observed. Sorting coefficient is lowest for the three shallow stations, indicating a better distribution of grain sizes within the substratum compared to the other stations.

3.2.2. Hyperbenthos

According to the working definition (see chapter 2) a selection of the taxa in the samples was made, meaning that some organisms not belonging to the hyperbenthos (*i.e.* juvenile or adult organisms belonging to the phyla Cnidaria, Echinodermata, Annelida, Brachiopoda and Mollusca) were totally excluded from the dataset, resulting in a hyperbenthos taxa abundance dataset, on which these results are based. The dataset used for this chapter is given in appendix 1.

In order to obtain information on the distribution of the hyperbenthic fauna in the 100 cm sampled benthic boundary water layer, the data of the two nets from the hyperbenthic sledge, the lower net (0-50 cm) and the upper net (50-100 cm), are treated separately in the first part of the results, describing the vertical or stratified distribution of the hyperbenthic fauna. The bathymetric distribution of the hyperbenthos along the continental slope is discussed in a second part, by taking the eight stations, as the sum of the two nets, into account.

3.2.2.1. Taxonomic composition and density of the hyperbenthos at Porcupine Seabight

The number of hyperbenthic individuals counted at Porcupine Seabight was 41 964. In total twelve hyperbenthic taxa were found over the eight stations sampled. The systematic position of the different taxa is given below (Table 3.3). Besides the eleven hyperbenthic taxa, the group 'larvae' comprising all Decapoda larvae is considered as a taxon and belongs to the merohyperbenthos. The amount of merohyperbenthos caught is very small compared to the holohyperbenthic abundances. Table 3.4 lists the twelve taxa together with the total number of individuals and the total density (individuals/100 m^2) respectively per net (lower and upper net) and per station. Note that the different taxa considered belong to different taxonomical levels (*e.g.* Phylum, Classis, Ordo).

Table 3.3 Systematic position of the twelve hyperbenthic taxa (in bold) sampled at Porcupine Seabight.

- Phylum **Chaetognatha**
- Phylum Arthropoda
  - Subphylum Crustacea
    - Classis **Copepoda**
    - Classis **Ostracoda**
    - Classis Malacostraca
      - Subclassis Phyllocarida
        - Ordo **Leptostraca**
      - Subclassis Eumalacostraca
        - Superordo Eucarida
          - Ordo **Euphausiacea**
        - Superordo Peracarida
          - Ordo **Mysidacea**
          - Ordo **Cumacea**
          - Ordo **Amphipoda**
          - Ordo **Isopoda**
          - Ordo **Tanaidacea**
  - Subphylum Chelicerata
    - Classis **Pycnogonida**
- Group **larvae**

Table 3.4 A) Total number of individuals for the twelve hyperbenthic taxa B) Total density (ind./800 m^2) for the twelve hyperbenthic taxa for both nets and for the sum of the nets (per station).

A.

Taxon	Lower nets	Upper nets	Station
Amphipoda	11830	535	12365
Isopoda	5347	36	5383
Cumacea	12479	248	12727
Tanaidacea	138	0	138
Mysidacea	1689	184	1873
Euphausiacea	155	87	242
Leptostraca	5	0	5
Copepoda	1141	1026	2167
Chaetognatha	269	213	482
Pycnogonida	537	3	540
Larvae	208	41	249
Ostracoda	5682	111	5793
sum	**39480**	**2484**	**41964**

B.

Taxon	Lower nets	Upper nets	Station
Amphipoda	9830,81	395,67	10226,48
Isopoda	4279,10	29,23	4308,33
Cumacea	11006,54	213,18	11219,73
Tanaidacea	129,83	0,00	129,83
Mysidacea	1159,94	141,25	1301,19
Euphausiacea	86,64	53,45	140,10
Leptostraca	5,70	0,00	5,70
Copepoda	826,93	867,21	1694,14
Chaetognatha	177,12	157,17	334,29
Pycnogonida	571,65	1,96	573,61
Larvae	105,31	20,79	126,09
Ostracoda	5028,66	95,23	5123,88
sum	**33208,24**	**1975,14**	**35183,38**

The difference in total number of individuals and density of the hyperbenthos caught with the lower nets (0-50 cm zone) and the upper nets (50-100 cm zone) of the hyperbenthic sledge is very obvious (Table 3.4). All densities (except for Copepoda) are much lower for the upper net samples compared to the densities for the lower net samples. Crustaceans are the dominant fauna in the BBL at the study site sampled with the hyperbenthic sledge. Within the hyperbenthos of the lower zone (0-50 cm) of the BBL along the sampled continental slope, Cumacea are most abundant with a total density in the lower nets of 11006 ind./800 m², followed by Amphipoda with 9830 ind./800 m², Ostracoda with 5028 ind./800 m², Isopoda with 4279 ind./800 m², Mysidacea with 1159 ind./800 m² and Copepoda with a density in the lower nets of 826 ind./800 m². The upper 50-100 cm zone is mainly dominated by Copepoda with a density of 867 ind./800 m², followed by Amphipoda with 395 ind./800 m².

3.2.2.2. Vertical distribution

Absolute densities

Most taxa show a different pattern in their vertical distribution throughout the two BBL layers 0-50 cm and 50-100 cm, which is illustrated by the absolute density of each taxon for the lower and upper nets separated (Fig. 3.2). Note the different scales used in both sets of graphs.

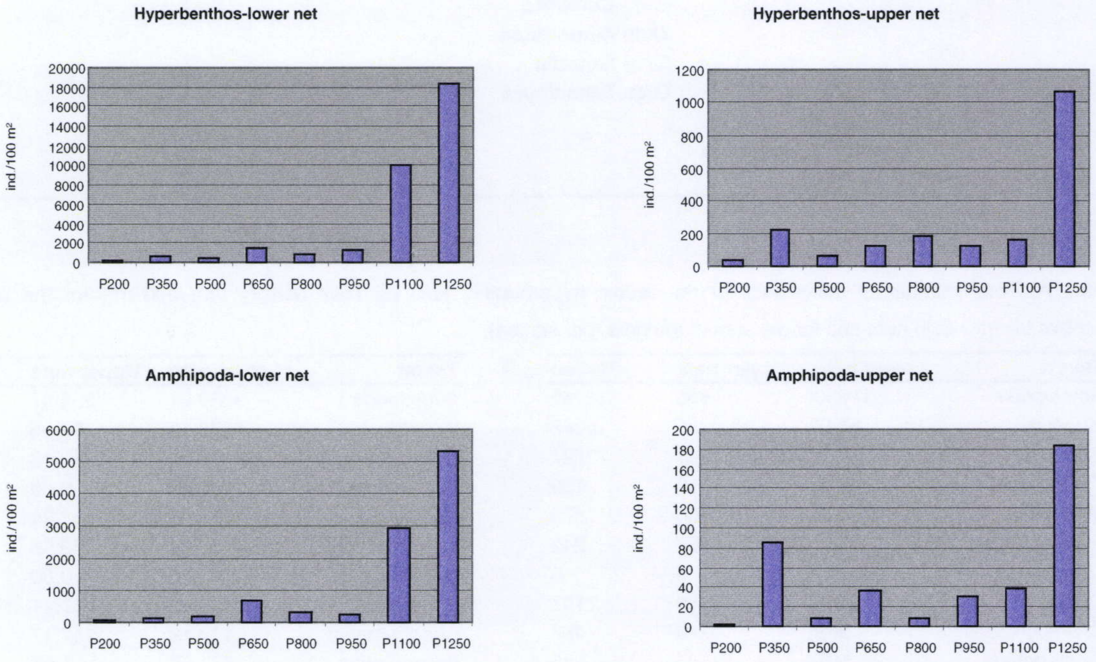


Figure 3.2 The absolute density (ind./100 m²) of the total hyperbenthos and all hyperbenthic taxa in the lower nets (0-50 cm) and upper nets (50-100 cm) sampled separately along the continental slope of Porcupine Seabight (P200-P1250) (continued).

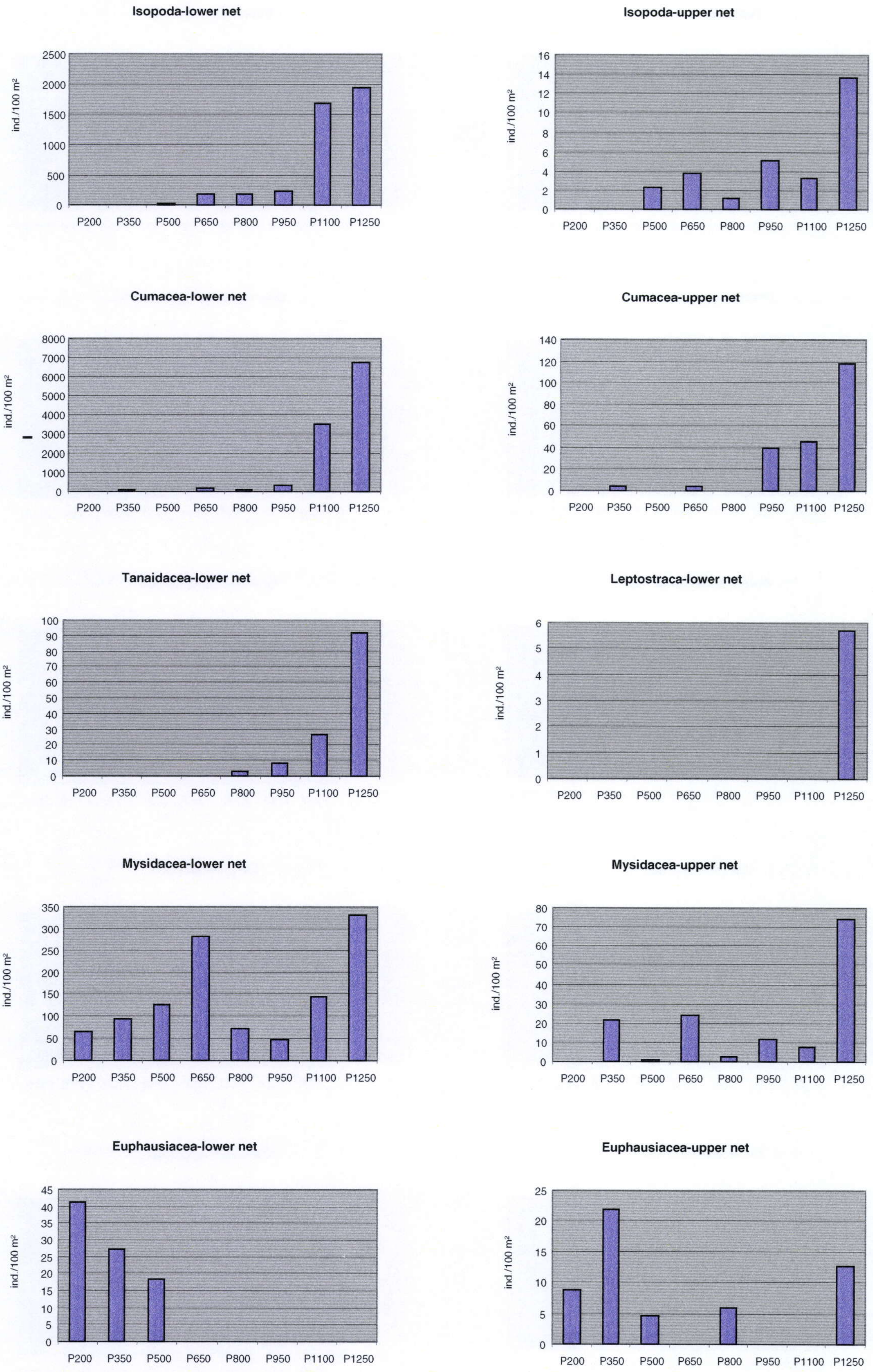
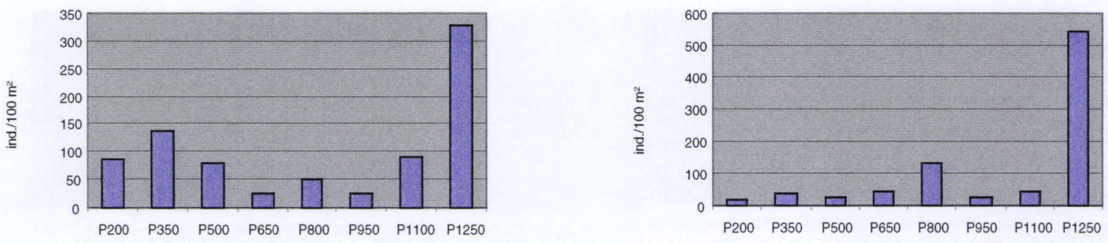
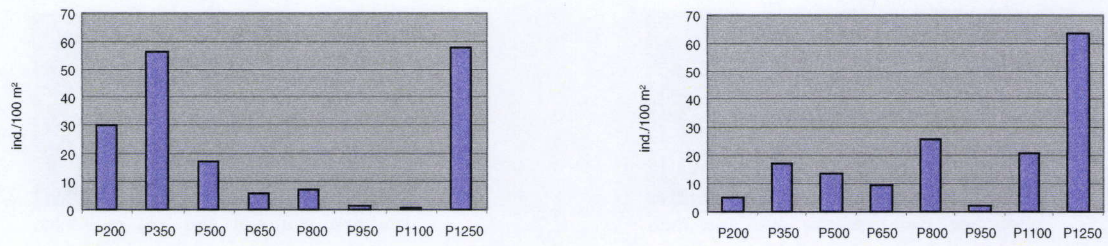


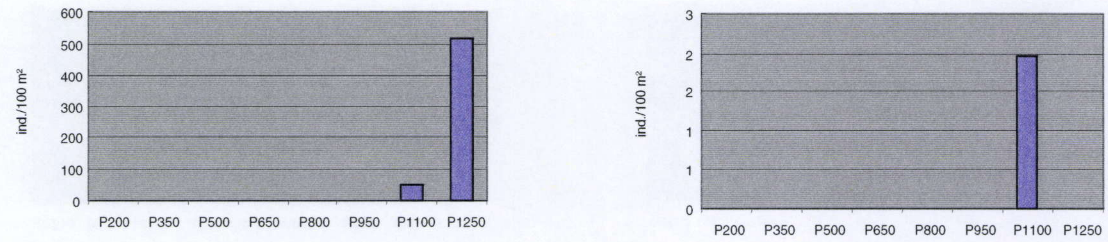
Figure 3.2 The absolute density (ind./100 m²) of the total hyperbenthos and all hyperbenthic taxa in the lower nets (0-50 cm) and upper nets (50-100 cm) sampled separately along the continental slope of Porcupine Seabight (P200-P1250) (continued).


Copepoda-lower net

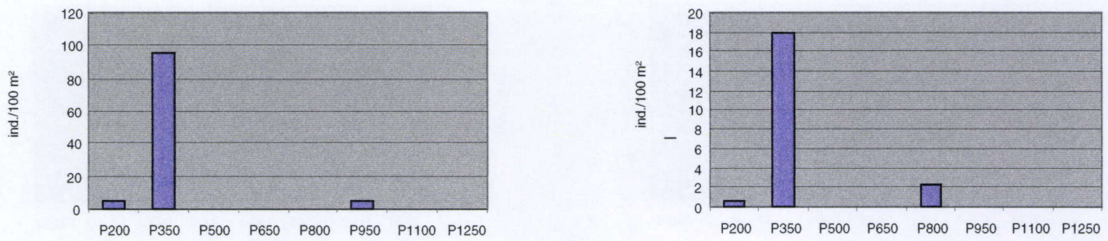
Copepoda-upper net


Chaetognatha-lower net

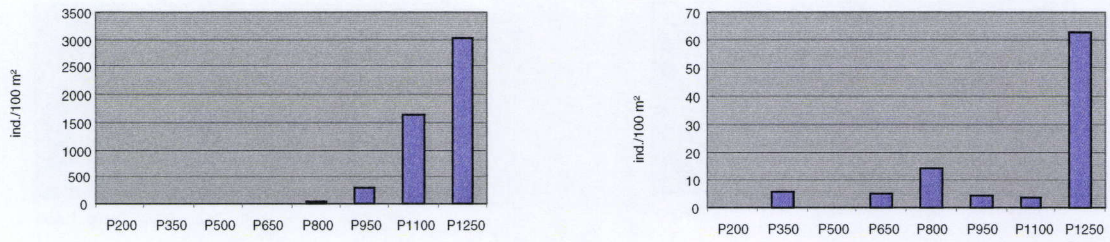
Chaetognatha-upper net


Pycnogonida-lower net

Pycnogonida-upper net


Larvae-lower net

Larvae-upper net


Ostracoda-lower net

Ostracoda-upper net

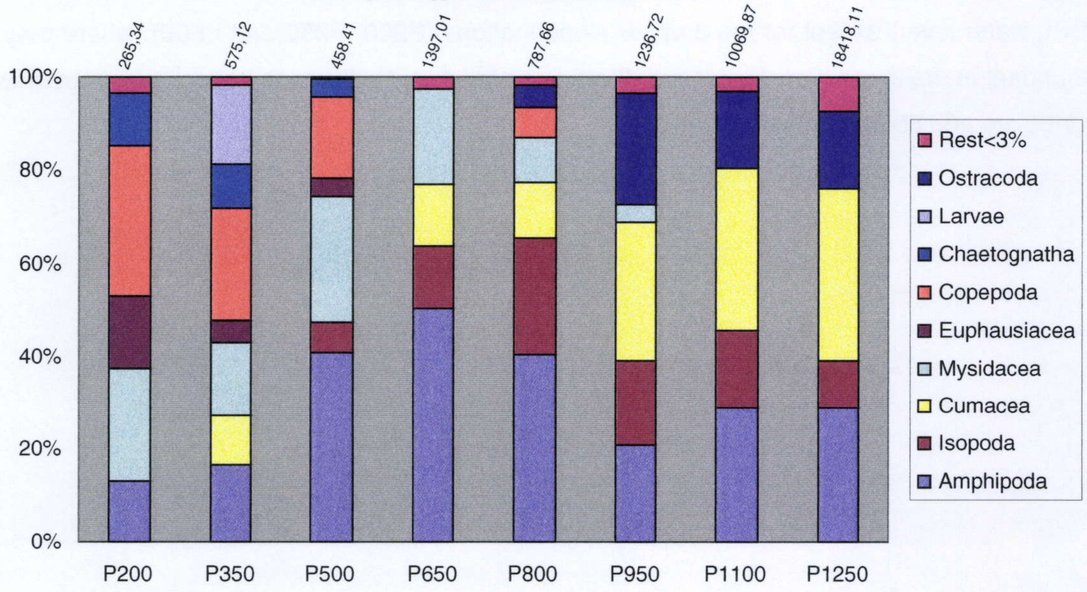
Figure 3.2 The absolute density (ind./100 m²) of the total hyperbenthos and all hyperbenthic taxa in the lower nets (0-50 cm) and upper nets (50-100 cm) sampled separately along the continental slope of Porcupine Seabight (P200-P1250).

Total absolute density for the hyperbenthos is higher in the lower nets compared to the upper nets at each station sampled (P200-P1250). In the lower net samples density values range from 265 ind./100 m² at station P200 to a maximum of 18418 ind./100 m² at the deepest station P1250. In the upper net samples the minimum density value was also found at station P200 (34 ind./100 m²) and a maximum density value was found at station P1250 (1069 ind./ 100 m²). A higher density in the lower nets or 0-50 cm BBL zone is also a general feature for the Amphipoda, Isopoda, Cumacea, Mysidacea, Euphausiacea, Pycnogonida and Ostracoda. Two taxa, Tanaidacea and Leptostraca are only found in the lower nets and the latter taxon only at station P1250. Copepoda show a different trend, in certain stations they are more abundant in the lower nets, while for the deeper stations they show higher densities in the upper layer. Chaetognatha densities remain similar in the lower and upper BBL water layer, except for the 3 upper slope stations (P200, P350 and P500), where they are more abundant in the lower nets. In general, there is an important difference in densities in both water layers (0-50 cm and 50-100 cm) in the BBL.

Relative composition

The vertical distribution of the different taxa is illustrated by the relative composition at each station for the lower and upper nets separately (Fig. 3.3). To keep this stacked bars figure orderly, a 'rest' group was created. This 'rest' group is the sum of the percentages of the taxa that make up less than 3 % of the hyperbenthos in a certain sample. The composition of this 'rest' group and the number of taxa consequently differs for each station. Only the taxa Tanaidacea, Pycnogonida and Leptostraca belong to the 'rest' group at each station.

A. **Porcupine hyperbenthos lower nets**



B. **Porcupine hyperbenthos upper nets**

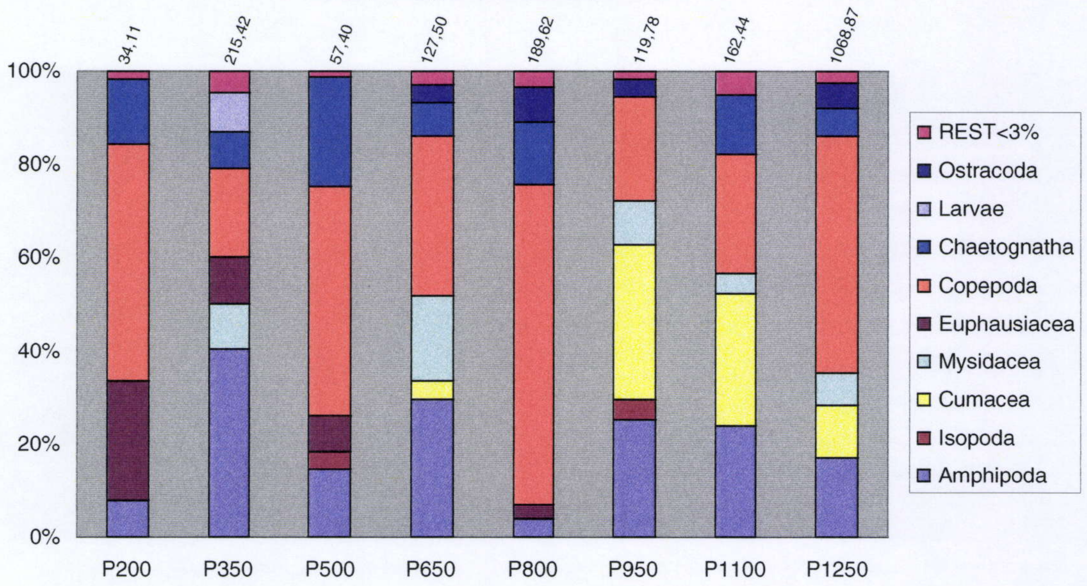
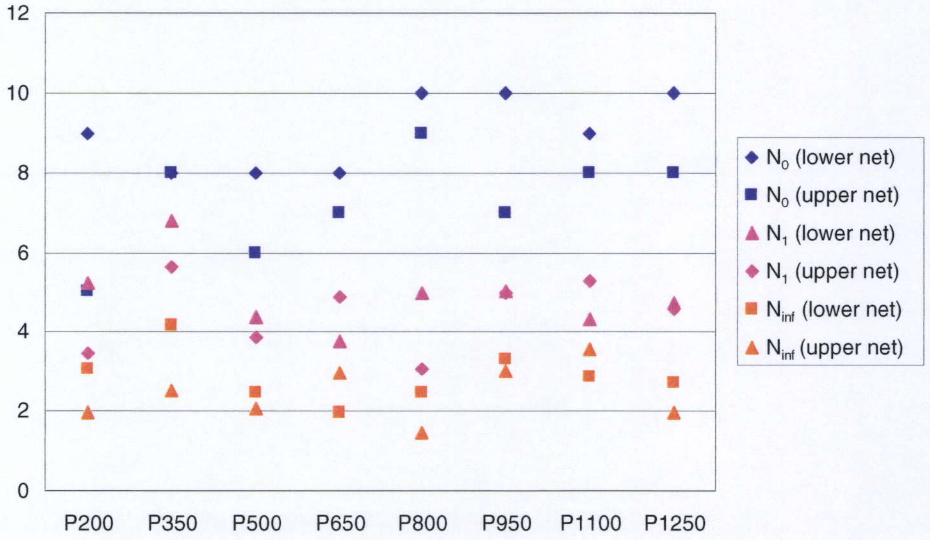


Figure 3.3 Relative hyperbenthic taxa composition for the A) lower nets (0-50 cm) and B) upper nets (50-100 cm) for the eight stations (P200-P1250) at Porcupine Seabight. The absolute total hyberbentic density per sample is indicated above each bar.

Comparing the relative composition (Fig. 3.3) of the different hyperbenthic taxa for the lower and upper BBL zone gives some striking results. Generally the upper zone is dominated by Copepoda at each station, while in the lower zone they are only abundant in the upper slope area (stations P200, P350 and P500). A similar trend is observed for Chaetognatha, although they are generally less abundant and belonging to the rest group at station P950 in the upper zone. In addition Cumacea are abundant in the lower zone especially in the mid and lower slope part (650-1250 m), and also in the upper BBL zone, but here only at the three deepest stations. Euphausiacea, Amphipoda and Ostracoda show a quite similar distribution in both zones at the different stations. Mysidacea show a rather uneven distribution, they are very abundant at the upper and mid slope area, decreasing with depth, in the lower nets, while in the upper BBL zone they also appear in the deeper stations and in P350 and P650. Larvae are only abundant at station P350 in the two BBL layers.

Alpha and beta diversity

The diversity of the hyperbenthic taxa is vertically structured as well. Diversity indices of Hill (Hill, 1973) (Fig. 3.4) are higher for hyperbenthic samples from the lower BBL zone, except N_1 and N_∞ at stations P650 and P1100, indicating a higher dominance. The k-dominance plot (Fig. 3.5) indicate a stronger dominance of Amphipoda (50 %) in the lower net sample of P650 compared to a dominance of 34 % of Copepoda in the upper net sample of the same station. Also for station P1100 a higher dominance of Cumacea (35 %) is illustrated for the lower net sample in comparison to the 28 % dominance of the same taxon in the upper net sample (Fig. 3.5). At station P350 species richness (N_0) is equal for both BBL zones.



	N_0 (lower net)	N_0 (upper net)	N_1 (lower net)	N_1 (upper net)	N_{inf} (lower net)	N_{inf} (upper net)
P200	9	5	5,24	3,45	3,08	1,97
P350	8	8	6,76	5,63	4,14	2,49
P500	8	6	4,35	3,88	2,44	2,05
P650	8	7	3,76	4,89	1,98	2,96
P800	10	9	4,97	3,07	2,47	1,46
P950	10	7	5,01	4,95	3,33	3,02
P1100	9	8	4,34	5,25	2,87	3,56
P1250	10	8	4,73	4,56	2,72	1,97

Figure 3.4 Diversity indices of Hill (N_0, N_1 and N_{inf}) for the hyperbenthic taxa at each Porcupine Seabight station (P200-P1250) for the lower nets (0-50 cm) and upper nets (50-100 cm) separated.

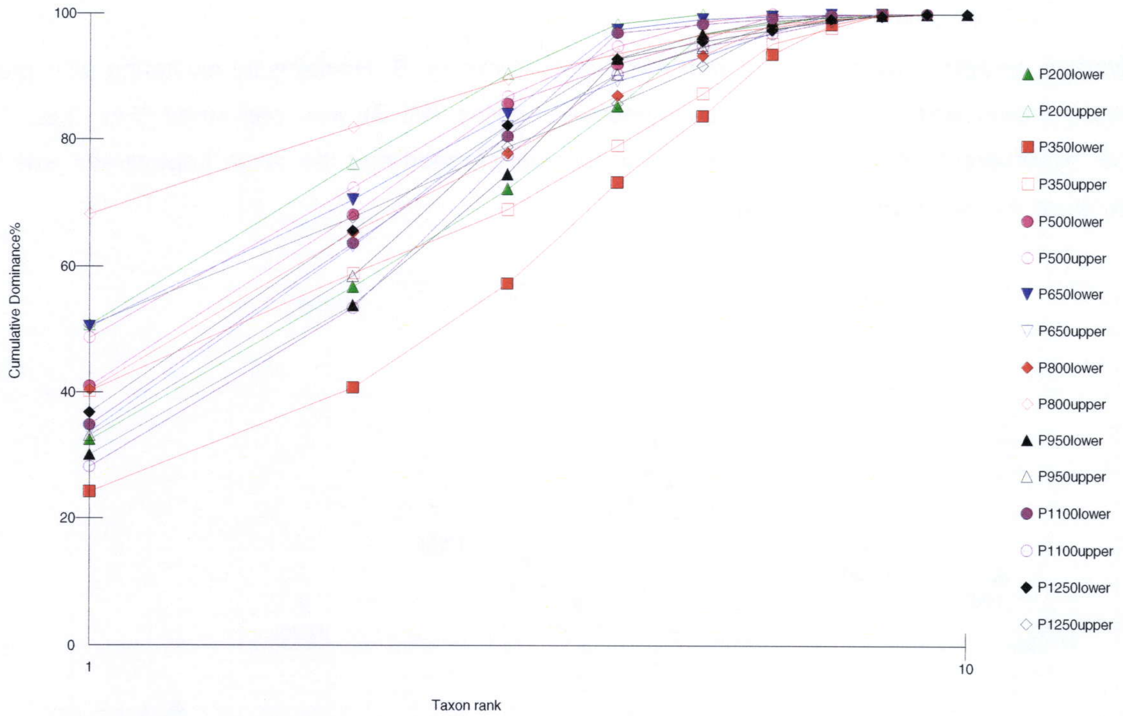


Figure 3.5 K-dominance plot of the hyperbenthic taxa of the 16 net samples (eight upper nets 50-100 cm; eight lower nets 0-50 cm) at the eight stations (P200-P1250) at Porcupine Seabight.

Community structure

Multivariate analysis was performed with the PRIMER version 5. Hierarchical clustering with group averaged linking and non-metric multi-dimensional scaling (MDS) was performed (Fig. 3.6). The original hyperbenthos density data were fourth-root transformed and the taxon Leptostraca was left out because it only occurred in one station.

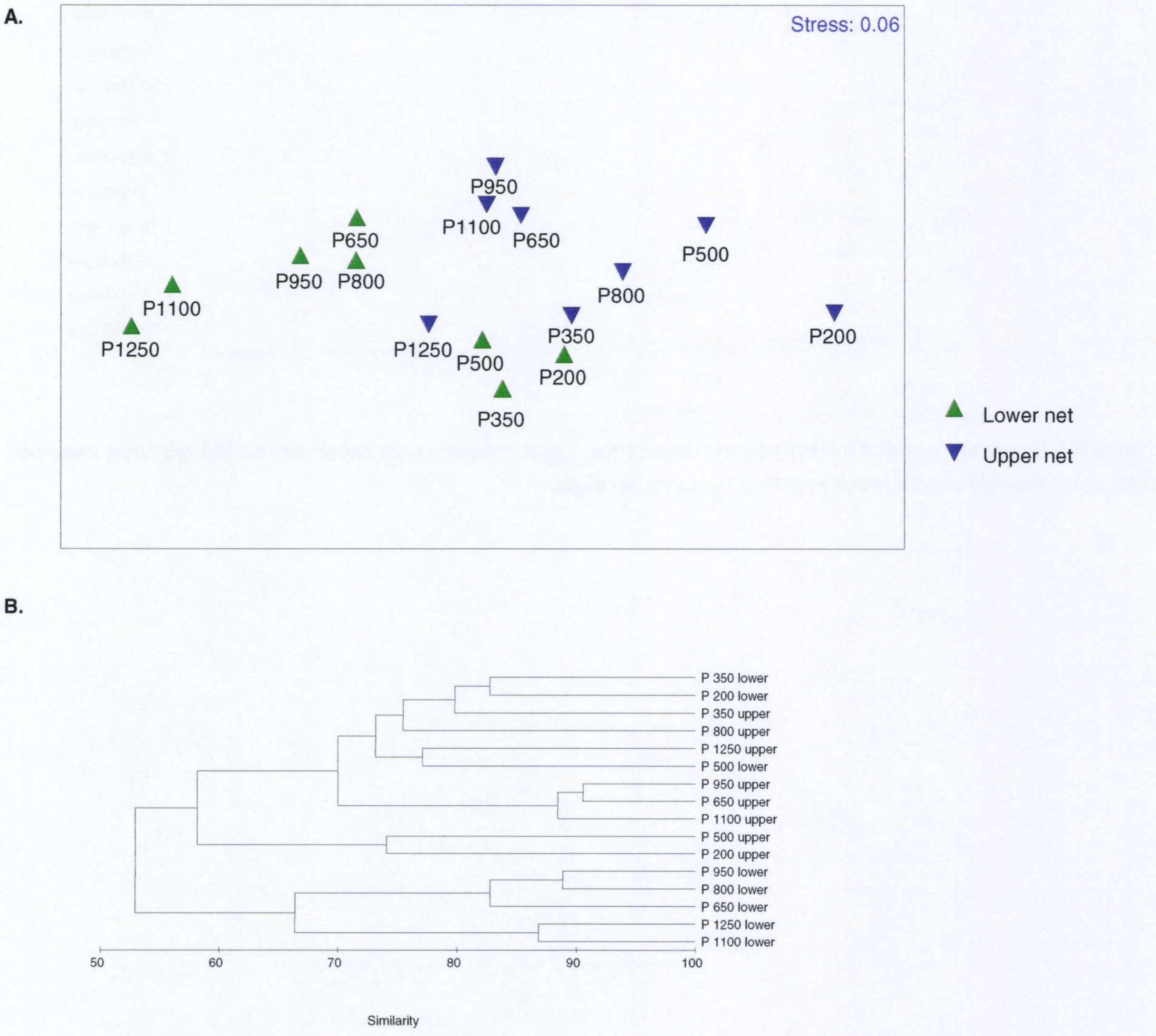


Figure 3.6 A) Multi-dimensional scaling (MDS) plot and B) cluster analysis dendrogram based on fourth-root transformed hyperbenthic taxa data of the eight Porcupine Seabight stations (P200-P1250) with the nets (lower and upper) separated.

The MDS diagram (Fig. 3.6A) shows a pronounced distinction between the lower and upper nets samples for all stations. In addition with the cluster analysis (Fig. 3.6B), this distinction can be refined and four groups can be distinguished. There is a clear separation of the 5 lower net samples from the lower slope area (P650-P1250), while the upper net samples of these stations are divided over two other groups. One group clusters the upper BBL samples of stations P650, P950 and P1100 together. The same samples of stations P800 and P1250 are clustered together with the lower net samples of the 3 upper slope stations (P200, P350 and P500) and with the upper net sample of station P350. The two upper nets from the upper slope area, P200 and P500, are also similar in taxa composition. The vertical distribution for the lower slope zone seems more pronounced than for the upper slope zone illustrated by the clear separation of the lower net samples and the upper net samples of the stations P650, P800, P950, P1100 and P1250. Although MDS and cluster analysis divide the different hyperbenthic samples in four hyperbenthic communities, the one-way ANOSIM test indicate that these four groups are not significantly different from each other (global R= 0.291, significance level= 0.7 %).

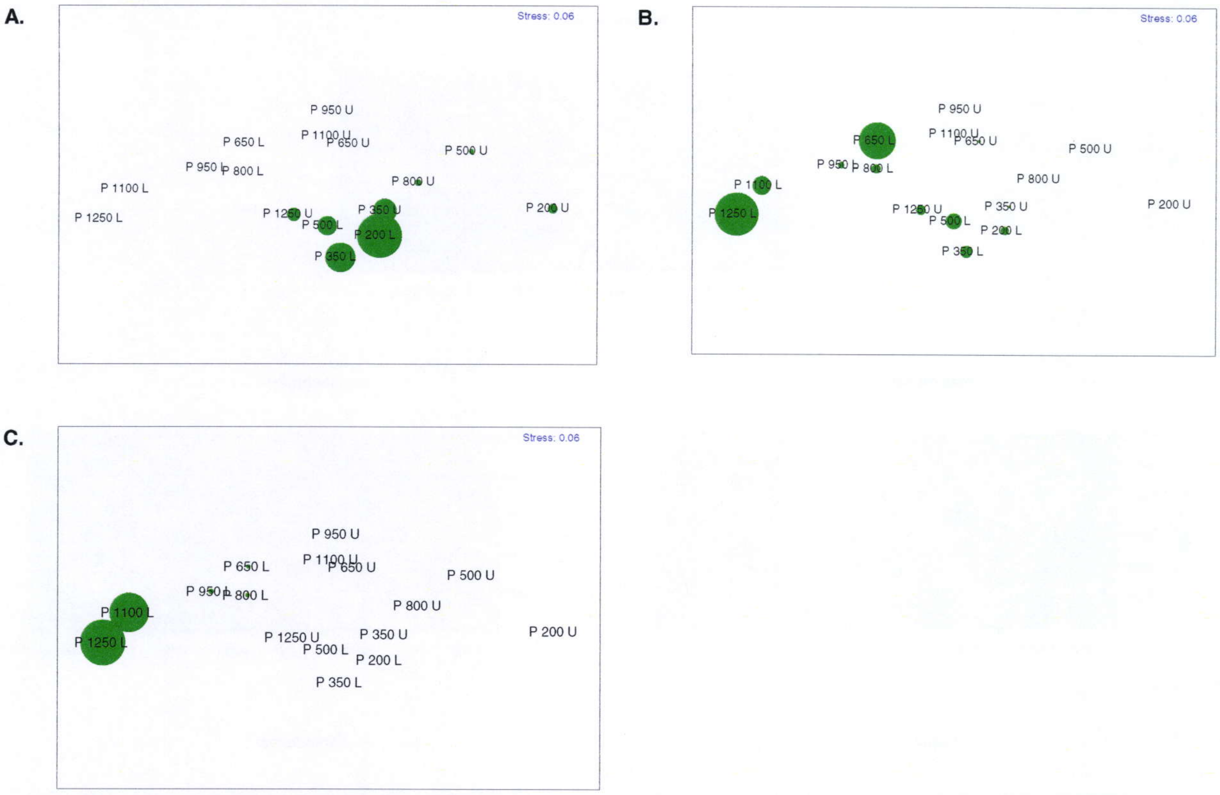


Figure 3.7 Bubble plots based on the MDS plot (*cfr.* Fig. 3.5), indicating the absolute density (ind./100 m$^{2^{-2}}$) of A) Euphausiacea, B) Mysidacea and C) Isopoda for each Porcupine Seabight station (P200-P1250). U= upper net sample; L= lower net sample.

Three bubble plot diagrams based on the MDS diagram (*cfr.* Fig.3.6A) illustrate which taxa contribute to the division of the different samples. Euphausiacea (Fig. 3.7A) are important at the upper slope stations, while Isopoda (Fig. 3.7C) show a high abundance at the two deepest stations. Note that the very high abundance of Isopoda in the lower net at the two deepest stations P1100 and P1250 cause a slightly distorted picture. Isopoda are also present in other samples but due to a large difference in abundance compared to the deep stations, the bubbles are very small. Mysidacea (Fig. 3.7B) are mainly important in the division of the lower net samples from the upper net samples.

3.2.2.3. Bathymetric distribution: zonation of the hyperbenthic taxa

The bathymetric distribution of the hyperbenthos from eight stations along the Porcupine slope (200-1250 m) is reported as the total of the upper and lower nets for each station (Fig. 3.8).

Absolute densities

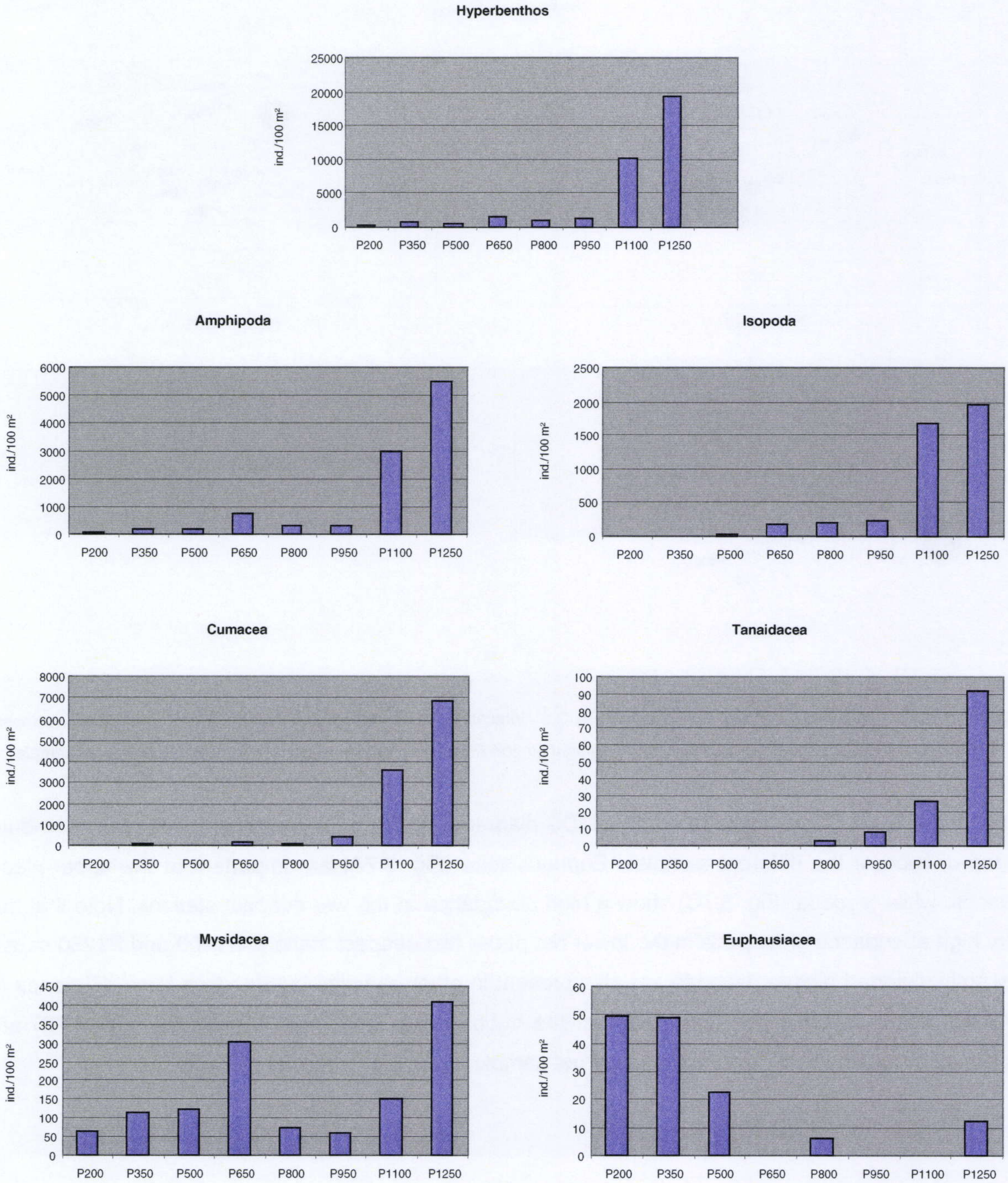


Figure 3.8 The absolute density (ind./100 m²) of the total hyperbenthos and all hyperbenthic taxa for the eight Porcupine Seabight stations (P200-P1250) along the continental slope (continued).

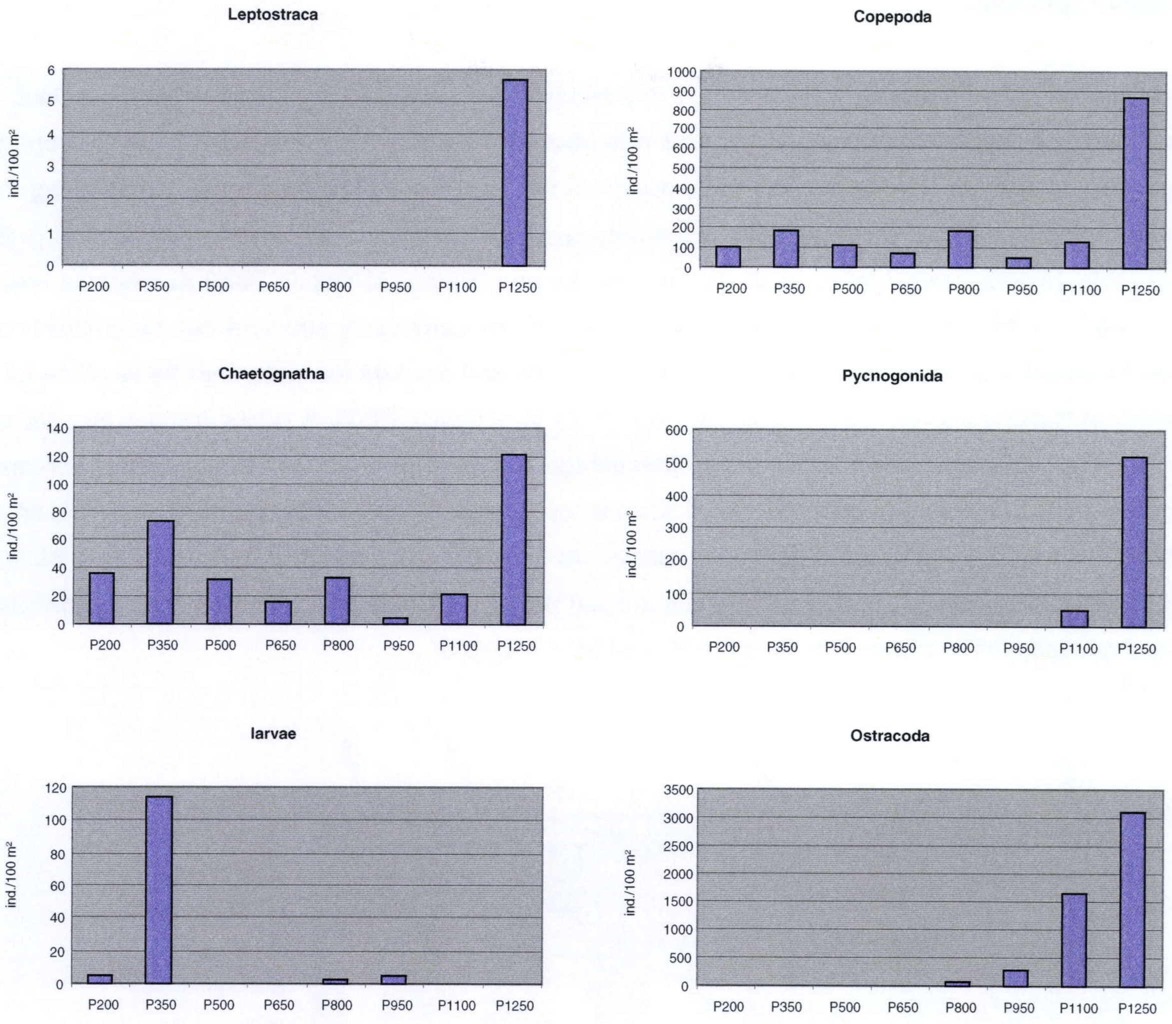


Figure 3.8 The absolute density (ind./100 m²) of the total hyperbenthos and all hyperbenthic taxa for the eight Porcupine Seabight stations (P200-P1250) along the continental slope.

Total absolute density of the hyperbenthos along the depth gradient shows an obvious increase towards the two deepest stations (P1100 and P1250). Density values of the hyperbenthos range from 299 ind./100 m² at station P200 to 19487 ind./100 m² at the deepest station P1250. Amphipoda, Isopoda, Cumacea, Tanaidacea, Pycnogonida and Ostracoda show a conspicuous increase at stations P1100 and P1250 (Fig. 3.8). In contrast, the Euphausiacea are more abundant at the three upper slope stations. Other taxa like Mysidacea, Copepoda and Chaetognatha display a rather irregular distribution along the continental slope.

Relative composition

The stacked bars figure (Fig. 3.9), illustrates the relative taxa composition along the depth gradient. A 'rest' group (*i.e.* group comprising all the taxa with abundance < 3 %) was created in order to keep the figure uncomplicated. The taxonomic composition of the hyperbenthos differs considerably along the continental slope (Fig. 3.9). Amphipoda is the only taxon that accounts for a substantial fraction (> 20 %) of total hyperbenthic density at all stations, except one (P200). At station P650 Amphipoda reach up to 48 % of the total density. Some important shifts in the community structure can be pointed out. Mysidacea are very abundant at the upper slope stations and account for more than 14 % of the total density in station P200 to P650, with a maximum of 24 % at station P500. A similar trend is recognized for the Euphausiacea, which show a high percentage in the three upper slope stations. In contrast, Isopoda and Cumacea appear in very high abundance at station P650 and account for a large part at all the deep stations. Isopoda percentage ranges from 10 % at station P1250 up to 20 % at station P800, while the relative part of the Cumacea is even higher, up to 35 % at the three deepest stations. A pronounced shift in community structure is illustrated (Fig. 3.9).

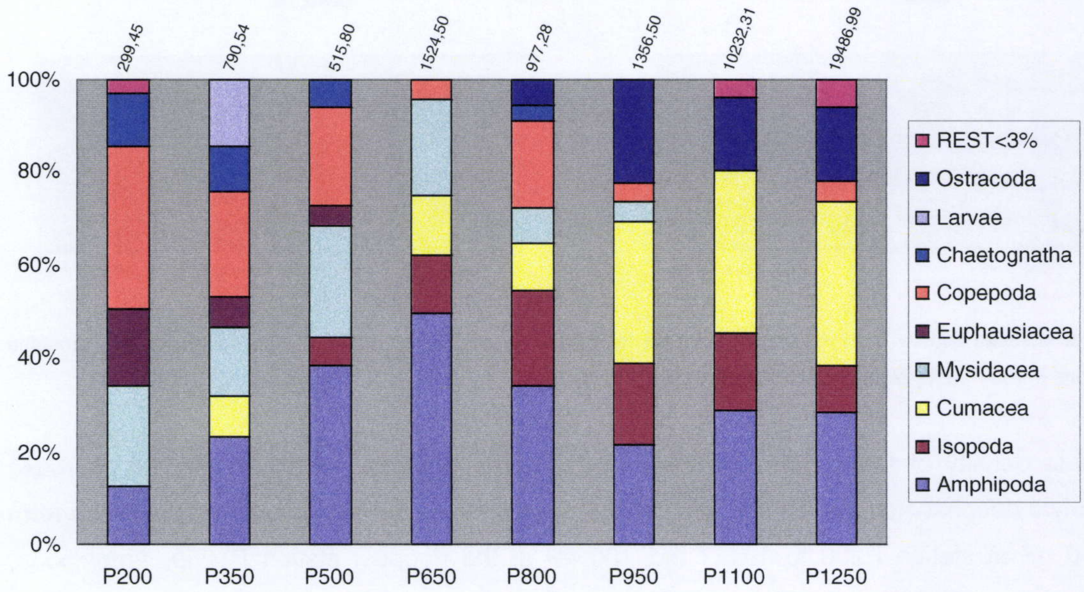
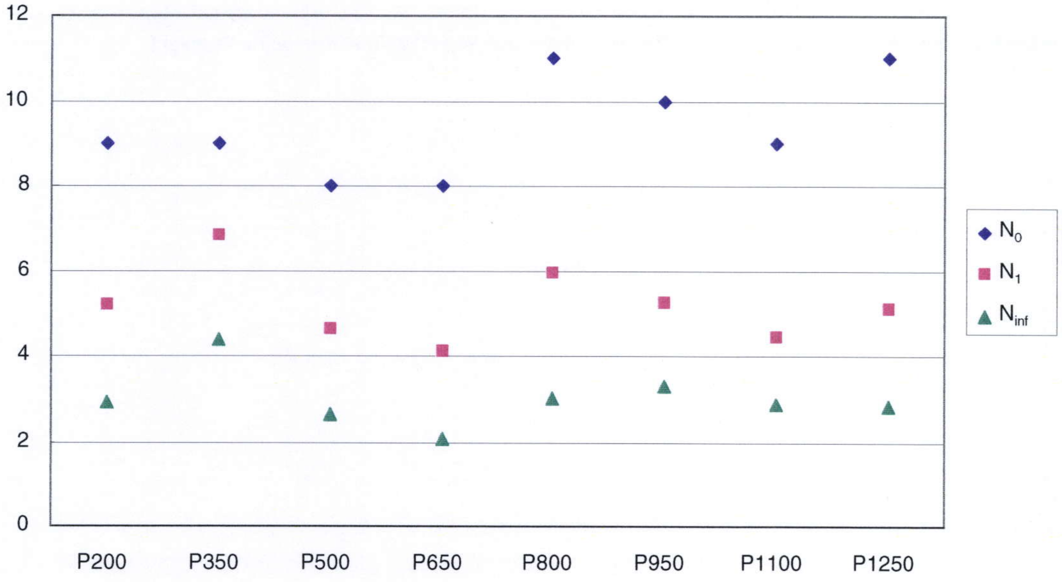


Figure 3.9 Relative taxa composition along the eight stations (P200-P1250) on the Porcupine Seabight slope. The absolute total hyberbentic density per station is indicated above each bar.

Alpha and beta diversity

Alpha diversity of the hyperbenthic taxa at each station (P200-P1250) at Porcupine Seabight is illustrated by the diversity indices of Hill (Fig. 3.10) and the corresponding k-dominance plot (Fig. 3.11). By comparing the alpha diversity of the different stations along the depth gradient on the continental slope, beta diversity is illustrated. The number of hyperbenthic taxa is higher for the four deepest stations compared to the upper slope stations. Taxa diversity expressed as N_1 is highest at station P350 and station P800, although at the latter a dominance of 34 % for Amphipoda was found, resulting in the k-dominance curve lying higher than the P950 curve (with Cumacea as the most abundant taxon, 30 %) in the plot (Fig. 3.11). At station P350 Amphipoda are most abundant (23%). The highest dominance effect was found for the hyperbenthos at station P650 (49 % for Amphipoda), resulting in the lowest diversity.



	P200	P350	P500	P650	P800	P950	P1100	P1250
N_0	9	9	8	8	11	10	9	11
N_1	5,18	6,82	4,63	4,11	5,95	5,24	4,44	5,09
N_{inf}	2,90	4,35	2,63	2,05	3,00	3,30	2,88	2,83

Figure 3.10 Diversity indices of Hill (N_0, N_1 and N_{inf}) for the hyperbenthic taxa at each station (P200-P1250) at Porcupine Seabight.

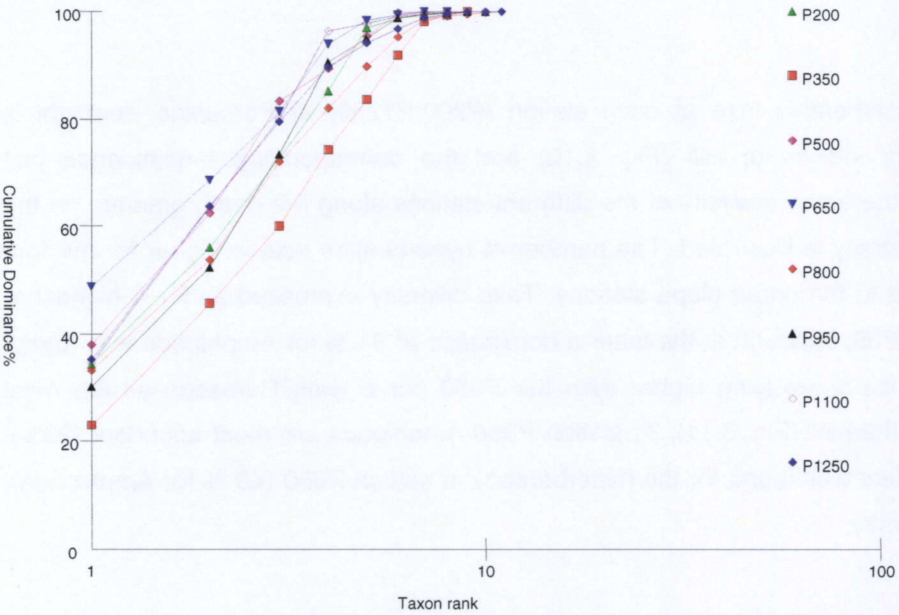


Figure 3.11 K-dominance plot of the hyperbenthic taxa at the eight stations (P200-P1250) at Porcupine Seabight.

Community structure

Multi-dimensional scaling (MDS) performed on the eight station samples along the Porcupine Seabight continental slope shows an obvious depth gradient (Fig. 3.12A). Also in the cluster analysis dendrogram (hierarchical clustering with group averaged linking) (Fig. 3.12B) this gradient along the slope is illustrated and an upper slope (stations P200, P350 and P500), mid slope (stations P650, P800 and P950) and lower slope (stations P1100 and P1250) group can be recognised. An ANOSIM-analysis indicated these groups as not significantly different (global R= 0.959, significance level= 0.4 %). This is probably due to the low number of taxa and the occurrence of most taxa in most samples.

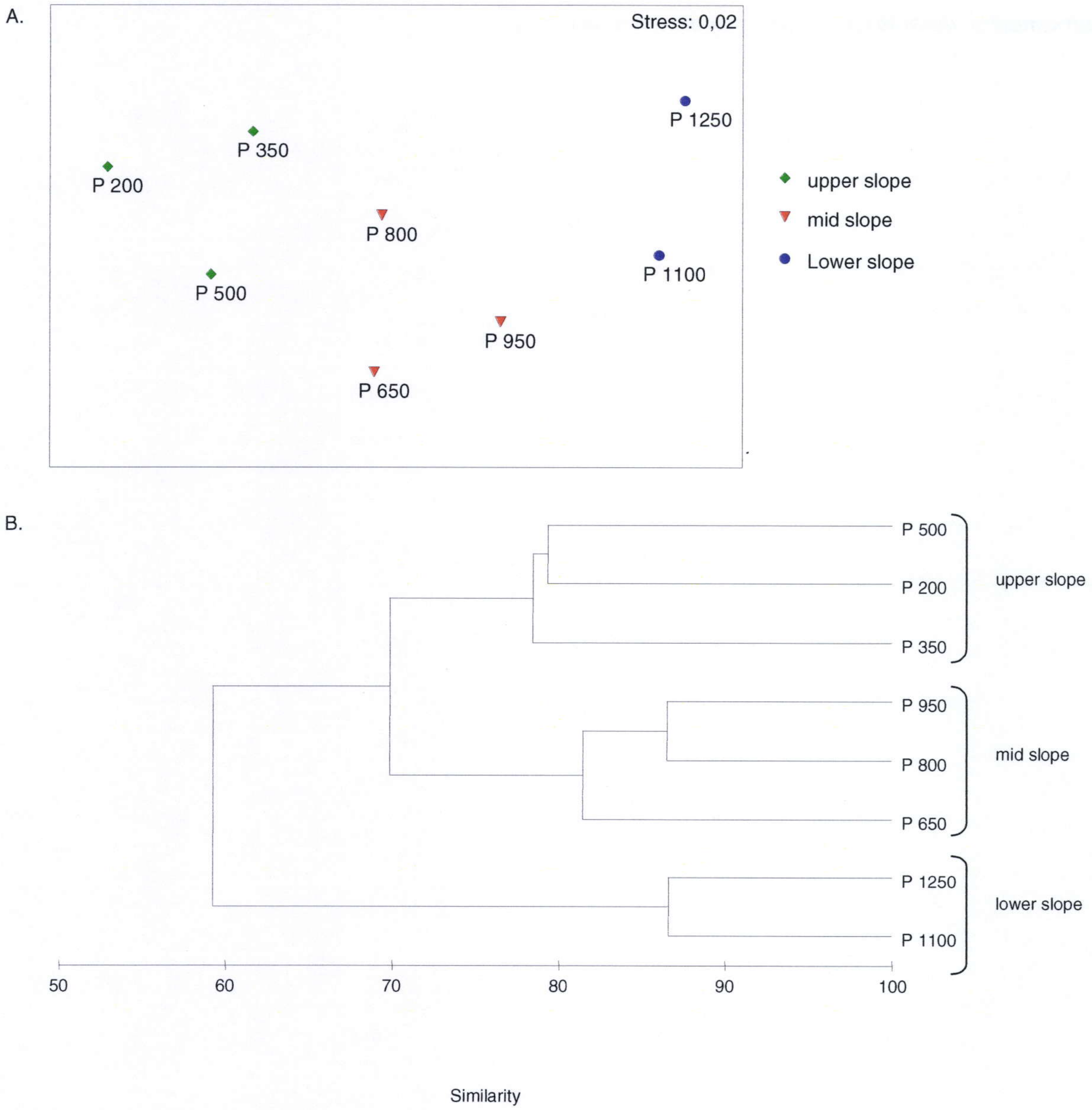


Figure 3.12 A) Multi-dimensional scaling (MDS) plot and B) cluster analysis dendrogram based on fourth-root transformed hyperbenthic taxa data of the eight Porcupine Seabight stations (P200-P1250).

Link with environmental variables

Due to the paucity of environmental variables measured at Porcupine Seabight, the BIO-ENV analysis was limited to the sediment characteristics (percentage mud, median grain size and sorting coefficient) and depth. BIO-ENV analysis was performed with the similarity matrix from the hyperbenthic taxa data and the log(x+1) transformed environmental dataset, using a Spearman rank correlation method. The draftsman plot indicated no correlations between the used environmental variables. The BIO-ENV analysis was performed for the upper net samples and the lower net samples separate. For both sets of samples a combination of the four environmental variables best explain the hyperbenthic community structure, with $\rho=0.222$ for the upper net samples and $\rho=0.539$ for the lower net samples, indicating a closer link with the sediment of the lower net samples. Due to the paucity of the different environmental variables, cautious interpretation is in order.

3.3. Discussion and conclusions

3.3.1. Vertical distribution

Density, community structure and diversity

The hyperbenthic fauna is recently recognised as a specific fauna, living in the benthic boundary layer (BBL) and conducting a specific role in the marine ecosystem functioning. As reviewed by Angel (1990) the hyperbenthic fauna can be considered as a combination of pelagic species, benthic species and other species specialized to the hyperbenthic environment. This combination of species in the specific BBL zone should be expected to be very diverse and comprising high densities of various ecological taxa. The results of the vertical distribution of the hyperbenthos at Porcupine Seabight in the present study verify this species combination, as 12 hyperbenthic taxa show a specific distribution throughout the slope BBL. In this research the BBL water layer is divided, by means of the sampling device, in two separate layers, one from 0-50 cm above the bottom, the second layer 50-100 cm above the sediment. There is a clear division of certain taxa throughout this 1 m water layer, characterized by a pelagic fauna in the upper 50-100 cm layer, dominated by Copepoda and a benthopelagic fauna in the 0-50 cm layer, mainly composed of peracarid crustaceans.

All taxa except the Copepoda reach higher densities in the lower zone (0-50 cm) compared with the higher zone (50-100 cm) of the BBL. Copepods are more abundant in the upper water layer, with densities doubling those in the first 50 cm of the water layer. All copepods caught, belong to the Order of the Calanoida (Mauchline, 1998), but no further determination was done for this taxon in this PhD research. Nevertheless certain copepods are referred to as typical hyperbenthic copepods, with some species endemic to this environment (Mauchline, 1998). On the other hand, many of the species normally living in the pelagic water column can have downward extensions of their populations into the BBL. Hyperbenthic species tend to be small in body size and are often robustly built but studies of their biology are few (Mauchline, 1998).

Besides the pelagic copepods, several benthopelagic taxa like Amphipoda, Cumacea, Isopoda, Tanaidacea, Pycnogonida and Ostracoda are an important portion of the hyperbenthos in the studied area. Tanaidacea are strictly limited to the lower 50 cm of the BBL. Very little is known about the ecology of tanaids, especially those living offshore. Most species are benthic, while some species are able to swim very fast for short periods by beating their pleopods (Holdich & Jones, 1983). Amphipoda, Isopoda and Cumacea, belonging to the Peracarida, and the taxa Pycnogonida and Ostracoda show strong differences in densities between the two BBL layers, with very high densities in the lower layer for all five taxa. The obvious increase of benthic taxa in the lower nets and particularly in the deeper stations is also reported by Sorbe (1999) for the Cap-Ferret Canyon in the Bay of Biscay. It is important to mention that the catch by the hyperbenthic sledge may have been slightly contaminated by benthic fauna present in the upper centimetre of the bottom triggered by disturbance and resuspension of the soft bottom. Despite this possible contamination, most of these benthopelagic animals are described as hyperbenthos, showing high swimming capability, which enable them to migrate into the water column, indicating no strict benthic life style.

Mysidacea, Euphausiacea and Chaetognatha are also more abundant in the 0-50 cm water layer, but with a smaller discrepancy with the 50-100 cm BBL zone. In the Catalan Sea a similar trend for mysids was described (Cartes & Sorbe, 1995). Hargreaves (1985) mentions that food supply is probably one of the causal factors for the increase in numerical abundance of some species near-bottom when considering the vertical distribution of Mysidacea.

Such a stratified distribution pattern of the fauna in the immediate vicinity of the seafloor was also noticed for shallower assemblages from the continental shelves and slopes at least in their daytime structure (Sorbe, 1989; Fosså, 1985, 1986; Sainte-Marie & Brunel, 1985; Brattegard & Fosså, 1991; Wildish *et al.*, 1992). Dauvin & Sorbe (1995) also found higher amphipod densities in the lower BBL zone at the Cap-Ferret Canyon in the Bay of Biscay. Similar results were reported along the Norwegian coasts and Gullmarfjord (Buhl-Jensen, 1986; Buhl-Jensen & Fosså, 1991). In contrast to the English Channel, the amphipods occupied the full BBL (1 m) sampled by a sledge and the density showed no drastic reduction from the lower net to the upper net (Vallet & Dauvin, 1995). As a general trend, most of the motile species within these assemblages performed noctural migrations upwards into the water column (Macquart-Moulin, 1984, 1991; Sorbe, 1989; Kaartvedt, 1985, 1989) and the amplitude of such migrations seem to be species-specific. Overall, these migration patterns together with other factors such as light, currents or food availability determine the swimming activity of the hyperbenthic taxa and thus the vertical distribution.

3.3.2. Bathymetric distribution

Zonation of the hyperbenthos

Studying one of the major environmental gradients, that relating to depth on the sloping parts of the seabed and the associated faunal zonation is one of the challenges of this PhD. Important faunal boundaries, found globally, are believed to occur at around the shelf break/upper slope 200-500 m and around 1000-1400 m depth (Day & Pearcy, 1968; Rowe & Menzies, 1969; Sanders & Hessler, 1969; Dayton & Hessler, 1972; Rex, 1977; Hecker, 1990). The depth at which faunal boundaries occur varies with taxa studied and geographical location (Gage & Tyler, 1991). Observations of these depth boundaries occurring at many locations worldwide, indicates that important controlling variables are present at these depths and that these may occur globally. The present study, at Porcupine Seabight, finds comparative faunal boundaries for hyperbenthos at ~500 m and ~1000 m. These boundaries involve some important taxon shifts determining three zones along the continental slope. An upper slope zone (stations P200, P350 and P500) characterised by high abundances of Euphausiacea, Mysidacea and Copepoda and with a relatively low taxon richness. The other two zones, the mid slope zone (stations P650, P800 and P950) and the lower slope zone (stations P1100 and P1250) are mainly characterised by the significant increase of the Cumacea and Isopoda. The mid slope zone, in contrast to the lower slope zone, also comprise an important share of Mysidacea and Copepoda.

Similar studies have focused either on general faunal zonation patterns (Le Danois, 1948; Rowe & Menzies, 1969; Haedrich *et al.*, 1975; Ohta, 1983) or on the zonation of specific taxa, *e.g.* fish (Day & Pearcy, 1968), gastropods (Rex, 1977), echinoderms (Gage, 1986; Howell *et al.*, 2002), holothurians (Billet, 1991) and decapod crustaceans (Cartes & Sardà, 1993). These studies have shown, regardless of the taxon examined, that deep-sea fauna undergo a non-repeating sequential change with depth and most species have predictable and restricted depth ranges (Rowe & Menzies, 1969; Carney *et al.*, 1983; Gage & Tyler, 1991).

Few studies on hyperbenthic communities have considered the continental slope area, including the shelf break transition (see Table 1.2 chapter 1). This area nevertheless coincides with strong gradients in the physical environment and it is characterised by a very pronounced transition in fauna, as was already reported for the macro-endobenthic and mega-epibenthic fauna (Rex, 1981; Flach & Thomsen, 1998; Duineveld *et al.*, 1997; Flach & de Bruin, 1999). For hyperbenthos Dauvin & Sorbe (1995) defined two bathymetric faunistic changes for Amphipoda at the Cap-Ferret Canyon in the Bay of Biscay: 400-500 m and 1000 m. On the same set of samples Elizalde *et al.* (1991) identified three bathymetric zones for Amphipoda and Mysidacea: 350-520 m, 520-925 m and stations lower than 1000 m.

Howell *et al.* (2002) recognised different faunal zones for starfish in the Porcupine Seabight and Porcupine Abyssal Plain, which are very similar to the zones defined in the present study for hyperbenthic taxa. They defined six zones between the shelf break zone (~150 m) and 4950 m depth with every zone characterised by specific starfish species. Similar boundaries at ~700 m and ~1100 m, also found in the present study were recognised.

In the present study, as with most deep-sea zonation studies, there is a paucity of environmental data available. The discussion is therefore limited to those environmental factors that show, often very loosely, a relationship to the faunal changes observed. Some characteristics from the physical oceanography at Porcupine Seabight (as described in chapter 2) can complement the interpretation of the zonation patterns found in the present study. At Porcupine Seabight, the start of a permanent thermocline occurs at 600 m. Temperature decreases from 10°C at 600 m to 4°C at 1400 m, the base of the permanent thermocline (Rice *et al.*, 1991). Both the 10°C and 4°C isotherms have been suggested to mark important faunal boundaries (Gage *et al.*, 1985; Gage, 1986). Deep-sea animals are thought to be very sensitive to small changes in temperature (Somero *et al.*, 1983). Other important factors are the hydrographic conditions of the study area. Water mass structure at Porcupine Seabight has been reported by Hargreaves (1984) and Rice *et al.* (1991). The boundary between Eastern North Atlantic Water (ENAW) and Mediterranean Outflow Water (MOW) occur at ~750 m depth in the Porcupine Seabight. Boundaries between water masses have been correlated with changes in the composition of benthic fauna (Tyler & Zibrowius, 1992; Bett, 2001). At Porcupine Seabight no common boundary in the hyperbenthic zonation pattern and water mass structure could be established.

In the present study the mid slope zone extends to about 1000 m. Previous studies have found a comparative faunal boundary at 1200-1300 m for decapod crustaceans (Cartes & Sardà, 1993) and 1000 m for cerianthid anemones (Shepard *et al.*, 1986). At Porcupine Seabight the 1000 m boundary is associated with changes in currents. The variability in the currents will have an effect on sediment transport, food supply and larval dispersal and is likely to affect the faunal zonation. Flach *et al.* (1998) found flow velocities to be important in structuring the benthic community at Goban Spur. The change in currents at about 1000 m water depth is also reflected in the sediment composition along the studied continental slope and can be linked to the hyperbenthic zonation pattern observed. At stations P1100 and P1250 a dominant fine sand fraction was found indicating a high-energy environment. Along the sampled transect the upper slope is characterized by fine sand sediments, while a high percentage of mud was found at the mid slope with smaller median grain size. The interpretation of the observed zonation pattern and possible causes will be discussed on species level for the main group, the Peracarida, in chapter 5 and in comparison with the bathymetric distribution patterns found at Meriadzek Terrace in chapter 4 and chapter 6.

Chapter 4

Hyperbenthic communities at Meriadzek Terrace (in comparison with Porcupine Seabight)

4.1. Introduction and objectives

Geographical patterns in the distribution of species (or higher taxa) and the causes of those patterns are poorly known for animals of the deep-sea floor. This situation arises, in part, because of the great mismatch between the vastness of the habitat and the low sampling intensity (Thistle, 2003). The shape of the ocean floor sets the stage for deep-sea biogeography. Briefly, within major ocean basins at slope depths, the habitat is more or less continuous along isobaths, interrupted by relatively small structures, such as submarine canyons. The major oceans and most of the world's seas are connected at these depths. Below about 2500 m, the mid-ocean ridges and submarine mountain ranges divide the major oceans into regions, for instance, the eastern Atlantic and the western Atlantic. Below about 3500 m, the deep-sea floor consists of isolated basins (Allen & Sanders, 1996).

These major geographical features have led to different studies based on distribution of fauna **along isobaths** and patterns with depth or **across isobaths**. Few studies combined the along- and across-isobaths patterns, mainly because of the incomplete sampling. The distribution of higher taxa along isobaths is unusually homogeneous in the deep sea (Gage & Tyler, 1991). For example, of the 143 genera of asellote isopods known from the World Oceans, all but nine are found in the Atlantic (Hessler *et al.*, 1979). For deep-sea species, the distribution is slightly different, some species are widespread, but many have restricted distributions (Kussakin, 1973; Hessler & Thistle, 1975; Svavarsson, 1988).

Concerning the patterns with depth or the across isobaths distribution, the faunal break at the shelf/slope transition (at circa 200 m water depth) has been confirmed repeatedly (Sanders & Hessler, 1969; Haedrich *et al.* 1975; Carney & Carey, 1982). Below 200 m, regions of relatively slow faunal change (= zones) are separated by bands of more rapid faunal change. The depths of zone boundaries vary among higher taxa and locations, but in the North Atlantic appear to be at about 500, 1000, 1500 and 2000 m (Gage & Tyler, 1991). Below 2000 m, the rate of change of the fauna decreases, and zonation does not appear to be as marked, perhaps partly due to the smaller sampling effort at these depths. Combining the along- and across-isobaths patterns was done in relatively few deep-sea studies (Allen & Sanders, 1996; Carney *et al.*, 1983; Grassle & Maciolek, 1992; Maynou *et al.*, 1996).

Specific hyperbenthos studies at greater depths (> 200 m) in the NE Atlantic, have been performed along the continental slope and adjacent canyons in the south-eastern Bay of Biscay (Elizalde *et al.*, 1993; Dauvin *et al.*, 1995; Sorbe & Weber, 1995; Sorbe, 1999; Marquiegui & Sorbe, 1999; Corbari & Sorbe, 2001), in the Catalan Sea (Cartes, 1998) and at the shelf break off Portugal (Cunha *et al.*, 1997). The hyperbenthos of polar areas has been studied in Antarctic regions (around the South Shetland Islands and in the Bransfield Strait, San Vicente *et al.*, 1997) and in Arctic waters (the Laptev Sea, Sirenko *et al.*, 1996). Other studies again focused on the entire peracarid community of the benthic boundary layer (BBL) or concentrated on separate orders such as Amphipoda, Isopoda, Cumacea, Mysidacea or Euphausiacea (see Table 1.2 in Chapter 1).

This study deals with the hyperbenthic component of the BBL fauna, defined as the small (1 - 20 mm) animals that swim in the vicinity of the seabed (Mees & Jones, 1997). The main representatives of the hyperbenthos are peracarid crustaceans, a group that shows a rich diversification in the deep sea often reaching high abundances (Gage & Tyler, 1991). Since the last decade, evidence for their potential function in deep-sea trophic webs is growing. Vertical migration behaviour may affect the energy transfer between the pelagic and benthic realm, either in the form of gut contents or as a result of predation (Angel, 1990; Longhurst & Harrison, 1988). Swimming activities might also contribute to the fragmentation of marine snow in the water column, as was shown for euphausiids (Dilling & Alldredge, 2000; Graham *et al.*, 2000). Extremely high feeding rates were reported for scavenging amphipods, which are numerous in the deep-sea BBL (Angel, 1990). Recently, certain asellote isopods have been shown to feed predominantly on benthic foraminifers, suggesting an important trophic link (Svavarsson *et al.*, 1993; Gudmundsson *et al.*, 2000). Several hyperbenthic crustaceans constitute an important part of the food exploited by megafaunal decapods (Cartes, 1998) and demersal fish (Mauchline, 1982; Mauchline & Gordon, 1991). Cartes (1998) could even indicate a link in seasonal abundance of the hyperbenthos and megafaunal decapods.

The first part of this chapter present the investigations made on the hyperbenthic communities of the second study area Meriadzek Terrace (see chapter 2 for study site description). In a second part these results are compared with the data collected from a similar bathymetric transect at Porcupine Seabight (raw data presented in chapter 3). The two slope areas in the NE Atlantic were sampled from 200 to 1250 m depth, following a standardised sampling strategy (see chapter 2: methodology). Three important distribution patterns will be studied and discussed: 1) vertical or stratified distribution of the hyperbenthos in the BBL, 2) across isobaths or bathymetric distribution and 3) along isobaths or geographical distribution of the hyperbenthic fauna. This near-bottom or hyperbenthic fauna, a link between the benthos and the water column, may quantitatively as well as qualitatively differ from the rest of the deep-sea plankton (pelagial) and may be important in biological interactions within the BBL. These animals, because of their proximity to the bottom, inhabit a more heterogeneous and possibly richer environment than deep plankton higher in the water column and may show a clear stratified distribution within the BBL. More niches may be available, and a specialized hyperbenthic fauna probably exists along with the regular deep-sea zooplankton (Wishner, 1980a).

By comparing the data from both study sites by means of multivariate analysis, some specific questions can be addressed here: are the major hyperbenthic stratified and bathymetric or across isobaths distribution patterns similar for both slope areas and can they be explained by environmental variables sampled along the slope? Can comparison of the hyperbenthic community structure found in Porcupine Seabight and Meriadzek Terrace put forward some general trends in geographical distribution patterns (*i.e.* along isobaths distribution), depth related distribution patterns (*i.e.* across isobaths distribution) or stratified distribution patterns (*i.e.* lower BBL zone 0-50 cm versus upper BBL zone 50-100 cm) of hyperbenthic fauna?

The results will be discussed in terms of higher taxa composition, hyperbenthic densities and environmental variables and in relation to other hyperbenthic community studies from the northeastern Atlantic described in literature.

4.2. Results

4.2.1. Environmental variables at Meriadzek Terrace

A description of the study site Meriadzek Terrace and the sampling strategy used, are presented in chapter 2.

4.2.1.1. Abiotic data

The different environmental variables measured by the 'Seabird Conductivity Temperature Depth' (SCTD) instrument are data from three metres above the ocean floor, this is a safety margin to prevent the oceanographic instrument from touching the bottom. The SCTD data were collected during the first sampling campaign to Meriadzek Terrace in 2002 (see chapter 2). At each station (M200-M1250) the SCTD data were collected immediately after the hyperbenthic sledge was hauled in. A summarize of the SCTD data, together with depth for each station is given in Table 4.1.

Table 4.1 SCTD data for the eight stations sampled at the Meriadzek Terrace (M200-M1250).

	M 200	M 350	M 500	M 650	M 800	M 950	M 1100	M 1250
depth (m)	227	352	494	678	795	953	1110	1215
temperature (°C)	11.64	11.53	11.00	10.47	9.75	9.26	8.18	7.52
salinity (psu)	35.58	35.58	35.55	35.57	35.68	35.71	35.58	35.49
dissolved oxygen (µmol/kg)	258.90	255.97	231.82	215.74	202.65	203.11	214.45	220.45
water density (kg/m^3)	27.12	27.13	27.22	27.33	27.54	27.65	27.72	27.75

Depth values range from 227 m to 1215 m, with a difference in depth of 141 m on the average between two stations. Water temperature values measured during this study decreased from 11.64 to 7.52 °C with depth. Salinity values are constant along the depth gradient. Dissolved oxygen concentration decreases from 258.90 µmol/kg at station M200 to a minimum of 202.65 µmol/kg at station M800 and then increases again with depth. Water density slightly increases with increasing depth.

4.2.1.2. Sediment characteristics

Sediment samples were taken during the second cruise to Meriadzek Terrace in 2003 (see chapter 2: methodology) and were performed at the same locations of the hyperbenthic samples taken during the first expedition to Meriadzek Terrace in 2002. Table 4.2 and figure 4.1 give an overview of the granulometric analysis. The median grain size (µm) and the sorting coefficient are given in table 4.3, the latter being an index for the range of the grain size distribution present in a sediment sample (Dyer, 1986).

Table 4.2 Sediment composition of the eight sampling stations at the Meriadzek Terrace (M200-M1250).

station	clay vol%	silt vol%	very fine sand vol%	fine sand vol%	medium sand vol%	coarse sand vol%	very coarse sand mass%	granule mass%	mud (=clay+silt) vol%
M200	0.80	2.90	7.60	63.30	23.92	1.48	3.63	8.35	3.70
M350	0.60	2.40	16.40	57.40	21.40	1.80	0.16	0.07	3.00
M500	1.20	7.70	36.10	41.50	11.61	1.89	0.00	0.00	8.90
M650	1.30	5.70	17.80	45.30	28.33	1.57	0.00	0.00	7.00
M800	25.90	33.40	9.90	17.30	10.76	2.74	0.00	0.00	59.30
M950	41.60	53.17	5.23	0.00	0.00	0.00	0.00	0.00	94.77
M1100	40.00	43.30	5.00	6.78	4.46	0.46	0.00	0.00	83.30
M1250	48.30	48.90	2.70	0.10	0.00	0.00	0.00	0.00	97.20

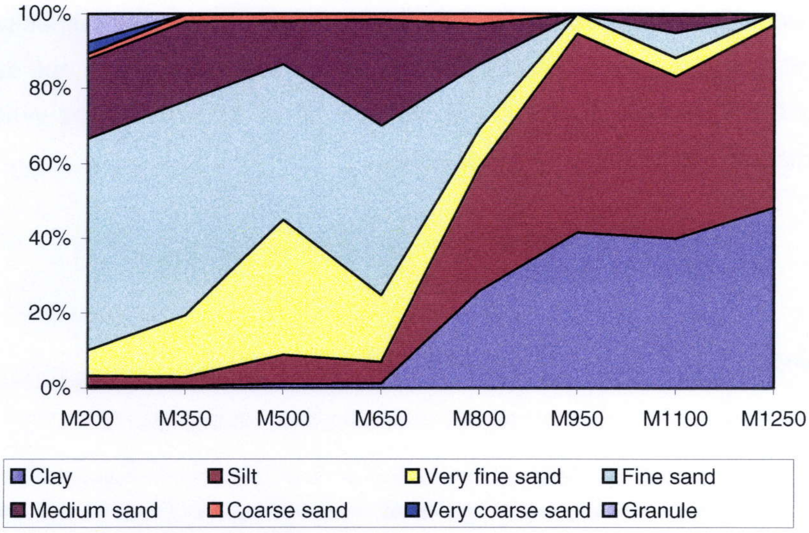


Figure 4.1 Relative sediment composition at the eight sampling stations at the Meriadzek Terrace (M200-M1250).

Table 4.3 Median grain size (µm) and the sorting coefficient of the eight sampling stations at the Meriadzek Terrace (M200-M1250).

station	median grain size (µm)	sorting coefficient
M200	200	0.34
M350	180	0.42
M500	134	0.54
M650	185	0.55
M800	28	2.74
M950	6	1.56
M1100	6	1.81
M1250	4	1.32

Granulometric analyses (Table 4.2 and Fig. 4.1) indicate an obvious increase of very fine sediments (clay and silt), starting at station M650. Clay, silt and very fine sand represent the entire 100 % of the sediment composition at station M950 and almost the entire 100 % at station M1250, resulting in a very low median grain size of 6 µm and 4 µm respectively. Median grain size at station M1100 is also 6 µm, this stations also contains a very small share of coarse, medium and fine sand. At the more shallow stations (M200-M650) fine sand is the major component of the sediment, ranging from 41,5 % to circa 63,3 % at stations M500 and M200 respectively. The general trend is a continuous increase of very fine sediments with depth. Sorting coefficient (Table 4.3) is lowest for the four shallow stations, indicating a better distribution of grain sizes within the substratum.

4.2.1.3. Environmental variables along the slope transect

The distribution of the environmental data (STD and sediment data: percentage mud, median grain size, sorting coefficient, depth, temperature, salinity, dissolved oxygen, water density and chla) along the transect was analysed using correlation-based principal-component analysis (PCA) (Fig. 4.2). Data were converted to approximately normality using a log(x+1) transformation prior to the analysis as described by Clarke (1993). The first two components of the ordination plot accounted for 90.8 % of the total variance of the data with 75.1 % and 15.7 % for the first and the second axis respectively. The first PC axis (PC1) is that of decreasing (from left to right) values of mud, water density and depth and explains the largest part of the variance while the second axis (PC2) is explained by the variable salinity, but only a small percentage is ascribed to this second axis.

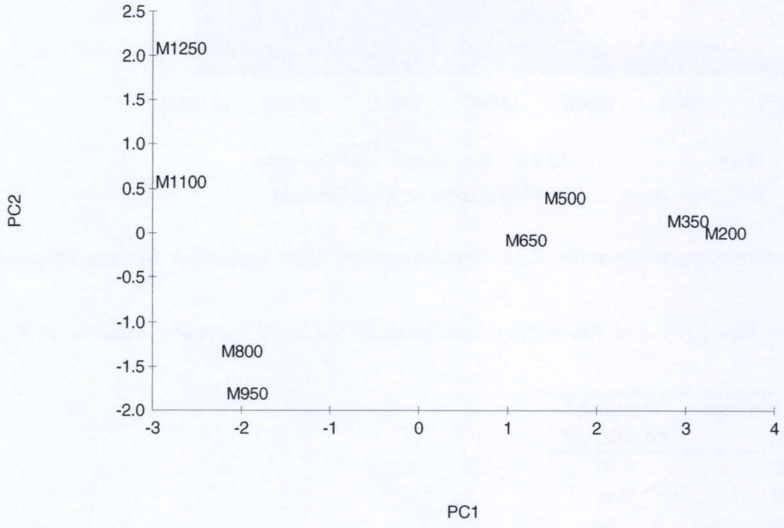


Figure 4.2 Principal component analysis (PCA) ordination on the log(x+1) transformed environmental variable matrix.

The draftsman plot (pairwise scatter plots) (Fig. 4.3) of all environmental variables illustrates the fact that some environmental variables are strongly correlated (see result file in appendix 4). Variable sets whose mutual correlation coefficients, after log(x+1) transformation, average more than 0.95 were reduced to a single representative. For this environmental data set these were the sets mud/median grain size, median grain size/density and temperature/density. The abiotic variable 'density' was left out, reducing the correlated variable sets to only the 'mud/median grain size' set. For this latter median grain size was left out, because the variable mud is a frequent used variable in other studies, so comparison is allowed. For further analysis based upon this environmental data set, the abiotic variables 'density' and 'median grain size' were left out.

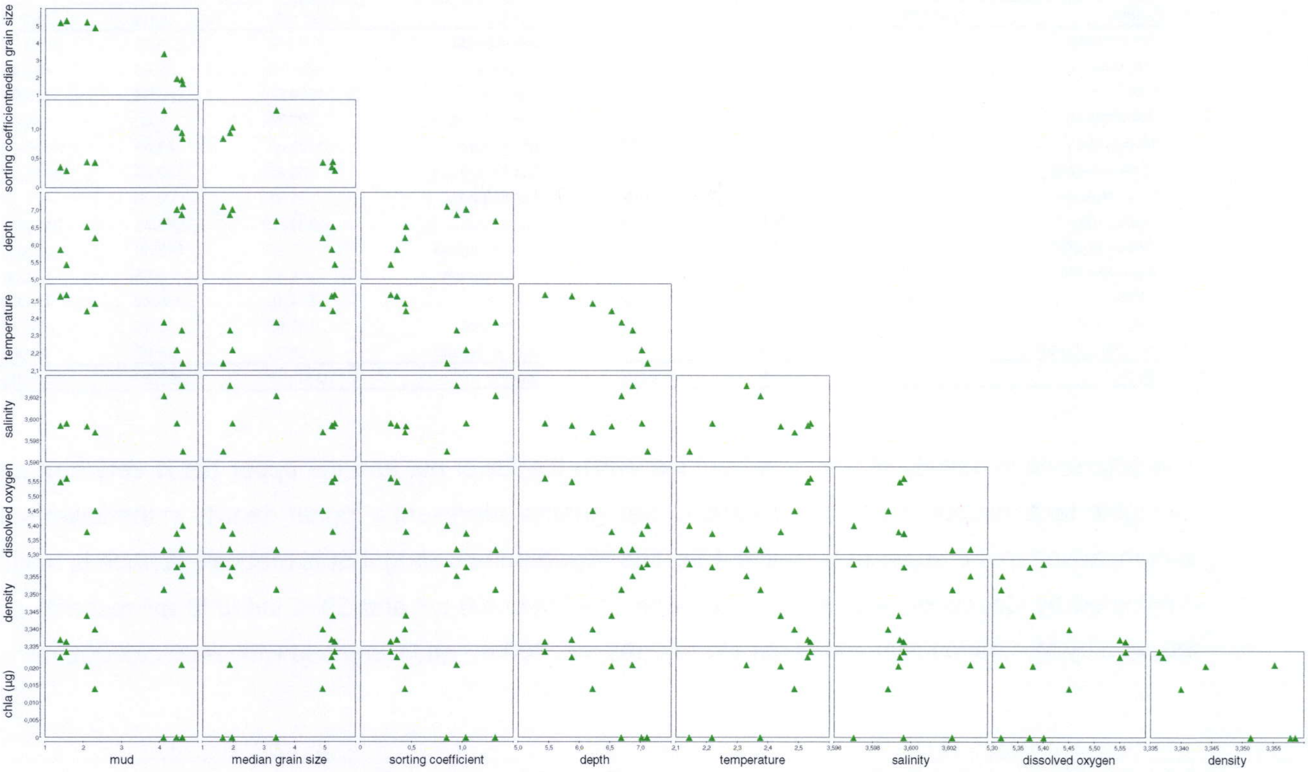


Figure 4.3 Scatter plot (Draftsman plot) for the different abiotic variable pairs illustrating correlation of certain variables.

The reduced dataset of environmental variables is used for the BIO-ENV procedure (Clarke & Warwick, 1994) to define suites of environmental variables that best determine the hyperbenthos community structure (see further in this chapter).

4.2.2. Hyperbenthic density at Meriadzek Terrace

In total 22 403 hyperbenthic individuals were counted at Meriadzek Terrace from all samples, belonging to 13 hyperbenthic higher taxa (Table 4.5) (including juvenile Polychaeta and larvae). This latter group mainly comprises Decapoda larvae, which were considered as a taxon. Densities are given (Table 4.5) for the sum of the lower nets (0-50 cm zone) and the sum of the upper nets (50-100 cm zone) separated and for the sum of the nets or eight stations at the Meriadzek Terrace.

Table 4.4 A) Total number of individuals for the 13 hyperbenthic taxa. B) Total density (ind./800 m²) for the 13 hyperbenthic higher taxa for the lower and upper nets and for the sum of the nets (station) at the Meriadzek Terrace.

A.

Taxon	Lower nets	Upper nets	Station
Amphipoda	4753	389	5142
Isopoda	1101	114	1215
Cumacea	1836	259	2095
Tanaidacea	41	12	53
Mysidacea	4677	112	4789
Euphausiacea	886	924	1810
Leptostraca	2	0	2
Copepoda	2871	2441	5313
Chaetognatha	166	176	342
Pycnogonida	180	4	184
Larvae	669	63	732
Ostracoda	265	165	431
Juv. Polychaeta	240	54	294
Sum	17689	4715	22403

B.

Taxon	Lower nets	Upper nets	Station
Amphipoda	2809,08	245,20	3054,28
Isopoda	717,78	71,63	789,42
Cumacea	1298,60	167,38	1465,99
Tanaidacea	27,85	7,60	35,44
Mysidacea	2522,83	72,65	2595,47
Euphausiacea	503,29	540,09	1043,38
Leptostraca	1,25	0,00	1,25
Copepoda	1635,95	1560,96	3196,91
Chaetognatha	103,02	118,05	221,06
Pycnogonida	119,48	2,58	122,06
Larvae	374,16	36,90	411,07
Ostracoda	165,67	110,65	276,32
Juv. Polychaeta	159,31	33,92	193,22
Sum	10438,27	2967,60	13405,88

The difference in density of the hyperbenthos within the lower net and the upper net is very obvious. All higher taxa, except Euphausiacea and Chaetognatha, represent a higher density in the lower nets in comparison to the upper nets (Table 4.5). The hyperbenthos caught at Meriadzek Terrace is mainly dominated by Copepoda and Amphipoda, with 3197 ind./800 m² and 3054 ind./800 m² respectively, followed by Mysidacea with a total density of 2595 ind./800 m² and Cumacea with 1466 ind./800 m².

4.2.2.1. Vertical distribution of the hyperbenthos at Meriadzek Terrace

The vertical distribution of the hyperbenthos in the two superimposed nets of the hyperbenthic sledge is studied. The densities of the lower nets (0-50 cm) are compared to the densities in the upper nets (50-100 cm).

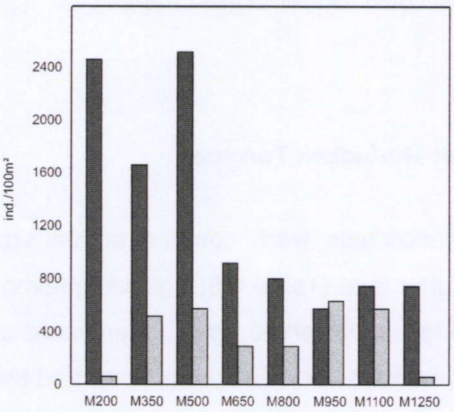


Figure 4.4 Total absolute density (ind./100 m²) of the hyperbenthos in the lower nets (dark grey) versus the upper nets (light grey) for each station at Meriadzek Terrace (M200-M1250).

Relative abundance of the hyperbenthic higher taxa

Relative hyperbenthic higher taxa composition illustrates the vertical distribution of the fauna (Figure 4.5). To keep this stacked bars figure orderly, a 'rest' group was created. This 'rest' group is the sum of the percentages of the taxa that make up less than 3 % of the hyperbenthos in a certain sample. The composition of this 'rest' group and the number of taxa it comprises differs for each station. For all lower net samples the taxa Tanaidacea, Leptostraca and Chaetognatha always belong to the 'rest' group, while for the upper nets Tanaidacea, Leptostraca and Pycnogonida are part of the 'rest' group in each station.

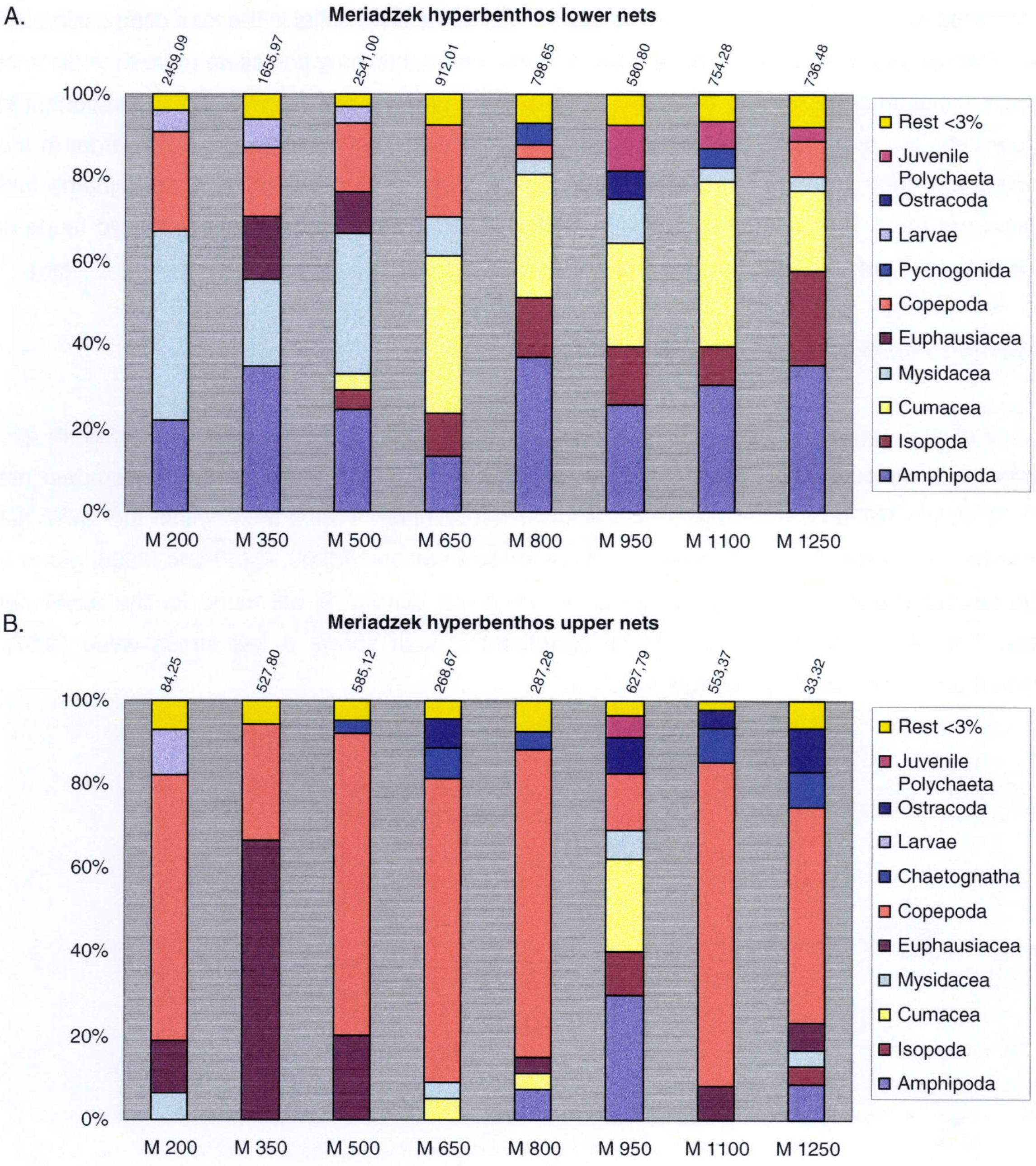


Figure 4.5 Relative hyperbenthic higher taxa composition for the A) lower nets (0-50 cm) and B) upper nets (50-100 cm) for the eight stations at the Meriadzek Terrace (M200-M1250). The absolute total hyperbentic density per sample is indicated above each bar.

The Amphipoda are very abundant in the hyperbenthos caught by the lower nets along the complete depth gradient. Also in the lower nets starting at 500 m depth (M500) the Isopoda exceed the 3 % and start to increase with depth. A similar trend is observed for the Cumacea. In contrast the Mysidacea are strongly abundant between 200 m and 500 m, but an obvious decrease with depth is observed. Euphausiacea only exceed the 3 % at stations M350 and M500. The Copepoda are very abundant in the lower nets at the stations M200-M650, but they also make up a significant part at the stations M800 and M1250. Larvae are only found at M200, M350 and M500 while the juvenile polychaetes appear at the three deepest stations. Generally this picture shows an increase in number of taxa with depth, station M500 shows the highest number of taxa (seven plus 'rest' group).

Comparing the two figures, lower nets versus upper nets, some clear shifts in the taxa composition are obvious: Copepoda becomes the dominant taxon in the upper nets, they constitute more than 50 % of the hyperbenthos in six of the eight stations. Amphipoda, Cumacea and Isopoda are still important in the upper nets, but only in the deeper stations. The percentage of the Euphausiacea is larger in the upper nets and they are also found at greater depths. Other taxa such as the Chaetognatha and Ostracoda are more abundant in the upper nets than in the lower nets. Overall, a pelagic fauna is found in the upper nets (50-100 cm) and a benthopelagic fauna dominated the lower nets (0-50 cm).

Hyperbenthic communities at Meriadzek Terrace

MDS- and cluster-analysis show an obvious division between the upper net samples (group III) and the lower net samples (group I and group II) (Fig. 4.6 and Fig. 4.7). As an exception, the upper net sample of station M950 is more related to the lower net samples. Furthermore within the lower net samples there is a clear division between the three shallow stations (M200, M350 and M500, group I) and the deeper stations (M650-M1250, group II), while this division is not found for the upper net samples. The MDS-ordination (Fig. 4.6) for hyperbenthic taxa shows a low stress value (0.07), indicating a good and useful 2D-representation.

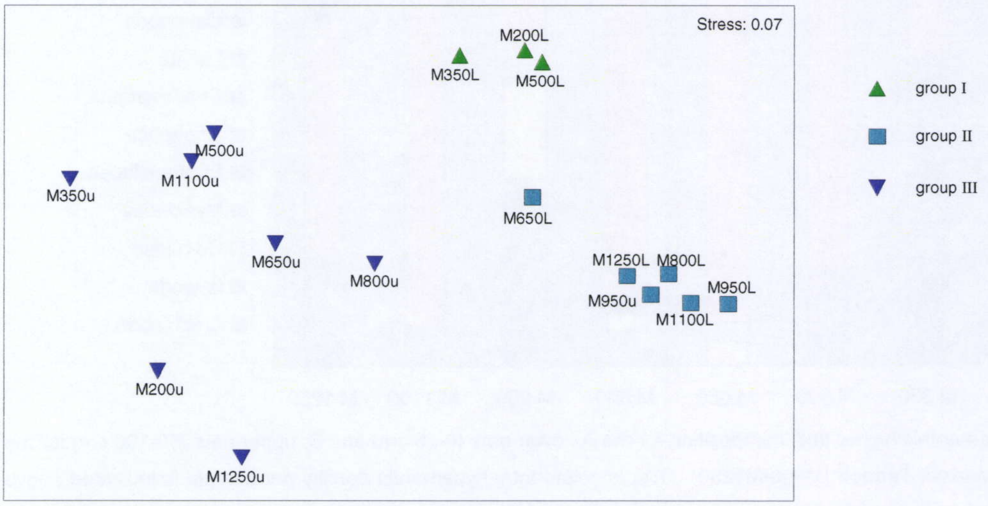


Figure 4.6 Multi-dimensional scaling (MDS) plot based on fourth-root transformed hyperbenthic taxa data of the eight sampling stations at the Meriadzek Terrace (M200-M1250) with the lower and upper nets separated. u= upper net, L= lower net.

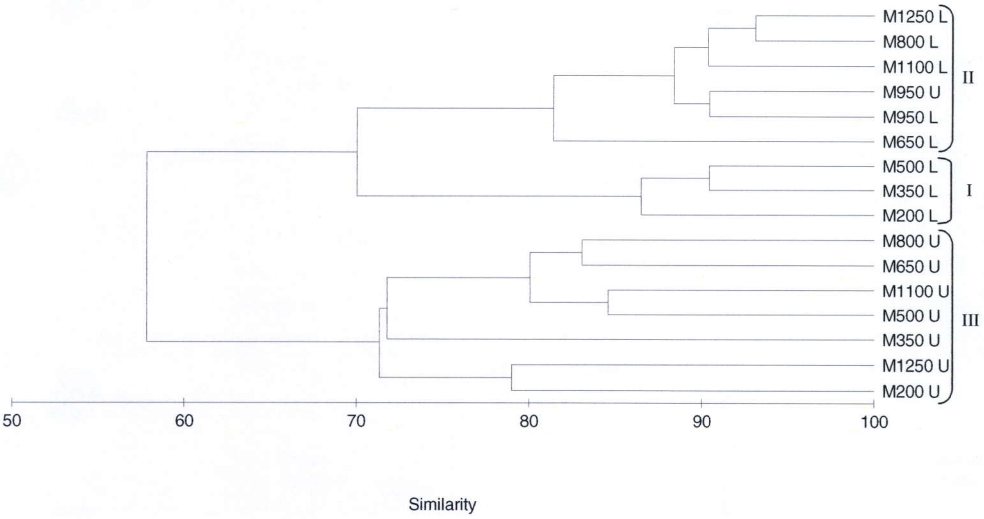


Figure 4.7 Cluster analysis dendrogram based on fourth-root transformed hyperbenthic taxa data of the eight sampling stations at the Meriadzek Terrace (M200-M1250) with the lower (L) and upper (U) nets separated. The three groups (I, II and III) are indicated.

In general MDS- and cluster-analysis divide the total hyperbenthos community on the continental slope into three different taxa associations, reflecting their position in the BBL zone and along the continental slope: the lower BBL zone (0-50 cm) on the upper part of the slope (group I), the lower BBL zone on the lower part of the continental slope (group II) and the upper BBL zone (50-100 cm) along the whole slope (group III), with sample M950u as exception.

Plotting the absolute densities (ind./100 m^2) (as a bubble value) of certain taxa on the MDS plot (*cfr.* Fig. 4.6) illustrates the taxa responsible for the community structure patterns for the hyperbenthos along the Meriadzek Terrace slope (Fig. 4.8) (see also SIMPER-lists Table 4.6). Group I or the lower BBL on the upper slope is discriminated by the taxa Amphipoda, Mysidacea and Copepoda. This latter taxon, together with the taxa Euphausiacea and Chaetognatha, are the taxa characterizing group III or the upper BBL along the complete slope. Clustering of the samples from group II is mainly based on the high abundances of the taxa Amphipoda, Cumacea, Isopoda and Tanaidacea.

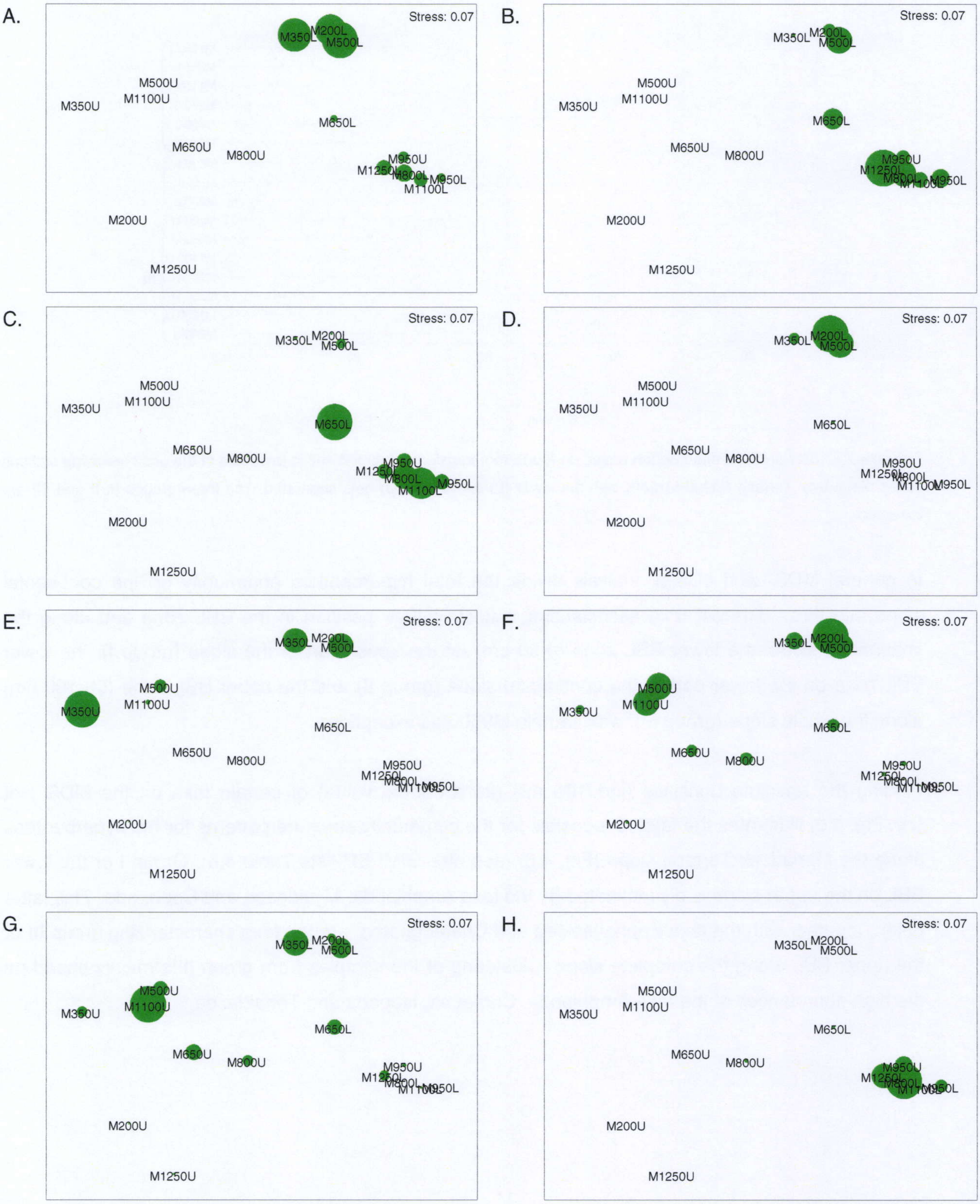


Figure 4.8 Bubble plots based on the MDS plot (*cfr.* Fig. 4.6), indicating the absolute density (ind./100 m²) of A) Amphipoda, B) Isopoda, C) Cumacea, D) Mysidacea, E) Euphausiacea, F) Copepoda, G) Chaetognatha and H) Tanaidacea for each Meriadzek Terrace station (M200-M1250). U= upper net sample; L= lower net sample.

Significance tests for differences in the hyperbenthic community structure between the three defined groups (I, II and III) were performed using the one-way ANOSIM tests (Clarke, 1993). The ANOSIM results (Table 4.5) indicate that the three hyperbenthic taxa associations are significantly different, with the highest dissimilarity (44 %) between the groups II and III. The average dissimilarity between all assemblages is 37 %.

Table 4.5 Results of the ANOSIM and pair-wise tests for difference on hyperbenthic community structure between the zones of the benthic boundary layer and along the continental slope (I= lower BBL on upper slope; II= lower BBL zone on lower slope; III= upper BBL zone along the whole slope).

	Dissimilarity	R-value	*p*-value
Global test	37%	0.871	0.001
groups compared			
I - II	30%	0.861	0.008
I - III	38%	0.975	0.012
II - III	44%	0.925	0.002

The taxa contributing to dissimilarities between the three groups were investigated using a similarity-percentages procedure (SIMPER, Clarke, 1993). The SIMPER-list (Table 4.6) shows the contribution percentages of the top three discriminating taxa for each defined group. Group III shares no top three taxon with any of the other two groups, while the lower BBL associations have Amphipoda as the most discriminating taxon.

Table 4.6 SIMPER-lists, showing the contribution percentages of the top three discriminating taxa for each taxa association.

Group I: lower BBL on upper slope		Group II: lower BBL on lower slope		Group III: upper BBL along whole slope	
Amphipoda	18%	Amphipoda	15%	Copepoda	26%
Mysidacea	17%	Cumacea	15%	Euphausiacea	15%
Copepoda	16%	Isopoda	13%	Chaetognatha	14%

Alpha diversity and dominance structure of hyperbenthic communities

Diversity indices of Hill of the three defined groups are significantly different (Kruskall-Wallis test significance levels: p= 0.0155 for N_0, p= 0.0482 for N_1, p= 0.0319 for N_{inf}; $p<0.05$ for all Hill indices) (Fig. 4.9A). Highest diversity is found for the lower BBL on the lower Meriadzek Terrace slope. Overall, very similar patterns are found for the three communities in the k-dominance plots (Fig. 4.9B). The upper BBL community (group III) shows the highest dominance, 63 % Copepoda. For the two lower BBL communities this is 35 % Mysidacea and 29 % Cumacea for the upper slope and lower slope community respectively.

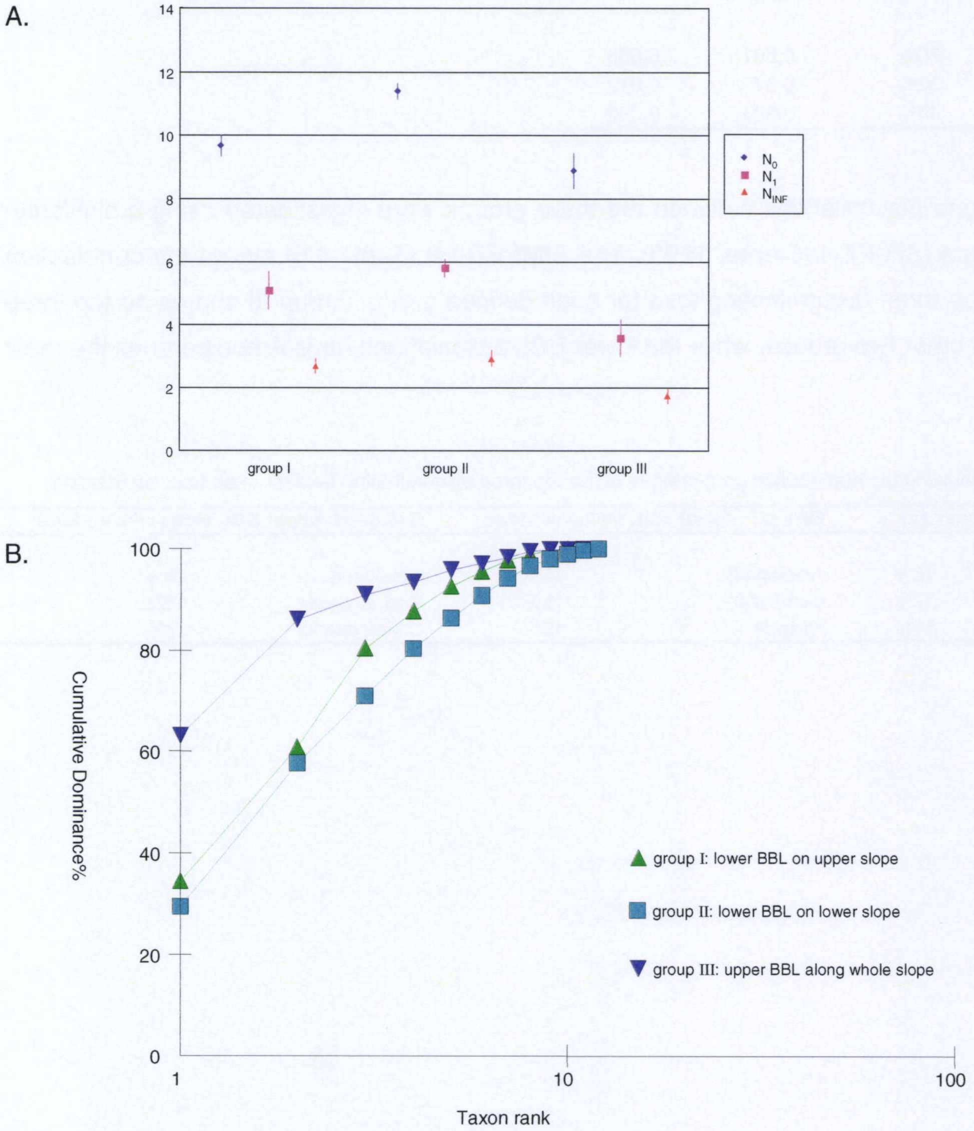


Figure 4.9 Alpha diversity of the hyperbenthic communities within the BBL along the Meriadzek Terrace slope: A) diversity indices of Hill (N_0, N_1 and N_{inf}) and B) corresponding k-dominance curves.

Link with environmental variables

A BIO-ENV analysis, with a Spearmann rank correlation method, with the similarity matrix from the hyperbenthic taxa density data and the reduced environmental variables dataset (see Draftsman plot) was performed for the upper and lower BBL zone (net) samples separated. For the lower BBL samples along the continental slope a combination of mud and dissolved oxygen best explain (ρ=0.883) the hyperbenthic community structure. A slightly different combination is found for the upper BBL samples, where salinity and dissolved oxygen best explain (ρ=0.553) the hyperbenthic community structure, thus indicating a closer link of the hyperbenthic taxa (mainly Cumacea and Isopoda) in the lower BBL zone with the very fine sediments, while the upper BBL zone taxa seem to be more influenced by environmental variables linked to the water column. This latter may be a reflection of a 'pelagial' fauna in the 50-100 cm BBL zone.

4.2.2.2. Bathymetric distribution of the hyperbenthos at Meriadzek Terrace

For the bathymetric distribution (*i.e.* along the slope in the zone 0-100 cm above the sediment) the station samples as the sum of the upper and lower net sample are considered and analysed.

Relative abundance

The distribution of the hyperbenthic taxa along the continental slope is illustrated by the relative taxa composition of each station (M200-M1250) (Fig. 4.10). The distribution of the hyperbenthos along the depth gradient on the continental slope is studied by means of the eight stations ranging from 200 m to 1250 m of water depth.

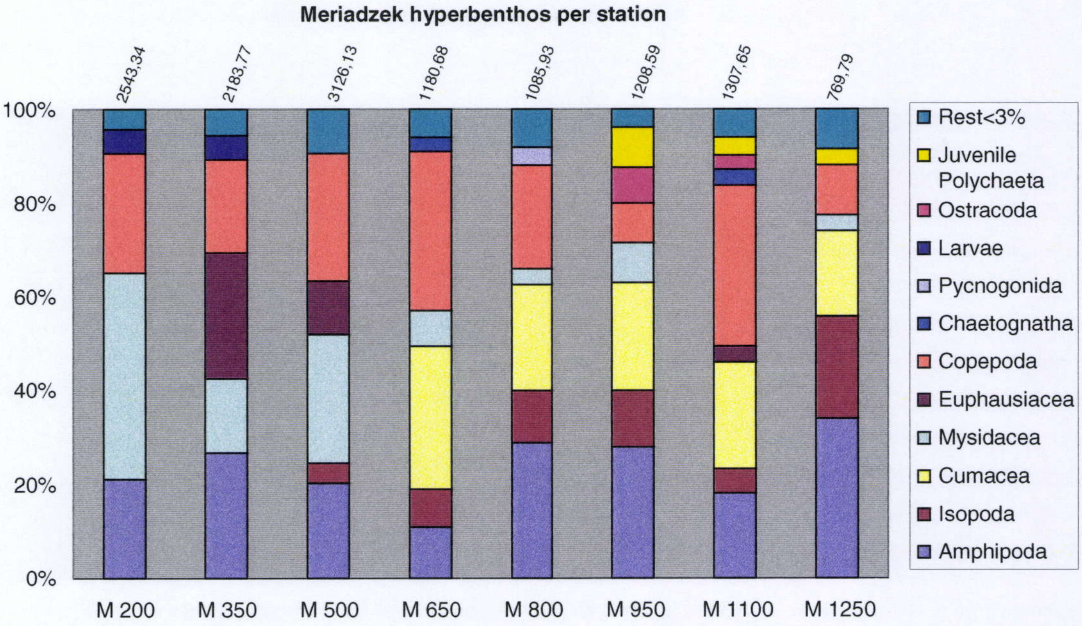


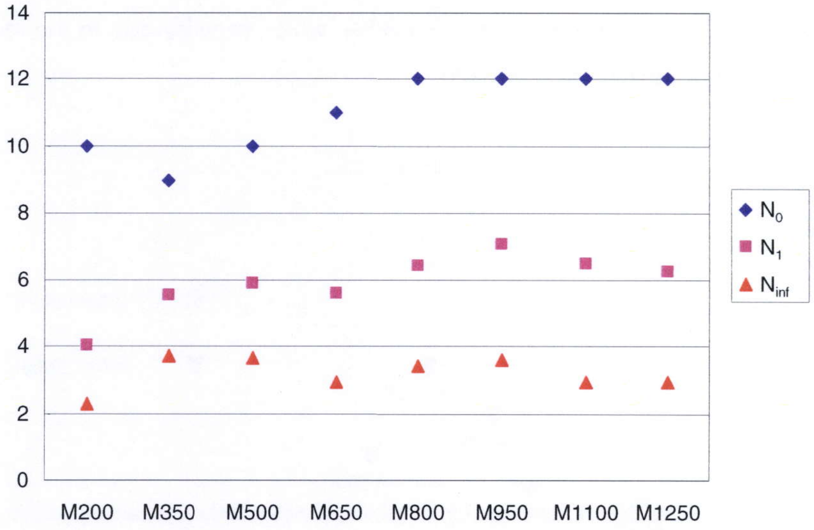
Figure 4.10 Relative hyperbenthic taxa composition for the eight stations (M200-M1250) at the Meriadzek Terrace. The absolute total hyperbentic density per station is indicated above each bar.

Amphipoda are of great importance along the complete continental slope (across isobaths), ranging from 11 % at station M650 to 34 % at station M1250. The Isopoda exceed the 3 %-limit at station P500 and then show an increase with depth, except at station M1100, with a maximum of 21 % at station M1250. A similar pattern is observed for the Cumacea which display relative high percentages starting at station M650 (30 %) with a high share in all deeper stations. Mysidacea are present in all stations, decreasing with depth, in station M1100 they belong to the 'rest' group. Euphausiacea are mainly present at stations M350 (27 %) and M500 (12 %).

Alpha and beta diversity

Diversity indices of Hill are very similar for the eight stations at Meriadzek Terrace (Fig. 4.11A), at station M950 a very small peak is observed. The k-dominance plot (Fig. 4.11B) confirms this trend and indicates the lowest diversity at station M200, with the highest dominance of 44 % Mysidacea.

A.



	M200	M350	M500	M650	M800	M950	M1100	M1250
N_0	10	9	10	11	12	12	12	12
N_1	4,00	5,49	5,84	5,56	6,42	7,07	6,46	6,23
N_{inf}	2,29	3,70	3,66	2,95	3,44	3,59	2,92	2,93

B.

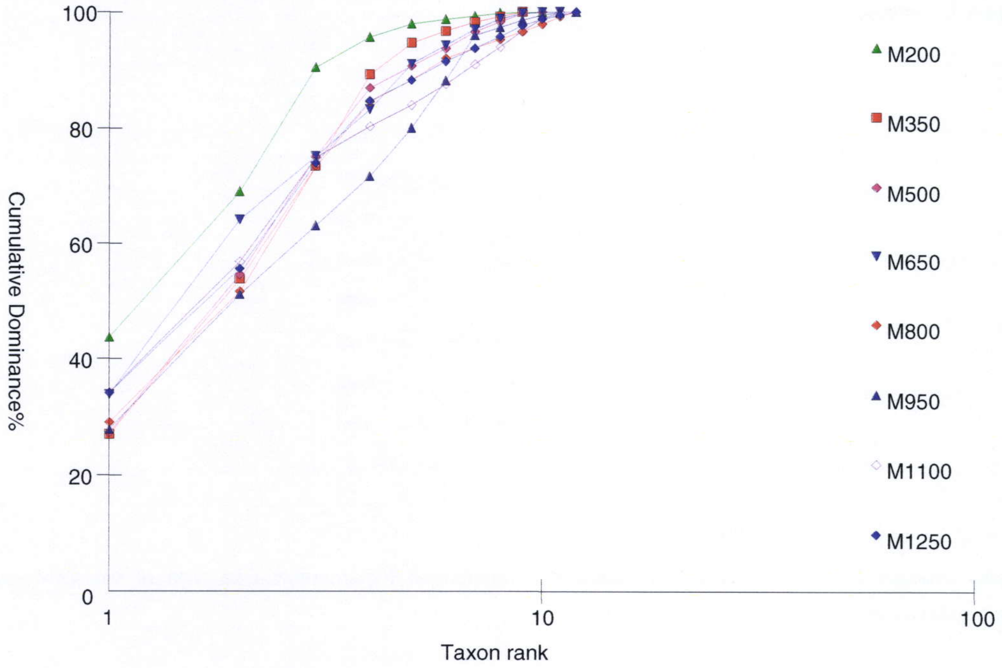


Figure 4.11 Alpha and beta diversity of the hyperbenthic taxa along the Meriadzek Terrace continental slope (M200-M1250): A) diversity indices of Hill (N_0, N_1 and N_{inf}) and B) corresponding k-dominance plot.

Hyperbenthic communities along the Meriadzek continental slope

MDS-analysis clearly divides an upper slope group from a lower slope group (Fig. 4.12). The distance between two groups of stations clearly illustrates the faunal break at the shelf/slope transition (at circa 500 m). This pattern is confirmed by the hierarchical clustering with group averaged linking illustrated by the cluster-analysis dendrogram (Fig. 4.13) but an ANOSIM-analysis indicated these groups as not significantly different (global R= 0.99, significance level= 1.8 %), which may be due to the low number of taxa and the occurrence of most taxa in each sample.

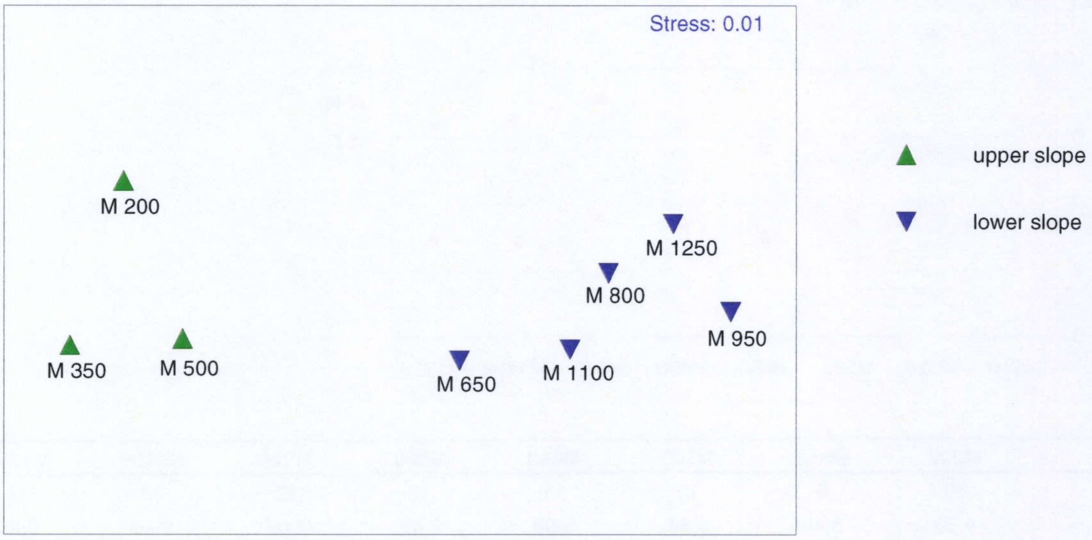


Figure 4.12 Multi-dimensional scaling (MDS) plot based on fourth-root transformed hyperbenthic taxa data of the eight stations (M200-M1250) at the Meriadzek Terrace.

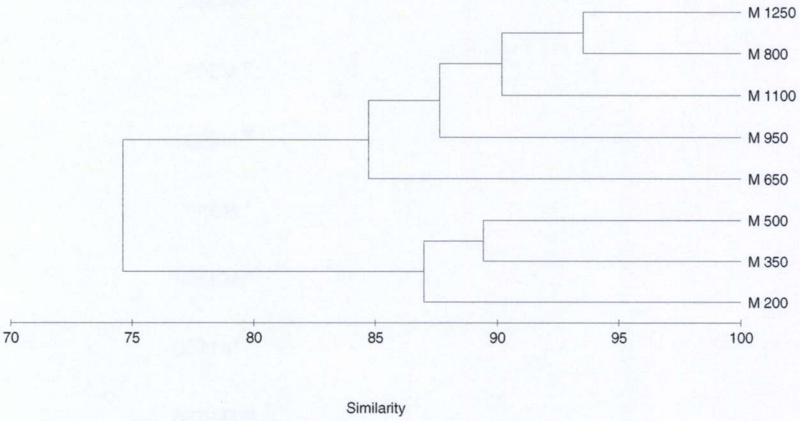


Figure 4.13 Cluster analysis dendrogram based on fourth-root transformed hyperbenthic taxa data of the eight stations (M200-M1250) at the Meriadzek Terrace.

Compared to the community structure of the hyperbenthos with the two BBL zones separated (*i.e.* two nets, see vertical distribution Fig. 4.6), the effect of the upper net samples is minimal in the community structure pattern when the stations are considered (see further 4.2.2.3.)

Plotting the absolute densities of four dominant taxa (Fig. 4.14) on the MDS plot (*cfr.* Fig.4.12) illustrates the taxa reflecting the community structure pattern found. Mysidacea (Fig. 4.14A) and Euphausiacea (Fig. 4.14B) mainly characterize the upper slope community, while the taxon Cumacea (Fig. 4.14C) plays an important role in shaping the lower slope community (also for Isopoda but not shown). Amphipoda (Fig. 4.14D) are found along the complete gradient, but an obvious difference in density between the two slope communities is illustrated.

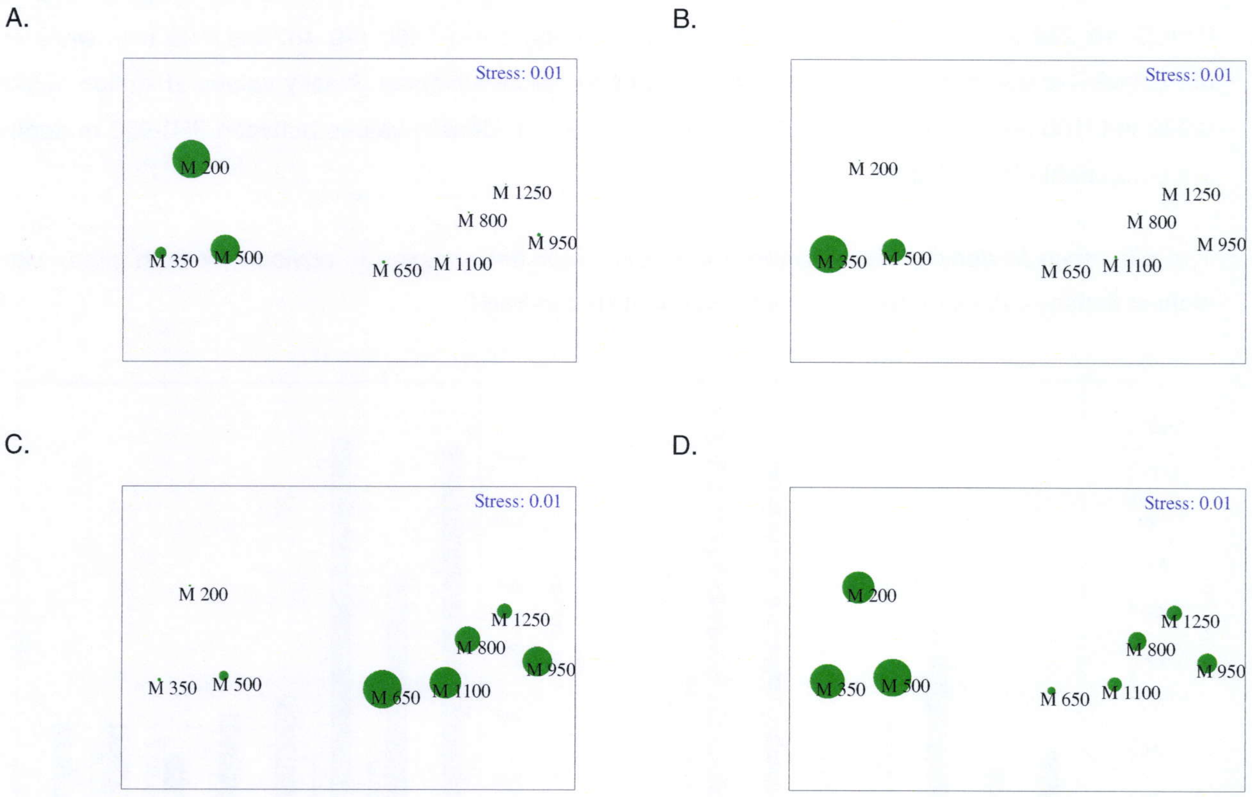


Figure 4.14 Bubble plots based on the MDS plot (*cfr.* Fig. 4.12), indicating the absolute density (ind./100 m^2) of A) Mysidacea, B) Euphausiacea, C) Cumacea and D) Amphipoda.

Link with environmental variables

A BIO-ENV analysis, with a Spearmann rank correlation method, with the similarity matrix from the hyperbenthic taxa data and the reduced environmental variables dataset (see above) was performed. A combination of mud, depth and dissolved oxygen best explain (ρ=0.846) the hyperbenthic community structure along the continental slope, thus the effect of the lower BBL taxa is also found here, in combination with depth being a structuring factor for the distribution of the hyperbenthos along the continental slope.

4.2.2.3. Comparing the hyperbenthic distribution and community structure along continental slopes: Porcupine Seabight versus Meriadzek Terrace

Comparing the hyperbenthic absolute density (Fig. 4.15) along the depth gradient of Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250) a different trend is observed. At Porcupine Seabight density increases with depth reaching highest density at the two deepest stations P1100 (10 232 ind./100 m² in the lower and upper nets) and P1250 (19 487 ind./100 m²), while at Meriadzek Terrace density decreases with depth and reaches highest density values at station M200 (2543 ind./100 m²) and at station M500 (3126 ind./100 m²). Density values between 650-950 m depth are comparable for both sites.

The difference in density between the upper and lower net samples is obvious for both sites, with highest density values for the lower nets except at station M950.

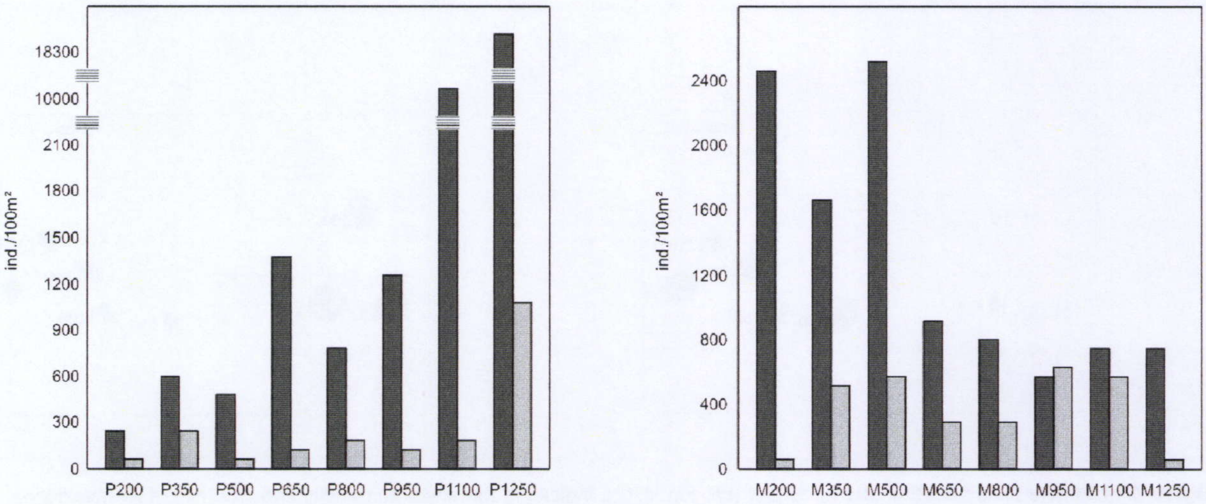


Figure 4.15 Total absolute density (ind./100 m²) of the hyperbenthos in the lower nets (dark grey) versus the upper nets (light grey) for each station at both study sites Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250). Note the different scales used.

Community structure is illustrated in the MDS plot based on the upper and lower net samples of the eight Porcupine Seabight stations and the eight Meriadzek Terrace stations (Fig. 4.16).

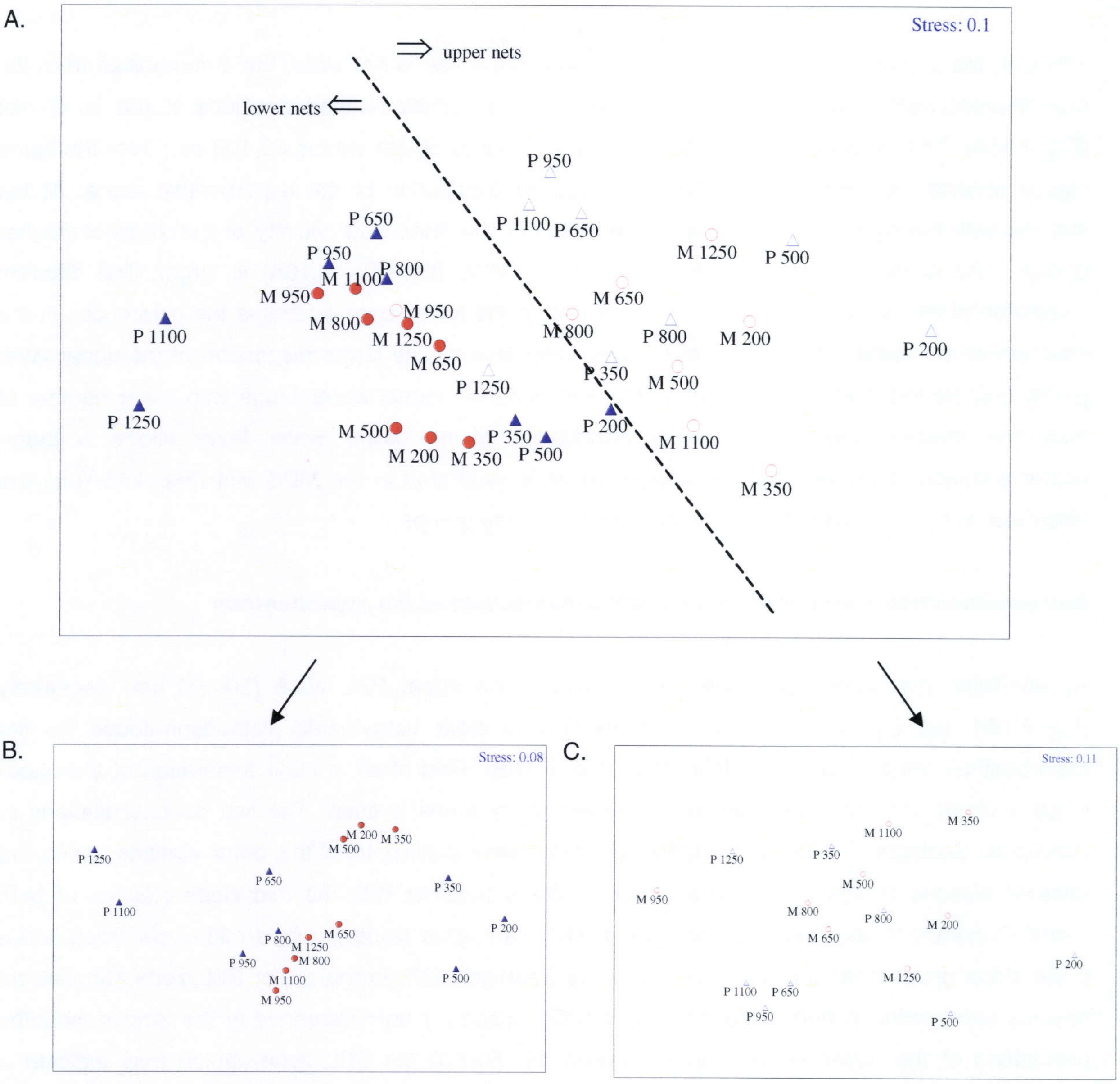


Figure 4.16 Multi-dimensional scaling (MDS) plot based on the fourth-root transformed hyperbenthic taxa data for A) the eight lower net samples (full symbols) and upper net samples (open symbols) of the eight stations of Porcupine Seabight (P, triangle symbol) and Meriadzek Terrace (M, circle symbol); for B) the 16 lower net samples of Porcupine Seabight (P, triangle symbol) and Meriadzek Terrace (M, circle symbol) and for C) the 16 upper net samples of Porcupine Seabight (P, triangle symbol) and Meriadzek Terrace (M, circle symbol).

Between geographical areas or hyperbenthic distribution along isobaths

The MDS plot (Fig. 4.16A) shows no clear separation of the samples of the two geographic areas Porcupine Seabight and Meriadzek Terrace indicating small differences in faunal composition between the two study sites, thus the hyperbenthic taxa distribution along isobaths in the present study seem to be quite homogeneous.

Stratified distribution within the BBL

Although the separation of the samples by geographic areas is not clear, the communities from the two different water layers (0-50 cm and 50-100 cm) occupy defined positions in the MDS plot (Fig. 4.16A). The distance between the two water layers (0-50 cm versus 50-100 cm) from the same station reflects the near-bottom vertical or stratified distribution of the hyperbenthic fauna. At the stations with the hyperbenthos more concentrated in the immediate vicinity of the seafloor (higher density), the distance between water layers in the MDS plot (Fig. 4.16A) is larger. The different dispersion of the points referring to the upper and to the lower layer illustrates the differences in the structure of the faunal assemblage of the two water layers. The larger dispersion of the upper layer points may be interpreted as a result of the impoverished faunal assemblage with lower number of taxa and density values. The higher abundance of the lower water layer allows a better characterization of the faunal assemblages which is illustrated in the MDS plot (Fig. 4.16A) by the closeness of the points and the marked delineation of the groups.

Bathymetric distribution or across isobaths distribution of the hyperbenthos

By analyzing the lower BBL zone (0-50 cm) and the upper BBL zone (50-100 cm) separately (Fig. 4.16B and Fig. 4.16C respectively) there is a clear bathymetric distribution found for the hyperbenthos living in the lower BBL zone (Fig. 4.16B). First of all, a clear separation of the upper slope stations (200, 350 and 500 m) of the two study areas is seen. The two deepest stations of Porcupine Seabight (P1100 and P1250) are completely distinct from the other stations, while the deepest stations of Meriadzek Terrace are clustered together with the mid slope stations of both areas. Generally three groups can be distinguished, an upper slope group, a mid slope group and a lower slope group (the latter only for Porcupine Seabight). Within the upper BBL zone samples no obvious bathymetric pattern is found (Fig. 4.16C), indicating no differences in the across isobaths distribution of the hyperbenthic taxa occupying the 50-100 cm BBL zone, which may indicate a reflection of a 'pelagic' assemblage.

4.3. Discussion and conclusions

4.3.1. Hyperbenthic communities at Meriadzek Terrace and Porcupine Seabight: along isobaths distribution

The two study sites, Porcupine Seabight and Meriadzek Terrace, were sampled during the spring/early summer period by a standardized sampling strategy (see Chapter 2). At Porcupine Seabight hyperbenthic sampling was done in June 2000, while at Meriadzek Terrace hyperbenthic sampling was performed in April-May 2002. A similar hyperbenthic taxa composition was found at the two slope sites. Density values differ significantly between the two areas, with higher total densities at Porcupine Seabight, for the eight stations this values 35 183 ind./800 m², while for Meriadzek Terrace this is about 2.6 times less (13 406 ind./800 m²). This difference in total density is mainly ascribed to the lower net samples, more specifically those of the two deepest stations, at Porcupine Seabight, tripling the density of the lower net samples at Meriadzek Terrace. For the upper net samples the densities are very comparable with the highest total value for Meriadzek Terrace, 2967 ind./800 m² and 1975 ind./800 m² for Porcupine Seabight. Amphipoda, Isopoda, Cumacea, Ostracoda and Pycnogonida are the taxa attributing to the higher density values in the lower net samples at Porcupine Seabight, while the Mysidacea, Euphausiacea and Copepoda show higher densities at Meriadzek Terrace.

According to Gage & Tyler (1991), distribution of higher taxa is rather homogeneous along isobaths in the deep sea. This is also confirmed for hyperbenthic higher taxa along the two studied continental slopes as no clear separation between the two geographical areas was found, so the along isobaths distribution of the hyperbenthic higher taxa is wide spread. Although the geographic distribution of individual taxa is quite homogeneous, this cannot be generalized for all species belonging to these higher taxa. Some deep-sea species are widespread while many others have a restricted distribution. In the present study, the species-specific distribution of the major hyperbenthic higher taxa (Peracarida) is studied in detail in chapter 5. It is difficult to compare the present density estimates of major higher taxa to other published observations on abyssal benthic assemblages from the NE Atlantic due to the disparity of sampling and sorting methods (*e.g.* different sampling devices and mesh size).

4.3.2. Stratified distribution of the hyperbenthos at Meriadzek Terrace and Porcupine Seabight

The most striking division found for the hyperbenthic higher taxa of the two study sites (each separate and both sites together) was the one related to their stratified or near-bottom distribution. An obvious separation of the lower (0-50 cm) and the upper (50-100 cm) BBL zone was found in the analysis, reflecting a stratification of pelagic higher taxa inhabiting the upper BBL zone and benthopelagic higher taxa concentrated in the 0-50 cm BBL zone. This **vertical distribution** within the BBL zone of the hyperbenthic higher taxa is very obvious in both study areas. Copepods make up the largest percentage in the **upper BBL zone** (50-100 cm) in both continental slope areas with an average percentage of 40 % and 57 % at Porcupine Seabight and Meriadzek Terrace respectively. At Porcupine Seabight, in contrast to Meriadzek Terrace, Amphipoda and Cumacea still make up a significant part in the upper BBL zone with an average of 20 % and 19 % respectively. At Meriadzek Terrace Euphausiacea are more important (average of 20 %) in the upper BBL zone than in Porcupine Seabight, even in the deeper stations. Although the general patterns in higher taxa composition in the upper BBL zone in the two areas are very similar, some differences in relative share of the different higher taxa were found.

Comparing the higher taxa composition found in the **lower BBL zone** (0-50 cm), this also shows similar patterns for both study sites. Amphipoda appear along the complete slope in both areas with an average of circa 30 %, followed by the Cumacea with an average of circa 25 % for both areas. This latter taxon belongs to the rest group in some upper slope stations (P200, M200 and M350) of both areas and is absent in station P500. Both Cumacea and Isopoda increase significantly with depth starting from circa 500 m depth in both sites. Mysidacea are strongly abundant at the upper slope stations but a decrease with depth is observed at both Porcupine Seabight and Meriadzek Terrace. Moreover, the multivariate analysis of only the upper BBL zone samples of the two slope areas did not reveal any significant differences in the hyperbenthic distribution related to depth and the associated environmental factors. Previous results in this PhD research already revealed the dominance of Copepoda in the upper BBL zone. Euphausiacea are important, mainly at Meriadzek Terrace, while Mysidacea displays higher densities at Porcupine Seabight. For both areas Amphipoda, Cumacea and Chaetognatha also determine a small part of the upper BBL zone fauna. These organisms, mainly Copepoda, Euphausiacea and Mysidacea have higher swimming capabilities and their bottom dependence is much smaller then for benthopelagic taxa. Moreover they display different feeding strategies, but this subject will be studied and discussed in more detail in chapter 5.

Despite the problem of comparison to other published observations on bathyal benthic assemblages from other deep-sea areas due to the disparity of sampling and sorting methods (*e.g.* different sampling devices and mesh size), some general vertical distribution patterns can be demonstrated based on previous studies on hyperbenthic communities conducted on the continental margins in the Bay of Biscay (Dauvin *et al.*, 1995; Elizalde *et al.*, 1993; Sorbe & Weber, 1995; Sorbe, 1999; Marquiegui & Sorbe, 1999; Corbari & Sorbe, 2001; Vanquickelberghe, 1999; Dewicke, 2002), the Portuguese margin (Cuhna *et al.*, 1997, 1999) and the Catalan Sea (NW Mediterranean) (Cartes, 1998). These studies, where sampling was performed with similar hyperbenthic sledges (sampling one meter of the water column), report a similar taxonomic composition and indicate distinct differences in the near-bottom environment. On the continental margin, the BBL fauna shows a general trend of decreasing numerical density with increasing distance to the ocean floor. This near-bottom distribution was also illustrated in this PhD research. Swimming activity and diel changes in the vertical distribution of hyperbenthic organisms have been studied and described by several authors (Macquart-Moulin, 1984, 1991; Dauvin & Zouhiri, 1996). Species-specific behavioural patterns together with other factors such as light, currents or food availability determine the swimming activity and thus the vertical distribution of hyperbenthic animals (Fosså, 1985, 1986; Elizalde *et al.*, 1991; Vallet *et al.*, 1995). The results discussed here are based on data on higher taxonomic level, while information on causes for the vertical distribution of organisms is very species-specific. The lack of knowledge on specific species ecology therefore restricts further insight into possible direct relations.

4.3.3. Across isobaths distribution: zonation of the hyperbenthos at the two continental slopes

Studying the **bathymetric distribution** of the hyperbenthic higher taxa along the two continental slope areas Porcupine Seabight and Meriadzek Terrace, some patterns become even more pronounced. There is a clear shift in higher taxa composition with depth, which can be generalized for the two sites. A significant increase of Cumacea and Isopoda is seen starting at the station at circa 650 m depth, this in contrast to a decrease of Mysidacea and Euphausiacea with depth. Copepoda and Amphipoda show a more evenly spread distribution along the slope.

Similar bathymetric distribution patterns for the hyperbenthic higher taxa as found for Porcupine Seabight and Meriadzek Terrace are described in literature. High percentages of **mysids** at the upper slope zone and the obvious decrease with depth were also reported for other Atlantic deep-sea communities (Fosså & Brattegard, 1990; Elizalde *et al.*, 1991; Cartes & Sorbe, 1995; Sorbe, 1999; Vanquickelberghe, 1999; Dewicke, 2002). This bathymetric zonation of hyperbenthic mysids is quite similar for different geographical areas (Cartes & Sorbe, 1995; Fosså & Brattegard, 1990), and might be caused by their feeding strategy in combination with other factors (see chapter 5). The relatively importance of **Amphipoda** in the one meter BBL in both Porcupine Seabight and Meriadzek Terrace was also found at the Cap-Ferret Canyon (Sorbe, 1999) and on the Catalan Sea slope (Cartes,1998). **Cumacea** and **Isopoda** were nearly absent at the upper slope region and tended to expand with depth along the slope. At bathyal depths of the Cap-Ferret canyon, isopods accounted for more than 40 % of the total hyperbenthos density (Sorbe, 1999). The numerical importance of the Isopoda in the deep sea was also previously recognized in many other Atlantic communities (Sander *et al.*, 1965; Dahl *et al.*, 1976; Gage, 1977, 1979; Gage *et al.*, 1980; Laubier & Sibuet, 1979; Sibuet *et al.*, 1984; Thistle *et al.*, 1985).

Grain size distribution of the sediment was often correlated with abundances of hyperbenthic amphipods (Buhl-Jensen, 1986; Marques & Bellan-Santini, 1993; Dauvin & Sorbe, 1995), isopods (Svavarsson *et al.*, 1990) and cumaceans (Roccatagliata, 1991). The increased density for amphipods, cumaceans and isopods at the lower slope at Porcupine Seabight and Meriadzek Terrace coincides with a decrease in median grain size and a higher mud content of the sediment. This trend is more pronounced at Meriadzek Terrace, for Porcupine Seabight the sediment composition along the slope is slightly different, with a very fine sediment between 650 and 950 m water depth, but an increase of fine sand and thus the median grain size at the deepest stations (between 1100-1250 m) (see chapter 3). It is also important to mention that catches by the hyperbenthic sledge may have been slightly contaminated by the fauna present in the upper centimeter of the bottom triggered by disturbance and resuspension by the biting of the sledge into the sediment, which may be a parameter to keep in mind especially for the stations where the sediments is mainly composed of mud (< 63 µm). Sediment characteristics of the biotope in which species are found, are generally reported in hyperbenthic literature (*e.g.* Cunha *et al.*, 1997; Dauvin *et al.*, 2000). Dauvin *et al.* (1994) mentioned that the highest densities were generally recorded on fine sediments in regions with an important input of organic matter to the bottom environment. Still, evidence for species-specific relations remains poorly documented. Muddy bottoms are often thought to have potential food availability. The grain size distribution is here believed to reflect the exposure and dynamics of the area. The majority of the hyperbenthic fauna is non-burrowing and may rather be dependant on the hydrodynamical mechanisms causing deposition and resuspension, than on the sediment structure itself. Yet, several exceptions certainly exist, as there are some burrowing mysids, several amphipod and cumacean species (Jones, 1976; Lincoln, 1979).

Bathymetric distribution and more specifically the distribution related to the shelf break area is a hot topic in deep-sea research. Early studies related the major physiographical and hydrographical features of the continental margin to boundaries of major zones of the fauna down the depth gradient. In the present study a marked distinction could be made concerning the community structure patterns related to depth found in the lower versus the upper BBL zone, when separating the samples of both BBL zones. It was clear that no depth related structure was found within the upper BBL samples, indicating a homogeneous distribution of the hyperbenthic higher taxa within the 50-100 cm water layer along the complete continental slope in both study sites. This in contrast to the hyperbenthic higher taxa distribution in the lower 50 cm of the BBL, which shows an obvious depth related distribution or zonation along the depth gradient of both slopes.

The **lower BBL zone** samples of Porcupine Seabight are clearly divided in three depth zones: an upper slope, a mid slope and a lower slope community. The lower BBL zone samples of Meriadzek Terrace are divided in only two depth zones. For both sites, the shelf break (or upper slope) is clearly split of from the deeper slope although there is no common separation for the deepest stations of the two sites: the deepest stations at Porcupine Seabight (P1100 and P1250) are clearly distinct from all the other deeper stations. Explanation for the observed bathymetric patterns can be looked for in the measured environmental variables and in the oceanographical data available.

Shelf/slope transition

As mentioned before, patterns with depth linked to the shelf/slope transition zone has been confirmed repeatedly (Sanders & Hessler, 1969; Haedrich *et al.*, 1975; Carney & Carey, 1982). The shelf break is likely to be intermediate between the two contrasting situations of shelf and slope and this affects various marine organisms.

Nevertheless this shelf break coincides with strong gradients in the physical environment and it is characterized by a very pronounced transition in fauna. Zonation control however can be explained by a wide variety of depth related gradients including physical (*e.g.* temperature, currents) and biological (*e.g.* resource availability, interspecific competition) factors, but it still remains poorly understood which factors causes hyperbenthic zonation patterns. Dewicke (2002) studied the bathymetric distribution of hyperbenthos along the shelf break and upper slope zone at Meriadzek Terrace between 200-700 m and found a pronounced shift in community structure between the shelf break (250-300 m depth) and the upper slope (600-700 m depth). The bathymetric distribution of mysids, euphausiids and decapods (good swimmers) is believed to be rather related to properties of the water column (*e.g.* light transmission, suspended matter concentration), than to sediment characteristics (Dewicke, 2002). The increase at the upper slope of bottom-dependant taxa such as amphipods, cumaceans and isopods is suggested to be more related to a change in sediment structure, in addition to variations in organic particle transport in the benthic boundary layer (Dewicke, 2002).

Mid- and lower slope communities

A clear discontinuity in sediment composition below 1000 m was observed at Porcupine Seabight in contrast to Meriadzek Terrace. The sediment at the two deepest stations (P1100 and P1250) becomes coarser than the above stations, revealing the existence of a high energy environment. Besides the discontinuities in sediment composition at Porcupine Seabight, the explanation for the separation of stations P1100 and P1250 related to higher densities found at those depths, can be searched for in the local hydrographical features. These features can result in an ample supply of food. The most obvious agency by which this might be explained is the resuspension of sedimented organic particles by near-bed water currents. Besides the general poleward flows (the slope current as described in chapter 2), there exist relatively strong internal tides and associated internal waves inducing these near-bed currents. Internal tides and waves have been observed at several locations along the NE Atlantic margin (Sherwin & Taylor, 1987). They are periodic oscillations in the water column formed by disturbances in the vertical density stratification (White, 2001). They generally originate from the interaction of the stratified water column with sharp changes in the seabed topography. The Celtic slope is one of the classical examples, and appears to be one of the most energetic slopes of the world, from this respect (Baines, 1982). Locations along the continental slope where the slope of the bathymetry is equal or exceeds the characteristic slope angle (α), as defined by Huthnance (1986), are likely locations for internal tide and wave generation. This characteristic slope (α) is defined as a function of the wave frequency, the Coriolis frequency at this latitude, the depth and the degree of water stratification (Huthnance, 1986). This is in particular the case in the eastern Porcupine Seabight, where the local slope exceeds the characteristic slope (α). This can result in enhanced near-bottom currents and turbulence (Rice *et al.*, 1990), which dependant on their velocity can induce resuspension. The strongest across-slope near-bottom tidal currents in the Porcupine Seabight are probably of the order of 15-20 cm/s, and occur around the 500-1000 m depth contours on the eastern flank (Rice *et al.*, 1990). Such currents are certainly sufficiently powerful to resuspend flocculent phytodetrital material (Lampitt, 1985) and might even resuspend less flocculent sedimented material. They would also delay the deposition of any sinking material entering the region compared with areas where the near-bed currents are less rapid. These rather perturbed conditions can be considered as natural causes of stress or instability that certainly influence the community structure of the hyperbenthos of Porcupine Seabight.

These observations were also the argumentation of Rice *et al.* (1990) who found dense aggregations and high biomass of the hexactinellid sponge *Pheronema carpenteri* in the Porcupine Seabight in a very restricted bathymetric zone between 1000 and 1300 m depth. Although *Pheronema* is not found within these areas of enhanced currents, Rice *et al.* (1990) states that the suspension feeding sponge is probably unable to withstand exposure to the high current speeds directly, but is dependent upon the resulting increased organic particulate load being deposited downslope or carried along the slope in the generally northward drift of the slope current.

A peak in density and biomass of suspension feeding taxa within macrofauna, megafauna and benthic foraminifera was observed at circa 1000-1500 m along the continental slope in the Goban Spur area (NE Atlantic) (Flach *et al.*, 1998). These peaks coincided with a zone where the highest flow velocities were measured along this continental slope. Thus, at these depths a high load of (re)suspended material provides good feeding conditions for suspension and interface feeders.

In contrast to Porcupine Seabight, the fine particles enrichment trend with increasing depth at Meriadzek Terrace indicates calmer conditions along this continental slope. Hydrodynamic conditions are less pronounced in this area due to the less steep slope, reducing the current velocities. These features can possibly explain the observed hyperbenthic density and community patterns at Meriadzek Terrace and the differences with the patterns found at Porcupine Seabight.

Chapter 5

Biodiversity of peracarid crustaceans of two continental slope areas in the NE Atlantic

- 5.1. Introduction and objectives
- 5.2. Results
- 5.3. Discussion and conclusions

5.1. Introduction and objectives

Diversity has been a major topic of deep-sea biology since the discovery that deep-sea faunas are highly diverse (Sanders *et al.*, 1965; Sanders & Hessler, 1969). The pattern of diversity in the deep sea appears to be less predictable than previously thought and the pattern differs between taxa and even within short distances (Jumars, 1976), suggesting that local environmental phenomena may be involved in maintaining a high diversity. With high diversity now accepted as a characteristic of the deep-sea fauna, several hypotheses were offered to explain this: among them the 'time-stability theory" (Sanders, 1968) and the 'spatial heterogeneity theory' (Grassle, 1977) are tested. The 'time-stability theory' attributes diversification to evolutionary time: older communities are more diverse than younger ones (Sanders, 1968). 'Spatial heterogeneity theory' argues that the more heterogeneous and complex the physical (topographical) environment is the more complex and diverse its fauna becomes (Grassle, 1977). Both disturbance in the long term and spatial heterogeneity obviously play a major role in structuring and maintaining highly diverse deep-sea species assemblages, as long as the disturbance is not too severe (Brandt, 1997c).

In addition to the theories, a number of factors have been discussed which possibly shape abundance and biodiversity in the deep sea. Some of these factors are absence of light and the high hydrostatic pressure (Dayton & Hessler, 1972), the low temperature (about 4°C; at 4500 m only 2.5°C), the currents and the seamounts. Generally also a low food supply (Hessler & Jumars, 1974; Hessler & Wilson, 1983) has been assumed to be important for a high spatial variability of feeding conditions on the ocean floor. The search for food is one of the most important tasks in marine environments (Kaïm-Malka, 1997). Food determines animals' activities, reproduction, development, juvenile recruitment and the maintenance of the species in the field. It is widely recognized that the food available becomes scarcer as the depth increases and that species have evolved very elaborate behavioural patterns to find food and make the best possible use of it.

In addition, as deep-sea sediments are usually very fine, it is not astonishing that deposit feeders comprise the overwhelming majority (Hessler & Jumars, 1974). Lampitt *et al.* (1986) published data from a survey of the Porcupine Seabight between 500 and 4100 m depth and found about a 30-fold decrease in biomass over this depth range. Within this biomass suspension-feeding crustaceans were dominating.

Among the more diverse major (hyper)benthic taxa in the deep sea are **peracarid crustaceans** belonging to the orders Amphipoda, Isopoda, Cumacea, Tanaidacea and Mysidacea (Jones & Sanders, 1972; Cartes & Sorbe, 1996). However the Mysidacea are distributed mainly in the upper bathyal and seem to have originated from the continental shelf (Gage & Tyler, 1991). Peracarid crustaceans are well adapted for a life in the deep sea due to their small body size and brood protection in the marsupium (Hessler & Wilson, 1983). This latter might favour the Peracarida over other Crustacea, such as larger decapods, which are relatively rare in the deep sea (Brandt, 1997c). The long evolutionary history of peracarids in the deep sea, as can be deduced from fossil records of

isopods and cumaceans from the upper Carboniferous and Permian respectively (Hessler & Wilson, 1983), might represent another advantageous factor (Gage & Tyler, 1991). Amphipods were probably not present until the Tertiary period (Hessler & Wilson, 1983).
Peracarid crustaceans are mostly deposit feeders, their aggregations might cause small-scale disturbances on the seafloor due to bioturbation, which can also be associated with some level of organic enrichment (Gage & Tyler, 1991). Bioturbation and sediment mixing are known to enhance microbial activity (Kristensen & Blackburn, 1987). Peracarids are potentially important in maintaining high faunal diversity in the deep sea. Piepenburg *et al.* (1997) documented that peracarid crustaceans are primarily correlated with the potential food supply and sediment composition. However, the relationship between productivity and diversity in the deep sea is still poorly understood (Warwick, 1996).

As peracarid crustaceans are known to increase in importance with depth (Dahl *et al.*, 1976; Grassle & Maciolek, 1992), one might expect that a vertical transect along the continental slope areas would reveal highly diverse peracarid communities.

Hyperbenthic data from this PhD research along two continental slope areas (Porcupine Seabight and Meriadzek Terrace) suggest that Peracarida are important in terms of abundance. At Porcupine Seabight and Meriadzek Terrace respectively 77 % and 59 % of the total hyperbenthos belong to the Peracarida (see chapters 3 and 4). Are these high abundances translated in high diversity along both continental slopes? What might favour Peracarida in this environment? Species which posses a certain degree of eurybathy are usually considered as pre-adapted for an abyssal life (Bruun, 1957).

In addition, there are strong relationships between sampling scale and the processes that influence diversity (Huston, 1994). At small scales all species are presumed to interact with each other and to compete for similar limiting resources (Gray, 1997). This is called within-habitat diversity or **alpha diversity** (Fisher *et al.*, 1943; Whittaker, 1960, 1967). At slightly larger scales, habitat and/or community boundaries are crossed and sampling covers more than one habitat or community. This level is referred to as between-habitat diversity or **beta diversity** (Whittaker, 1960, 1975). At an even larger scale (regional scale) where evolutionary rather than ecological processes operate the patterns are defined as **gamma diversity** or landscape diversity (Whittaker, 1960; Cody, 1986).

This chapter emphasizes the depth related distribution of peracarid species along the two slope areas Porcupine Seabight and Meriadzek Terrace and how the species of the different taxa Amphipoda, Mysidacea, Cumacea, Isopoda and Tanaidacea behave along this bathymetric gradient. One might expect different strategies within the different taxa, *e.g.* occurrence in a preferred depth range. In addition to the distribution this chapter deals with the alpha and beta component of diversity of peracarid crustaceans along both continental slope areas. Alpha diversity is translated into diversity of the peracarid species associated with one station or one depth along the continental slope. Beta diversity is designated as the degree of species change along the depth gradient characteristic of the studied continental slopes. Are both spatial levels of diversity similar for the five major peracarid taxa, Amphipoda, Mysidacea, Isopoda, Cumacea and Tanaidacea on species level and how does the species turn-over (beta diversity) along the continental slope relates between the different taxa? These interpretations will be discussed in terms of the ecology (*e.g.* feeding strategy) of the different species.

5.2. Results

5.2.1. Importance of Peracarida within the hyperbenthos

The importance of the peracarid crustaceans within the hyperbenthic fauna in the two studied areas is illustrated by their relative abundance: at Porcupine Seabight 77 % of the total hyperbenthos belong to the Peracarida, at Meriadzek Terrace this is 59 %. These percentages correspond with an absolute total Peracarida density of 27 186 ind./800 m² at Porcupine Seabight and 7940 ind./800 m² at Meriadzek Terrace (see chapters 3 and 4).

Further identification on species level of all Amphipoda, Mysidacea, Cumacea, Isopoda and Tanaidacea was performed in order to obtain detailed information on the diversity of this group along the continental slope areas. The species list with the taxonomic information and the density for all species per station are given in appendix 2 and 3. The number of species, genera and families for each order within the Peracarida (Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea) is given for both study sites separate and for the total over the two sites (Table 5.1).

Table 5.1 Number of species, genera and families for the peracarid orders Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea for Porcupine Seabight (PSB), Meriadzek Terrace (M) and total dataset over the two sites (T).

	# Species PSB / M / T	**# Genera** PSB / M / T	**# Families** PSB / M / T
Amphipoda	97 / 126 / 152	68 / 90 / 101	29 / 32 / 35
Cumacea	34 / 33 / 45	16 / 16 / 18	6 / 6 / 6
Isopoda	19 / 27 / 30	15 / 20 / 22	11 / 13 / 14
Mysidacea	15 / 19 / 26	12 / 15 / 19	2 / 3 / 4
Tanaidacea	2 / 5 / 5	2 / 4 / 4	2 / 4 / 4

From both transects combined, 258 peracarid species have been identified comprising 164 peracarid genera and 63 peracarid families belonging to the orders Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea. Among these species 152 are Amphipods, 45 belong to the Cumacea, 30 to the Isopoda, 26 to the Mysidacea and 5 to the Tanaidacea (Table 5.1). On a generic level amphipods are also most diverse with 101 genera, followed by Isopoda with 22, Mysidacea with 19, Cumacea with 18 and Tanaidacea with 4 genera (Table 5.1). Amphipoda show usually the highest abundance, except at the deeper stations Cumacea are more numerous (see chapter 3 and 4).

5.2.2. Stratified distribution of the Peracarida

As illustrated before (see chapter 3 and 4) the hyperbenthic fauna shows an obvious distribution within the benthic boundary layer of one meter, as seen in the abundances and composition of the different hyperbenthic taxa in the lower (0-50 cm) and upper (50-100 cm) nets of the hyperbenthic sledge. A clear distinction of pelagic taxa, as chaetognaths, euphausiids and copepods, in the upper nets and a benthopelagic (related to the bottom) fauna in the lower nets was found, mainly composed of the peracarids.

As a result an obvious vertical distribution of the Peracarida is found in both study sites (Fig. 5.1). The absolute densities in the lower net at each station are much higher at every station than for the upper nets, with the exception of station M950 of Meriadzek Terrace (Fig. 5.1). At this station the peracarid density is evenly distributed between the two nets (49 % in the lower net, 51 % in the upper net). For the remaining stations the percentage peracarids in the lower nets ranges from a minimum of 69 % (P350) to more than 95 % in twelve stations.

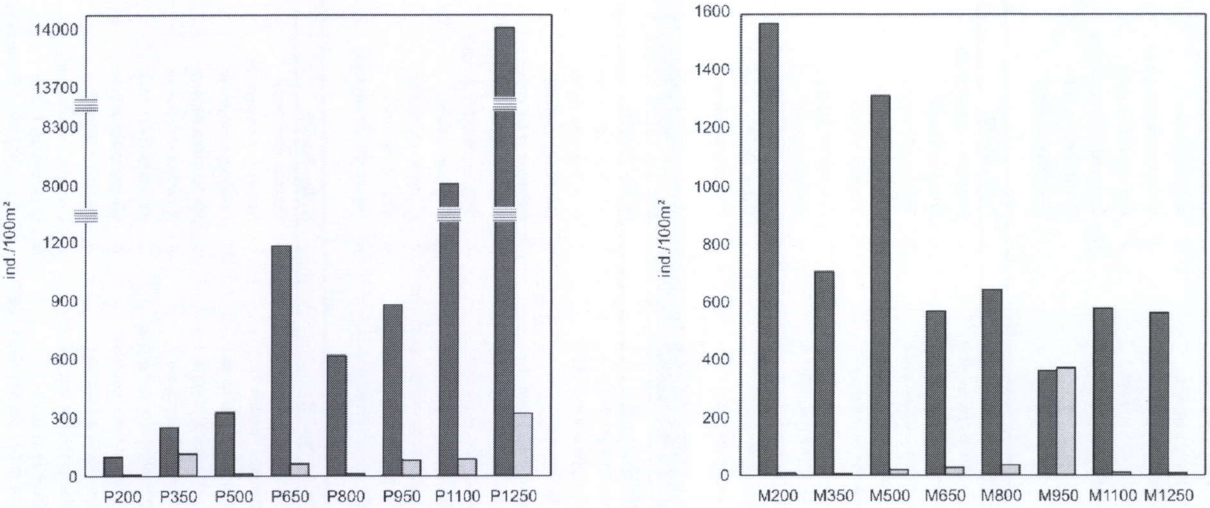


Figure 5.1 Total absolute density (ind./100 m²) of the Peracarida in the lower nets (dark grey) versus the upper nets (light grey) for each station at both study sites Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250). Note the different scales used.

In addition to the observed stratified distribution, another important trend is observed in terms of differences between the two studied areas. If the total absolute abundances of all Peracarida (*e.g.* sum of lower and upper nets) are considered, the abundance seems to differ significantly between the two sites Porcupine Seabight and Meriadzek Terrace. At Porcupine Seabight the abundance is low at the shallower stations and increases significantly with depth. Only station P650 shows a higher abundance than the two deeper stations P800 and P950. An opposite pattern is observed at Meriadzek. Here the highest abundance is found at the shallow stations and decreases with depth. Within the deeper stations an increase of abundance is found between 650 m and 950 m and decreases towards 1100 m and 1250 m.

Besides the share of Peracarida in each net, the species composition per net in the different stations is illustrated by the top 10 of the peracarid species based on the absolute abundance per net (Table 5.2). The total number of peracarid species (N_o) for each sample (*e.g.* net) is also given and for each station, again with the exception of station M950, N_o is always lower for the upper net sample compared to the lower net sample at the same depth. Due to the large number of species, the top 10 of each net sample does not show a general trend.

Porcupine Seabight

P200U (N_0=1)		P350U (N_0=27)		P500U (N_0=7)		P650U (N_0=24)		P800U (N_0=8)		P950U (N_0=28)		P1100U (N_0=27)		P1250U (N_0=41)	
Parathemisto oblivia	A	*Scopelocheirus hopei*	A	*Epimeria parasitica*	A	*Orchomene pectinatus*	A	*Parathemisto oblivia*	A	*Campylaspis verrucosa*	C	*Hemilamprops uniplicata*	C	*Boreomysis tridens*	M
		Mysidopsis didelphys	M	*Natatolana borealis*	I	*Pseudomma affine*	M	Janiridae species 1	I	*Unciola planipes*	A	*Campylaspis verrucosa*	C	*Ampelisca gibba*	A
		Nicippe tumida	A	*Scopelocheirus hopei*	A	*Astyra abyssi*	A	*Amblyops abbreviata*	M	*Hemilamprops uniplicata*	C	*Ampelisca gibba*	A	*Tmetonyx cicada*	A
		Hippomedon denticulatus	A	*Parathemisto oblivia*	A	*Hemilamprops uniplicata*	C	*Epimeria cornigera*	A	*Pseudomma affine*	M	*Cyclaspis longicaudata*	C	*Campylaspis horridoides*	C
		Orchomenella nana	A	*Rhachotropis rostrata*	A	*Carangolia* aff *barnardi*	A	*Epimeria parasitica*	A	*Ampelisca gibba*	A	*Boreomysis tridens*	M	*Cyclaspis longicaudata*	C
		Campylaspis macrophthalma	C	*Acidostoma sarsi*	A	*Rhachotropis rostrata*	A	*Acidostoma sarsi*	A	*Makrokylindrus longipes*	C	*Campylaspis rostrata*	C	*Rhachotropis gracilis*	A
		Acidostoma sarsi	A	*Hippomedon denticulatus*	A	*Proboloides grandimanus*	A	Pleustidae species 2	A	*Amblyops abbreviata*	M	*Rhachotropis rostrata*	A	*Metacirolana hanseni*	I
		Trischizostoma nicaeense	A			*Syrrhoe affinis*	A	*Hemilamprops uniplicata*	C	*Stegocephaloides auratus*	A	*Stegocephaloides auratus*	A	*Campylaspis rostrata*	C
		Orchomene pectinatus	A			*Astacilla intermedia*	I			*Bathycopea typhlops*	I	*Paralamprops* species 1	C	*Tryphosella horingi*	A
		Epimeria parasitica	A			*Eusirus longipes*	A			*Campylaspis glabra*	C	*Epimeria cornigera*	A	*Syrrhoe affinis*	A

P200L (N_0=17)		P350L (N_0=36)		P500L (N_0=22)		P650L (N_0=43)		P800L (N_0=59)		P950L (N_0=53)		P1100L (N_0=71)		P1250L (N_0=87)	
Erythrops serrata	M	*Leptostylis villosa*	C	*Scopelocheirus hopei*	A	*Gammaropsis palmata*	A	*Hemilamprops uniplicata*	C	*Hemilamprops uniplicata*	C	*Ampelisca gibba*	A	*Campylaspis rostrata*	C
Leptomysis lingvura	M	*Erythrops serrata*	M	*Pseudomma affine*	M	*Pseudomma affine*	M	*Astacilla intermedia*	I	*Unciola planipes*	A	*Metacirolana hanseni*	I	*Metacirolana hanseni*	I
Parathemisto oblivia	A	*Stegocephaloides auratus*	A	*Paramblyops rostrata*	M	*Hemilamprops uniplicata*	C	*Gammaropsis palmata*	A	*Natatolana borealis*	I	*Campylaspis rostrata*	C	*Diastyloides serrata*	C
Rhachotropis integricauda	A	*Mysidopsis didelphys*	M	*Rhachotropis grimaldii*	A	*Haploops setosa*	A	*Laetmatophilus tuberculatus*	A	*Campylaspis macrophthalma*	C	*Hemilamprops normani*	C	*Ampelisca gibba*	A
Erythrops neapolitana	M	*Scopelocheirus hopei*	A	*Natatolana borealis*	I	*Astacilla intermedia*	I	*Metacirolana hanseni*	I	*Astacilla longicornis*	I	*Cumellopsis puritani*	C	*Cyclaspis longicaudata*	C
Mysidopsis didelphys	M	*Campylaspis glabra*	C	*Epimeria parasitica*	A	Janiridae species 1	I	*Cressa dubia*	A	*Bathycopea typhlops*	I	*Hemilamprops uniplicata*	C	*Makrokylindrus longipes*	C
Melphidipella macra	A	*Hypererythrops serriventer*	M	*Syrrhoe affinis*	A	*Astyra abyssi*	A	*Astacilla longicornis*	I	*Ampelisca gibba*	A	*Cyclaspis longicaudata*	C	*Lepechinella manco*	A
Epimeria cornigera	A	*Rhachotropis integricauda*	A	*Harpinia antennaria*	A	*Astacilla longicornis*	I	*Campylaspis macrophthalma*	C	*Astacilla intermedia*	I	*Paralamprops* species 1	C	*Hemilamprops uniplicata*	C
Stegocephaloides auratus	A	*Pseudomma affine*	M	*Hippomedon denticulatus*	A	*Urothoe elegans*	A	Janiridae species 1	I	*Makrokylindrus longipes*	C	*Makrokylindrus josephinae*	C	*Lilljeborgia fissicornis*	A
Leptostylis villosa	C	*Epimeria parasitica*	A	*Amblyops abbreviata*	M	*Stenothoe marina*	A	*Ampelisca gibba*	A	*Pseudomma affine*	M	*Tryphosella insignis*	A	*Argissa hamatipes*	A

Meriadzek Terrace

M200U (N_0=4)		M350U (N_0=3)		M500U (N_0=19)		M650U (N_0=13)		M800U (N_0=32)		M950U (N_0=84)		M1100U (N_0=9)		M1250U (N_0=9)	
Erythrops neapolitana	M	*Orchomene humilis*	A	*Hippomedon denticulatus*	A	*Hemilamprops uniplicata*	C	*Eurydice grimaldii*	I	*Hemilamprops normani*	C	*Parathemisto oblivia*	A	*Lilljeborgia fissicornis*	A
Atylus species 1	A	*Stegocephaloides auratus*	A	*Ampelisca gibba*	A	*Boreomysis arctica*	M	*Campylaspis rostrata*	C	*Lilljeborgia fissicornis*	A	*Eucopia unguiculata*	M	*Lepidepecreum clypeatum*	A
Leucothoe liljeborgii	A	*Hyperia schizogeneois*	A	*Syrrhoe affinis*	A	*Lamprops fasciata*	C	*Byblis guerni*	A	*Ceratocuma horrida*	C	*Lepidepecreum* aff *umbo*	A	*Tryphosella* species 1	A
Melita obtusata	A			*Rhachotropis rostrata*	A	*Hippomedon denticulatus*	A	*Campylaspis glabra*	C	*Bathycopea typhlops*	I	*Tmetonyx similis*	A	*Stegocephaloides auratus*	A
				Parathemisto oblivia	A	*Bathymedon* species 1	A	*Pseudomma affine*	M	*Metacirolana hanseni*	I	*Stegocephaloides auratus*	A	*Janirella nanserii*	I
				Cyclaspis longicaudata	C	*Bruzelia typica*	A	*Rhachotropis grimaldii*	A	*Stegocephaloides auratus*	A	*Phrosina semilunata*	A	*Ilyarachna longicornis*	I
				Pseudomma affine	M	*Syrrhoe affinis*	A	*Gammaropsis maculata*	A	*Syrrhoites walkeri*	A	*Campylaspis rostrata*	C	*Hemilamprops normani*	C
				Ampelisca brevicornis	A	*Syrrhoites walkeri*	A	*Bathymedon monoculodiformes*	A	*Campylaspis rostrata*	C	*Boreomysis microps*	M	*Eucopia sculpticauda*	M
				Lepechinella manco	A	*Natatolana borealis*	I	*Harpinia truncata*	A	*Natatolana caeca*	I	*Boreomysis tridens*	M	*Eucopia unguiculata*	M
				Anonyx liljeborgi	A	*Campylaspis squamifera*	C	*Stegocephaloides auratus*	A	*Hemilamprops uniplicata*	C				

M200L (N_0=45)		M350L (N_0=46)		M500L (N_0=58)		M650L (N_0=57)		M800L (N_0=73)		M950L (N_0=70)		M1100L (N_0=79)		M1250L (N_0=62)	
Erythrops neapolitana	M	*Siphonoecetes striatus*	A	*Pseudomma affine*	M	*Hemilamprops uniplicata*	C	*Hemilamprops normani*	C	*Ceratocuma horrida*	C	*Ceratocuma horrida*	C	*Ceratocuma horrida*	C
Melphidipella macra	A	*Rhachotropis grimaldii*	A	*Rhachotropis inermis*	A	*Lamprops fasciata*	C	*Cerapus* species 1	A	*Hemilamprops normani*	C	*Bathycopea typhlops*	I	*Janirella nanserii*	I
Melita gladiosa	A	*Erythrops neapolitana*	M	*Natatolana borealis*	I	*Ilyarachna longicornis*	I	*Ilyarachna longicornis*	I	*Lilljeborgia fissicornis*	A	*Lilljeborgia fissicornis*	A	*Lilljeborgia fissicornis*	A
Parerythrops obesa	M	*Hypererythrops serriventer*	M	*Syrrhoe affinis*	A	*Bathycopea typhlops*	I	*Campylaspis rostrata*	C	*Metacirolana hanseni*	I	*Hemilamprops normani*	C	*Metacirolana hanseni*	I
Rhachotropis integricauda	A	*Lembos longipes*	A	*Ampelisca gibba*	A	*Pseudomma affine*	M	*Lilljeborgia fissicornis*	A	*Ilyarachna longicornis*	I	*Makrokylindrus josephinae*	C	*Ilyarachna longicornis*	I
Disconectes latirostris	I	*Tryphosites longipes*	A	*Melita gladiosa*	A	*Diastyloides bacescoi*	C	*Makrokylindrus josephinae*	C	*Paramblyops rostrata*	M	*Bathyamaryllis haswelli*	A	*Ampelisca aequicornis*	A
Hypererythrops serriventer	M	*Westwoodilla caecula*	A	*Westwoodilla caecula*	A	*Cyclaspis longicaudata*	C	*Ampelisca macrocephala*	A	*Campylaspis rostrata*	C	*Ileraustroe* species 1	A	*Cressa dubia*	A
Lembos longipes	A	*Epimeria parasitica*	A	*Hippomedon denticulatus*	A	*Campylaspis glabra*	C	*Carangolia* aff *barnardi*	A	*Lembos* species 1	A	*Platysympus typicus*	C	*Bathyamaryllis haswelli*	A
Megamphopus cornutus	A	*Pseudomma affine*	M	*Amblyops abbreviata*	A	*Siphonoecetes striatus*	A	*Makrokylindrus longipes*	C	*Cyclaspis longicaudata*	C	*Hemilamprops uniplicata*	C	*Hemilamprops normani*	C
Orchomenella nana	A	*Rhachotropis integricauda*	A	*Tryphosites longipes*	A	*Synchelidium maculatum*	A	*Lembos longipes*	A	*Rhachotropis inermis*	A	*Stegocephaloides auratus*	A	*Ileraustroe* species 1	A

Table 5.2 Top 10 of peracarid species in each net sample (U= upper net (50-100 cm), L= lower net (0-50 cm) for every station (200-1250) in both sampling sites Porcupine Seabight (P) and Meriadzek Terrace (M).
A=Amphipoda, I=Isopoda, C=Cumacea, M=Mysidacea.

5.2.3. Bathymetric distribution of the Peracarida

For the discussion on the bathymetric distribution, all the data are pooled as the sum of the two nets, which makes comparison with literature possible.

5.2.3.1. Composition of the Peracarida

An obvious shift in peracarid taxon composition along the depth gradient is observed (Fig. 5.2). Amphipoda make up a significant part at all stations in both areas. Mysidacea show high percentages at the upper slope stations (200-500 m) at Porcupine Seabight and Meriadzek Terrace, but their share decrease with depth, starting at 650 m. Isopoda and Cumacea show a reverse trend which is more pronounced for the latter taxon. The general trends are similar for the two study sites.

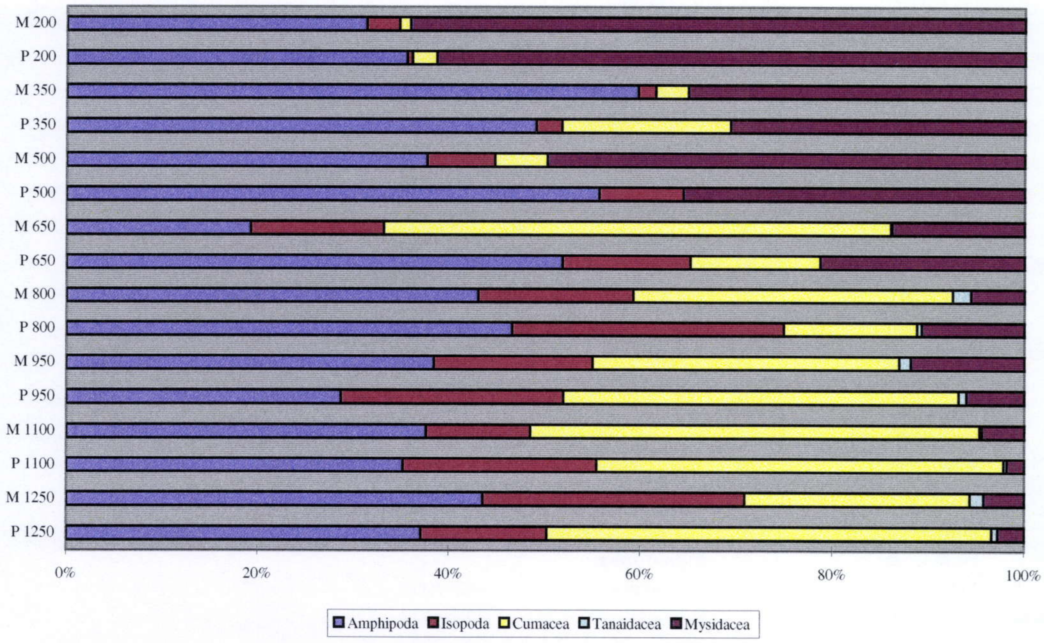


Figure 5.2 Relative composition of Peracarida in the two study sites Porcupine Seabight (P) and Meriadzek Terrace (M) with stations at similar depths (200-1250) of the two areas put together in the figure.

Considering the two sampling sites together, 119 peracarid species of the total of 258 species (see Table 5.1.) are sampled in both areas Porcupine Seabight and Meriadzek Terrace. These are 72 species of Amphipoda, 22 species of Cumacea, 15 species of Isopoda, 8 species of Mysidacea and 2 species of Tanaidacea. At a generic level this correspond with 56 genera of Amphipoda, 14 genera of Cumacea, 13 genera of Isopoda and 8 and 2 genera of Mysidacea and Tanaidacea respectively (Table 5.3). Of these, genera which had a bathymetric range of more than 1000 m, *i.e.* sampled along the complete bathymetric range on the continental slope, were considered as eurybathic, and may have had the potential to submerge into the deep sea from the shelf (Table 5.3). These are 22 genera, with only one genus of Mysidacea, the 21 others belonging to the Amphipoda, Cumacea and Isopoda.

Table 5.3 Peracarid genera sampled in both study sites Porcupine Seabight and Meriadzek Terrace with their maximal depth range found in the present study. Genera indicated with (*) are considered as eurybathic (> ~1000 m bathymetric range).

Taxon	Depth (m)	Taxon	Depth (m)
Amphipoda		**Cumacea**	
Acidostoma	336-953	*Campylaspis*	336-1215
Ampelisca *	227-1215	*Ceratocuma*	953-1215
Amphilochoides	207-494	*Cumellopsis*	953-1215
Argissa	795-1215	*Cyclaspis**	227-1215
Astyra	336-1215	*Diastylis*	336-1215
*Atylus**	227-1215	*Diastyloides**	207-1215
Bathyamaryllis	628-1215	*Hemilamprops**	227-1215
*Bathymedon**	207-1215	*Leptostylis**	207-1215
Bruzelia	494-1215	*Leucon*	953-1215
Byblis	628-953	*Makrokylindrus*	494-1215
*Carangolia**	227-1215	*Paralamprops*	678-1215
Cerapus	795-1215	*Platysympus*	678-1215
Chevreuxius	678-1215	*Procampylaspis*	352-1215
Cressa	765-1215	*Vaunthompsonia*	795-1215
Epimeria *	207-1215		
Euonyx	1110-1215	**Isopoda**	
*Eusirus**	207-1215	*Aega*	227-914
*Gammaropsis**	227-1215	*Astacilla*	227-1067
Halicoides	795-1215	*Bathycopea*	336-1215
Haliragoides	678-1215	*Disconectes**	227-1215
Haploops	628-1215	*Eurydice**	227-1215
Harpinia	469-1215	*Gnathia**	227-1215
Hippomedon	336-1215	*Ilyarachna*	336-1215
Ileraustroe	914-1215	*Metacirolana*	628-1215
Laetmatophilus	628-1215	*Munna**	207-1215
*Lembos**	227-1215	*Munnopsis*	678-1215
Lepechinella	494-1215	*Munnopsurus**	227-1215
*Lepidepecreum**	227-1215	*Natatolana*	336-1215
Lilljeborgia	678-1215	*Tytthocope*	678-1215
Lysianassa	795-1067		
Melphidipella	207-953	**Tanaidacea**	
Melphidippa	628-1215	Apseudes	795-1215
Metambasia	953-1215	Typhlotanais	765-1215
Nicippe	336-1110		
Orchomene	336-1215	**Mysidacea**	
Orchomenella	227-1110	Amblyops	469-1215
Paracentromedon	914-1215	Boreomysis	336-1215
Paraphoxus	628-1110	Erythrops	207-795
Parathemisto *	207-1215	Hypererythrops	227-494
Pardalisca	1067-1215	Mysidopsis	207-336
Pontocrates	227-914	Paramblyops	469-1215
Proboloides	336-1215	Parerythrops	227-765
Rhachotropis *	207-1215	Pseudomma*	227-1215
Scopelocheirus	336-1215		
Siphonoecetes	352-1215		
Sophrosyne	953-1067		
Stegocephaloides *	207-1215		
Stenopleustes	628-795		
Stenothoe	628-795		
Synchelidium	469-1110		
Syrrhoe	336-1215		
Tmetonyx	469-1215		
Tryphosella	628-1215		
Tryphosites	352-1067		
Unciola	628-1067		
Urothoe	336-1215		

5.2.3.2. Community structure

MDS-analysis (Fig. 5.3) and cluster-analysis (Fig. 5.4) divided the total peracarid community of the continental slope at Porcupine Seabight and Meriadzek Terrace into four species associations, reflecting their geographical and bathymetrical distribution: a first division in an upper slope (200-500 m) and a lower slope (650-1250) association and within the upper and lower slope association the division of both study sites Porcupine Seabight (P) and Meriadzek Terrace (M) exists. The MDS-analysis showed a low stress value (0.1), indicating a good and useful 2D-representation of the groups.

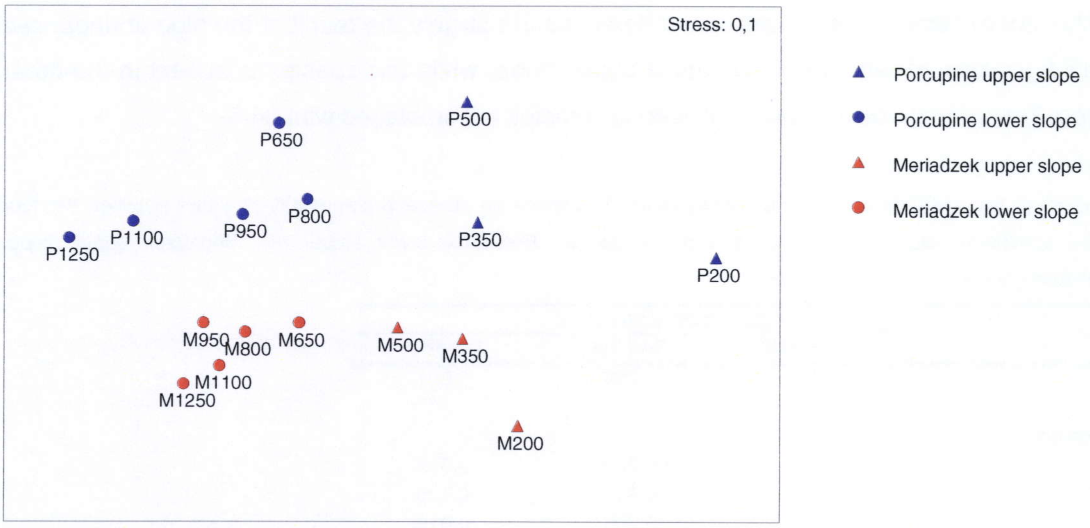


Figure 5.3 MDS plot based on the square-root transformed Peracarid species dataset of the eight samples of both sampling sites Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M).

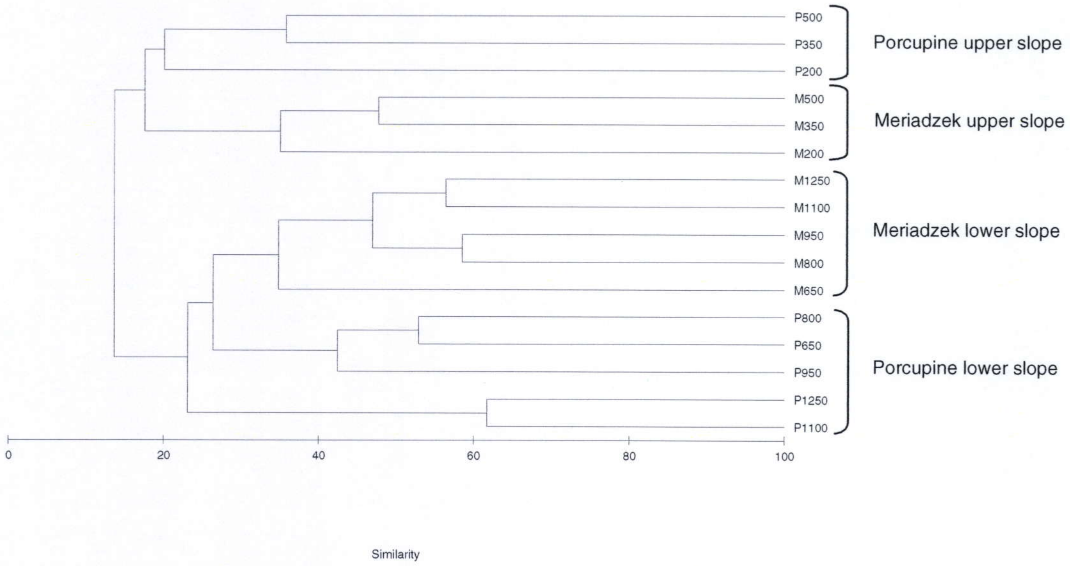


Figure 5.4 Cluster dendrogram from a group average sorting using Bray-Curtis similarities of the square-root transformed Peracarid species dataset of the eight stations of both sampling sites Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250).

The ANOSIM-results (Table 5.4) indicate that the four peracarid species associations were significantly different. An additional SIMPER-analysis indicates a strong dissimilarity between the upper and lower assemblage of both study sites: 89 % between the upper and lower slope assemblage at Porcupine Seabight, 81 % dissimilarity between both associations at Meriadzek Terrace. The difference between the upper slope assemblage and the lower slope assemblage of both areas is characterized by the high number of Mysidacea species and Amphipoda species at both upper slope groups and the higher number of Cumacea and Isopoda species at both lower slope assemblages (Table 5.5). In addition, a strong dissimilarity is found between the Porcupine upper slope assemblage and the other assemblages: 89 % with the Meriadzek lower slope and 83 % with the Meriadzek upper slope. These significant differences are largely the result of the high abundances of the mysid *Erythrops serrata* at the Porcupine upper slope, while this species is absent in the other assemblages. The average dissimilarity between all species assemblages was 84 %.

Table 5.4 Results of the ANOSIM and SIMPER analysis for differences on peracarid community structure between the four groups on the continental slope (I= Porcupine upper slope, II= Porcupine lower slope, III= Meriadzek upper slope, IV= Meriadzek lower slope).

	Hyperbenthic community structure		
	Dissimilarity	**R-value**	***p*-value**
Global test	84%	0,759	0,001
Groups compared			
I-II	89%	0,795	0,018
I-III	83%	0,741	0,100
I-IV	89%	0,908	0,018
II-III	86%	0,805	0,018
II-IV	75%	0,540	0,080
III-IV	81%	0,938	0,018

Table 5.5 SIMPER lists, showing the contribution percentages of the top ten discriminating species for each species association. For each species, the order they belong to is indicated: M= Mysidacea, A= Amphipoda, C= Cumacea, I=Isopoda.

Species association 1 Porcupine upper slope			**Species association 2 Porcupine lower slope**		
Erythrops serrata	M	16%	*Hemilamprops uniplicata*	C	11%
Scopelocheirus hopei	A	15%	*Pseudomma affine*	M	5%
Parathemisto oblivia	A	11%	*Ampelisca gibba*	A	5%
Stegocephaloides auratus	A	9%	*Bathycopea typhlops*	I	4%
Rhachotropis integricauda	A	6%	*Metacirolana hanseni*	I	4%
Pseudomma affine	M	5%	*Astacilla intermedia*	I	4%
Bathymedon species 1	A	5%	*Astacilla longicornis*	I	3%
Mysidopsis didelphys	M	5%	*Harpinia pectinata*	A	3%
Epimeria parasitica	A	5%	*Orchomene pectinatus*	A	3%
Hippomedon denticulatus	A	3%	*Laetmatophilus armatus*	A	3%

Species association 3 Meriadzek upper slope			**Species association 4 Meriadzek lower slope**		
Lembos longipes	A	8%	*Bathycopea typhlops*	I	5%
Erythrops neapolitana	M	7%	*Hemilamprops normani*	C	5%
Melita gladiosa	A	7%	*Lilljeborgia fissicornis*	A	5%
Westwoodilla caecula	A	6%	*Ilyarachna longicornis*	I	5%
Hypererythrops serriventer	M	6%	*Campylaspis glabra*	C	4%
Pseudomma affine	M	5%	*Platysympus typicus*	C	4%
Hemilamprops uniplicata	C	4%	*Stegocephaloides auratus*	A	4%
Stegocephaloides auratus	A	4%	*Makrokylindrus josephinae*	C	3%
Amphilochoides boecki	A	3%	*Hemilamprops uniplicata*	C	3%
Megamphopus cornutus	A	3%	*Pseudomma affine*	M	3%

This distinct preference or zonation of certain taxa and species along the depth gradient on the continental slope will be discussed in more detail in a next part of this chapter. Three case studies will be worked out and explanations for this pronounced zonation will be looked for in the ecology of the different species (see 5.2.4.).

5.2.3.3. Alpha and beta diversity

In order to illustrate alpha and beta diversity, different diversity indices were calculated, based on the relative peracarid species abundances per station (*i.e.* alpha diversity) along the depth gradient in both study areas (*i.e.* beta diversity) (Table 5.6 and Fig. 5.5). Generally species richness and diversity is higher for the lower slope stations (650-1250 m) compared to the upper slope stations (200-500 m). For both areas a similar trend is observed for the upper slope stations: the station at 350 m depth shows the highest diversity in comparison to 200 m and 500 m station. At Porcupine Seabight P350 also shows the highest species richness. Within the lower slope stations peracarid diversity for both study sites shows a different pattern. At Porcupine Seabight diversity shows two peaks, first at station P800 and after decreasing towards P1100, diversity increases again at P1250. At Meriadzek Terrace, peracarid diversity increases towards an obvious peak at stations M800 and M950 and then decreases again with a very small increase at M1250. The species richness (N_0) is highest at 1250 m water depth at Porcupine Seabight (96 species), while at Meriadzek this is the case at 950 m depth (102 species). Overall, species richness is higher at Meriadzek Terrace than at Porcupine Seabight when similar depths are compared, except for the deepest station (1250 m).

The Hill index N_1 and the Shannon Wiener index (H') indicate that dominance is most pronounced at the shallower stations. Diversity expressed as the expected number of species (ES(100)) (Table 5.6 and Fig. 5.5) is highest at P800 (41) and P1250 (37) at Porcupine Seabight, for Meriadzek Terrace highest ES(100) is found around 800-950 m depth (38 at M800, 45 at M950). Average taxonomic diversity (delta (Δ)) and average taxonomic distinctness (delta* (Δ^*)) (Warwick & Clarke, 1995) (Table 5.6) do not show large differences between the different stations at each site, indicating small differences in taxonomic composition between the stations. Only the shallowest station in both sites (P200 and M200) shows a significant lower value for both indices.

Table 5.6 Alpha and beta diversity of the peracarid species expressed in terms of different diversity indices for each station in both study site: A) Porcupine Seabight (P200-P1250) and B) Meriadzek Terrace (M200-M1250). The dashed line indicates the separation of the upper and lower slope community.

A.

	Upper slope			**Lower slope**				
	P200	**P350**	**P500**	**P650**	**P800**	**P950**	**P1100**	**P1250**
Number of species (N_0)	17	47	23	50	63	63	77	96
Hill Diversity (N_1)	8,46	16,47	8,56	15,92	32,21	20,29	18,66	32,74
Hill Diversity (N_{inf})	3,19	4,40	3,46	5,73	9,27	4,90	5,04	6,74
Evenness (J')	0,75	0,73	0,68	0,71	0,84	0,73	0,67	0,76
Shannon Diversity (H')	2,13	2,80	2,15	2,77	3,47	3,01	2,93	3,49
ES(100)	17	24	12	24	41	27	25	37
Delta	30	36	34	37	39	38	37	38
Delta*	36	40	40	41	41	41	41	40

B.

	Upper slope			**Lower slope**				
	M200	**M350**	**M500**	**M650**	**M800**	**M950**	**M1100**	**M1250**
Number of species (N_0)	48	48	63	63	86	102	84	66
Hill Diversity (N_1)	6,86	19,72	15,09	19,50	43,05	46,43	28,05	29,44
Hill Diversity (N_{inf})	1,80	4,87	2,76	3,78	8,84	10,86	4,42	8,01
Evenness (J')	0,50	0,77	0,66	0,72	0,84	0,83	0,75	0,81
Shannon Diversity (H')	1,93	2,98	2,71	2,97	3,76	3,84	3,33	3,38
ES(100)	14	30	24	31	38	45	33	33
Delta	27	35	35	35	39	40	38	39
Delta*	40	38	41	39	41	41	40	41

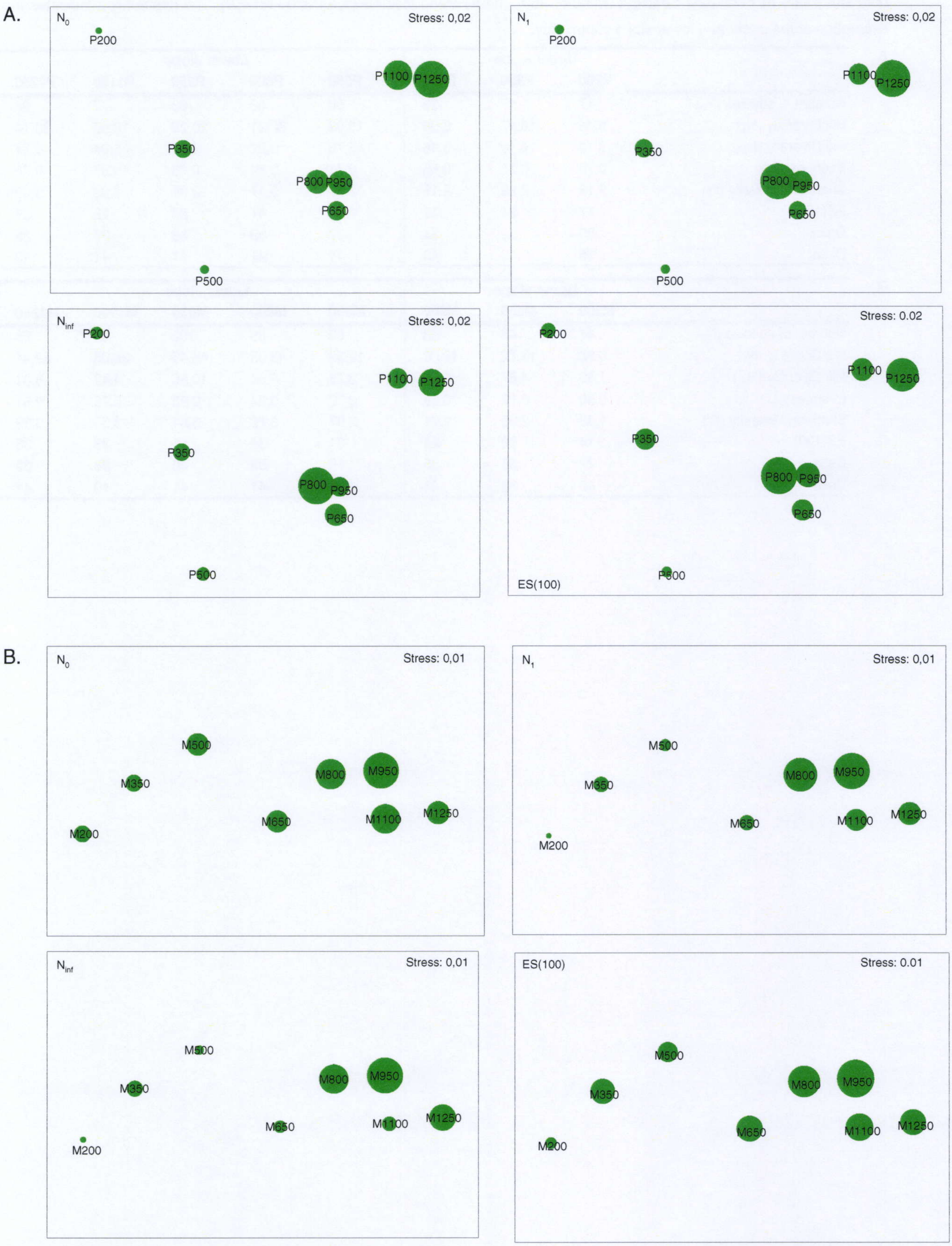


Figure 5.5 MDS bubble plots based on the square-root transformed absolute densities of the Peracarid species per sampling site A) Porcupine Seabight (P200-P1250) and B) Meriadzek Terrace (M200-M1250). The bubbles value four different diversity indices: Hill diversity indices N_0, N_1 and N_{inf} and ES(100).

The MDS bubble plots illustrating the Hill diversity numbers (N_0, N_1 and N_{inf}) and ES(100) (Fig. 5.5), plotted on the peracarid community structure, are based on the MDS analysis of the Peracarid species of the eight stations of each study site separated. Comparing these MDS plots with the community structure found based on the complete hyperbenthic fauna (see chapter 3 and chapter 4), a very similar community structure, with an upper and lower slope community, was found for Meriadzek Terrace for both the hyperbenthos and the Peracarida. For the Peracarida community structure at Porcupine Seabight the distance between the three upper slope stations (P200, P350 and P500) becomes larger and the separation of the mid and lower slope becomes more pronounced.

The k-dominance plots (Fig. 5.6) and the top ten of the most abundant species per station (see appendix 5) based on the peracarid species composition of all samples for both Porcupine Seabight and Meriadzek Terrace add some extra information on diversity in combination with the diversity indices. The k-dominance plot for Meriadzek Terrace (Fig. 5.6 A) explains the major difference for the Hill number N_1 for the stations M200 and M350 compared to the very similar species richness (N_0=48). The curve for station M200 clearly indicates a very high dominance of 55.5 % of the mysid species *Erythrops neapolitana*, compared to the relative abundance of 20.5 % of *Siphonoecetes striatus*, the most dominant species sampled at station M350 (see appendix 5). Generally, both plots illustrate a lower diversity for the upper slope stations (mainly 200 and 500 m) compared to the lower slope stations. As mentioned before, highest peracarid diversity and lowest dominance is found for the stations P800 and P1250 at Porcupine Seabight and for M800 and M950 at the Meriadzek Terrace. Overall, caution should be taken into account with the interpretation of the different curves, especially these of the remaining stations as the corresponding k-dominance curves intersect (Lambshead *et al.*, 1983; Platt *et al.*, 1984).

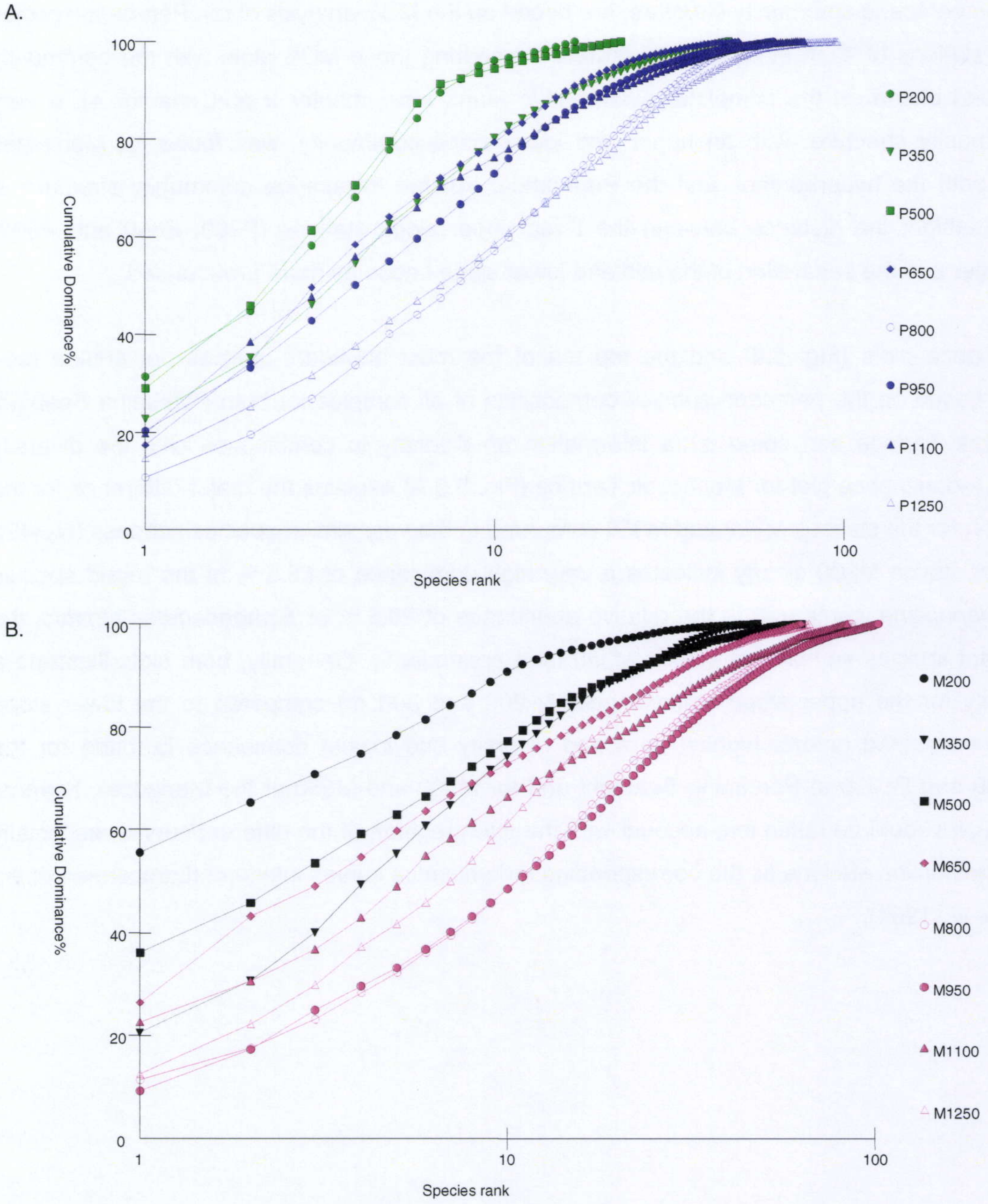


Figure 5.6 K-dominance plot indicating beta diversity of Peracarida species in each station along the depth gradient in both sampling sites A) Porcupine Seabight (P200-P1250) and B) Meriadzek Terrace (M200-M1250). In each plot the upper slope and lower slope stations are indicated by a different color.

5.2.4. Three case studies

5.2.4.1. Mysidacea: upper slope preference

A total of 26 mysid species, belonging to 19 genera was collected during the two expeditions, with 15 species sampled at Porcupine Seabight and 19 species at Meriadzek Terrace (see appendix 2 for full species list and appendix 3 for absolute density values). Both study sites have eight mysid species of the total of 26 in common and eight genera of the total of 19. *Pseudomma affine* (406 ind./800 m²), *Paramblyops rostrata* (292 ind./800 m²) and *Boreomysis tridens* (79 ind./800 m²) are the three most abundant species at Porcupine Seabight. At Meriadzek Terrace these are *Erythrops neapolitana* (940 ind./800 m²), *Pseudomma affine* (584 ind./800 m²) and *Hypererythrops serriventer* (114 ind./800 m²). For both study sites the distributional range of each mysid species is showing an obvious zonation along the depth gradient on both continental slope sites (Fig. 5.7). Only one species, *Pseudomma affine*, can be said to be eurybathic in both sampling sites. This species shows a maximal depth range between 200 and 1250 m depth, only at station P200 it was not found in the samples. At both sites the upper slope stations comprise more mysid species than the lower slope stations. Within this upper slope part some differences between the two sampling sites Porcupine Seabight and Meriadzek Terrace can be outlined. At the upper slope, seven mysid species in both sites are restricted to the shallowest three stations (200-500). Most of the species from the upper slope at Porcupine Seabight show a smaller distributional range (200-350) compared to the species at Meriadzek Terrace, where most species are distributed from 200-500 m depth. From these seven species only two species are found in both sites: *Mysidopsis didelphys* and *Hypererythrops serriventer*. Both species show a slightly different distribution along both continental slopes (Fig. 5.7), but their maximum distributional range over the two sites is 200-350 m and 200-500 m respectively. Besides these two species at Porcupine Seabight, five other species have their distribution restricted to the upper slope and none of these five species were sampled at Meriadzek Terrace. At Meriadzek Terrace in contrast only three other species which were not sampled at Porcupine Seabight are found at the upper slope. Two other species found restricted to the upper slope at Meriadzek Terrace, show a rather different distribution at Porcupine Seabight: *Erythops neapolitana* and *Parerythrops obesa*. *Erythrops neapolitana* was also sampled deeper at Porcupine Seabight (at 800 m), while *Parerythrops obesa* was, in contrast to Meriadzek Terrace, not sampled at the upper slope at Porcupine Seabight but was found in the samples from 650-800 m depth.

The lower slope part at Meriadzek Terrace is characterized by a higher total number of mysid species compared to Porcupine Seabight although N_0 (Fig. 5.8) is only higher at M650 and M1100. Only three species are common for both sites: *Amblyops abbreviata*, *Paramblyops rostrata* and *Boreomysis tridens*. From this latter genus, two other species are found at the lower slope at Meriadzek Terrace. Besides this genus the upper slope community at Meriadzek is characterized by species belonging to the genera *Eucopia*, *Hansenomysis*, *Dactylerythrops* and *Parapseudomma*. These genera were not sampled at Porcupine Seabight. At each site only two species are sampled which are only found at the deepest station (1250 m) and both sites have none of these species in common.

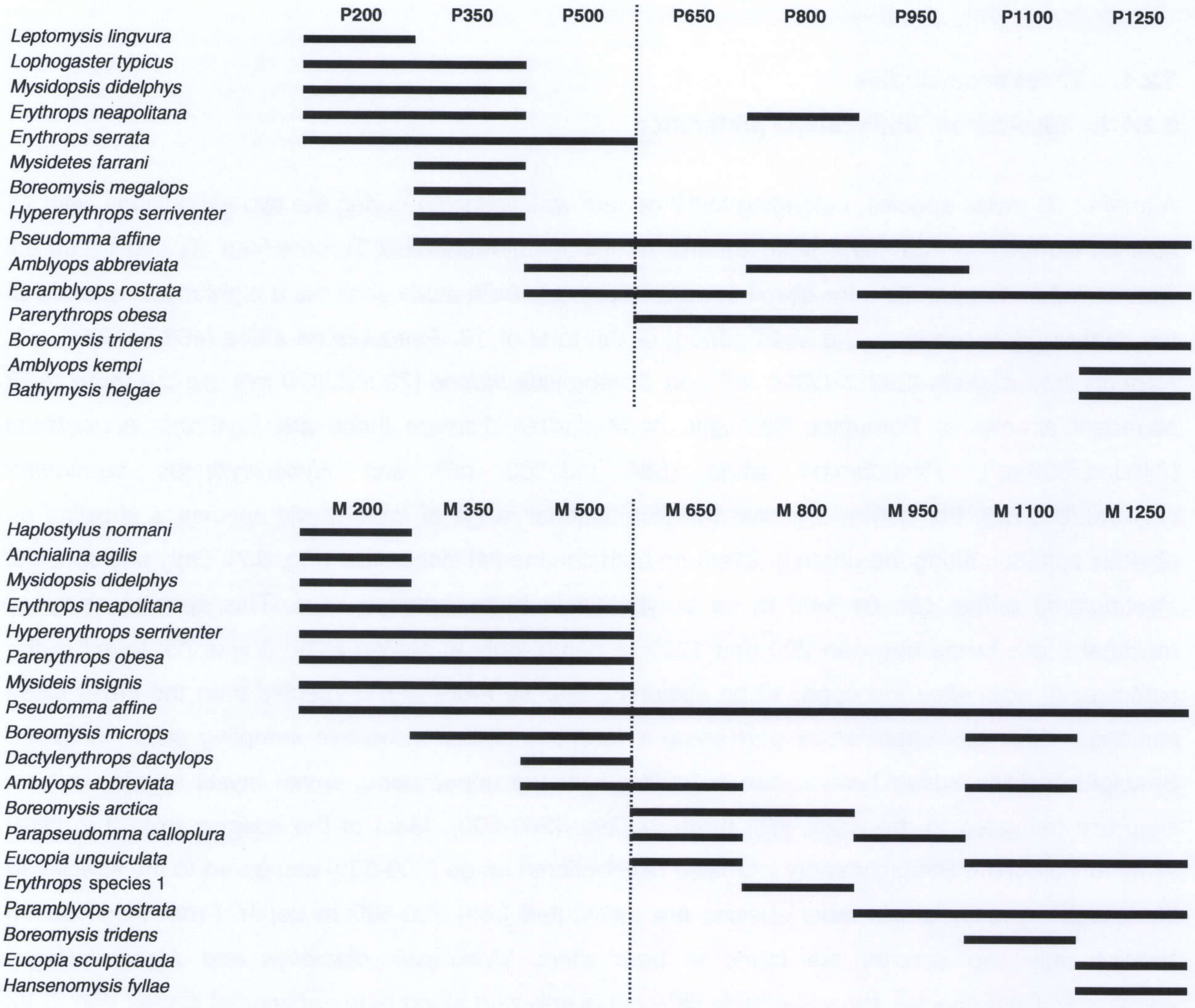


Figure 5.7 Mysidacea species occurrence along the continental slope at Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250). The dashed line indicates the boundary between the upper and lower slope zone.

The diversity indices off Hill (Fig. 5.8A) indicate higher species richness at the three upper slope stations (200, 350 and 500 m) compared to the lower slope for both sites. The highest diversity is found for the station at 350 m depth at both sites Porcupine Seabight and Meriadzek Terrace. A second peak of mysid diversity was found at P800 and M1100 for Porcupine Seabight and Meriadzek Terrace respectively. The corresponding k-dominance plot (Fig. 5.8B) shows a high dominance of mysid species for the majority of the lower slope stations of both sites.

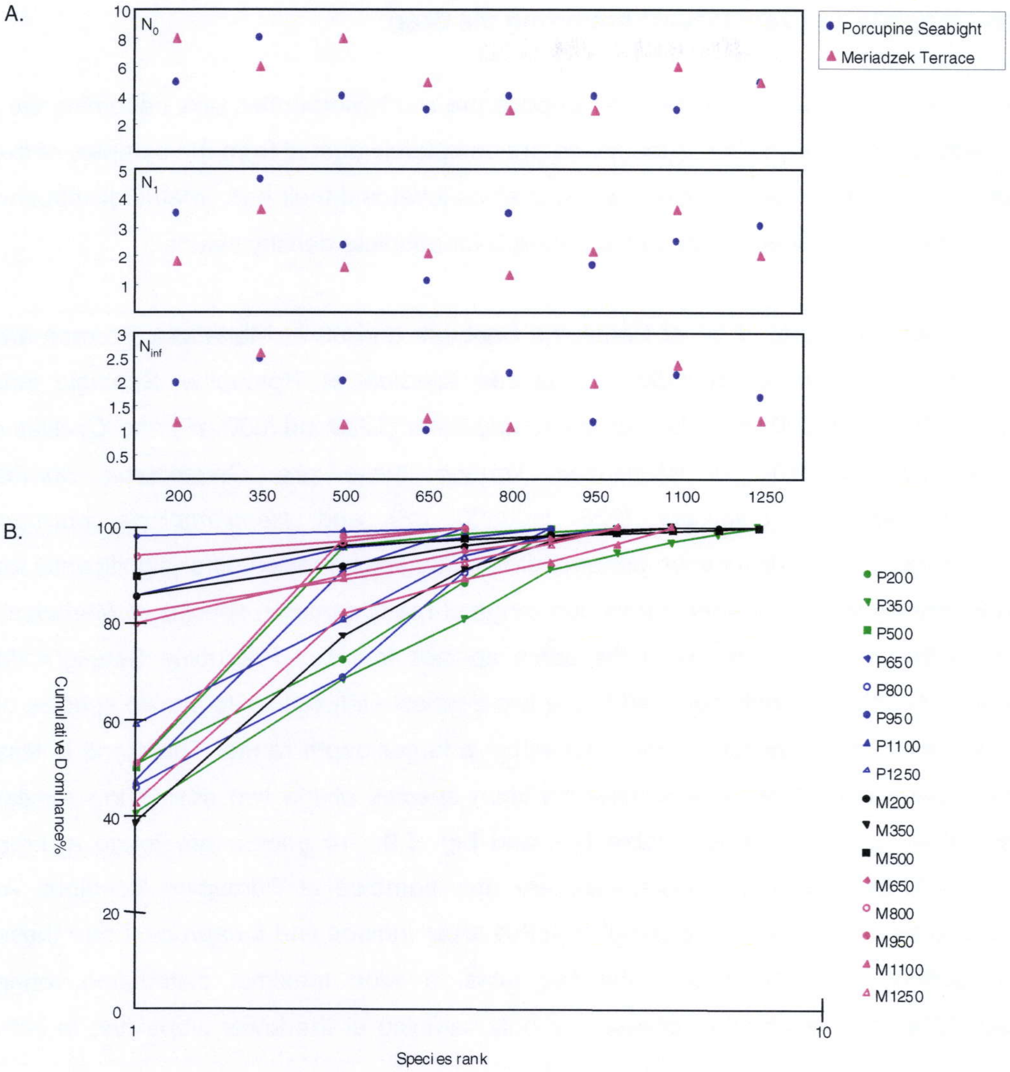


Figure 5.8 Alpha diversity of Mysidacea species along the depth gradient (200-1250 m) at Porcupine Seabight and Meriadzek Terrace: A) Diversity indices of Hill (N_0, N_1 and N_∞ and B) corresponding k-dominance curves.

5.2.4.2. Cumacea, Isopoda and Tanaidacea: preferring the deep

As illustrated before (see figure 5.2.), Cumacea and Isopoda are two hyperbenthic taxa becoming very abundant with increasing depth. In addition Tanaidacea are completely absent from the samples of the upper slope stations. These three taxa are identified at species level and their bathymetric distribution is studied (see appendix 2 for full species list and appendix 3 for absolute density values).

For Cumacea 22 species on a total of 34 at Porcupine Seabight and 33 at Meriadzek Terrace are sampled in both areas. The most abundant cumacean species at Porcupine Seabight are *Campylaspis rostrata* (2921 ind./800 m^2), *Hemilamprops uniplicata* (1239 ind./800 m^2) and *Cyclaspis longicaudata* (1116 ind./800 m^2), for Meriadzek Terrace these are *Ceratocuma horrida* (259 ind./800 m^2), *Hemilamprops uniplicata* (236 ind./800 m^2) and *Hemilamprops normani* (245 ind./800 m^2). The bathymetric distribution patterns of the Cumacea species differ significantly for both areas (Fig. 5.9), mainly due to a larger distribution range of many common species at Meriadzek Terrace compared to the distribution range of the same species found at Porcupine Seabight. At Porcupine Seabight 19 species are only sampled in the two deepest stations, while eleven species of these 19 are also sampled at Meriadzek Terrace but within a larger depth range. This trend is less pronounced at the shallower stations, where most common species of the two sites show similar distribution ranges. At a generic level (see table 5.3. and Fig. 5.9), 14 genera are found at both sampling sites, while *Bathycuma* and *Cyclaspoides* are only sampled at Porcupine Seabight. At Meriadzek Terrace also two genera are only sampled in this area: *Iphinoe* and *Lamprops*. From these 14 genera seven genera have, seen over the two sites, a wide maximal distribution range (200-1250 m or 350-1250 m). Seven other genera are only sampled at the lower slope part in both sampling sites.

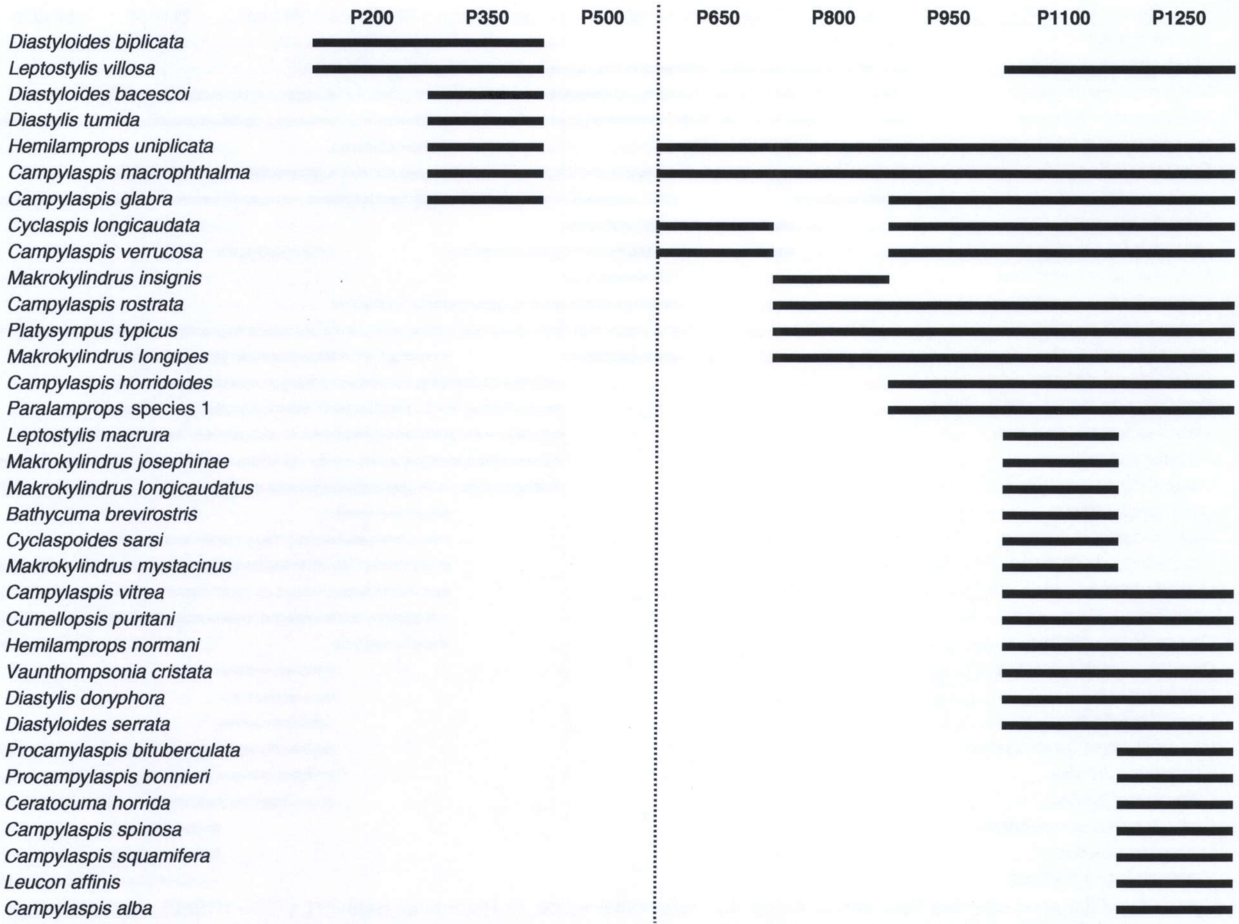


Figure 5.9 Cumacea species occurrence along the continental slope at Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250). The dashed line indicates the boundary between the upper and lower slope zone (continued).

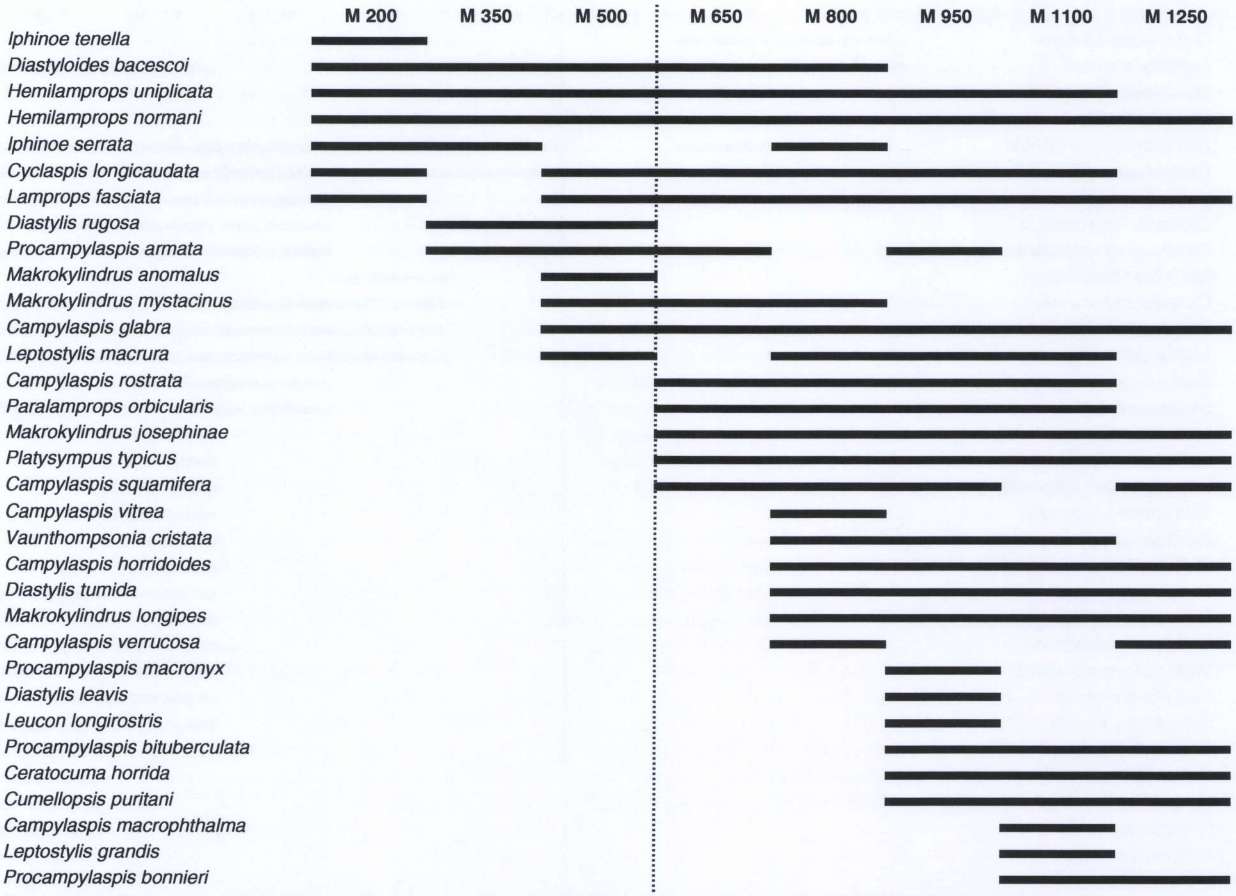


Figure 5.9 Cumacea species occurrence along the continental slope at Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250). The dashed line indicates the boundary between the upper and lower slope zone.

The diversity indices of Hill (Fig. 5.10A) indicate a higher species richness and diversity of the Cumacea for Meriadzek Terrace, with the exception of the two deepest stations, which are more diverse at Porcupine Seabight. At Meriadzek Terrace a gradual increase of species richness with depth is observed, with a peak at 950 m depth (22 species) and then a decrease is initiated. This trend is not seen at Porcupine Seabight. Here a gradual increase of species richness with depth is observed with a maximum N_0 at P1250 (24 species). Overall, species richness and diversity of cumaceans is higher at the deeper stations compared to the upper slope stations. The k-dominance plot (Fig. 5.10B) indicates a larger dominance effect for Cumacea at the upper slope of Porcupine Seabight compared to the upper slope stations at Meriadzek Terrace.

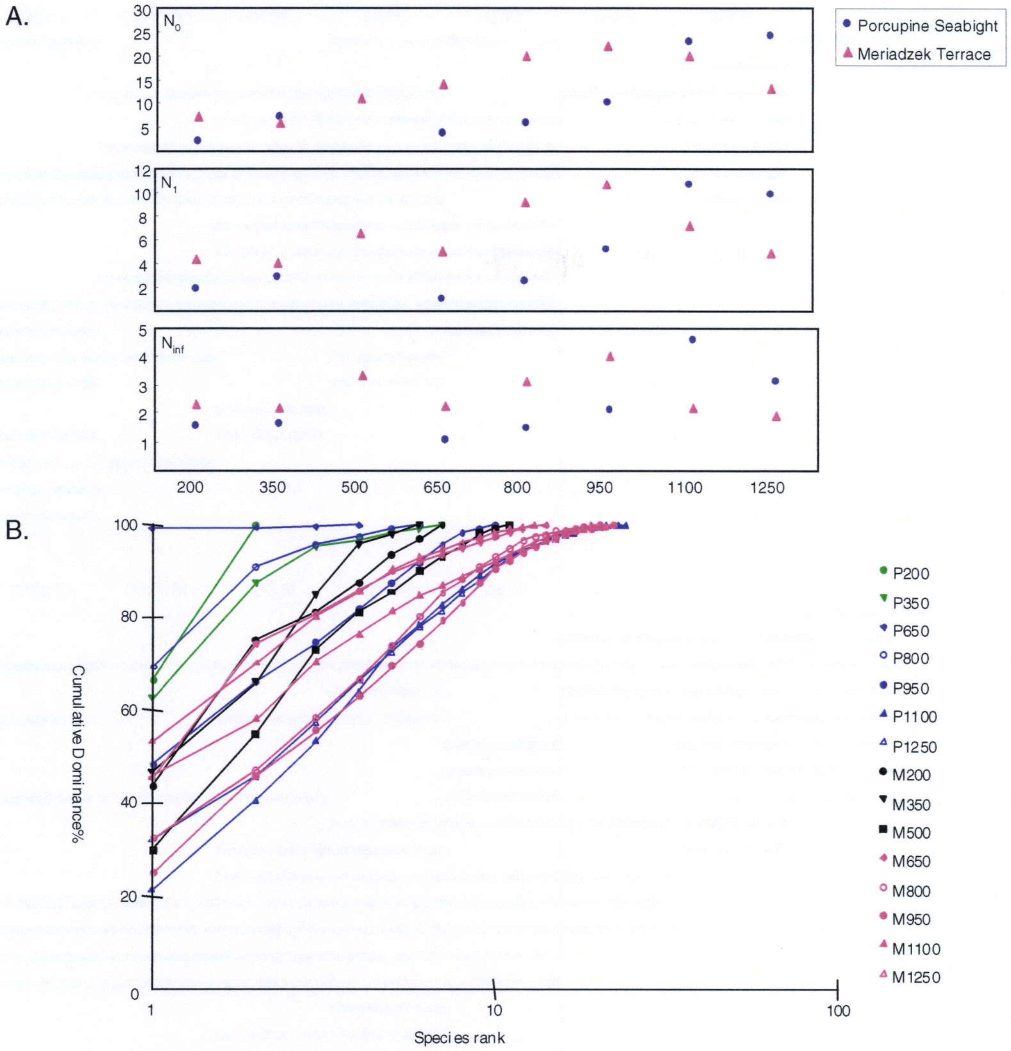


Figure 5.10 Alpha diversity of Cumacea species along the depth gradient (200-1250 m) at Porcupine Seabight and Meriadzek Terrace: A) Diversity indices of Hill (N_0, N_1 and N_∞ and B) corresponding k-dominance curves.

The most abundant Isopoda sampled at both sites differ. At Porcupine Seabight these are *Metacirolana hanseni* (3058 ind./800 m²), *Bathycopea typhlops* (267 ind./800 m²) and *Ischnomesus* species 1 (178 ind./800 m²). For Meriadzek Terrace these are *Bathycopea typhlops* (138 ind./800 m²), *Ilyarachna longicornis* (126 ind./800 m²) and *Natatolana borealis* (112 ind./800 m²). The bathymetric distribution of the Isopoda (Fig. 5.11) in both sampling sites differs in the higher species richness at Meriadzek Terrace compared to Porcupine Seabight. The diversity indices of Hill (Fig. 5.12A) confirm this observation, although only at 950 m depth the diversity is significant higher at Meriadzek Terrace compared to Porcupine Seabight, at the other depths diversity is comparable.

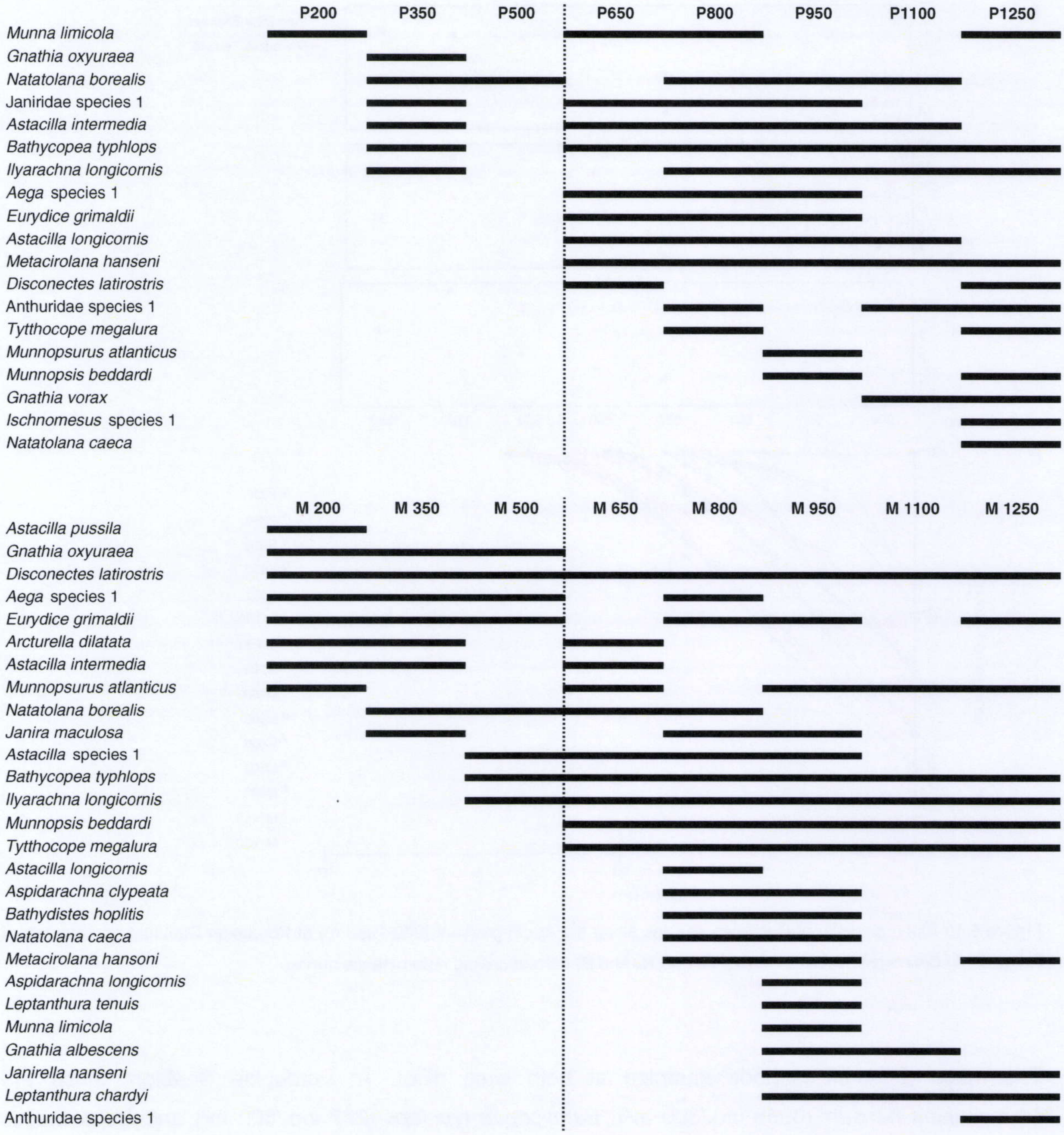


Figure 5.11 Isopoda species occurrence along the continental slope at Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250). The dashed line indicates the boundary between the upper and lower slope zone.

Overall, species richness and diversity increase with depth reaching a maximum value at 800 m at Porcupine Seabight (12 species) and at 950 m at Meriadzek Terrace (19 species). For the deepest stations a small decrease in both sites is observed. From the eleven species sampled only at Meriadzek Terrace, nine were found at 950 m resulting in the higher N_0 at this depth. Besides the different species, both study sites have 16 species of a total of 19 at Porcupine Seabight and 27 at Meriadzek terrace in common. Most of the common species show a deeper distribution at Porcupine Seabight compared to Meriadzek Terrace. Only one species has a limited distribution in the upper slope part: *Gnathia oxyuraea*. At a generic level, 13 genera are found in both sites (see Table 5.3 and Fig. 5.11). From these 13 genera only three are restricted to the lower slope part (650-1250). Most genera show a wide distribution along the continental slopes. The k-dominance curve indicates a large dominance effect at the stations P200 and P500 (Fig. 5.12B).

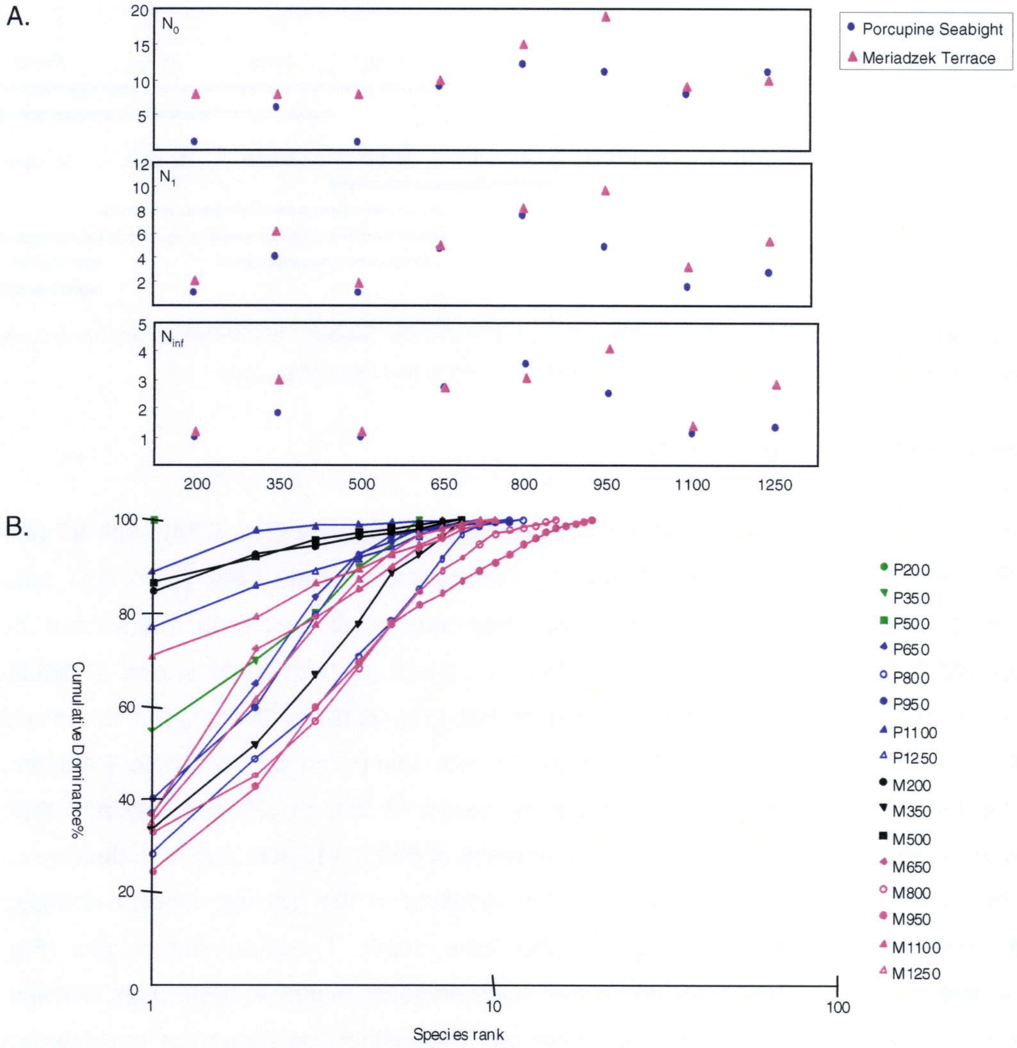


Figure 5.12 Alpha diversity of Isopoda species along the depth gradient (200-1250 m) at Porcupine Seabight and Meriadzek Terrace: A) Diversity indices of Hill (N_0, N_1 and N_∞ and B) corresponding k-dominance curves.

Tanaidacea are sampled in small abundances and also the species number is very low (see Table 5.1 and Fig. 5.13). A total of five species was sampled, only two at Porcupine Seabight, five at Meriadzek Terrace. All tanaids are sampled in the deeper stations and are completely absent at the upper slope from both sites.

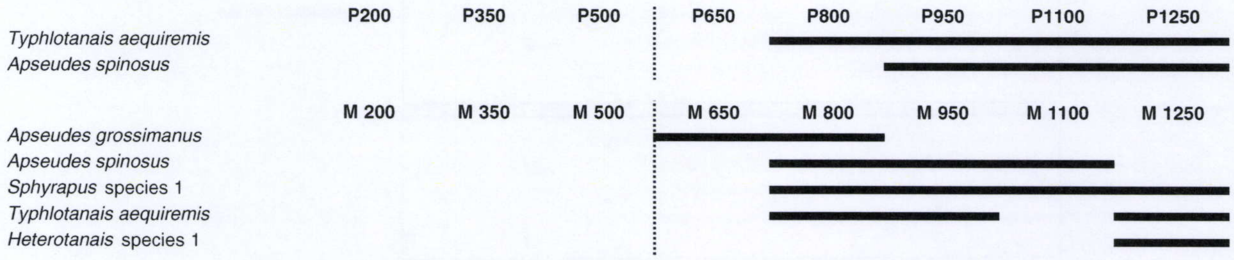
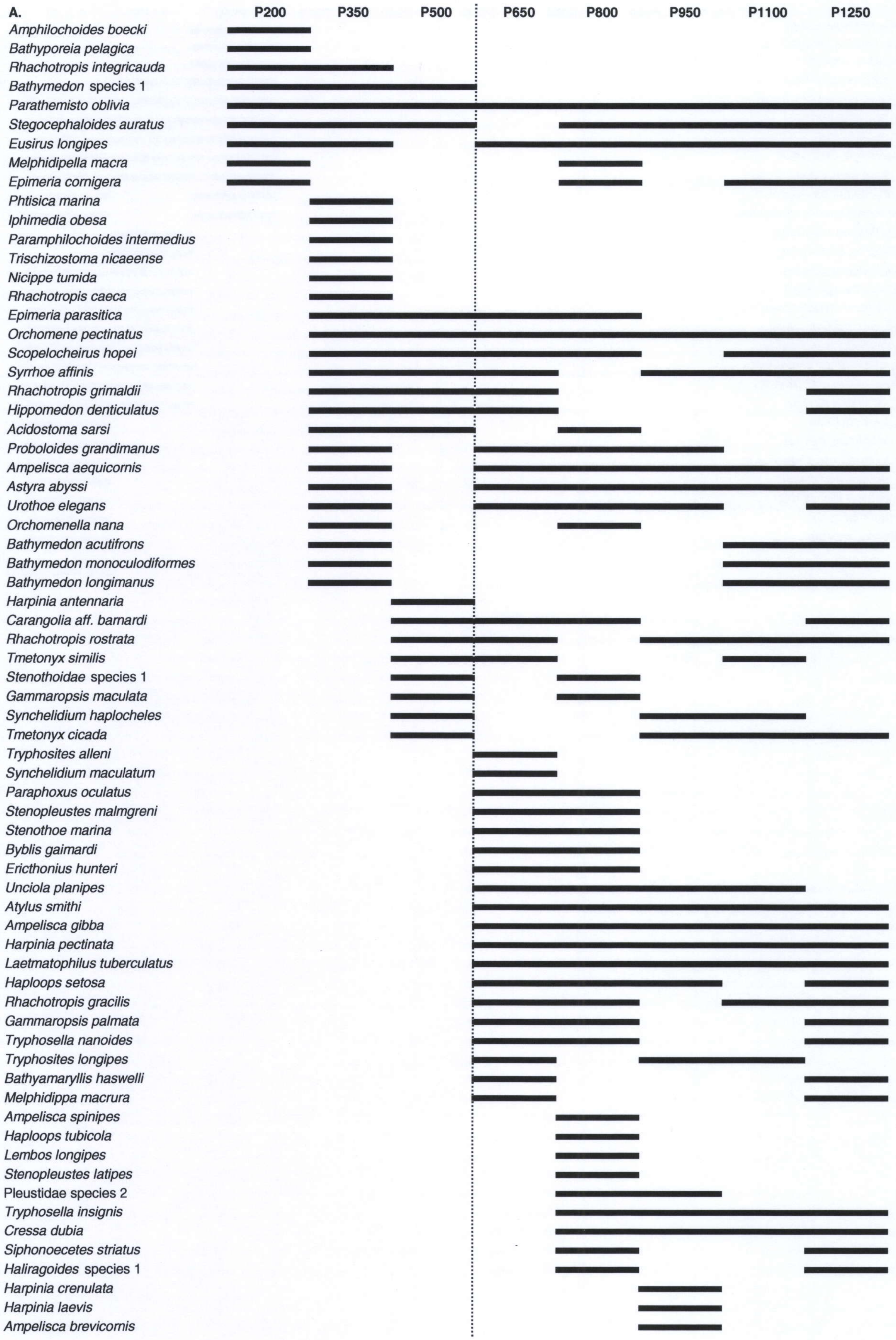


Figure 5.13 Tanaidacea species occurrence along the continental slope at Porcupine Seabight (P200-P1250) and Meriadzek Terrace (M200-M1250). The dashed line indicates the boundary between the upper and lower slope zone.

5.2.4.3. Generalists: patterns of Amphipoda

The peracarid taxon with the highest total number of species is Amphipoda (Fig. 5.14), with 97 and 126 species at Porcupine Seabight and at Meriadzek Terrace respectively (see Table 5.1) (see appendix 2 for full species list and appendix 3 for absolute density values). Both areas have 72 amphipod species and 56 genera in common. The diversity pattern for both areas shows a slightly different picture as illustrated by the diversity indices of Hill (Fig. 5.15A). Overall, the amphipod species richness and diversity is higher at Meriadzek Terrace compared to Porcupine Seabight, except for the deepest station. At Meriadzek Terrace N_0 peaks at 950 m (55 species) and than decrease with depth, while at Porcupine Seabight N_0 first peaks at 800 m (40 species) than decreases with depth, but increases again at 1100 m and 1250 m resulting in the highest species richness (54 species) and diversity at Porcupine Seabight at this latter depth. The k-dominance plot (Fig. 5.15B) indicates a clear division of the upper and lower slope stations, mainly at Meriadzek Terrace, with a larger dominance effect for the upper slope stations. The distribution pattern of the different amphipod species along both continental slopes is rather difficult to interpret due to the large amount of species. Some general patterns can be outlined and further interpretation is done on genus level. In the distribution of the amphipod species (Fig. 5.14) an obvious zonation or species turnover can be seen between the upper and lower slope, but both zones comprise a high number of species. From the 56 common amphipod genera, twelve were sampled along the complete depth gradient from 200-1250 m and can be considered as eurybathic genera (see Table 5.3.). Only one genus, *Amphilochoides*, was sampled only at the upper slope (200-500 m), while eight genera covered the complete lower slope (650-1250 m) and were not found on the upper slope: *Bathyamaryllis*, *Chevreuxius*, *Haliragoides*, *Haploops*, *Laetmatophilus*, *Liljeborgia*, *Melphidippa* and *Tryphosella*. Another 18 genera comprise a wide distribution range over five or more sampling depths/stations. 17 genera have a rather limited depth distribution (over less than five sampling depths) and these are only found within the lower slope area: *e.g.* *Euonyx* and *Pardalisca* are two genera found from 1100-1250 m depth.



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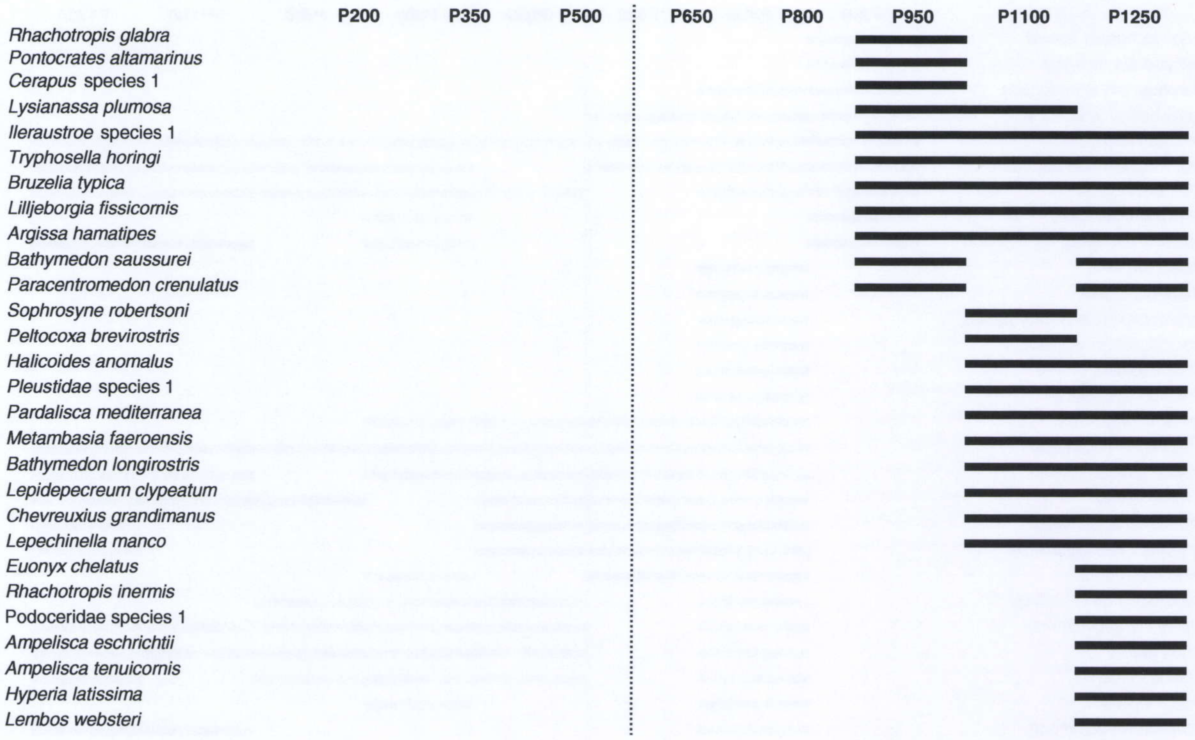

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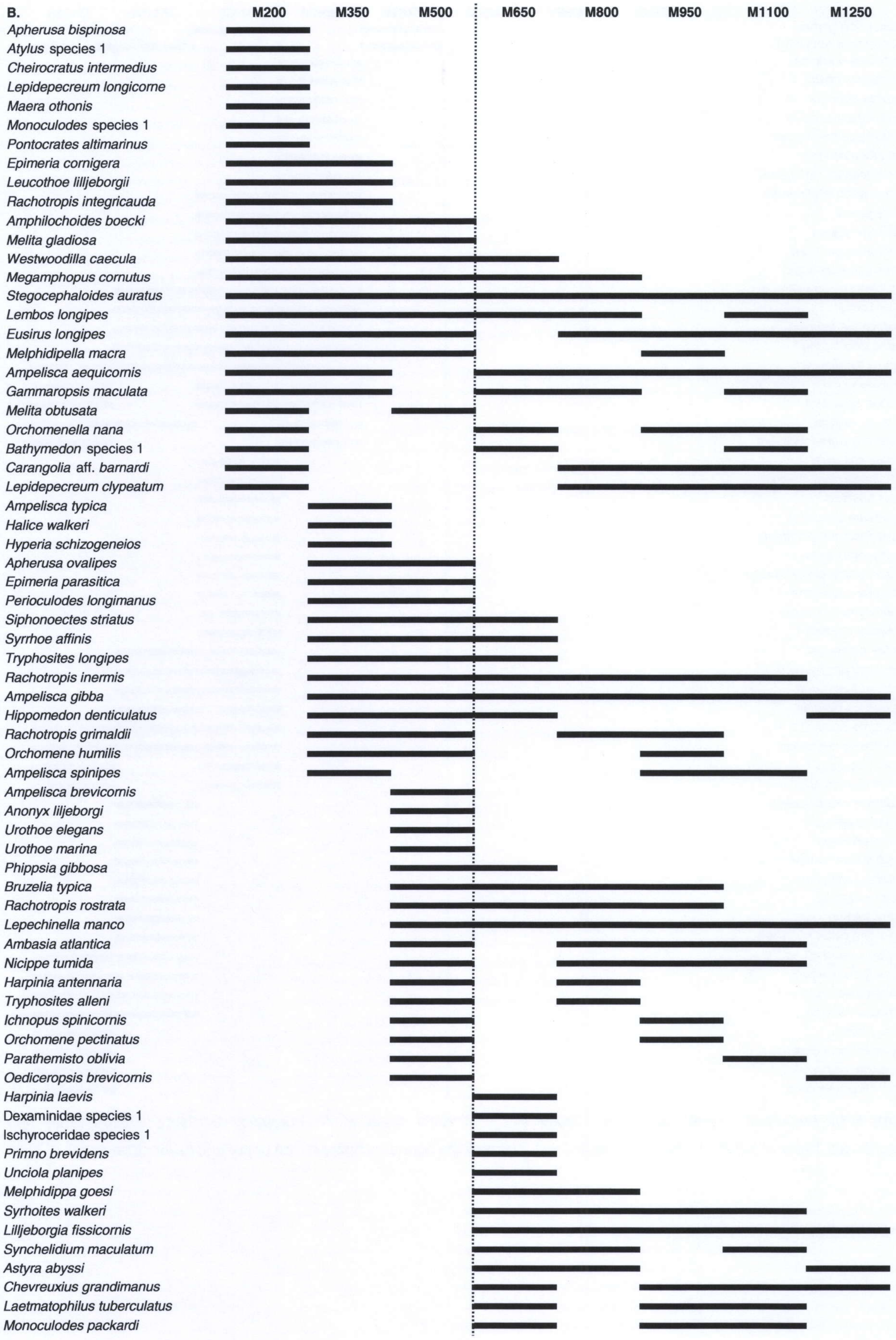

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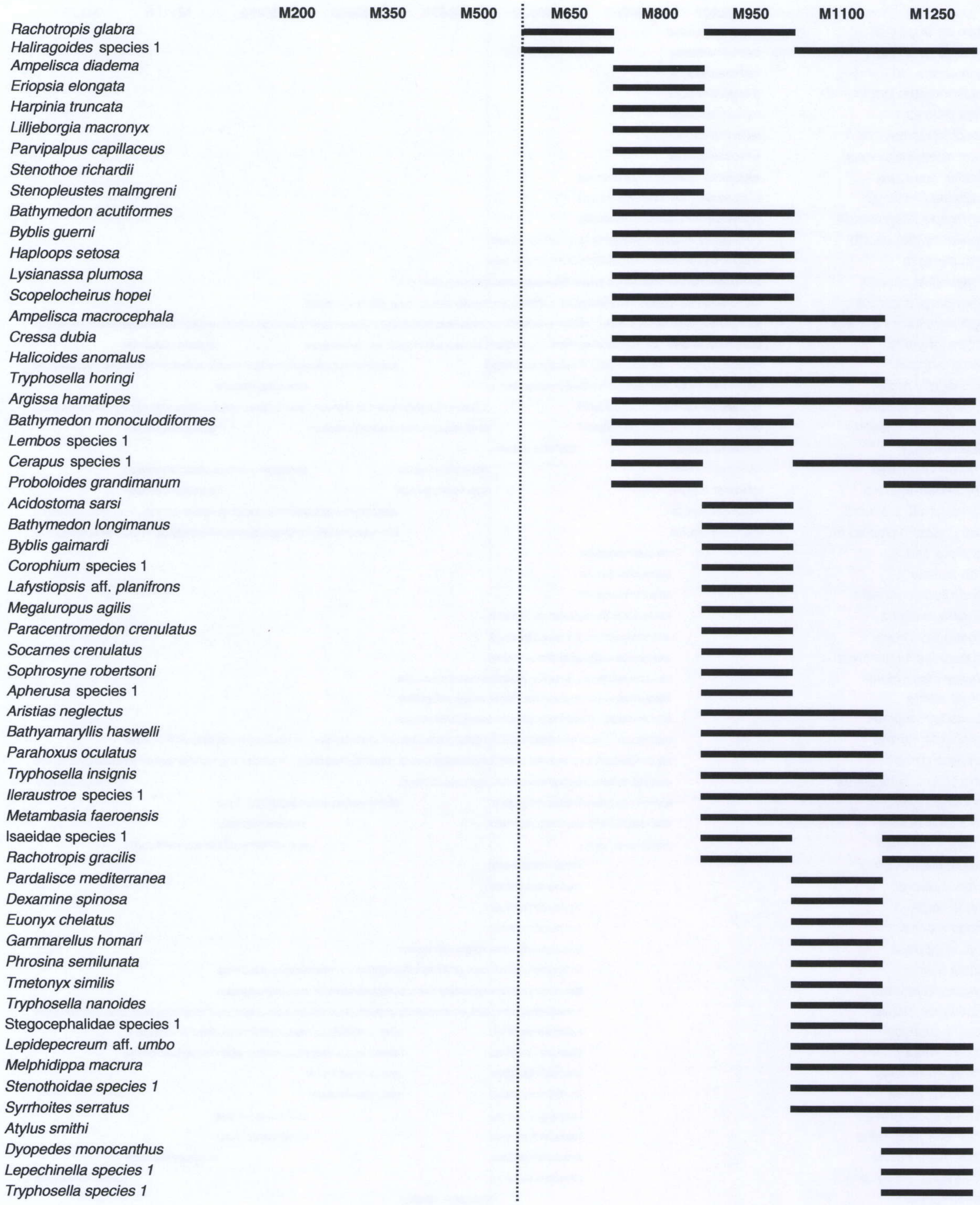


Figure 5.14 Amphipod species occurrence along the continental slope at A) Porcupine Seabight (P200-P1250) and B) Meriadzek Terrace (M200-M1250). The dashed line indicates the boundary between the upper and lower slope zone.

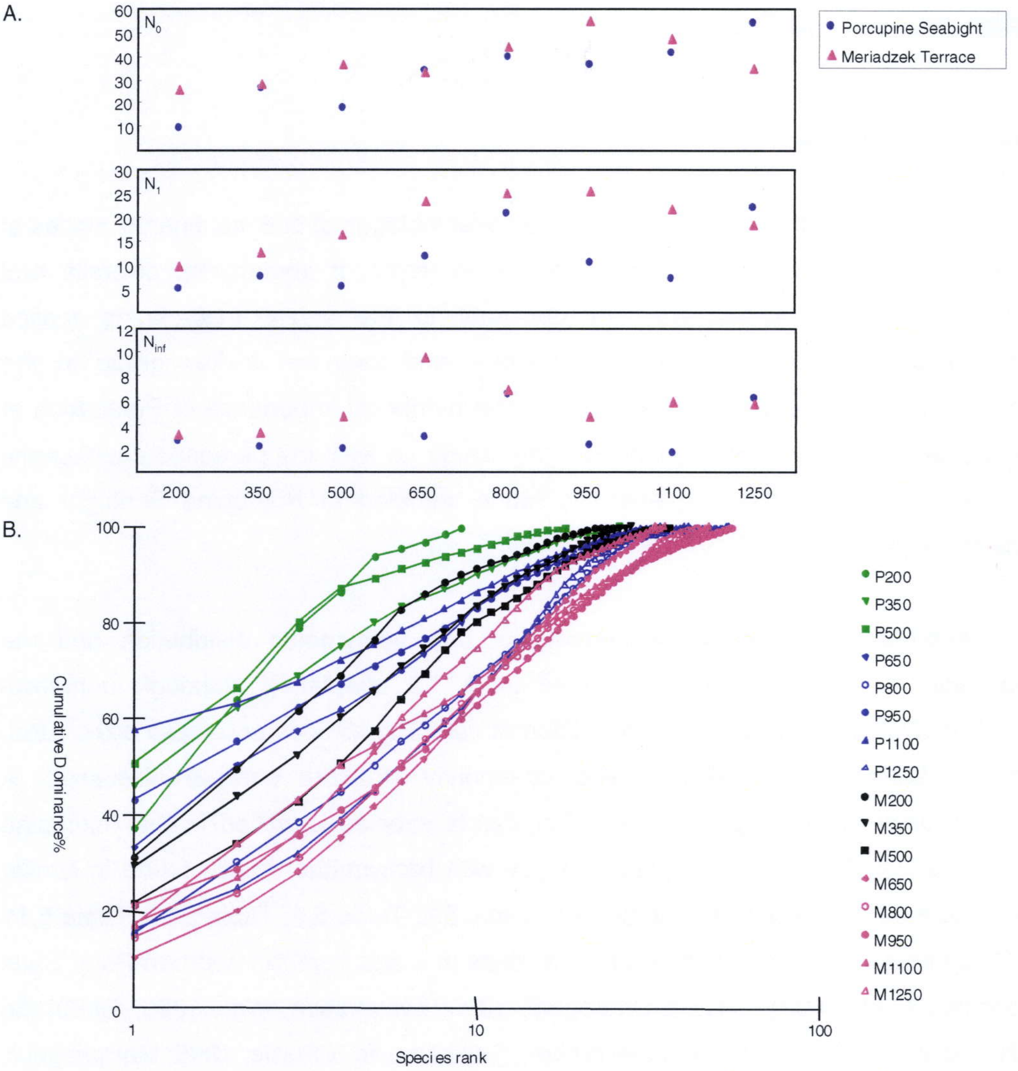


Figure 5.15 Alpha diversity of Amphipoda species along the depth gradient (200-1250 m) at Porcupine Seabight and Meriadzek Terrace: A) Diversity indices of Hill (N_0, N_1 and N_∞ and B) corresponding k-dominance curves.

5.3. Discussion and conclusions

5.3.1. Importance of Peracarida

In the present study, the hyperbenthic peracarid crustacean assemblages of both continental slopes at Porcupine Seabight and Meriadzek Terrace were studied in terms of abundance, diversity and community structure. Peracarid crustaceans are dominant in the vagile macrofauna (called suprabenthos or hyperbenthos) in deep-sea assemblages, and they are a key group in the benthopelagic coupling (Graf, 1992; Cartes *et al.*, 2002). The numerical importance of Peracarida at bathyal depths in the deep sea has been confirmed in this study as well: the peracarid crustaceans made up 77 % and 59 % of the total hyperbenthic fauna sampled at Porcupine Seabight and Meriadzek Terrace respectively.

Most studies on deep-sea hyperbenthos concentrate on the bathymetric distribution and the community composition of deep-sea peracarids (see table 1.2 chapter 1). Although numerical comparison with these studies is difficult due to the different sampling devices and mesh sizes used, some information on bathymetric distribution and community structure can be discussed. A comparison of the maximal depth range of all the Peracarida species identified in the Porcupine Seabight and the Meriadzek Terrace in the present study with bathymetric ranges found in similar peracarid studies performed on species level is given in Table 5.8, Table 5.9, Table 5.10, Table 5.11 and Table 5.12. These studies comprise bathymetric transects in areas from the northern Polar Seas (Brandt, 1997c; Sirenko *et al.*, 1996; Fosså & Brattegard, 1990; Svavarsson *et al.*, 1990, 1993), the Bay of Biscay (Elizalde *et al.*, 1991, 1993; Sorbe & Weber, 1995; Dauvin & Sorbe, 1995; Marquiegui & Sorbe, 1999; Dewicke, 2002), the Portuguese margin (Cunha *et al.*, 1997) and the Mediterranean waters (Cartes & Sorbe, 1995, 1997, 1999a; Cartes *et al.*, 2003). Most of these studies concentrate on one particular peracarid crustacean order (Amphipoda: Dauvin & Sorbe, 1995; Cartes & Sorbe, 1999a; Mysidacea: Cartes & Sorbe, 1995; Fosså & Brattegard, 1990; Elizalde *et al.*, 1991; Isopoda: Svavarsson *et al.*, 1990, 1993; Cumacea: Cartes & Sorbe, 1997), others studied all the Peracarida (Brandt, 1997c; Cartes *et al.*, 2003;) or the complete hyperbenthic fauna (Sirenko *et al.*, 1996; Elizalde *et al.*, 1993; Sorbe & Weber, 1995; Marquiegui & Sorbe, 1999; Cunha *et al.*, 1997; Dewicke, 2002). Comparing the peracarid species composition and depth ranges found in the present study to these other studies (Table 5.8 to Table 5.12), a significant resemblance was found mainly with the peracarid fauna sampled in areas in the Bay of Biscay and the Mediterranean. The number of common species with northern areas is much lower indicating the importance of the south to north directed slope current (Pingree & Le Cann, 1989, 1990; Huthnance *et al.*, 2001) in the faunal dispersal. Peracarid species richness (N_0) found at Porcupine Seabight and Meriadzek Terrace is comparable to areas in the Bay of Biscay (Table 5.8-5.12), where the relatively high species richness can be explained by the presence of a major gradient of substrate (for Porcupine Seabight and Meriadzek Terrace see chapter 3 and chapter 4) and depth, and the conjunction of the northern limit of warm-temperate species and the southern limit of cold-temperate species (Dauvin & Bellan-Santini, 1996). In our results some cold-temperate peracarid species (*e.g.* the amphipods *Atylus smithi* and *Lepedepecreum* aff *umbo*) were sampled which were not found in more southern regions in the Bay of Biscay, indicating their southern limit in these areas. A comparison of peracarid species diversity found in this study (see Table 5.6 in this chapter) with other bathymetric gradient studies (Brandt, 1993, 1995, 1997a; Cunha *et al.*, 1997; Vanquickelberghe, 1999) is given in Table 5.13. Similar diversity pattern with depth for the Peracarida are found. Moreover, the diversity and density patterns observed at Meriadzek Terrace confirm the general view of deep-sea diversity and density, which postulates that diversity increases with depth (Sanders, 1968), while abundance is high at shallower sites and decreases with depth (Dahl *et al.*, 1976, Dauvin *et al.*, 1995). Additionally, the predominant pattern of species diversity in both macrobenthos and megabenthos appears to be parabolic, with a peak at intermediate depths and lower values on the upper slope and abyssal depths (Rex, 1983). The density and diversity patterns found at Porcupine Seabight show a different trend, indicating the existences of different environmental conditions or other factors influencing the hyperbenthos distribution at both study sites. Community structure analysis illustrated that the continental slope hyperbenthic peracarid species of the two areas adjust to two more or less clearly delimited faunistic zones: an upper slope zone (200-500 m), where species diversity is low and a lower slope zone (650-1250 m), where species diversity attain maximum values. This analysis additionally indicated that the upper and lower slope faunistic zones of both study sites showed significant differences in species composition between the two sites. Similar zonation patterns for Peracarida have been observed in the Mediterranean by Cartes *et al.* (2003), who found three faunistic slope zones: an upper slope belt above approximately 400 m, a mid slope belt from 400-1200 m and a lower slope belt below approximately 1200 m.

Abundance, diversity and community analysis all indicate the importance of Mysidacea on the upper part of both continental slopes, while Cumacea, Isopoda and Tanaidacea prefer the deep (as also illustrated previously in chapter 3 and 4). Amphipoda seem to be important along the complete depth gradient. This observation was studied in this chapter in more detail in three case studies: 1) Mysidacea: upper slope preference; 2) Cumacea, Isopoda and Tanaidacea: preferring the deep; 3) Generalists: patterns of Amphipoda, and indicated different diversity patterns for the different Peracarida groups. Mysidacea showed a high species richness and diversity at the upper slope in both sites, followed by a decrease till 950 m to increase slightly towards the deepest stations. Cumacea species richness and diversity increased with depth, with a maximum at 1100 m at Porcupine Seabight and at 950 m at Meriadzek Terrace. Also an increasing trend with depth was found for the Isopoda although maximum diversity was found at 800 m at Porcupine Seabight and at 950 m at Meriadzek Terrace. A similar trend was found for Amphipoda. Tanaidacea were not frequently caught and were restricted to the deepest stations.

However, the study of diversity and the relationships between community structure and environmental gradients such as depth or food supply has rarely been attempted (Brandt, 1995, 1997a, 1997b, 1997c; Cartes *et al.*, 2003), and the results obtained are often inconclusive. Studies trying to relate changes in hyperbenthic assemblages with environmental variables that could explain possible zonation patterns are almost nonexistent. Factors limiting the presence of Peracarida are a combination of biogenic microhabitat heterogeneity, which is also influenced by the peracarid crustaceans themselves and other small-bodied animals. Other limiting factors could be sedimentological conditions, disturbance created by feeding and burrowing activities, predation, food resources and availability and their dependence on hydrography and depth (Brandt, 1997c).

All observation of the peracarids combined with the results on the hyperbenthic taxa (see chapter 3 and chapter 4) clearly indicate that different combinations of factors might play a structuring role for the benthic boundary layer fauna along the two slope sites Porcupine Seabight and Meriadzek terrace. This will be discussed in chapter 6 (general discussion and conclusions), taking into account the different patterns found at the two sites. The next part of this discussion concentrates on the link of specific distribution patterns of Peracarid families, genera and species with food availability along the continental slopes.

5.3.2. Zonation of Peracarida in the deep sea: a matter of food availability?

Most aspects concerning the organization of animal communities in the deep sea remain poorly understood. Despite this there are some relatively well-documented patterns such as species replacement with depth and depth zonation (Gage & Tyler, 1991). Causes responsible for observed changes in these patterns are difficult to establish, although both physical and biological causes in origin have been argued. Among the possible causes of biotic origin, food resource partitioning between coexisting species is one of the most widely discussed (Cartes, 1998).

The deep-sea ecosystem is considered as an environment dependant on the import of energy from outside (Rowe, 1981). In such a system the decline of faunal abundance seems to be related to the amount and the quality of organic matter reaching the sea floor and thus influencing the faunal zonation (Sanders *et al.*, 1965; Rowe *et al.*, 1974; Laubier & Sibuet, 1979). On continental slopes, the abundance of life in benthic assemblages is intermediate between those of the shallow continental shelf (highest) and the abyssal plain (lowest). In this environment two major pathways of energy are recognized: the first one from the euphotic zone (vertical flux) and the second from the adjacent continental shelf via bottom nepheloid layers and submarine canyons (advective flux) (Sorbe, 1999). As the particulate organic matter (POM) produced by primary production in the euphotic zone sinks to the sea floor, it provides a potential link between surface and the deep-sea communities (Rowe, 1983; Watts *et al.*, 1992; Cartes *et al.*, 2003). Recently there has been increasing interest in studying benthopelagic coupling in order to establish these pathways linking secondary production in the benthos and top predators in demersal communities to primary production at the surface. This topic has been increasingly documented in deep-sea environments (Graf, 1992; Gooday *et al.*, 1992, 1996; Dell'Anno *et al.*, 2000) where it is generally assumed that availability of food is the main factor limiting secondary production in benthic organisms (Gage and Tyler, 1991).

In the deep sea evidence for the arrival of phytodetritus at the water-sediment interface has been documented photographically (Lampitt, 1985; Hecker, 1990), or by sediment cores collected at bottoms as deep as 5000 m depth or more (Rice *et al.*, 1994; Smith *et al.*, 1996). Whereas the dynamics of many deep-living deposit-feeders appear to be closely linked to phytodetritus events (Billet & Rice, 2001), several dominant species of macrofauna are indirectly coupled to temporal changes in particle flux, because they feed mainly on meiofaunal taxa such as foraminiferans. Moreover, peracarid crustaceans, a dominant faunal component in deep-sea assemblages, are a key group linking lower trophic levels with top predators such as fish (Cartes, 1998; Carrassón & Cartes, 2002; Cartes *et al.*, 2003).

Additionally, evidence has accumulated that the deep-sea floor is not a stable environment, but shows seasonal variation. Billett *et al.* (1983) reported seasonal pulses of phytodetrital material to bathyal and abyssal depths in the Porcupine Seabight. This material appears to originate directly from the surface primary production and to sink rapidly (100-150 m d^{-1}) to the deep-sea floor (Billett *et al.*, 1983). Once on the seabed, the detrital material is moved over the sediment surface by bottom currents. When currents exceed about 7 cm/s (at 1 m above the bottom), the material is resuspended (Lampitt, 1985). Lampitt (1985) speculates that because resuspension of the detritus will make the material more readily available to suspension feeders, quite subtle changes in the near-bottom current regime may have substantial effects on the structure of benthic and hyperbenthic (benthopelagic) communities.

Furthermore large differences in timing of the spring bloom were reported between 1982 and 1983 in the Porcupine Seabight (Lampitt, 1985). In 1982 the bloom occurred in early April and the detritus reached a depth of 2000 m on 1 May, whereas in 1983 the bloom did not occur until mid May and detritus reached a depth of 4000 m in mid-June. No data on bottom detritus were included in this research but interpretation of satellite images (http://seawifs.gsfc.nasa.gov/) of both study sites before, during and after the sampling periods indicated sampling at Porcupine Seabight was performed during a post-bloom period (bloom in May); at Meriadzek Terrace a phytoplankton bloom was present at the moment of sampling. In this study, changes in assemblages and zonation patterns found in both continental slope areas, may be related to differences in the regime of flux and deposition of organic matter between both slope areas but an analysis of these causes is difficult due to the lack of simultaneous environmental data and to the absence of detailed information on food consumed by Peracarid species. Although some studies on feeding biology of deep-sea organisms were performed, the feeding biology of bathyal and abyssal crustaceans is complex and poorly understood (Elizalde *et al.*, 1999).

Mysidacea: upper slope preference

Deep-water mysids have mainly been described from faunistic and systematic viewpoints, resulting in relatively well known systematics (Bacescu, 1989; Tattersall & Tattersall, 1951; Lagardère & Nouvel, 1980; Mauchline, 1980), but little information exists on their ecological role in deep-water communities. In general, mysids are detritivores or carnivores (Mauchline, 1980; Hargreaves, 1985) though there are hardly any data on their trophic preferences in the deep sea. Generally the species occurrence (*i.e.* zonation and community structure) of the mysids found at Porcupine Seabight and Meriadzek Terrace was consistent with previously known geographical distributions (Hargreaves, 1985; Anadón, 1993; Mauchline, 1986; Cartes & Sorbe, 1995, 1998; Cartes & Maynou, 2001; Fosså & Brattegard, 1990; Elizalde *et al.*, 1991) (Table 5.11).

Some mysid species normally associated with the continental shelf and coastal waters were present at Porcupine Seabight and Meriadzek Terrace: *e.g. Lophogaster typicus, Haplostylus normani, Anchialina agilis and Mysidopsis didelphys, Leptomysis lingvura.* Downslope penetration to the upper continental slopes at Porcupine Seabight and Meriadzek Terrace by these shelf species can be supposed. These shelf species all have a very restricted depth distribution along the Porcupine and Meriadzek slopes, they are only found between 200-350 m depth, *i.e.* around the shelf break, confirming a limited downslope movement.

Two species, *Amblyops kempi* and *Bathymysis helgae* at Porcupine Seabight and two species, *Eucopia sculpticauda* and *Hansenomysis fyllae* were only sampled in the deepest station (1215 m). Three of these four species were also sampled at the Rockall Trough (Mauchline, 1986) (northerly of Porcupine Seabight). Information on *Amblyops kempi* is scarce, this species occurred in stomach of fish caught at 1000 and 1250 m depth in the Rockall Trough. *Eucopia sculpticauda* is a cosmopolitan, bathypelagic species with a bathymetric range of 800-1500 m. Another representative of this genus *Eucopia unguiculata* was also found only at Meriadzek Terrace but within a wider range (650-1250m). *Hansenomysis fyllae* was found in the Rockall Trough between 1000 and 1750 m. It has been recorded off southwestern Ireland near 51° N, 11° 40' W and this is described as its southern limit (Tattersall & Tattersall, 1951). Although in this study, this species was sampled at Meriadzek Terrace at 47° N, 8° 13' W what lies more to the south.

A general pattern which was illustrated by the hyperbenthic and Peracarida data was the obvious zonation of the Mysidacea along the continental slope characterized by a numerical decrease with depth. The high abundance of Mysidacea on the upper slope part in both study sites might be explained by the feeding strategy of these organisms. Species-specific trophic preferences can also partially explain their distribution with depth in the present study. Mysids can have a very diversified diet. Depending on the food availability, certain mysids seem to prefer crustacean remains (*e.g.* mainly copepods) above detritus of phytoplankton origin (Cartes & Sorbe, 1998). This change in diet possibly could explain the gradient distribution of the mysids at the upper slope because their dominant food source is also very abundant at the upper slope (see chapter 3 and 4). The relative abundance of copepods at the upper slope in both areas Porcupine Seabight and Meriadzek Terrace is respectively 26 % and 24 %, compared to 7 % and 22 % at the lower slope. The difference in copepod abundance at Meriadzek is rather small, but for the Euphausiacea this is more pronounced: 13 % at the upper slope, 1.3 % at the lower slope, while at Porcupine Seabight the relative abundance of Euphausiacea is 9 % and 0.13 % for the upper and lower slope respectively. At Meriadzek the abundances of Mysidacea, Copepoda and Euphausiacea are higher compared to Porcupine Seabight (see chapter 3 and 4). Moreover Cartes & Sorbe (1998) also found an increase of phytodetritus as a food source in the stomach content of mysids, which were caught on greater depths (between 1250-1350 m in the Catalan Sea). This lower specificity in the diet of some mysid species (*e.g. Boreomysis arctica*) would support different characteristics in its biology, such as its wide bathymetric distribution range (Cartes & Sorbe, 1998). Moreover, mysids are well-known aggregators (Mauchline, 1980), which can possibly reinforce the numerical dominance of certain mysids at the upper slope stations (*e.g.* 55.5 % Erythrops *neapolitana* at M200; 31.4 % *Erythrops serrata* at P200; 36.2 % *Pseudomma affine* at M500).

Isopoda and Cumacea: preferring the deep

Carey (1972) observed changes in feeding types with increasing depth from predators to detritus-feeding forms. Moreover, as deep-sea sediments are usually very fine, it is not astonishing that deposit feeders comprise the overwhelming majority (Hessler & Jumars, 1974). Lampitt *et al.* (1986) published data from a survey in the Porcupine Seabight between 500 and 4100 m depth and found about a 30-fold decrease in invertebrate megabenthos biomass over this depth range. Within this biomass, again, suspension-feeding crustaceans were dominating.

According to Wilson (1998) most **isopod** crustaceans in the North Atlantic deep sea belong to the suborder Asellota. In contrast, South Atlantic isopod faunas have a significant component of flabelliferan isopods (Wilson, 1998). This study shows that both suborders are important in the studied areas, with Flabellifera dominating in seven of the 16 bathyal slope stations.

Many **flabelliferans**, especially **Cirolanidae**, have a high proportion of scavengers or predators that may be disadvantaged in the abyss owing to the rarity of prey (Hessler & Wilson, 1983; Gage & Tyler, 1991). In contrast, some highly active swimmers among the Cirolanidae seek out food falls (Wong & Moore, 1995, 1996) and may be well adapted to deep-sea conditions owing to their ability to find food over long distances (Wilson, 1998). The Cirolanidae species *Natatolana borealis,* an important scavenging isopod species was found in this study within a depth range of 350-1100 m in Porcupine Seabight and between 350 and 800 m at Meriadzek Terrace. This species construct U-shaped burrows in soft sediments and shows a circadian rhythm of emergence from the substratum (Taylor & Moore, 1995; Kaïm-Malka, 1997). Furthermore swimming behaviour controlled by smell has been described for this isopod (Kaïm-Malka, 1997), which may explain its rather wide distribution along the studied continental slopes. At the deeper stations another Cirolanidae species becomes abundant, *Metacirolana hanseni.* Other isopods are parasitic during some stages of their life cycle and may be similarly disadvantaged. A predominance of these life styles among flabelliferans (*e.g.* Anthuridae, some Cirolanidae, Aegidae, **Gnathiidae**) might explain some of their decline with depth, but only partially. Parasitic *Gnathia* species were mainly caught at the upper slope of Meriadzek Terrace. Dependance on carnivory or parasitism does not explain reduced diversity in other abundant groups among the flabelliferans that are detritivorous (*e.g.* the family **Sphaeromatidae**) (Wilson, 1998). This latter family showed a similar distribution pattern in both study sites, becoming very important with increasing depth.

Asellote isopod crustaceans are among the most divers group in the deep sea (Hessler & Wilson, 1983). Little is still known of the ecological factors that shape their diversity and abundance in the deep-sea environment. The deep-water asellote isopods have generally been considered detritus feeders (Wolff, 1962) but recently Svavarsson *et al.* (1993) and Gudmundsson *et al.* (2000) showed that certain deep-sea **munnopsid** asellote isopod species feed on foraminifers (Protozoa) and that their selection of food may depend upon the shape of their mouthparts. Another isopod species, *Munnopsurus atlanticus* potentially feeds on meiofauna (Elizalde *et al.*, 1999; Cartes *et al.*, 2000). This species was also sampled in this study, but mainly at Meriadzek Terrace between 950 and 1100 m.

Another family within these Asellota, **Eurycopidae**, was shown to be important along the complete studied continental slope (200-1215 m) at Meriadzek Terrace, compared to the very low abundances found at Porcupine Seabight. Species belonging to the family Eurycopidae are considered as epifaunal isopods, characterized by natatory legs,which enables the animals to walk on the surface of the sediment or to swim rapidly (Thistle & Wilson, 1987). Therefore these animals will be more subject to erosion (*e.g.* caused by benthic storms) than animals that live in or can shelter in the seabed (Thistle & Wilson, 1987). In contrast, infaunal isopods are likely to be unaffected by a few millimeters' increase or decrease in the amount of overburden (Thistle & Wilson, 1987). Eurycopidae are foraminifera eaters. Furthermore, the asellote families **Ilyarachnidae** and **Munnopsididae** are modified for swimming (Hessler *et al.*, 1979). The latter family shows insignificant abundances in both study site compared to the dominance of the family Ilyarachnidae mainly at the deeper stations at Meriadzek terrace. Species within this family have enlarged heads to accommodate crushing jaws enabling them to eat foraminifera (Hessler *et al.*, 1979). The family **Janirellidae** is considered as epifaunal but no other information concerning the biology of this family is known (Thistle & Wilson, 1987). **Ischnomesidae** are considered infaunal, tube-burrow dwellers commonly found in sudsurface layers (Thistle & Wilson, 1987). In this study these are only found at station P1250, which can be an indication of a limited contamination in the hyperbenthic sledge at this particular station. The **Arcturidae** is a dominant isopod family sampled between 650 and 1100 m at Porcupine Seabight and which is less important at Meriadzek Terrace. The Arcturidae are isopods that have developed a unique body morphology enabling them to live as passive filter feeders among plants and plant-like (in structure) animals such as bryozoans and sponges. In arcturids, the posterior pereopods are adapted for clinging while the anterior pereopods are long and hold rows of long setae (hairs). Their bodies are often elongated at the fourth segment so that they are able to tilt upwards and get their anterior legs higher in the water column (for more food). They swash their anterior pereopods around, collect small food particles out of the water and send them to the mouthparts.

Overall different isopod families show a different dominance pattern along the depth gradient between the two sampling sites Porcupine Seabight and Meriadzek Terrace. At Porcupine Seabight a dominance of filter feeding isopods (*e.g.* Arcturidae) and Cirolanidae are found, in contrast to a dominance of scavengers and predators at Meriadzek Terrace.

Compared to other groups of peracarid crustaceans (*e.g.* mysids and amphipods), **cumaceans** are more closely associated with the substratum (Cartes & Sorbe, 1997). Most deep-sea cumacean species have close relatives in shallow waters (Gage *et al.*, 2004), the exception being one family, the Ceratocumidae, which is a small overwhelmingly deep-water family (Gage *et al.*, 2004). This is also illustrated in this study where this family makes up around 50 % of all cumaceans caught at the two deepest stations at Meriadzek Terrace and 21 % at 950m. At Porcupine Seabight this family is only present at the deepest station, but in a relatively small amount. One might expect the difference in substrate between both sites may play an important role in the distribution of this typically deep-sea family. At Meriadzek Terrace very fine sediment is found at those depths, compared with coarser sediment at Porcupine Seabight at the same depths (see chapter 3 and chapter 4). Furthermore at Meriadzek Terrace, the cumacean family Lampropidae (*e.g.* species *Hemilamprops* species) is the dominant family in all stations except at the two deepest stations where the Ceratocumidae (*e.g. Ceratocuma horrida*) are dominant. At Porcupine Seabight, where the abundance of cumaceans is much higher, the Nannastacidae (*e.g. Campylaspis* species) make up the largest percentage in the two deepest stations, while the Lampropidae (*e.g. Hemilamprops* species) are dominant (more than 50 %) between 650 and 950 m. Around the shelf break (200-350 m) a dominance of Diastylidae was found. Within the former family, the Nannastacidae, the genus *Campylaspis* and some related genera the mandibles and second maxillipeds are modified as piercing organs and they probably feed on foraminiferans and perhaps small crustaceans (Jones, 1976). This dominance may be explained by the coarser sediment type at stations P1100 and P1250. Other deep-sea cumaceans are believed to live partially or completely buried in the top layer of the sediment, with many species being surface deposit-feeders or resuspension filter-feeders (Gage *et al.*, 2004). The food-manipulating appendages and mouthparts are suitable armed with spines and bristles (Jones, 1976). In some bathyal species, movement off the bottom is known predominantly to involve adult males (Cartes & Sorbe, 1997). Some bathyal cumaceans show a reproductive response to seasonally pulsed fluxes of organic material to the seabed (Bishop & Shalla, 1994; Cartes & Sorbe, 1996). It follows that utilization of this material may also fuel population expansion among these cumaceans similar to the way in which it increases abundance among foraminiferan phytodetritus opportunists (Gage *et al.*, 2004).

In both sites more cumacean families are represented at the lower slope compared the upper slope part, resulting in higher diversity. Due to the smaller amount of feeding strategies and the intense relationship of cumaceans with the sediment, no large differences were detected between the two study sites. In both sites the importance of Cumaceans increases with increasing depth, probably mainly explainable by the sediment change with depth along the continental slopes.

Amphipoda: generalists?

Amphipoda are an important and a diversified part of the bathyal and abyssal fauna. Concerning the diet and food sources exploited, amphipods seem a more heterogeneous taxon than, for instance, cumaceans or mysids, since they have different feeding strategies, which range from filter-feeding to scavenging or predation (Mills, 1967; Sainte-Marie, 1992), which might partly explain the high number of species and a wide bathymetric distribution along the studied slopes. There is limited detailed information about the feeding habits of deep-sea amphipods (Sainte-Marie, 1992; Cartes & Sorbe, 1999a) and other ecological aspects, such as oxygen consumption and food assimilation (Smith & Baldwin, 1982; Hargrave *et al.*, 1995). Some indirect ecological data on the role of amphipods in deep-sea food webs have been obtained from studies of trophic relationships with megafauna (Lagardère, 1977; Cartes, 1998). Many species or families of amphipods are widely consumed by fishes and decapod crustaceans. Among them, Lysianassidae and Eusiridae are the most commonly preyed upon by deep-water shrimps in the western Mediterranean (Cartes, 1998).
Also related to feeding preferences, amphipods show different swimming capacities and a distribution above the sediment surface that ranges from infaunal to bathypelagic or hyperbenthic species (Sainte-Marie & Brunel, 1985; Sainte-Marie, 1992). Many are nektonic and are dispersed by migration and water mass movements. Others presumably are obligatorily benthic, swimming only small distances (Barnard, 1962). Cartes & Sorbe (1999a) studied the swimming capacity of bathyal amphipods sampled at the Catalan Sea slope. Generally swimming activity of bathyal Gammaridea species was low, demonstrating their close relationship to the water-sediment interface, but was higher for Hyperiidea. All Lysianassidae and some Eusiridae had relatively high swimming capacities, while all the Liljeborgiidae, some small Oedicerotidae, Phoxocephalidae, Gammaridae, Aoridae and Haustoriidae were linked more closely to the substratum and thus showing none or very low swimming activity (Cartes & Sorbe, 1999a).

The zonation of the amphipod families shows some differences in the two studied continental slope areas, which may, in combination to the trophic diversity, be linked to changes in the flux of particulate organic matter from the water column. At Meriadzek Terrace the upper and mid slope (200-800 m) is mainly inhabited by a mixture of suspension-feeding families (*e.g.* Melphidippidae and Corophiidae) (Dauby *et al.*, 2001) and scavengers (Lysianassidae and Eusiridae) (Ruffo, 1982; Dauby *et al.*, 2001), while the deeper stations are dominated by Lilljeborgidae and Lysianassidae, a deposit-feeding/predatory type and a scavenger family respectively (Ruffo, 1982; Dauby *et al.*, 2001). Scavenging is a widespread feeding mode in deep-sea species (Kaïm-Malka, 2003) with Amphipods being one of the main groups of scavengers in the deep sea. The importance of suspension-feeding amphipods at the deeper stations of Meriadzek Terrace significantly decreases.

At Porcupine Seabight the trophic diversity and the bathymetric zonation relate different. Here, the upper slope (350-500 m) is dominantly occupied by Lysianassidae and the shelf break (200 m) by Hyperiidae and Eusiridae, though mainly scavengers. At the lower Porcupine slope (650-1250 m) an increase of suspension-feeding families (*e.g.* Ampeliscidae, Isaeidae, Corophiidae) (Dauby *et al.*, 2001) is obvious. Amphipoda of this group are typically epibenthic and feed selectively on discrete particles of organic matter (Barnard, 1962), which suggests that they can be sensitive to changes in the flux of particles and organic matter deposition (Cartes & Sorbe, 1999a). These animals are always weakly motile, or sedentary. It may be an indication of an important flux of particulate organic matter from the water column after a phytoplankton-bloom at Porcupine Seabight as illustrated also for the Isopods and to a less extend for the Cumacea.

5.3.3. Comparison of distribution and biodiversity patterns of Peracarida with shelf/coastal systems

It was thought to be useful to discuss the results in relation with the current knowledge on the peracarid fauna of continental shelf systems and coastal systems in order to confirm the high diversity subscribed to deep-sea habitats like the continental slope. Comparison with the peracarid fauna from different sites in the North Sea (Dogger Bank (do), Frisian front (ff) and the Belgian continental shelf (bcs)) after Dewicke (2002) was performed. The work of Dewicke (2002) provides a baseline study of the species composition and spatio-temporal distribution of the hyperbenthic communities of the North Sea. This comparison is possible because a similar standardized methodology, as described in the present study, was used in the study of Dewicke (2002). Three areas in the southern North Sea are compared to the continental slope areas at Porcupine Seabight and Meriadzek Terrace. Two North Sea areas are situated at the transition between mixed and stratified water masses, *i.e.* in a frontal boundary area. The **Dogger Bank** is located in the central North Sea and borders the southern North Sea to the north. This vast, submerged sandbank is regarded as a special ecological region (Kröncke & Knust, 1995). Phytoplankton production is nearly continuous throughout the year related to near-stable abundances for macrofauna and fish. The Dogger Bank (between 15 and 70 m depth) has a significant impact on the circulation in the central and southern North Sea and is an important fishing area (Dewicke, 2002). The **Frisian front** (located off the northwest Dutch coast at the boundary between the Southern Bight and the Oyster Ground; situated between the 30-40 m isobaths) approximately coincides with the position of the summer tidal mixing front and has very particular characteristics regarding its benthic community (Creutzberg, 1985). High sedimentation of organic matter occurs in the area leading to an enriched bottom fauna (Baars *et al.,* 1991). The largest area for comparison of the peracarid fauna is the **Belgian continental shelf** (on average 30 m deep). This area is characterized by numerous linear sandbanks, reflected as sets of parallel groups. Their close position to the coastline and the shallowness of the area makes them unique, both from an ecological as well as from a geological point of view. The continuous interaction between morpho- and hydrodynamics results in a complex heterogeneous structure, generating a variety of habitats for marine life. It has additionally often been hypothesized that the protective character of this sandbank system possibly sustains a nursery function for several fish and crustacean species (Dyer & Huntley, 1999).

The total number of peracarid species of each taxon (Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea) is higher for the continental slope fauna compared to the North Sea areas (Table 5.7). In terms of species number, the Dogger Bank shows the highest number of species in common (39 peracarid species) with the continental slope fauna (Porcupine Seabight and Meriadzek Terrace) (Table 5.7). Frisian front and Belgian continental shelf have a similar number of species in common with the continental slope fauna (17 and 15 peracarid species for the Frisian front and the BCS respectively) (Table 5.7). Tanaidacea were not sampled in any of the shallow areas.

Table 5.7 The total number of Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea species found along the continental slope studied in this work (Porcupine Seabight and Meriadzek Terrace) and in three coastal systems: Dogger Bank, Frisian Front and Belgian Continental Shelf (after Dewicke, 2002). The number of common species in each coastal system in comparison with the continental slope fauna is also indicated.

	Continental slope	**Dogger Bank**		**Frisian Front**		**BCS**	
	# spec	**# spec**	**# common**	**# spec**	**# common**	**# spec**	**# common**
Amphipoda	152	61	30	36	16	30	13
Cumacea	45	14	3	6	0	7	0
Isopoda	30	2	2	2	0	3	0
Mysidacea	26	14	4	9	1	10	2
Tanaidacea	5	0	0	0	0	0	0
Peracarida	258	91	39	53	17	50	15

The maximum depth range of all sampled amphipods, cumaceans, isopods, mysids and tanaids in the present study along both continental slope areas are listed in Table 5.8, Table 5.9, Table 5.10, Table 5.11 and Table 5.12 respectively, with indication of the presence of these species in the three shelf/coastal systems after Dewicke (2002). The small portion of species found in common between the deep slope habitat and the shallow North Sea habitats indicate that most species caught along the continental slope are typical deep-sea species. This observation is very obvious for most of the cumacean and isopod species, which became very abundant with increasing depth in the present study.

Moreover alpha and beta diversity for the Peracarida of the Dogger Bank, Frisian front and the Belgian continental shelf *i.e.* the different sandbank groups and Westerschelde were calculated in the present study in order to compare with diversity data of the continental slope areas (Table 5.6 in this chapter) and are listed in Table 5.14. Highest peracarid diversity in the North Sea is found at the Dogger Bank, but overall a higher peracarid diversity is established on the continental slope. Lowest diversity is found at the Westerschelde. Diversity on the Belgian continental shelf is lower compared to the Frisian front and the Dogger Bank and is much lower in comparison with the peracarid diversity found along the deeper continental slope. The sample-size independent diversity index ES(100) of the Dogger Bank ranges between 9 and 27 expected number of species (Table 5.14) and is comparable to the upper slope diversity of Porcupine Seabight (12-24 expected number of species) and Meriadzek Terrace (14-30 expected number of species) (Table 5.6). ES(100) of the lower slope of both study sites is much higher: between 25-41 and 31-45 expected number of species at Porcupine Seabight and Meriadzek Terrace respectively. The Dogger Bank and Frisian front as frontal zones have often been mentioned as biological 'hot spots' (Nielsen & Munk, 1998). Within short distance, not only the productivity, but also the structure and the trophic diversity of the communities may change significantly. It is hypothesized that such areas might in particular be attractive for the holohyperbenthos, through their motility and omnivorous behaviour.

It can be concluded that much higher peracarid diversity was found along the depth gradient of both deep continental slope areas Porcupine Seabight and Meriadzek Terrace compared to the different shallow areas in the North Sea *i.e.* Dogger Bank, Frisian front, Belgian continental shelf. The high species richness at the continental slope is mainly ascribed to the high number of Cumacea and Isopoda species. The orders Cumacea and Isopoda has been described as showing their most impressive radiation in the deep sea, where they are found at all depths down to the deepest trench (Gage & Tyler, 1991).

Table 5.8 All identified Amphipoda from Porcupine Seabight and Meriadzek Terrace in the present study with their maximal depth range in comparison with depth ranges for the different species found in similar hyperbenthic research along depth gradients. For each study the range of the sampled bathymetric transect and the total number of species is indicated. In the last column the presence of the Amphipoda species in coastal systems (do=Dogger Bank, ff=Frisian Front, bcs=Belgian Continental Shelf) is indicated (continued).

Author			Brandt, 1997	Sirenko 1996	Elizalde et al., 1993	Sorbe & Weber, 1995	Dauvin & Sorbe, 1995	Marquiegui & Sorbe, 1999	Cunha et al., 1997	Cartes & Sorbe, 1999	Cartes et al. 2003	Dewicke, 2002	Dewicke, 2002
Geographical area	Porcupine Seabight	Meriadzek Terrace	Three Artctic exp	Laptev Sea	Cap-Ferret	Golfe de Gasconge	Cap Ferret	Capbreton Canyon	Portuguese margin	Catalan Sea	SW Balearic Islands	Meriadzek Terrace	Coastal systems
Depth range	207-1215 m	227-1215 m	45-2681 m	51-3042 m	425-1043 m	392-717 m	346-1098 m	923-1009 m	21-299 m	389-1589 m	249-1622 m	201-695 m	9-70 m
Total number of species (N_0)	97	126	148	40	74	74	108	46	71	82	45	84	do 61, ff 36, bcs 30
Acidostoma sarsi	336-765*	953				395-717	1098				1586-1594		
Ambasia atlantica		494-1110*					1098						
Ampelisca aequicornis	336-1215*	227-1215*										312-695	
Ampelisca brevicornis	914	953											do/bcs
Ampelisca diadema		795								396-400			ff
Ampelisca eschrichtii	1215		50-328										
Ampelisca gibba	628-1215	352-1215								400-402		253-695	ff
Ampelisca macrocephala		795-1110											
Ampelisca spinipes	765	352-1110*										253-695	
Ampelisca tenuicornis	1215												do/ff
Ampelisca typica		352											
Amphilochoides boecki	207	227-494				392-395	346		185-188			312-592	
Anonyx liljeborgi		953	186-1525										
Apherusa bispinosa		227	321-2681				346		91-188			201-312	do/bcs
Apherusa ovalipes		352-494					346					201-312	do/ff/bcs
Apherusa species 1		953											
Argissa hamatipes	914-1215	795-1215			708-1043	669-717	711-1098	1009	21-185			695	do/ff
Aristias neglectus		953-1110											
Astyra abyssi	336-1215*	678-1215*	174-940										
Atylus smithi	628-1215	1215	45-310										
Atylus species 1		227											
Bathyamaryllis haswelli	628-1215*	953-1110											
Bathymedon acutifrons	336-1215*	795-953				669-717				389-1859	601-1594		
Bathymedon longimanus	336-1215*	953	411		708-714	392-717	610-1098	923-1009					
Bathymedon longirostris	1067-1215										398-1594	592-695	
Bathymedon monoculodiformes	336-1215*	795-1215*			708-1043	392-717	523-1098		299	389-1859	802-900		
Bathymedon saussurei	914-1215*				708-714	669-717	610-923						
Bathymedon species 1	207-469	227-1110*											
Bathyporeia pelagica	207												
Bruzelia typica	914-1215	494-953			708-714	392-717	346-711	923		389-1859	398-1594	592-695	
Byblis gaimardi	628-765	953	45-326										
Byblis guerni		795-953				669	610	923				592-695	
Carangolia aff barnardi	469-1215*	227-1215*											
Cerapus species 1	914	795-1215*											
Cheirocratus intermedius		227			425-437	392-395	346-687		185			253	ff
Chevreuxius grandimanus	1067-1215	678-1215*			1024-1043	669	923-1098	1009					
Corophium species 1		953											
Cressa dubia	765-1215	795-1110	328-425										
Dexamine spinosa		1110											
Dexaminidae species 1		678											
Dyopedes monocanthus		1215											do/bcs
Epimeria cornigera	207-1215*	227-352					747-1098	923	188			201-695	
Epimeria parasitica	336-765	352-494			425-1043	395-669	346-1034		125-299	393-601	249-1204		
Ericthonius hunteri	628-765												
Eriopsia elongata		795			1024-1043		791-1034	923		389-601			
Euonyx chelatus	1215	1110			1024-1043								
Eusirus longipes	207-1215*	227-1215*	411		425-1043	395-717	346-1098	923	125-299	389-1859	601-1594	201-695	
Gammarellus homari		1110											
Gammaropsis maculata	469-765*	227-1110*										253-312	
Gammaropsis palmata	628-1215*												do
Halice walkeri		352											
Halicoides anomalus	1067-1215	795-1110			1024-1043		687-1098		188	389-600	601-804	253-312	

Table 5.8 All identified Amphipoda from Porcupine Seabight and Meriadzek Terrace in the present study with their maximal depth range in comparison with depth ranges for the different species found in similar hyperbenthic research along depth gradients. For each study the range of the sampled bathymetric transect and the total number of species is indicated. In the last column the presence of the Amphipoda species in coastal systems (do=Dogger Bank, ff=Frisian Front, bcs=Belgian Continental Shelf) is indicated (continued).

Author			Brandt, 1997	Sirenko 1996	Elizalde et al., 1993	Sorbe & Weber, 1995	Dauvin & Sorbe, 1995	Marquiegui & Sorbe, 1999	Cunha et al., 1997	Cartes & Sorbe, 1999	Cartes et al. 2003	Dewicke, 2002	Dewicke, 2002
Geographical area	Porcupine Seabight	Meriadzek Terrace	Three Artctic exp	Laptev Sea	Cap-Ferret	Golfe de Gasconge	Cap Ferret	Capbreton Canyon	Portuguese margin	Catalan Sea	SW Balearic Islands	Meriadzek Terrace	Coastal systems
Depth range	207-1215 m	227-1215 m	45-2681 m	51-3042 m	425-1043 m	392-717 m	346-1098 m	923-1009 m	21-299 m	389-1589 m	249-1622 m	201-695 m	9-70 m
Total number of species (N_0)	97	126	148	40	74	74	108	46	71	82	45	84	do 61, ff 36, bcs 30
Haliragoides species 1	765-1215*	678-1215*											
Haploops setosa	628-1215*	795-953	232-1525	1006-1016								592-695	
Haploops tubicola	765		174-1525										
Harpinia antennaria	469	494-795*						923					do/ff
Harpinia crenulata	914				1024-1043	717	523-1034	923					do/ff
Harpinia laevis	914	678			425-437		431-687						
Harpinia pectinata	628-1215		198-315						125	396-1255		592-695	ff
Harpinia truncata		795								389-1275			
Hippomedon denticulatus	336-1215*	352-1215*			425-437	395	346-431					201-695	do
Hyperia latissima	1215												
Hyperia schizogeneois		352											
Ichnopus spinicornis		494-953*							185				
Ileraustroe species 1	914-1215	953-1215											
Iphimedia obesa	336						346	923	91		1204	201-253	do
Isaeidae species 1		953-1215*											
Ischyroceridae species 1		678											
Laetmatophilus tuberculatus	628-1215	678-1110*										592-695	
Lafystiopsis aff *planifrons*		953											
Lembos longipes	765	227-1110*											do
Lembos species 1		795-1215*											
Lembos websteri	1215												
Lepechinella manco	1067-1215	494-1215			708-714	669-717	687-923		299	1250-1355	896-1049	592-695	
Lepechinella species 1		1215											
Lepidepecreum aff *umbo*		1110-1215											
Lepidepecreum clypeatum	1067-1215	227-1215*										*201*	
Lepidepecreum longicorne		227											do
Leucothoe liljeborgii		227-352							185	389-1263	398-402	253-312	
Lilljeborgia fissicornis	914-1215	678-1215	45-2681									650-695	
Lilljeborgia macronyx		795			1024-1043		485-1034						
Lysianassa plumosa	914-1067	795-953				717	687-923		299			592-695	
Maera othonis		227				392			125-299			201-253	do
Megalopurus agilis		953							21				do/ff/bcs
Megamphopus cornutus		227-795										201	do
Melita gladiosa		227-494										253-312	
Melita obtusata		227-494*											do/ff/bcs
Melphidipella macra	207-765*	227-953*			425-437	392-395	346-747		91-299			201-312	do/bcs
Melphidippa goesi		678-795	45-411									312-650	
Melphidippa macrura	628-1215*	1110-1215										592-695	
Metambasia faeroensis	1067-1215	953-1215											
Monoculodes packardi		678-1110*			425-1043	392-717	346-1098	1009	299	389-1859	617-1594	592-695	
Monoculodes species 1		227											
Nicippe tumida	336	494-1110*			425-1043	392-717	346-1034			389-1263	601-603	201-695	
Oediceropsis brevicornis		494-1215*			425-714	392-669	346-791		299	396-1355	398-1594	592-650	
Orchomene humilis		352-953*			708-714	392-717	610-747	923					
Orchomene pectinatus	336-1215	494-953*	180-315	1006-1016			1098						
Orchomenella nana	336-765*	227-1110*			425-1043	392-717	346-1034		21-299	523-1263	398-1204	592-695	do/ff/bcs
Paracentromedon crenulatus	914-1215*	953			1024-1043		1034			1263-1355			
Paramphilochoides intermedius	336												do
Paraphoxus oculatus	628-765	953-1110	174-830							389-601			
Parathemisto oblivia	207-1215	494-1110*	321-1525										
Pardalisca mediterranea	1067-1215	1110			1024-1043	669	346-1098	923-1009		396-1859	802-1594		
Parvipalpus capillaceus		795											

Table 5.8 All identified Amphipoda from Porcupine Seabight and Meriadzek Terrace in the present study with their maximal depth range in comparison with depth ranges for the different species found in similar hyperbenthic research along depth gradients. For each study the range of the sampled bathymetric transect and the total number of species is indicated. In the last column the presence of the Amphipoda species in coastal systems (do=Dogger Bank, ff=Frisian Front, bcs=Belgian Continental Shelf) is indicated (continued).

Author			Brandt, 1997	Sirenko 1996	Elizalde et al., 1993	Sorbe & Weber, 1995	Dauvin & Sorbe, 1995	Marquiegui & Sorbe, 1999	Cunha et al., 1997	Cartes & Sorbe, 1999	Cartes et al. 2003	Dewicke, 2002	Dewicke, 2002
Geographical area	Porcupine Seabight	Meriadzek Terrace	Three Artctic exp	Laptev Sea	Cap-Ferret	Golfe de Gasconge	Cap Ferret	Capbreton Canyon	Portuguese margin	Catalan Sea	SW Balearic Islands	Meriadzek Terrace	Coastal systems
Depth range	207-1215 m	227-1215 m	45-2681 m	51-3042 m	425-1043 m	392-717 m	346-1098 m	923-1009 m	21-299 m	389-1589 m	249-1622 m	201-695 m	9-70 m
Total number of species (N_0)	97	126	148	40	74	74	108	46	71	82	45	84	do 61, ff 36, bcs 30
Peltocoxa brevirostris	1067												
Perioculodes longimanus		352-494			708-714	395-669	687-747		21-188	389-600			do/ff/bcs
Phippsia gibbosa		494-678											
Phrosina semilunata		1110											
Phtisica marina	336								91-299				do/ff/bcs
Pleustidae species 1	1067-1215												
Pleustidae species 2	765-914												
Podoceridae species 1	1215												
Pontocrates altamarinus	914	227							21			201	do/bcs
Primno brevidens		678											
Proboloides grandimanus	336-914*	795-1215*											
Rhachotropis caeca	336					392-717	346-791	923		389-1859	398-1594		
Rhachotropis glabra	914	678-953*				395	346-610			389-1280			
Rhachotropis gracilis	628-1215*	953-1215*						923					
Rhachotropis grimaldii	336-1215*	352-953*			425-1043	392-717	346-1034	923-1009		389-1280	601-1204		
Rhachotropis inermis	1215	352-1110											
Rhachotropis integricauda	207-336	227-352					346		125-299	389-506	398-402	253-312	
Rhachotropis rostrata	469-1215*	494-953			708-1043	669-717	485-1098	1009	299	389-1859	601-1594	592	
Scopelocheirus hopei	336-1215*	795-953			425-714	392-717	346-1098	923	125-299	389-1263	294-804		do/ff
Siphonoecetes striatus	765-1215*	352-678							125-188			201-650	do
Socarnes crenulatus		953											
Sophrosyne robertsoni	1067	953											
Stegocephalidae species 1		1110											
Stegocephaloides auratus	207-1215*	227-1215			425-1043	392-717	346-1098	923	299				
Stenopleustes latipes	765		1525										
Stenopleustes malmgreni	628-765	795	321						91-188				
Stenothoe marina	628-765								91			695	do/ff/bcs
Stenothoe richardi		795											
Stenothoidae species 1	469-765*	1110-1215											
Synchelidium haplocheles	469-1067*											253	do
Synchelidium maculatum	628	678-1110*			708-1043	392-717	485-1034	923-1009		389-1355	398-804	201-650	
Syrrhoe affinis	336-1215*	352-678			425-437	392-717	346-687		21-299	389-601	1015-1049	592-695	
Syrrhoites serratus		1110-1215											
Syrrhoites walkeri		678-1110										592-695	
Tmetonyx cicada	469-1215*			1006-1016									do
Tmetonyx similis	469-1067*	1110			708-714		523-923			400-1284	601-1204	201-695	
Trischizostoma nicaeense	336					395	346-386		91-299		398-402		
Tryphosella horingi	914-1215	795-1110										592	
Tryphosella insignis	765-1215	953-1110						923-1009					
Tryphosella nanoides	628-1215*	1110										312	
Tryphosella species 1		1215											
Tryphosites alleni	628	494-795*			425-1043	392-717	346-1098			392-598		312-695	
Tryphosites longipes	628-1067*	352-678				392-395	485			389-600			do
Unciola planipes	628-1067	678	232-328										
Urothoe elegans	336-1215*	953			1024-1043		1034-1098			501-598		201-695	bcs
Urothoe marina		953											
Westwoodilla caecula		227-678	198		425-714	392-395	431		125-299	389-400		253-695	do

Table 5.9 All identified Cumacea from Porcupine Seabight and Meriadzek Terrace in the present study with their maximal depth range in comparison with depth ranges for the different species found in similar hyperbenthic research along depth gradients. For each study the range of the sampled bathymetric transect and the total number of species is indicated. In the last column the presence of the Cumacea species in coastal systems (do=Dogger Bank, ff=Frisian Front, bcs=Belgian Continental Shelf) is indicated.

Author			Brandt, 1997	Sirenko 1996	Elizalde et al., 1993	Sorbe & Weber, 1995	Marquiegui & Sorbe, 1999	Cunha et al., 1997	Cartes & Sorbe, 1997	Cartes et al. 2003	Dewicke, 2002	Dewicke, 2002
Geographic area	Porcupine Seabight	Meriadzek Terrace	Three Artctic exp	Laptev Sea	Cap-Ferret	Golfe de Gasconge	Capbreton Canyon	Portuguese margin	Catalan Sea	SW Balearic Islands	Meriadzek Terrace	Coastal systems
Depth range	207-1215 m	227-1215 m	45-2681 m	51-3042 m	425-1043 m	392-717 m	923-1009 m	21-299 m	389-1589 m	249-1622 m	201-695 m	9-70 m
Total number of species (N_0)	34	33	36	3	30	20	19	25	36	24	16	do 14, ff 6, bcs 7
Bathycuma brevirostris	1067			no common spec	1024-1043		1009		524-1859	802-1594		
Campylaspis alba	1215											
Campylaspis glabra	336-1215*	494-1215	198-940		425-714	392-717	1009	185-299	395-1859	617-1594	253-695	
Campylaspis horridoides	914-1215	795-1215						299	1253-1859	1024-1594	592	
Campylaspis macrophthalma	336-1215*	1110						299			253-312	
Campylaspis rostrata	765-1215	678-1110			1024-1043				593-598		695	
Campylaspis spinosa	1215											
Campylaspis squamifera	1215	678-1215*			708-714	392-717	1009		1258-1279		695	
Campylaspis verrucosa	628-1215*	795-1215*			425-437			299		601-804	592-695	
Campylaspis vitrea	1067-1215	795								896-1594		
Ceratocuma horrida	1215	953-1215										
Cumellopsis puritani	1067-1215	953-1215				669			595-1859	601-1594		
Cyclaspis longicaudata	628-1215*	227-1110*			1024-1043	669	1009		1253-1859	1204-1594	592-695	
Cyclaspoides sarsi	1067				1024-1043							
Diastylis doryphora	1067-1215											
Diastylis laevis		953						21-125				
Diastylis rugosa		352-494										do
Diastylis tumida	336	795-1215										
Diastyloides bacescoi	336	227-795									201-695	
Diastyloides biplicata	207-336							91-299				do
Diastyloides serrata	1067-1215				425-1043	392-717	923-1009		393-1859	1586-1594		
Hemilamprops normani	1067-1215	227-1215				669-717	1009				312-695	
Hemilamprops uniplicata	336-1215*	227-1110	198-1525								201-695	
Iphinoe serrata		227-795*						125-299				
Iphinoe tenella		227										
Lamprops fasciata		227-1215*										
Leptostylis grandis		1110										
Leptostylis macrura	1067	494-1110*						299	393-601	398-402		
Leptostylis villosa	207-1215*		50-1525		425-714	392-717	1009					do
Leucon affinis	1215				708-714	669			393-1263	802-900		
Leucon longirostris		953							395-1355			
Makrokylindrus anomalus		494			1024-1043							
Makrokylindrus insignis	765								395-1263			
Makrokylindrus josephinae	1067	678-1215			708-714						592-695	
Makrokylindrus longicaudatus	1067				1024-1043		1009	125				
Makrokylindrus longipes	765-1215	795-1215			1024-1043	669-717	923-1009	299	524-1859	1204-1594		
Makrokylindrus mystacinus	1067	494-795										
Paralamprops orbicularis		678-1110										
Paralamprops species 1	914-1215											
Platysympus typicus	765-1215	678-1215			708-1043	392-669			1253-1859	802-1594	592-695	
Procampylaspis armata		352-953*			708-1043	669-717	1009	299	450-1859	601-1594	592	
Procampylaspis bonnieri	1215	1110-1215							395-1859	896-1594		
Procampylaspis macronyx		953										
Procamylaspis bituberculata	1215	953-1215										
Vaunthompsonia cristata	1067-1215	795-1110										

Table 5.10 All identified Isopoda from Porcupine Seabight and Meriadzek Terrace in the present study with their maximal depth range in comparison with depth ranges for the different species found in similar hyperbenthic research along depth gradients. For each study the range of the sampled bathymetric transect and the total number of species is indicated. In the last column the presence of the Isopoda species in coastal systems (do=Dogger Bank, ff=Frisian Front, bcs=Belgian Continental Shelf) is indicated.

Author			Brandt, 1997	Sirenko 1996	Svavarsson et al., 1990	Svavarsson et al., 1993	Elizalde et al., 1993	Sorbe & Weber, 1995	Marquiegui & Sorbe, 1999	Cunha et al., 1997	Cartes et al. 2003	Dewicke, 2002	Dewicke, 2002
Geographic area	Porcupine Seabight	Meriadzek Terrace	Three Artctic exp	Laptev Sea	Norwegian and Greenland Sea	Northern Seas	Cap-Ferret	Golfe de Gasconge	Capbreton Canyon	Portuguese margin	SW Balearic Islands	Meriadzek Terrace	Coastal systems
Depth range	207-1215 m	227-1215 m	45-2681 m	51-3042 m	794-3709 m	0-3970 m	425-1043 m	392-717 m	923-1009 m	21-299 m	249-1622 m	201-695 m	9-70 m
Total number of species (N_0)	19	27	68	5	40	106	26	22	16	14	18	22	do 2, ff 2, bcs 3
Aega species 1	628-914	227-795*		no common spec									
Anthuridae species 1	765-1215*	1215											
Arcturella dilatata		227-678*										253-695	do
Aspidarachna clypeata		795-953				219-457						695	
Aspidarachna longicornis		953											
Astacilla intermedia	336-1067*	227-678*											
Astacilla longicornis	628-1067	795	774										do
Astacilla pussila		227											
Astacilla species 1		494-953											
Bathybadistes hoplitis		795-953											
Bathycopea typhlops	336-1215*	494-1215					708-714	669-717				592-695	
Disconectes latirostris	628-1215*	227-1215				274-366		392-717			802-900	253-695	
Eurydice grimaldii	628-914	227-1215*									1620-1624		
Gnathia albescens		953-1110											
Gnathia oxyuraea	336	227-494										253-312	
Gnathia vorax	1067-1215												
Ilyarachna longicornis	336-1215*	494-1215				54-92	425-1043	392-717	1009	299	617-1594	312-695	
Ischnomesus species 1	1215												
Janira maculosa		352-953*				10-731							
Janirella nanseni		953-1215							923				
Janiridae species 1	336-914*												
Leptanthura chardyi		953-1215											
Leptanthura tenuis		953					1024-1043	669-717	1009			695	
Metacirolana hanseni	628-1215	795-1215*										695	
Munna limicola	207-1215*	953				40-594						312-695	
Munnopsis beddardi	914-1215*	678-1215					708-714					592-695	
Munnopsurus atlanticus	914	227-1215*					425-714	392-717		299	398-1624		
Natatolana borealis	336-1067*	352-795									398-1204	253-695	
Natatolana caeca	1215	795-953										695	
Tytthocope megalura	765-1215*	678-1215	198-1525		800-845	250-1020						592-695	

Table 5.11 All identified Mysidacea from Porcupine Seabight and Meriadzek Terrace in the present study with their maximal depth range in comparison with depth ranges for the different species found in similar hyperbenthic research along depth gradients. For each study the range of the sampled bathymetric transect and the total number of species is indicated. In the last column the presence of the Mysidacea species in coastal systems (do=Dogger Bank, ff=Frisian Front, bcs=Belgian Continental Shelf) is indicated.

Author			Brandt, 1997	Sirenko 1996	Fossa & Brattegard, 1990	Elizalde et al., 1993	Sorbe & Weber, 1995	Marquiegui & Sorbe, 1999	Elizalde et al., 1991	Cunha et al., 1997	Cartes & Sorbe, 1995	Cartes et al. 2003	Dewicke, 2002	Dewicke, 2002
Geographic area	Porcupine Seabight	Meriadzek Terrace	Three Artctic exp	Laptev Sea	Norway fjords	Cap-Ferret	Golfe de Gasconge	Capbreton Canyon	Cap Ferret	Portuguese margin	Catalan Sea	SW Balearic Islands	Meriadzek Terrace	Coastal systems
Depth range	207-1215 m	227-1215 m	45-2681 m	51-3042 m	32-1260 m	425-1043 m	392-717 m	923-1009 m	346-1099 m	21-299 m	389-1589 m	249-1622 m	201-695 m	9-70 m
Total number of species (N_0)	15	19	15	11	19	22	22	5	27	26	16	16	23	do 14, ff 9, bcs 9
Amblyops abbreviata	469-914*	494-1110*	186-517		254-1260								592-695	
Amblyops kempi	1215													
Anchialina agilis		227								91-188	392-393	249	201-312	do/ff/bcs
Bathymysis helgae	1215					1024-1043		923	791-1099					
Boreomysis arctica		678-795	411-830	180-556	254-1260	425-1043	395-717		346-1099		389-1859	601-1624	592-695	
Boreomysis megalops	336				74-663		395		346-437	299	400-601	249-402	253-312	
Boreomysis microps		352-1110*					395							
Boreomysis tridens	914-1215	1110				1024-1043			608-1099				592	
Dactylerythrops dactylops		494												
Erythrops neapolitana	207-765*	227-494					392-395			185-299	389-1355	601-1624	201-312	
Erythrops serrata	207-469				40-490								201	do
Erythrops species 1		795												
Eucopia sculpticauda		1215												
Eucopia unguiculata		678-1215*												
Hansenomysis fyllae		1215												
Haplostylus normani		227									392-406		201-312	
Hyperythrops serriventer	336	227-494					392-395		523-608				253-312	
Leptomysis lingvura	207												253-312	do/bcs
Lophogaster typicus	207-336				32-296					185-299			201	
Mysideis insignis		227-494			110-1100	708-714	717		608-611				201-695	
Mysidetes farrani	336					425-1043	392-717		437-1099					
Mysidopsis didelphys	207-336	227			40-700					185-188			201-253	do
Paramblyops rostrata	469-1215*	953-1215				425-1043	392-717	923	346-1099	299	389-1859	601-1594	592-695	
Parapseudomma calloplura		678-953*				425-1043	392-717	923	346-1099	299	389-1355	601-1204	592	
Parerythrops obesa	628-765	227-494			135-509	708-714		923	791-1099				201-695	
Pseudomma affine	336-1215	227-1215			166-585	425-714	392-717		346-1024	299	389-601		253-695	

Table 5.12 All identified Tanaidacea from Porcupine Seabight and Meriadzek Terrace in the present study with their maximal depth range in comparison with depth ranges for the different species found in similar hyperbenthic research along depth gradients. For each study the range of the sampled bathymetric transect and the total number of species is indicated. In the last column the presence of the Tanaidacea species in coastal systems (do=Dogger Bank, ff=Frisian Front, bcs=Belgian Continental Shelf) is indicated.

Author			Brandt, 1997	Sirenko 1996	Elizalde et al., 1993	Sorbe & Weber, 1995	Marquiegui & Sorbe, 1999	Cunha et al., 1997	Cartes et al. 2003	Dewicke, 2002
Geographic are	Porcupine Seabight	Meriadzek Terrace	Three Artctic exp	Laptev Sea	Cap-Ferret	Golfe de Gasconge	Capbreton Canyon	Portuguese margin	SW Balearic Islands	Meriadzek Terrace
Depth range	207-1215 m	227-1215 m	45-2681 m	51-3042 m	425-1043 m	392-717 m	923-1009 m	21-299 m	249-1622 m	201-695 m
Total number of species (N_0)	2	5	21	-	3	3	2	1	1	3
Apseudes grossimanus		678-795				392-717				695
Apseudes spinosus	914-1215	795-1110			708-1043	669-717	923-1009	125	802-1204	695
Heterotanais species 1		1215								
Sphyrapus species 1		795-1215								
Typhlotanais aequiremis	765-1215	795-1215*								592-695

Table 5.13 Alpha and beta diversity of the peracarid species expressed in terms of different diversity indices for similar hyperbenthic research along depth gradients. Depth of the different stations is indicated. Diversity indices which were not mentioned in the different studies are indicated by '-'.

Brandt, 1993 Kolbeinsey Ridge

station	332	335	331	333	330
depth (m)	830	830	860	940	1100
Number of species (N_0)	33	52	21	71	22
Hill Diversity (N_1)	-	-	-	-	-
Hill Diversity (N_{inf})	-	-	-	-	-
Evenness (J')	0,88	0,73	0,88	0,73	0,90
Shannon Diversity (H')	3,09	2,88	2,68	3,11	2,78
ES(100)	23,3	20,3	21	24	18,2

Brandt, 1995 NEW Polynya

station	36	39	54	234	155	102	179	85	18	145	138	95	165	258	217	119	231	77	115	216
depth (m)	45	50	174	180	186	232	260	270	310	310	314	315	320	326	328	377	411	425	492	517
Number of species (N_0)	42	48	53	73	85	90	82	66	73	75	79	82	79	84	64	40	73	61	44	35
Hill Diversity (N_1)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hill Diversity (N_{inf})	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Evenness (J')	0,73	0,70	0,73	0,73	0,71	0,73	0,75	0,69	0,78	0,73	0,75	0,74	0,72	0,75	0,78	0,78	0,81	0,66	0,80	0,88
Shannon Diversity (H')	2,70	2,61	2,85	3,14	3,12	3,28	3,28	2,83	3,32	3,14	3,22	3,22	3,12	3,32	3,20	2,84	3,45	2,71	2,98	3,09
ES(100)	8,6	8	8,6	9,5	9,4	9,9	10,1	8,5	10,1	9,6	9,6	9,7	9,5	10	9,9	8,7	10,6	8	9,2	9,9

Brandt, 1997a 75°N off East Greenland

station	31-17	31-14	31-97	31-25	31-16	31-20	31-09	31-06
depth (m)	197	317	449	732	774	817	1525	2681
Number of species (N_0)	76	82	53	21	72	22	70	50
Hill Diversity (N_1)	-	-	-	-	-	-	-	-
Hill Diversity (N_{inf})	-	-	-	-	-	-	-	-
Evenness (J')	-	-	-	-	-	-	-	-
Shannon Diversity (H')	3,15	3,53	3,27	2,38	3,49	2,82	2,6	2,44
ES(100)	-	-	-	-	-	-	-	-

Cunha *et al*., 1997 Portuguese margin

station	TS333N	TS320D	TS302D	TS300D	TS298D	TS297D	TS299D
depth (m)	21	21	91	125	185	188	299
Number of species (N_0)	31	23	40	63	56	67	74
Hill Diversity (N_1)	-	-	-	-	-	-	-
Hill Diversity (N_{inf})	-	-	-	-	-	-	-
Evenness (J')	0,68	0,62	0,40	0,30	0,58	0,55	0,67
Shannon Diversity (H')	3,35	2,81	2,12	1,82	3,36	3,36	4,15
ES(100)	-	-	-	-	-	-	-

Vanquickelberghe, 1999 Meriadzek Terrace

station	ch200	ch250	ch300	ch600	ch650	ch700
depth (m)	201	253	312	592	650	695
Number of species (N_0)	43	51	52	73	59	79
Hill Diversity (N_1)	20,84	14,79	12,99	31,30	26,40	31,17
Hill Diversity (N_{inf})	5,82	3,84	4,76	10,56	9,98	9,43
Evenness (J')	0,81	0,69	0,65	0,80	0,80	0,79
Shannon Diversity (H')	3,04	2,69	2,56	3,44	3,27	3,44
ES(100)	26	21	20	32	31	34

Table 5.14 Alpha and beta diversity of the peracarid species expressed in terms of different diversity indices for different shallow area in the North Sea: Dogger Bank, Frisian front and Belgian continental shelf (divided in the different sandbank groups and Westerschelde). Depth of the stations/areas is indicated. MLLWS= Mean Lowest Low Water Spring Level. All diversity values were based on data after Dewicke (2002) and were calculated in the present study.

Dogger Bank	**do3**	**do4**	**do7**	**do2**	**do6**	**do5**	**do8**	**do1**	**do9**
depth (m)	**15**	**20**	**26**	**27**	**28**	**32**	**37**	**58**	**70**
Number of species (N_0)	20	22	25	30	20	21	30	47	72
Hill Diversity (N_1)	11,87	14,04	8,57	12,35	11,43	8,07	3,47	11,58	21,60
Hill Diversity (N_{inf})	4,33	4,92	3,23	3,41	3,75	2,06	1,41	4,66	6,05
Evenness (J')	0,83	0,85	0,67	0,74	0,81	0,69	0,37	0,64	0,72
Shannon Diversity (H')	2,47	2,64	2,15	2,51	2,44	2,09	1,25	2,45	3,07
ES(100)	13	9	14	20	16	15	10	18	27

Frisian Front	**A1**	**A2**	**A3**	**A4**	**A5**	**A6**	**B1**	**B2**	**B3**	**B4**
depth between 30-40 m isobath										
Number of species (N_0)	10	13	18	20	19	14	13	17	13	15
Hill Diversity (N_1)	8,85	3,25	4,86	4,11	4,39	4,35	8,58	6,94	4,10	4,45
Hill Diversity (N_{inf})	5,00	1,43	1,93	1,74	1,65	1,56	3,00	3,17	2,06	3,03
Evenness (J')	0,95	0,46	0,55	0,47	0,50	0,56	0,84	0,68	0,55	0,55
Shannon Diversity (H')	2,18	1,18	1,58	1,41	1,48	1,47	2,15	1,94	1,41	1,49
ES(100)	10	11	10	11	9	14	9	12	8	7

Westerschelde	**W2**	**W3**	**W4**	**W1**
Depth below MLLWS (m)	**9,0**	**18,0**	**12,4**	**14,1**
Number of species (N_0)	11	4	5	8
Hill Diversity (N_1)	1,54	1,31	1,43	3,16
Hill Diversity (N_{inf})	1,14	1,08	1,13	2,03
Evenness (J')	0,18	0,20	0,22	0,55
Shannon Diversity (H')	0,43	0,27	0,36	1,15
ES(100)	3	2	2	7

Coastal Banks	**C9s**	**C10c**	**C11c**	**C12s**	**C13c**	**C14s**	**C15s**	**C3c**	**C4s**	**C5s**	**C6s**	**C7c**	**C8s**	**C1c**	**C2s**
Depth below MLLWS (m)	**14,9**	**14,8**	**14,6**	**26,9**	**11,0**	**7,4**	**9,0**	**33,2**	**12,0**	**38,4**	**36,8**	**30,9**	**25,0**	**8,8**	**14,8**
Number of species (N_0)	16	9	7	9	9	7	7	27	15	18	13	17	16	12	14
Hill Diversity (N_1)	2,51	2,45	4,49	3,37	2,29	3,49	1,84	5,81	2,65	3,61	1,73	2,44	2,82	7,06	7,69
Hill Diversity (N_{inf})	1,31	1,36	2,99	1,77	1,28	2,01	1,17	2,56	1,39	1,87	1,16	1,53	1,84	4,00	4,45
Evenness (J')	0,33	0,41	0,77	0,55	0,38	0,64	0,31	0,53	0,36	0,44	0,21	0,32	0,37	0,79	0,77
Shannon Diversity (H')	0,92	0,90	1,50	1,21	0,83	1,25	0,61	1,76	0,98	1,28	0,55	0,89	1,04	1,95	2,04
ES(100)	7	5	6	6	5	5	5	9	7	9	4	5	6	11	11

Flemish Banks	**F9c**	**F10s**	**F11s**	**F1c**	**F2s**	**F3c**	**F4s**	**F5c**	**F6s**	**F7c**	**F8s**
Depth below MLLWS (m)	**21,8**	**16,5**	**34,2**	**12,3**	**12,7**	**12,7**	**21,3**	**10,2**	**38,2**	**18,8**	**23,2**
Number of species (N_0)	22	13	14	8	7	6	12	13	10	15	24
Hill Diversity (N_1)	2,59	2,58	3,32	5,80	4,26	3,36	6,08	6,26	2,60	3,69	5,64
Hill Diversity (N_{inf})	1,86	1,53	2,21	2,55	2,86	1,60	2,25	2,29	1,30	1,59	2,00
Evenness (J')	0,31	0,37	0,45	0,85	0,74	0,68	0,73	0,71	0,41	0,48	0,54
Shannon Diversity (H')	0,95	0,95	1,20	1,76	1,45	1,21	1,81	1,83	0,96	1,31	1,73
ES(100)	4	5	5	8	7	6	12	11	8	9	12

Zeeland Banks	**Z8s**	**Z9c**	**Z10s**	**Z11c**	**Z12s**	**Z18s**	**Z1c**	**Z2c**	**Z3s**	**Z4c**	**Z5s**	**Z6c**	**Z7s**	**Z13c**	**Z14s**	**Z15s**	**Z16c**	**Z17c**	**Z19c**	**Z20s**
Depth below MLLWS (m)	**13,1**	**38,5**	**12,9**	**10,9**	**21,8**	**18,5**	**9,6**	**13,5**	**11,6**	**22,6**	**16,0**	**25,7**	**15,7**	**19,0**	**13,6**	**36,3**	**16,8**	**27,6**	**13,8**	**20,0**
Number of species (N_0)	6	10	12	11	11	11	15	9	9	11	17	13	23	10	7	12	14	10	8	11
Hill Diversity (N_1)	4,06	2,53	4,43	4,55	3,33	4,51	4,41	3,04	2,66	5,01	7,64	4,29	8,95	6,66	1,67	6,06	4,64	6,90	5,63	4,03
Hill Diversity (N_{inf})	2,00	1,32	2,05	2,32	1,63	2,57	2,44	1,38	1,30	1,90	3,81	1,90	3,34	3,06	1,12	2,75	1,71	3,00	2,75	1,60
Evenness (J')	0,78	0,40	0,60	0,63	0,50	0,63	0,55	0,51	0,45	0,67	0,72	0,57	0,70	0,82	0,26	0,72	0,58	0,84	0,83	0,58
Shannon Diversity (H')	1,40	0,93	1,49	1,51	1,20	1,51	1,48	1,11	0,98	1,61	2,03	1,46	2,19	1,90	0,51	1,80	1,53	1,93	1,73	1,39
ES(100)	6	8	8	9	8	8	10	9	8	9	11	9	16	10	7	10	11	10	8	11

Hinder Banks	**H1c**	**H2s**	**H3c**	**H4s**	**H5c**	**H6s**	**H7s**	**H8**	**H9**	**H10**	**H11**	**H12**
Depth below MLLWS (m)	**11,6**	**21,4**	**24,0**	**17,5**	**29,8**	**16,4**	**10,3**	**14,0**	**22,4**	**35,5**	**34,6**	**36,1**
Number of species (N_0)	7	12	7	8	9	4	10	6	3	5	6	9
Hill Diversity (N_1)	1,92	5,24	2,86	3,52	2,00	1,81	4,70	4,23	2,30	3,10	4,45	4,17
Hill Diversity (N_{inf})	1,25	2,74	1,48	2,00	1,17	1,19	1,84	1,94	1,45	1,64	3,10	2,18
Evenness (J')	0,34	0,67	0,54	0,61	0,32	0,43	0,67	0,80	0,76	0,70	0,83	0,65
Shannon Diversity (H')	0,65	1,66	1,05	1,26	0,69	0,60	1,55	1,44	0,83	1,13	1,49	1,43
ES(100)	5	10	7	5	7	4	9	6	3	5	6	9

Chapter 6

General discussion and conclusions

6.1. Introduction

The hyperbenthic fauna living in the benthic boundary layer (BBL) of two continental slope areas in the northeastern (NE) Atlantic Ocean was studied. This faunal component has been defined in previous chapters (chapter 1 and chapter 2) and can be considered as a combination of pelagic species (*e.g.* copepods), (epi)benthic or benthopelagic species (*e.g.* isopods, cumaceans) and species specialized to the hyperbenthic environment (*e.g.* mysids) (Angel, 1990) (Fig. 6.2). The benthic boundary layer is the water layer above the sediment interface which is characterized by homogeneous temperature and salinity conditions (Turley, 2000) and which, at times, is enriched with resuspended detritus through increased bottom currents (Lampitt *et al.*, 2000). This detrital or particulate organic matter (POM) coming from the richer productive surface layer of the ocean (*e.g.* the euphotic zone) often forms a seasonal fluffy layer on the sediment and is the nutritional basis for benthic life on the ocean floor (Turley, 2000). In this PhD study, the BBL and its specific fauna was sampled by means of a hyperbenthic sledge, which covers the one metre water layer above the seafloor. Moreover, as a result of the used sampling device the fauna was sampled in two separate levels: 0-50 cm and 50-100 cm above the bottom, which made research on the stratified distribution of the fauna within the BBL possible.

The BBL hyperbenthos of two continental slope areas in the NE Atlantic, Porcupine Seabight (Ireland) and Meriadzek Terrace (France), was studied with emphasis on the taxonomic composition, the distribution patterns, community structure and diversity. Both study sites (for detailed description see chapter 2) are situated along the European continental margin and the sampling transect covers a part of the continental slope between 200-1250 m water depth.

Overall, the study's approach is to assess the BBL hyperbenthic fauna as an ecological entity at the interface between the pelagic and benthic realm along one of the major environmental gradients, that related to depth on the sloping parts of the ocean floor, in two NE Atlantic slope areas. This approach enabled us to clarify distributional patterns (stratified, bathymetric and geographical distribution) of the hyperbenthos, which are summarized and discussed here (Fig. 6.2). There are many logistic problems associated with identifying and measuring factors that may affect zonation and depth related distribution, and as a result, nearly all deep-sea studies looked at those factors that correlate with changes in the fauna such as temperature, pressure, oxygen minimum, sediment type, water mass structure, currents, topography and food supply, larval dispersion, competition, predation and trophic level (Howell *et al.*, 2002). Despite the paucity of environmental data available in the present study some possible explanations for the observed faunal distributional patterns were put forward. According to Carney *et al.* (1983) three types of depth related gradients control the distribution of benthic organisms across continental margins: physiologically important factors (*e.g.* temperature, salinity, pressure), 'partionable resources' (*e.g.* sediment structure, currents) and available resources (*e.g.* food, space) (Pfannkuche & Soltwedel, 1998).

6.2. Study site comparison

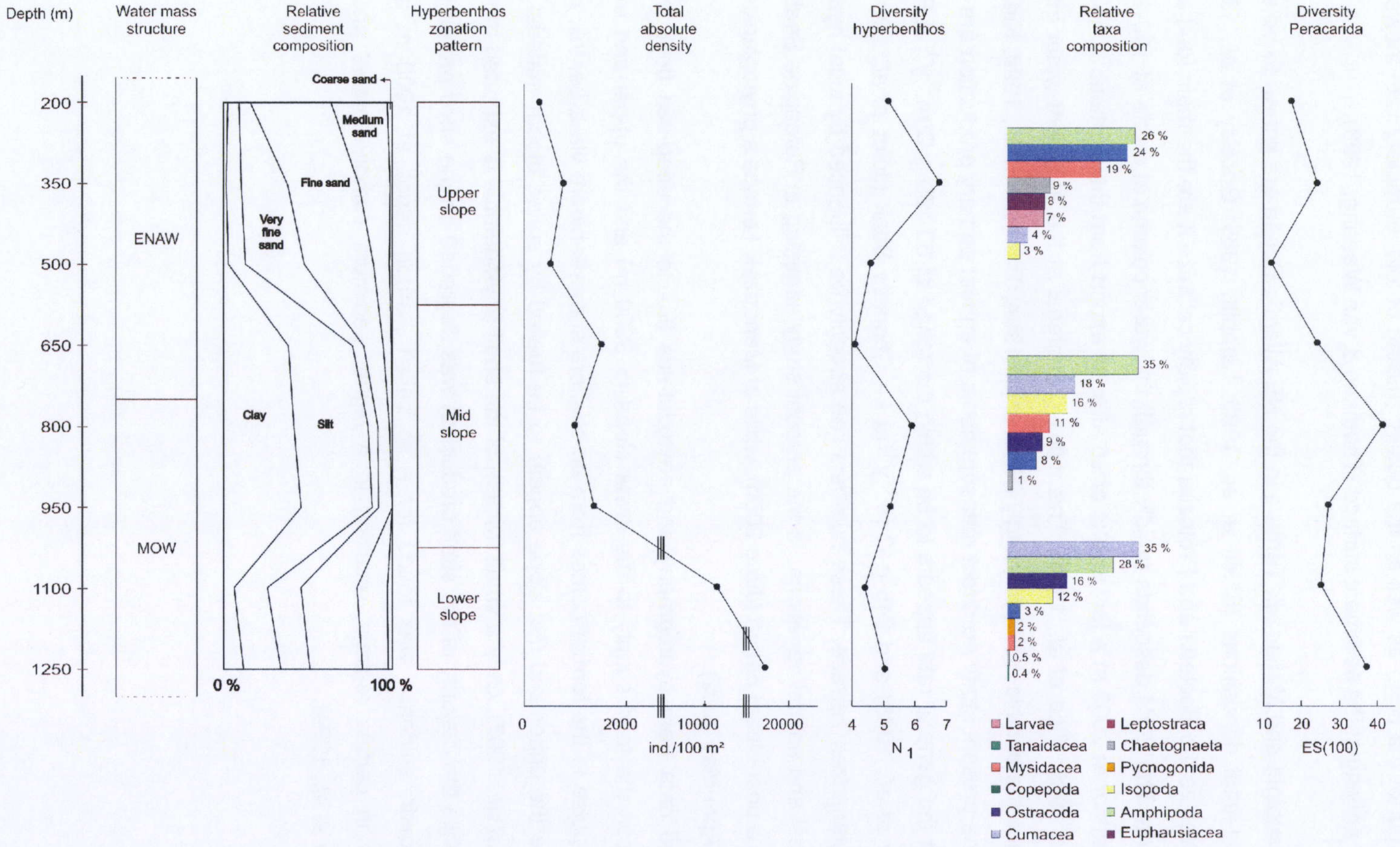
Porcupine Seabight and Meriadzek Terrace are two continental slope areas with similar physical oceanographic characteristics although some differences are illustrated in figure 6.1. Both sites are characterized by a Mediterranean Outflow Water (MOW) water mass layer between circa 750 m and circa 1500 m (Rice *et al.*, 1991) and the general south to north directed (*e.g.* poleward) slope current with a mean speed of 4 cm s^{-1} at the eastern flank of the Porcupine Seabight and a comparable mean speed at the Meriadzek Terrace slope (Pingree & Le Cann, 1989; Huthnance *et al.*, 2001; van Weering *et al.*, 2001). At Porcupine Seabight measurements of near-bed currents as part of the slope current showed that when current speed was higher than 7 cm s^{-1}, currents were able to resuspend phytodetrital matter, making it available for suspension feeders (Rice *et al.*, 1990). Besides the general poleward flows, there exist relatively strong diurnal and semidiurnal internal tides and associated internal waves (Huvenne *et al.*, 2002), which are directed across the slope (Rice *et al.*, 1990). These waves are present in the areas where the shelf slope exceeds the characteristic slope defined by Huthnance (1986) as a function of the semidiurnal frequency, the Coriolis frequency at this latitude, the depth and the degree of water stratification. This is in particular the case along the eastern flank of the Porcupine Seabight, where the local slope (2-3°) exceeds the characteristic slope. At the northern end of this eastern slope internal tides are found around 1000 m water depth, where they can result in enhanced near bottom currents and turbulence (Pingree & Le Cann, 1990; Rice *et al.*, 1990). For Meriadzek Terrace less detailed information on hydrography was found in literature, although Thomsen & van Weering (1998) described near bottom currents (between 1-6 m above the bottom) at mid depths along the continental slope between Meriadzek Terrace and Goban Spur, which were markedly directed downslope, reaching mean speeds of 15 cm s^{-1}.

Besides physical oceanographical characteristics of the study sites, food availability has been put forward several times as being a structuring variable for the deep-sea fauna (Hessler & Jumars, 1974; Hessler & Wilson, 1983; Kaïm-Malka, 1997). In recent years, it has been recognized that the biology and chemistry of the deep sea is strongly influenced by processes occurring in surface waters. Strong seasonal pulses of phytodetritus (particulate organic matter, POM) to the seafloor, which are exported from the euphotic zone are common in many areas of the oceans (*e.g.* Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, 1986, 1994; Baldwin *et al.*, 1998; Conte *et al.*, 1998). Generally export of organic material to the deep-sea floor ranges from 1 to 3 % of the primary productivity of the photic layer (Lampitt & Antia, 1997) and is the most important food source for deep-sea benthic communities (Bett & Rice, 1993; Gooday & Turley, 1990; Pfannkuche, 1993). Short bursts of rapid POM transport associated with productivity events control the composition of the settling particles (Conte *et al.*, 1995, 1998). Physical and biological conditions drive the fate and residence time of this material. Important physical factors include pressure, temperature, topography, currents and advection, while biological ones include degree and timing of flux via pelagic-benthic coupling, remineralisation, bioturbation and bioirrigation (Turley, 2000). However, the chemical characteristics of the settling POM changes significantly during its transit down through the water column (*e.g.* Lee & Wakeham, 1989; Wakeham & Lee, 1989; Conte *et al.*, 1995; Wakeham *et al.*, 1997, Turley, 2000). As a result of biological reworking and microbial colonisation (Cho & Azam, 1988), most labile organic compounds associated with sinking POM (*e.g.* polyunsaturated fatty acids: PUFA's; Wakeham *et al.*, 1997) are utilised before they reach the deep-sea floor. Resuspension and/or lateral advection of particulate material may also have an impact on the benthic boundary layer (BBL). It can affect the quantity (material can be advected into or out of the BBL) as well as the quality (mixing of 'old' refractory with 'newer' fresher material) of POM arriving at the sediment surface (Thomsen & van Weering, 1998).

The Porcupine Seabight and Meriadzek Terrace in the NE Atlantic Ocean are known to be subject to substantial phytodetrital depositions (Billett *et al.*, 1983; Lampitt, 1985; Gooday *et al.*, 1996). The detritus itself as well as the Bacteria and Protozoa that rapidly colonize it are the main food source for the deep-sea fauna. The POM descends rapidly through the water column at a rate of 100-150 m d^{-1}, arriving at the seafloor at 2000 m a few weeks or so after its export from the euphotic zone (Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, 1986). This influx of material at the sediment-water interface is thought to influence the benthic biology strongly (Rice *et al.*, 1994; Thurston *et al.*, 1998; Kiriakoulakis *et al.*, 2001). In the present study no direct measurements of annual primary production are available for both sites, but the general rate appears to be within the range of 60-100 g C m^{-2} y^{-1} at Porcupine Seabight (Berger *et al.*, 1988) and 245 g C m^{-1} y^{-1} at La Chapelle Bank (Joint *et al.*, 2001), a site northerly of the Meriadzek Terrace. These numbers can strongly be influenced by local hydrography and show seasonal and annual variations. In the present study sampling at Porcupine Seabight was performed during a post-bloom period (June 2000), while at Meriadzek Terrace a phytoplankton bloom was in progress (April-May 2002).

Overall, combined data from hydrography and phytodetritus flux to the deep-sea floor, indicate a decoupling between the food supply to the lower slope (> 3000 m) and the upper and mid slope, where the major pulse to the former comes from an offshore summer bloom via a benthic nepheloid layer (BNL), while the upper and mid slope appear to be fuelled by spring bloom material from the shelf (Duineveld *et al.*, 1997). Only a small fraction of the shelf phytodetritus is exported to the upper and mid slope, while the majority of the shelf production was degraded on the shelf proper (Rowe *et al.*, 1986). Moreover, evidence was found for a so called 'carbon depot' at 1000 m along the continental slope in certain regions, resulting in a higher sediment carbon content and benthic respiration (Rowe *et al.*, 1994).

Porcupine Seabight



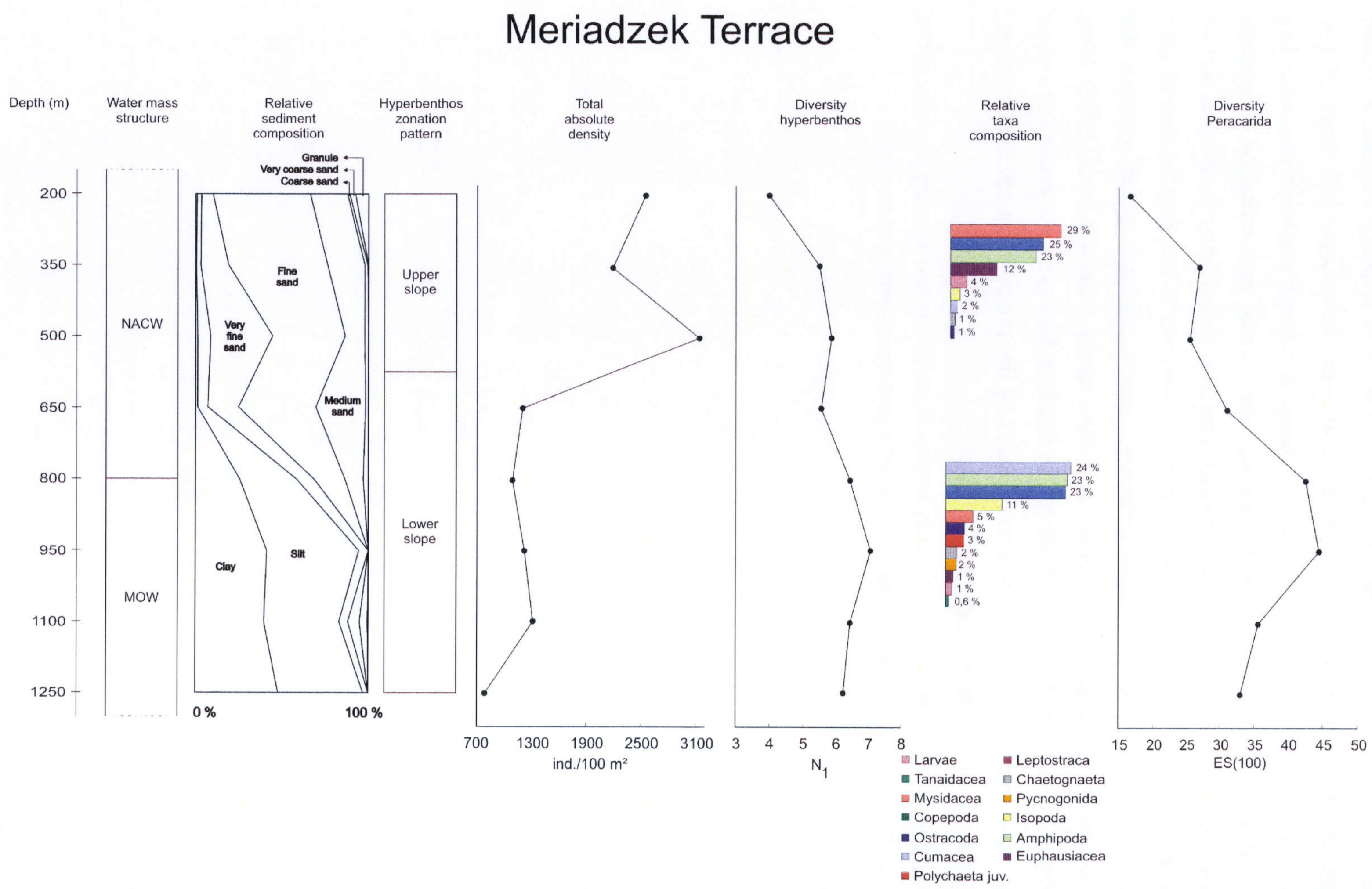


Figure 6.1 Overview of the physical environment (water mass structure and sediment composition) of both continental slope areas Porcupine Seabight and Meriadzek Terrace between 200-1250 m water depth and associated faunal characteristics: hyperbenthos zonation pattern along the slope, total hyperbenthic absolute density (ind./100 m²) and diversity (N_1) per station, relative taxa composition for the different slope communities and species diversity (ES(100)) of the Peracarida per station. ENAW= Eastern North Atlantic Water; MOW= Mediterranean Outflow Water; NACW= North Atlantic Central Water.

While no significant differences between the two sites can be proved based on previous characteristics, sediment structure of both sampling transect is different (Fig. 6.1). At Meriadzek Terrace there is a continuous decrease in median grain size with depth, the result of a large percentage of mud (> 50 %) at the stations between 800 m and 1250 m (M800-M1250). A similar sediment composition was found at Porcupine Seabight but was restricted between 650 m and 950 m. In contrast the deepest stations, P1100 and P1250, contained a coarser sediment structure. The sediment at the upper slope (200-500 m) of both sites was very similar in composition. A coarser sediment structure at the eastern Porcupine Seabight slope was also illustrated at the Belgica mound province (Huvenne *et al.*, 2002). The occurrence of coarser sediments in the Belgica mound area could be explained by the presence of locally enhanced current systems, which increase the resuspension of fine particles, leaving the coarser ones on the seabed (Huvenne *et al.*, 2002). Note also that the sampling transect at Porcupine Seabight is situated between two important mound provinces (see Fig. 2.2 in chapter 2), which are characterized by the presence of cold-water corals, but prove of direct influence on *e.g.* food supply do not exists.

The observed patterns in density, diversity, community structure, zonation and feeding strategy of the hyperbenthos and the Peracarida are summarized in figure 6.1 and discussed below in 6.3.

6.3. Major hyperbenthic patterns along the continental slope

In general three important distributional patterns of the hyperbenthos on the continental slopes were studied (Fig. 6.2): (1) a stratified distribution of the hyperbenthos within the one meter benthic boundary layer (BBL) at each sampling station, (2) an across isobaths distribution or zonation of the hyperbenthos with depth on each slope transect and (3) an along isobaths or geographical distribution between the two slope areas. The results of these patterns in Porcupine Seabight and Meriadzek Terrace are described in chapters 3, 4 and 5. A summary of the most important results of these patterns of the hyperbenthic fauna and the Peracarida will be discussed below and are illustrated in figure 6.1.

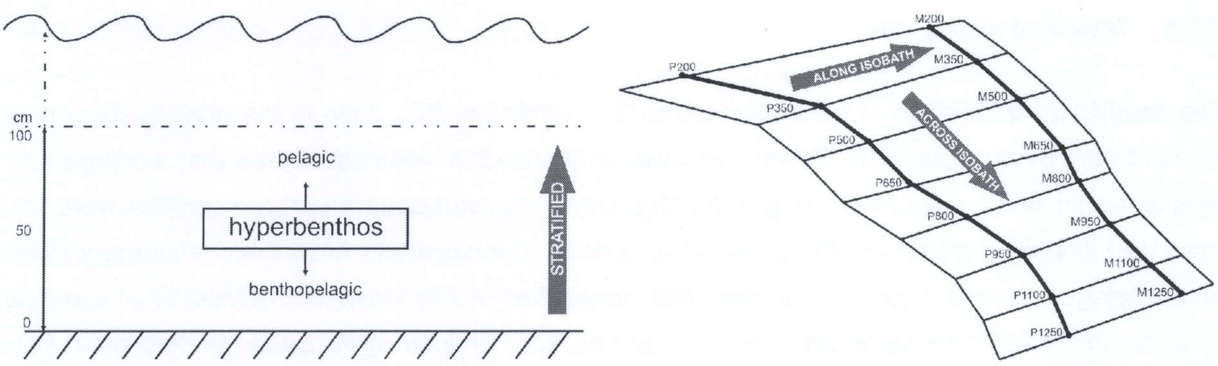


Figure 6.2 Overview of the major distributional patters studied in the present study: (1) stratified distribution of the hyperbenthos within the BBL, (2) across isobaths or bathymetric distribution and (3) along isobaths or geographical distribution of the hyperbenthos and the Peracarida.

6.3.1. General characteristics

On the higher taxonomical level, the hyperbenthic composition at both sites is very similar, with a high importance of the peracarid crustaceans (*i.e.* Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea) in both sites of 77 % and 59 % in Porcupine Seabight and Meriadzek Terrace respectively. Density values differ significantly between the two areas, with higher total densities at Porcupine Seabight, the total hyperbenthic density for the eight stations is 35 183 ind./800 m², while for Meriadzek Terrace this is about 2.6 times less (13 406 ind./800 m²) (see chapter 3 and chapter 4). This difference in total density is mainly due to the high values in the two deepest stations P1100 and P1250 at Porcupine Seabight. Absolute density values at the eight stations at Porcupine Seabight range from 299 ind./100 m² at station P200 to a maximum value of 19487 ind./100 m² at station P1250. For Meriadzek Terrace absolute density values range from 770 ind./100 m² at the deepest station M1250 to 3126 ind./100 m² at station M500. The absolute hyperbenthic density of the three shallowest stations (at 200, 350 and 500 m) is higher for the Meriadzek Terrace stations, while the total hyperbenthic abundance of the stations at 650, 800 and 950 m depth are very similar for both sites. The largest difference is found for the two deepest stations, as mentioned before, with a significant increase of the values at Porcupine Seabight. Furthermore, the higher total densities are mainly concentrated in the lower net samples at Porcupine Seabight, tripling the density of the lower net samples at Meriadzek Terrace. For the upper net samples the densities are very comparable with the highest total value for Meriadzek Terrace, 2967 ind./800 m² and 1975 ind./800 m² for Porcupine Seabight. Amphipoda, Isopoda, Cumacea, Ostracoda and Pycnogonida are the taxa attributing to the higher density values in the lower net samples at Porcupine Seabight, while the Mysidacea, Euphausiacea and Copepoda show higher densities at Meriadzek Terrace.

Diversity at taxon level can be considered as almost equal with depth for both sites (Fig. 6.1). At Meriadzek Terrace a more or less increase of diversity (N_1) is shown with depth, with the highest value at 950 m depth, in contrast to Porcupine Seabight were the diversity pattern is less uniform. In this area, a maximum value is found at 350 m depth and at 800 m depth. Detailed description of the diversity was given in previous chapters.

6.3.2. Stratified distribution

The **stratified distribution** of the hyperbenthic taxa within the BBL zone in the present study was characterized by an upper (50-100 cm) and lower (0-50 cm) BBL zone associated with a pelagic and benthopelagic fauna respectively (Fig. 6.2). Copepods, Euphausiacea and Chaetognatha were the main taxa inhabiting the upper BBL zone, while Isopoda, Cumacea and Amphipoda, showing a more benthopelagic life style, mainly in the lower BBL zone. Community structure analyses of all samples (0-50 cm and 50-100 cm samples) of both study sites (see chapter 4) indicated no clear trend with depth of the upper net samples, suggesting a homogeneous upper BBL zone along both depth transects. In contrast, the lower net samples showed a clear community structure pattern with depth which reflects the overall community structure (see further) found for the hyperbenthos when the samples were considered as stations (*e.g.* sum of the two net samples), indicating a closer link with the sediment and associated environmental variables. Total abundance in the upper and lower BBL layers also differed significantly, mainly at Porcupine Seabight (33 208 ind./800 m² in the eight lower nets, 1975 ind./800 m² in the upper nets), at Meriadzek the difference was smaller (10 438 ind./800 m² in the lower nets, 2967 ind./800 m² in the upper nets).

Such a stratified distribution pattern of the fauna in the immediate vicinity of the seafloor was also observed in other geographical regions including the Bay of Biscay (Sorbe, 1989, 1999; Dauvin & Sorbe, 1995) and the Portuguese continental margin (Cunha *et al.*, 1997). It has been described in terms of swimming activity and diel migrations of the organisms (Macquart-Moulin, 1984, 1991; Dauvin & Zouhiri, 1996). These studies documented an increasing swimming activity during the night. Amphipods and Cumaceans usually emerge from the sediment but do not commonly swim high up into the water column (Kaartvedt, 1986, 1989), thus limiting their distribution to the lower BBL zone just above the seafloor. In contrast to the amphipods and cumaceans, most of the hyperbenthic mysids migrate upwards during the night (Kaartvedt, 1985), indicating higher swimming capability which explains why some mysids were also caught in the upper BBL zone, although in smaller abundances than in the lower BBL zone. Moreover, among Peracarida, the natatory capability varies between species (Cartes & Sorbe, 1995) or even, as in the case of cumaceans, on the sexual state (Cartes & Sorbe, 1996). For the present study sampling was performed during daytime, explaining the higher abundances of the Peracarida in the lower BBL zone. Copepoda, Euphausiacea and Chaetognatha (dominant in the upper zone) are animals with high swimming capabilities which allow them to swim higher up in the BBL zone and in doing so actively searching for food. Overall, species-specific behavioural patterns together with other factors such as light, currents or food availability determine the swimming activity and thus the vertical distribution of hyperbenthic animals (Fosså, 1985, 1986; Elizalde *et al.*, 1991; Vallet *et al.*, 1995).

Vertical migration has also been studied in pelagic and demersal fish species which prey upon Mysidacea along the continental slope at the Rockall Trough (NE Atlantic Ocean) (Mauchline, 1982). Mysids contributed significantly to the diets of many demersal fish (*i.e.* fish caught in epibenthic trawls and living in close association with the sediment) but were not apparently important constituents of the food of pelagic fish (*i.e.* fish caught in pelagic trawls). Most of the fish are probably opportunistic feeders, the choice possibly being governed by availability and size spectrum of potential prey. Availability in the case of the mysids and other organisms may mean successful encountering of mysid aggregations, which was confirmed by Mauchline (1982) who found several mysid individuals of a same species in fish stomachs.

6.3.3. Across isobaths or bathymetric distribution

Different faunal (both within hyperbenthic taxa and Peracarida species) associations were found along the continental slope at Porcupine Seabight and Meriadzek Terrace indicating the faunal zonation with depth (Fig. 6.1). At Meriadzek Terrace an upper (M200-M500) and lower (M650-M1250) slope (or bathyal) hyperbenthic association was distinguished, while at Porcupine Seabight three hyperbenthic associations were found along the slope, an upper (P200-P500), mid (P650-P950) and lower slope (or bathyal) group (P1100-P1250). Overall, for both study sites a similar faunal boundary associated with the shelf break/upper slope zone (200-500m) was characterized by high abundances of Mysidacea and Euphausiacea, but between 650 and 1250 m both sites showed different faunal boundaries, although all characterized by an increase in abundance of cumaceans and isopods. Amphipoda were relatively important in all communities. Moreover, a similar community structure along the slope was also reflected in the peracarid community structure, when all samples of both sites were analyzed. Four significantly different peracarid species associations were found with highest dissimilarity (89 %) between the Porcupine upper slope associations and the lower slope associations of both study sites (see chapter 5). In this case the two deepest sampling stations at Porcupine Seabight (P1100 and P1250) showed a more similar species composition with the mid slope stations and were clustered together.

In general, in other studies examining general faunal change from the shelf break at 200 m to abyssal depths, up to seven different faunal zones have been recognized (Menzies *et al.*, 1973; Musick, 1976; Haedrich *et al.*, 1980). Three faunal zones have been reported consistently in the literature: (1) the shelf break/upper slope (200-500 m), (2) a less pronounced boundary around 1000-1400 m and (3) a general boundary at circa 3000 m for megafauna (Howell *et al.*, 2002). This latter boundary at 3000 m has been proposed as the start of the abyssal fauna (Hansen, 1975; Sibuet, 1979; Billett, 1991). That these depth boundaries occur at many locations worldwide indicates that important controlling variables are present at these depths and that these may occur globally (Howell *et al.*, 2002). Moreover the depth at which faunal boundaries occur varies with taxa studied and geographical location (Gage & Tyler, 1991).

For hyperbenthos specifically, the bathymetric distribution or zonation observed in the present study agreed with previous results on the same depth range. Le Danois (1948) distinguished for the Bay of Biscay macrofauna two levels in the bathyal zone between 200 and 1000 m with faunistic changes around 500 m depth. Lagardère (1977) defined three bathymetric assemblages for the crustacean fauna of the continental slope of the Bay of Biscay: (1) 200-400 m, transitional zone between the continental shelf and the bathyal, (2) 400-1000 m, upper horizon of the bathyal, and (3), deeper than 1000 m, lower horizon of the bathyal. Also in the Cap-Ferret Canyon Dauvin & Sorbe (1995) documented zonation of Amphipoda with faunal changes at 400-500 m and 1000 m.

As mentioned before, in this study, as with most deep-sea zonations studies, there is a paucity of environmental data available, which limits the discussion on possible explanations for the observed zonation patterns.

Structuring factors for the **faunal boundary associated with the shelf break** (~200 m) and the upper slope zone (200-500 m), which was observed in both study sites Porcupine Seabight and Meriadzek Terrace can be looked for in the physical environment. The shelf break is likely to be intermediate between the two contrasting situations of shelf and slope and this affects various marine organisms. Nevertheless this shelf break coincides with strong gradients in the physical environment. The upper slope in the present study is characterized by the start of the permanent thermocline at 600 m. Temperature decreases from 10 °C at 600 m to 4 °C at 1400 m, the base of the permanent thermocline (Rice *et al.*, 1991). Deep-sea animals are thought to be very sensitive to small changes in temperature (Somero *et al.*, 1983). Moreover other factors associated with this boundary around 500 m could be important. An obvious change of sediment structure at 500 m was also observed in both study sites, with finer sediments becoming more important deeper which might explain, in combination with other factors, the faunal change at this depth. It is known that cumaceans and isopods prefer muddy sediments, which could explain their low abundances at this upper slope zone. Furthermore this boundary around the shelf break possibly marks the change from shelf species to bathyal species. In the present study species data of the Peracarida illustrated this trend for the Mysidacea, where some shelf species were found along the continental slopes, but with a very restricted depth range (200-500 m) (see chapter 5). Furthermore, mysids are known to migrate actively to areas of high primary productivity (Wooldridge, 1989) and several authors (Clutter, 1967; Fosså, 1985; Hargreaves, 1985) suggest that increased food availability may be an important factor acting on the swimming activity and causing local increased abundance of these hyperbenthic organisms, which can be translated in their bathymetric distribution. Species-specific trophic preferences can also partially explain their distribution with depth in the present study. Mysids can have a very diversified diet. Depending on the food availability, certain mysids seem to prefer crustacean remains (*e.g.* mainly copepods) above detritus of phytoplankton origin (Cartes & Sorbe, 1998). This change in diet possibly could explain the gradient distribution of the mysids at the upper slope because their dominant food source is also very abundant at the upper slope. Moreover Cartes & Sorbe (1998) also found an increase of phytodetritus as a food source in the stomach content of mysids, which were caught on greater depths (between 1250-13500 m in the Catalan Sea). This lower specificity in the diet of some mysid species (*e.g. Boreomysis arctica*) would support different characteristics in their biology, such as their wide bathymetric distribution range (Cartes & Sorbe, 1998). Moreover, these peracarid crustaceans are also known as aggregators (Mauchline, 1980), which may also explain local increased abundances. In some upper slope samples certain mysid species were significantly dominant indicating swarms of mysids (*e.g.* at station M200 56 % *Erythrops neapolitana*, at M500 36 % *Pseudomma affine* and at P200 31 % *Erythrops serrata*).

Below the shelf break zone at the upper slope, a **lower bathyal zone** with specific characteristics was found in the present study (Fig. 6.1) (from 650-1250 m at Meriadzek Terrace; from 650-950 m at Porcupine Seabight). A very important shift in hyperbenthic taxa composition with depth was illustrated by the significant increased abundance and number of species of Cumacea and Isopoda. At both sites this faunal association is characterized by similar density values and a peak in hyperbenthic and peracarid diversity around 800-950 m. In both study sites this zone is also characterized by a very fine sediment structure with a high percentage of mud and a very low median grain size, which might be one of the main factors explaining the observed faunal patterns. Cumaceans and Isopods are known to prefer very fine sediments. The faunal association boundary found at Porcupine Seabight and Meriadzek Terrace do not match a boundary of water masses (Fig. 6.1), although the change in water masses has already been correlated with changes in composition of benthic fauna in other studies (Tyler & Zibrowius, 1992; Bett, 2001; Howell *et al.*, 2002): *e.g.* the MOW mass is associated with a decrease of the oxygen concentration, which could be a factor explaining faunistic changes. Besides these physical factors, biological causes for faunal zonation such as food availability could play a role. A change in feeding strategy along continental slopes is thought to be a result of the decrease in food availability with increasing depth. Food availability, both in terms of supply and composition, might be another factor affecting the distribution of hyperbenthic and peracarid populations in the Porcupine Seabight and Meriadzek Terrace (as discussed in chapter 5). Changes in feeding strategy with depth have been observed in asteroids (Carey, 1972; Howell *et al.*, 2002) and many other taxa (Gage & Tyler, 1991; Flach *et al.*, 1998). Feeding strategy of the different peracarid orders was discussed in detail in chapter 5, explaining the preferences of Mysidacea along the upper slope. Moreover these data could explain partially the differences found in the peracarid community structure between the two continental slopes (see further 6.3.4. geographical distribution).

Along the Porcupine continental slope a third hyperbenthic community was determined between 1100 and 1250 m depth, characterized by very high abundances (Fig. 6.1). The studied transect at Porcupine Seabight is located between two mound provinces, the Hovland mounds and the Belgica mounds, two sites associated with cold-water coral reefs (Huvenne *et al.*, 2002) (see chapter 2). To what extend this presence of coral reefs can have a direct influence on the observed hyperbenthic patterns is not clear. Some small dead coral parts were found in the hyperbenthic samples, indicating the presence of the cold-water corals, which might act as a factor increasing the habitat heterogeneity within the sediment. Several species of crustaceans, molluscs and other animals have been found to live in association with the corals (Jensen & Frederiksen, 1992; Mortensen et al., 1995; Rogers, 1999). Physically this part of the Porcupine slope is characterized by a coarser sediment structure compared to the zone between 650-950 m depth, which indicates a high-energy environment with enhanced currents (as described above, 6.2. Study site comparison). High speed currents have been shown to increase the (re)suspension of particulate matter on the seafloor, making it more available as food source for a high variety of animals, mainly filter-feeders and suspension feeders (Lampitt, 1985).

6.3.4. Along isobaths or geographical distribution

Overall, concerning the along isobaths distribution or geographical distribution, both slope areas have a similar hyperbenthic faunal composition when taxa are compared, but community structure showed differences as described above. Moreover, general density and diversity patterns along the two slopes were significantly different. Most explanations for these differences were looked for in the physical environment of both slope areas, although not every observed pattern could be explained based on these environmental parameters. Factors related to the distribution of species may vary with time and space (Cartes *et al.*, 2004). Marine species, particularly benthopelagic fish or crustaceans having swimming capacity, can perform daily or seasonal migrations upward or downward along the slope, presumably to feed, or related to their reproductive cycle (Cartes *et al.*, 1994). Such movements have been suggested, and sometimes relatively well documented, on the upper part of the continental slope (Wenner & Read, 1982). In the same way, species distributed across wide geographical areas may also exhibit variations in their depths of occurrence at different localities (Cartes *et al.*, 2004). Horizontal variability in the form of patchiness can originate from local phenomena (*e.g.* hydrography or geomorphology) (Maynou *et al.*, 1996). However, for deep-sea fauna, information on such changes are scarce (Maynou & Cartes, 2000).

For the Peracarida a similar bathymetric distribution pattern along both slopes was found, but the species composition were significantly different between the two study sites (see chapter 5). Results based on the Peracarida on family level showed a higher percentage of suspension-and filter-feeding cumacean, isopod and amphipod families along the Porcupine Seabight slope compared to higher percentages of scavengers and other peracarid families found at Meriadzek Terrace. This should not directly be a result of higher particulate matter on the seafloor at Porcupine Seabight, but might be linked to an enhanced current regime in this area.

6.4. General conclusions

Based on the results presented and discussed, and referring to the objectives of this study, following conclusions can be drawn:

- The two continental slope study sites Porcupine Seabight and Meriadzek Terrace comprised a specific hyperbenthic fauna in the 0-100 cm water column just above the ocean floor *(i.e.* the benthic boundary layer), which was characterized by a combination of pelagic species, benthopelagic species and species specialized to the hyperbenthic environment.

- The sampled hyperbenthic organisms belonged to a total of 13 hyperbenthic taxa, reaching high abundances and diversity values along both bathymetric transects. The abundances at Porcupine Seabight were significantly higher than the values found at Meriadzek Terrace.

- The hyperbenthos in both study sites was dominated by the peracarid crustaceans (i.e. Amphipoda, Isopoda, Cumacea, Mysidacea and Tanaidacea); 258 species were identified over the two continental slopes.

- Three important spatial distribution patterns of the hyperbenthos and the Peracarida on the continental slopes were observed:
    - ➢ a **stratified distribution** within the one meter benthic boundary layer (BBL) at each sampling station (with a clear difference between the 0-50 cm and the 50-100 cm layer)
    - ➢ an **across isobaths distribution or zonation** with depth on each slope transect .
    - ➢ an **along isobaths or geographical distribution** between the two study areas.

- The **stratified distribution** of the hyperbenthic higher taxa within the BBL zone was characterized by an upper (50-100 cm) and lower (0-50 cm) BBL zone associated with a pelagic (mainly copepods, Euphausiacea and Chaetognatha) and benthopelagic fauna (mainly Isopoda, Cumacea and Amphipoda) respectively. The data suggested a homogeneous upper BBL zone along both depth transects, while the lower net samples showed a clear community structure pattern with depth.

- An obvious higher taxa and species turnover or zonation along both bathymetric transects was observed, with Mysidacea and Euphausiacea dominating the upper slope (~200-500 m), while Amphipoda, Isopoda and Cumacea abundances increased significantly with depth (between ~650 m and 1250 m).

- The bathymetric distribution of Mysidacea and Euphausiacea seems to be rather related to physical properties of the water column (*e.g.* swimming ability, light transmission, currents) than to the sediment characteristics. The increase of more bottom dependent taxa, such as Amphipoda, Isopoda and Cumacea at the lower slope however is suggested to be related to a change in sediment structure and to the variations in organic particle transport in the BBL (*e.g.* deposition and resuspension events). Biological factors (e.g. species-specific trophic preferences) nevertheless might also contribute to this shift in community structure, as was illustrated for the Peracarida species.

- Concerning the along isobaths distribution, a similar hyperbenthic fauna was observed at Porcupine Seabight and Meriadzek Terrace, though differences in community structure on taxa and on species level were clear. Local differences in the physical environment, such as the current regime, sediment composition and the presence of carbonate mounds, of both study sites may play a role.

- Based on the comparison with similar hyperbenthic research along depth gradients performed in different regions in the NE Atlantic and Mediterranean, one can conclude that hyperbenthic distribution along continental margins hold uniform characteristics in terms of zonation along the depth gradient and the stratified distribution within the benthic boundary layer.

- From comparison with shallow coastal and shelf areas, it could be concluded that much higher peracarid diversity was found along the depth gradient of both deep continental slope areas Porcupine Seabight and Meriadzek Terrace compared to the different shallow areas in the North Sea *i.e.* Dogger Bank, Frisian front, Belgian continental shelf.

Summary

Summary

The **deep sea** is the part of the world's oceans below the continental shelves, covering almost two third of the earth's surface. The knowledge of the deep-sea fauna and its high species diversity is remarkably recent and mainly through the use of adequate sampling techniques, biological information (*e.g.* faunal zonation, species diversity) of this unique habitat has become available. Important topographical features of the deep sea, *i.e.* the **continental margins** and adjacent abyssal plains, have recently been the focus of a number of scientific research programs (*e.g.* the International Council for the Exploration of the Sea (ICES), the Ocean Margin Exchange project (OMEX)). Continental margins, which form the outer edges of the continents that lie under water, are built up of three important features: the continental shelf, the continental slope and the continental rise. The transition between the shallow, gently sloping continental shelf and the bathyal continental slope, called the shelf break, indicates the beginning of the deep sea at ~200 m. This physiographic feature coincides with the replacement of the basically shallow water fauna of the continental shelf to the deep-sea fauna (Sanders *et al.*, 1965; Hessler, 1974; Merrett, 1989). These sloping parts of the ocean floor are characterized by one of the major environmental gradients, the one related to depth and this bathymetric gradient consequently coincides with an associated faunal zonation. Important faunal boundaries occur around the shelf break and upper slope zone *i.e.* at ~200-500 m and around ~1000-1400 m water depth (Day & Pearcy, 1968; Rowe & Menzies, 1969; Sanders & Hessler, 1969; Dayton & Hessler, 1972; Rex, 1977; Hecker, 1990), nevertheless, the depth at which faunal boundaries occur varies with taxa studied and geographical location (Gage & Tyler, 1991). Observations of these depth boundaries indicate that important controlling factors are present at these depths and that these may occur globally.

Recognizing the importance of deep-sea research related to faunal diversity and distribution patterns along depth gradients, the present study aimed to investigate spatial distribution patterns of benthic communities and examine their underlying controlling environmental factors. In this study, focus is given on the hyperbenthic fauna which was sampled between ~200 m and ~1250 m water depth, using a standardized sampling strategy in two continental slope areas along the NE Atlantic continental margin: one transect (from 207-1215 m water depth) in the Porcupine Seabight (southwest of Ireland) and another transect (227-1215 m water depth) on the Meriadzek Terrace (west of France). Sampling at both study sites was performed with the R.V. Belgica during different sampling campaigns. Sampling at Porcupine Seabight was performed from 9-29 June 2000, while at Meriadzek Terrace sampling was conducted from 22 April-11 May 2002. A second cruise to Meriadzek Terrace for sediment sampling was performed from 11-18 May 2003.

The hyperbenthos is a term applied to the association of small animals living in the water layer close to the seabed (Mees & Jones, 1997). The species composition of the hyperbenthos is distinctly different from that of other benthic and planktonic groups and can be considered as a combination of pelagic species, benthopelagic species and species specialized to the hyperbenthic environment

(Angel, 1990). This fauna occupies the benthic boundary layer (BBL), *i.e.* the one metre water layer above the sediment interface which is characterized by homogeneous temperature and salinity conditions (Turley, 2000) and which, at times, is enriched with resuspended detritus through increased bottom currents (Lampitt *et al.*, 2000). In nearly all marine ecosystems investigated to date, there is a general increase in the biomass at the BBL relative to the water column immediately above it but the dynamics of the bathyal benthic boundary layer are still far from being understood. Despite the scattered knowledge on hyperbenthic communities, evidence of the potential role of this fauna in marine ecosystems has often been emphasized. Hyperbenthos plays an important role in marine food webs *e.g.* as a food source for juvenile demersal fish species and adult shrimp species in shallow coastal areas and estuaries (*e.g.* Mauchline, 1980; Mees & Jones, 1997; Hostens & Mees, 1999; Beyst *et al.*, 1999; Oh *et al.*, 2001) and more recently this was documented for the deep sea as well (Mauchline, 1986; Cartes, 1998; Bjelland *et al.*, 2000). Hyperbenthic species contribute to the conversion and recycling of organic matter as several species were indicated to feed on non-refractory detrital matter and in doing so contributing to the benthopelagic coupling (Kost & Knight, 1975; Jansen, 1985; Fockedey & Mees, 1999).
Among the more diverse major hyperbenthic higher taxa in the deep sea are peracarid crustaceans belonging to the orders Amphipoda, Isopoda, Cumacea, Tanaidacea and Mysidacea (Jones & Sanders, 1972; Cartes & Sorbe, 1996). They are well adapted for a life in the deep sea due to their small body size and brood protection in the marsupium (Hessler & Wilson, 1983).

In view of the characteristics of the selection of the organisms, the study sites and the sampling method, it was possible to analyse and discuss three important faunal distributional patterns: (1) a stratified distribution of the hyperbenthos within the one meter benthic boundary layer (BBL: 0-50 cm and 50-100 cm) at each sampling station, (2) an across isobaths distribution or zonation of the hyperbenthos and Peracarida with depth on each slope transect and (3) an along isobaths or geographical distribution between the two slope areas. Characterizing these three distribution patterns was approached by examining the hyperbenthic taxa composition, peracarid species composition, density and diversity of the hyperbenthos and peracarid crustaceans in eight sampling stations along a transect in both study sites. Patterns of hyperbenthic and Peracarid distribution were discussed in terms of what is known of their ecology and possible explanations were looked for in the physical environment of Porcupine Seabight and Meriadzek Terrace.

On the higher taxonomical level, the hyperbenthic composition of both sites was very similar, with a high importance of the peracarid crustaceans (*i.e.* Amphipoda, Cumacea, Isopoda, Mysidacea and Tanaidacea) in both sites of 77 % and 59 % in Porcupine Seabight and Meriadzek Terrace respectively. Density values differed significantly between the two areas, with higher total densities at Porcupine Seabight, the total hyperbenthic density for the eight stations was 35 183 ind./800 m^2, while for Meriadzek Terrace this was about 2.6 times less (13 406 ind./800 m^2). Diversity at taxon level could be considered as almost equal for both sites. At Porcupine Seabight and Meriadzek Terrace a total of 13 hyperbenthic taxa was sampled and 258 Peracarida species were identified for the two study sites together (152 Amphipoda species, 45 Cumacea species, 30 Isopoda species, 26 Mysidacea species and 5 Tanaidacea species).

The **stratified distribution** of the hyperbenthic taxa within the benthic boundary layer (BBL) in the present study was characterized by an upper (50-100 cm) and lower (0-50 cm) BBL zone associated with a pelagic and benthopelagic fauna respectively. Copepods, Euphausiacea and Chaetognatha were the main taxa inhabiting the upper BBL zone, while Isopoda, Cumacea and Amphipoda, showing a more benthopelagic life style, were mainly sampled in the lower BBL zone. Moreover, no clear trend with depth was found within the upper net samples, in contrast to the lower net samples, which showed a community structure related to depth. This suggested a homogeneous faunal composition in the upper BBL zone along the complete depth gradient and a closer link with sediment conditions and other depth related variables of the fauna of the lower BBL zone. Mainly species-specific behavioural patterns together with other factors such as light, currents or food availability determined the swimming activity and thus the vertical distribution of hyperbenthic animals (Fosså, 1985, 1986; Elizalde *et al.*, 1991; Vallet *et al.*, 1995).

Different hyperbenthic and Peracarida communities were observed along the continental slope at Porcupine Seabight and Meriadzek Terrace characterizing the **faunal zonation with depth**. At Meriadzek Terrace an upper (200-500 m) and lower (650-1250 m) slope hyperbenthic association was distinguished, while at Porcupine Seabight three hyperbenthic communities were found along the slope, an upper (200-500 m), mid (650-950 m) and lower slope group (1100-1250 m). Moreover, a similar community structure along the slope was also reflected in the peracarid community structure, when all samples of both sites were analyzed. Four significantly different peracarid species associations were found: an upper slope zone (200-500 m) with low species diversity and a lower slope zone (650-1250 m) with high species diversity for the two sites Porcupine Seabight and Meriadzek Terrace respectively. Overall, for both study sites a similar faunal boundary associated with the shelf break/upper slope zone (~200-500 m) was characterized by high abundances of Mysidacea and Euphausiacea. This zone coincides with strong gradients in the physical environment and possible structuring factors for the faunal zonation might be changes in temperature and sediment composition and species-specific trophic preferences. Between 650 and 1250 m water depth both sites showed different faunal boundaries, although all characterized by an increase in abundance of cumaceans and isopods. Amphipoda were relatively important in all communities. The 650-1250 m zone at Meriadzek Terrace and the 650-950 m zone at Porcupine Seabight were both characterized by a very fine sediment structure with a high percentage of mud and a very low median grain size, which might be one of the main factors explaining the observed faunal patterns. Besides the physical factors, biological causes for faunal zonation such as food availability could play a role. A change in feeding strategy along continental slopes is thought to be a result of the decrease in food availability with increasing depth. The third hyperbenthic community observed between 1100-1250 m at Porcupine Seabight, characterized by very high abundances might be the result of enhanced current regime and associated coarser sediment composition in combination with the presence of cold-water coral-reefs.

Overall, concerning the **along isobaths distribution or geographical distribution**, both slope areas have a similar hyperbenthic faunal composition when taxa are compared, but community structure showed differences as described above. General density and diversity patterns along the two slopes were significantly different. Most explanations for these differences were looked for in the physical environment of both slope areas, although not every observed pattern could be explained based on these environmental factors.

Based on the comparison with similar hyperbenthic research along depth gradients performed in different regions in the NE Atlantic and Mediterranean, one can conclude that hyperbenthic distribution along continental margins hold uniform characteristics in terms of zonation along the depth gradient and the stratified distribution within the benthic boundary layer. Although minor differences were illustrated indicating local environmental factors (*e.g.* currents, sediment composition) might act in the different continental margin regions.

Samenvatting

Samenvatting

De diepzee is het deel van de wereldzeeën dat zich onder het continentaal plat bevindt en dat ongeveer tweederde van het totale aardoppervlak omvat. Onderzoek naar diepzeefauna en geassocieerde hoge soortenrijkdom is zeer recent gestart en mede dankzij de ontwikkeling van geschikte staalnametechnieken werd tal van biologische informatie (zoals zonatie van fauna, soortenrijkdom) van dit uniek habitat beschikbaar. Belangrijke topografische eenheden van de diepzee zoals de continentale randen en nabijgelegen abyssale vlaktes zijn het onderwerp van talrijke recente wetenschappelijke onderzoeksprojecten (*i.e.* de International Council for the Exploration of the Sea (ICES), de Ocean Margin Exchange project (OMEX)).

De continentale randen zijn opgebouwd uit drie belangrijke onderdelen: het continentaal plat, de continentale helling en de continentale voet. De overgangszone van het ondiep, licht hellend continentaal plat, naar de bathyale continentale helling, de zogenaamde 'shelf break', wordt gedefinieerd als het begin van de diepzee en bevindt zich in veel gebieden op ongeveer 200 m diepte. Deze 'shelf break' zone wordt tevens gekenmerkt door een verandering in fauna: de fauna van het ondiepe continentaal plat wordt vervangen door een diepzeefauna (Sanders *et al.*, 1965; Hessler, 1974; Merret, 1989). Daarenboven zijn deze hellende onderdelen van de oceaanbodem gerelateerd aan een belangrijke diepte- of bathymetrische gradiënt die resulteert in een zonatie van de fauna langsheen de continentale helling. Belangrijke faunale grenzen tussen verschillende zones werden reeds beschreven in de omgeving van de 'shelf break' en de 'upper slope' op een diepte van ongeveer 200-500 m en eveneens op een diepte van ~1000-1400 m (Day & Pearcy, 1968; Rowe & Menzies, 1969; Sanders & Hessler, 1969; Dayton & Hessler, 1972; Rex, 1977; Hecker, 1990). De dieptes waarop deze grenzen van faunale zonatie zich bevinden varieert naargelang het bestudeerde taxon en de geografische locatie (Gage & Tyler, 1991). Observaties van deze faunagemeenschappen op welbepaalde dieptes impliceert dat op deze dieptes belangrijke factoren een rol spelen in de faunale structurering en dat deze wereldwijd kunnen voorkomen.

Met het oog op het belang van diepzee-onderzoek gerelateerd aan diversiteits-en distributiepatronen langsheen dieptegradiënten heeft dit onderzoek tot doel het bestuderen van ruimtelijke distributiepatronen van hyperbenthische gemeenschappen en hun onderliggende verklarende omgevingsfactoren. De nadruk ligt op de hyperbenthische fauna bemonsterd tussen ~200 m en ~1250 m waterdiepte op twee continentale hellingen langsheen de continentale randen in het noordoosten van de Atlantische Oceaan: een eerste transect (207-1215 m diepte) in Porcupine Seabight (ten zuidwesten van Ierland) en een tweede transect (227-1215 m diepte) ter hoogte van Meriadzek Terrace (ten westen van Frankrijk). Beide transecten werden bemonsterd volgens een gestandaardiseerde staalnamestrategie vanop het onderzoeksschip RV Belgica gedurende verschillende staalnamecampagnes. De staalnames in Porcupine Seabight werden uitgevoerd van 9-29 juni 2000, in Meriadzek Terrace van 22 april tot 11 mei 2002. Voor bemonstering van sediment in Meriadzek Terrace werd een tweede campagne georganiseerd van 11-18 mei 2002.

Hyperbenthos wordt gedefinieerd als de associatie van kleine organismen die in het onderste stratum van de waterkolom leeft in de nabijheid van de zeebodem (Mees & Jones, 1997). De soortensamenstelling van het hyperbenthos is duidelijk te onderscheiden van andere benthische en pelagische groepen en kan beschouwd worden als een combinatie van pelagische soorten, benthopelagische soorten en soorten gespecialiseerd voor een hyperbenthische levenswijze (Angel, 1990). Het hyperbenthon of de 'benthic bounday layer' (BBL) wordt gedefinieerd als de 1 m hoge waterkolom vlak boven de zeebodem, gekenmerkt door een constante temperatuur en saliniteit (Turley, 2000). Verhoogde stromingen kunnen in deze BBL regelmatig resulteren in aanrijking van geresuspendeerd detritus (Lampitt *et al.*, 2000). In alle tot op heden bestudeerde mariene ecosystemen, werd een algemene toename van biomassa ter hoogte van de BBL waargenomen in verhouding tot de erboven gelegen waterkolom, maar de structuur en dynamiek van de bathyale BBL zijn nog steeds onvoldoende gekend. Ondanks de beperkte kennis omtrent hyperbenthische gemeenschappen, heeft deze fauna een specifieke functie in mariene ecosystemen. Het hyperbenthos speelt een belangrijke rol in mariene voedselwebben bvb. als voedselbron voor juveniele bodemvissen en adulte garnalen in ondiepe kustzones en estuaria (*e.g.* Mauchline, 1980; Mees & Jones, 1997; Hostens & Mees, 1999; Beyst *et al.*, 1999; Oh *et al.*, 2001) en recent werd dit ook voor diepzeehyperbenthos aangetoond (Mauchline, 1986; Cartes, 1998; Bjelland *et al.*, 2000). Deze organismen zijn ook belangrijk in de conversie en recyclage van organisch materiaal door hun voedingsstrategieën en zijn hierdoor een belangrijke schakel in de bentho-pelagische koppeling (Kost & Knight, 1975; Jansen, 1985; Fockedey & Mees, 1999).
De meest diverse groep in diepzeehyperbenthos zijn de peracaride crustaceeën. Deze omvatten de orden van de Amphipoda, Isopoda, Cumacea, Mysidacea en Tanaidacea en blijken zeer goed aangepast aan een leven in de diepzee door hun kleine lichaamsafmetingen en broedzorg in een marsupium (Hessler & Wilson, 1983).

Gelet op de karakteristieken van de geselecteerde organismen, het geselecteerde studiegebied en de staalnamemethode was het mogelijk om drie belangrijke distributiepatronen van het hyperbenthos te analyseren en te bediscussiëren: (1) een verticale distributie van het hyperbenthos in de 1 m hoge BBL (0-50 cm en 50-100 cm) in elk staalnamepunt, (2) een 'across isobaths' distributie of zonatie van het hyperbenthos en de peracaride crustaceeën met de diepte langsheen beide continentale hellingen en (3) een 'along isobaths' of geografische distributie tussen beide staalnamegebieden. Om deze drie distributiepatronen te karakteriseren werd de hyperbenthische taxasamenstelling, de Peracarida soortensamenstelling, de densiteit en diversiteit van het hyperbenthos en de Peracarida bestudeerd in acht staalnamepunten langsheen de twee transecten op de continentale helling in Porcupine Seabight en Meriadzek Terrace. De geobserveerde patronen werden bediscusieerd op basis van de ecologie van de bestudeerde organismen en mogelijke verklaringen werden gezocht in de fysische omgeving van Porcupine Seabight en Meriadzek Terrace.

Op hoger taxonomisch niveau is de samenstelling van het hyperbenthos in beide gebieden zeer vergelijkbaar en wordt ze gekenmerkt door hoge abundanties van de peracaride crustaceeën (*i.e.* Amphipoda, Cumacea, Isopoda, Mysidacea en Tanaidacea). In Porcupine Seabight en Meriadzek Terrace maken de Peracarida respectievelijk 77 % en 59 % uit van het totale hyperbenthos. Absolute densiteiten vertoonden grote verschillen tussen de twee gebieden, met beduidend hogere waarden in Porcupine Seabight. De totale hyperbenthische densiteit over de acht staalnamestations bedroeg 35 183 ind./800 m^2, terwijl deze in Meriadzek Terrace slechts 13 406 ind./800 m^2 (~2.6 maal minder) bedroeg. Diversiteit op taxon niveau kan als zeer gelijk beschouwd worden. In beide gebieden werd een totaal van 13 hyperbenthische taxa bemonsterd en 258 Peracarida soorten werden geïdentificeerd, waarvan 152 Amphipoda soorten, 45 Cumacea soorten, 30 Isopoda soorten, 26 Mysidacea soorten en 5 Tanaidacea soorten.

De **verticale distributie van het hyperbenthos** in de BBL werd gekenmerkt door een boven (50-100 cm) en een onder (0-50 cm) BBL gemeenschap bestaande uit een pelagische en een benthopelagische fauna respectievelijk. Copepoda, Euphausiacea en Chaetognatha zijn de meest abundante taxa in de boven-BBL zone, terwijl Isopoda, Cumacea en Amphipoda de onder-BBL zone domineerden. Daarenboven werd voor de stalen uit de bovenste netten geen duidelijk patroon met de diepte aangetoond, terwijl voor de stalen van de onderste netten een duidelijke gemeenschapsstructuur geassocieerd aan de diepte gevonden werd. Dit suggereerde een zeer homogene boven-BBL zone langsheen de volledige dieptegradiënt en een sterkere link met het sediment en andere diepte-gerelateerde factoren van de fauna in de onder-BBL zone. Deze verticale distributie is voornamelijk het resultaat van soortspecifieke factoren in combinatie met andere factoren zoals licht, stromingen en/of voedselbeschikbaarheid (Fosså, 1985, 1986; Elizalde *et al.*, 1991; Vallet *et al.*, 1995).

Langsheen de continentale hellingen werden verschillende hyperbenthische en Peracarida gemeenschappen aangetoond, die een duidelijke **zonatie van deze fauna met de diepte** impliceerden. In Meriadzek Terrace werd een ‘upper slope’ (200-500 m) en een ‘lower slope’ (650-1250 m) hyperbenthisch gemeenschap onderscheiden in tegenstelling tot Porcupine Seabight waar drie hyperbenthische gemeenschappen langsheen de helling werden waargenomen: een ‘upper slope’ (200-500 m), een ‘mid slope’ (650-950 m) en een ‘lower slope’ (1100-1250 m) gemeenschap. Daarenboven werd een gelijkaardige gemeenschapsstructuur waargenomen voor de peracaride fauna van beide gebieden samen. Vier significant verschillende soortenassociaties werden aangetoond: een ‘upper slope’ zone (200-500 m), met een lage soortenrijkdom en een ‘lower slope’ zone (650-1250 m) gekenmerkt door een hoge soortenrijkdom voor Porcupine Seabight en Meriadzek Terrace respectievelijk.

Voor beide gebieden werd een verandering van de hyperbenthische zonatie aangetoond op een diepte van ~500 m. die gekarakteriseerd werd door hoge abundanties van Mysidacea en Euphausiacea. Deze ‘shelf break’ is een gebied dat gekenmerkt wordt door sterke gradiënten in de fysische omgeving en deze veranderingen in temperatuur, sedimentsamenstelling en stromingspatronen in combinatie met soortspecifieke voedingspatronen zouden mogelijke verklaringen kunnen bieden voor de waargenomen zonatiepatronen van het hyperbenthos en de Peracarida. Tussen 650 m en 1250 m vertoonden beide gebieden andere zonatiepatronen, maar allen werden ze gekenmerkt door een toename van Isopoda en Cumacea. Amphipoda bleken relatief belangrijk langsheen de volledige dieptegradient in de verschillende gemeenschappen. De zone tussen 650-1250 m diepte in Meriadzek Terrace en de zone tussen 650-950 m in Porcupine Seabight werden beide gekarakteriseerd door een zeer fijne sedimentstructuur, bestaande uit een zeer hoog percentage 'mud' (<63 µm) en een zeer kleine mediane korrelgrootte, wat een verklarende factor zou kunnen zijn voor de verandering in fauna op deze dieptes. Naast deze fysische factoren, kunnen biologische factoren zoals voedselbeschikbaarheid ook een belangrijke rol spelen in de structurering van de fauna. Verandering van voedingsstrategie met de diepte wordt toegeschreven aan de afname van beschikbaar voedsel met toenemende diepte. Tussen 1100-1250 m diepte in Porcupine Seabight werd een derde hyperbenthische gemeenschap waargenomen in dit onderzoek, met zeer hoge abundanties die het resultaat zouden kunnen zijn van versterkte stromingspatronen en daarmee geassocieerde grovere sedimentsamenstelling in combinatie met de aanwezige koud-water koraalriffen in dat gebied.

Betreffende de **'along isobaths' distributie of de geografische distributie** bevatten beide bestudeerde gebieden een vergelijkbare hyperbenthische fauna, maar zoals hierboven besproken vertoonden beide gebieden significante verschillen in densiteit, diversiteit en gemeenschapsstructuur. De meeste verschillen werden verklaard aan de hand van de kenmerken van de fysische omgeving van de twee continentale hellingen.

Vergelijking met gelijkaardig onderzoek van hyperbenthos langsheen dieptegradienten in vershillende regio's in de noordoostelijke Atlantische Oceaan, leert ons dat de hyperbenthische distributie langsheen continentale randen uniforme patronen vertonen betreffende zonatie langsheen de diepte en de verticale distributie in de BBL. Lokale factoren (e.g. stromingen en sedimentcompositie) spelen een belangrijke rol in de verklaring van de waargenomen verschillen in deze patronen.

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Appendix

Appendix 1

Absolute densities (ind. 100 m^{-2}) for the different hyperbenthic taxa sampled at the eight stations at Porcupine Seabight (P200-P1250). Densities are given for each net sample (L= lower net, 0-50 cm; U= upper net, 50-100 cm) and per station (*i.e.* sum of both nets) (P200-P1250). Total density per net sample and per station is also indicated.

	P200L	P200U	P350L	P350U	P500L	P500U	P650L	P650U	P800L	P800U	P950L	P950U	P1100L	P1100U	P1250L	P1250U
Amphipoda	34,66	2,71	95,02	86,57	188,05	8,31	704,50	37,60	318,56	7,58	256,15	30,30	2908,88	39,14	5324,99	183,46
Isopoda	0,54	0,00	9,95	0,00	28,70	2,27	186,89	3,81	197,21	1,17	226,56	5,05	1690,92	3,26	1938,33	13,67
Cumacea	2,71	0,00	60,20	4,98	0,00	0,00	189,06	4,90	96,85	0,58	371,59	39,68	3507,10	45,67	6779,02	117,37
Tanaidacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	3,50	0,00	7,94	0,00	26,09	0,00	92,30	0,00
Mysidacea	64,44	0,00	92,04	21,39	124,61	0,76	280,60	23,97	72,35	2,33	48,34	11,54	144,82	7,18	332,74	74,07
Euphausiacea	41,15	8,66	27,36	21,89	18,12	4,53	0,00	0,00	0,00	5,83	0,00	0,00	0,00	0,00	0,00	12,53
Leptostraca	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,70	0,00
Copepoda	86,10	17,33	138,81	40,30	80,05	27,94	24,52	43,04	50,18	129,53	25,98	26,70	91,98	41,10	329,32	541,27
Chaetognata	30,32	4,87	56,22	16,92	17,37	13,59	5,99	9,26	7,00	25,67	1,44	2,16	0,65	20,88	58,12	63,81
Pycnogonda	0,54	0,00	0,00	0,00	0,76	0,00	0,54	0,00	2,33	0,00	0,72	0,00	48,27	1,96	518,48	0,00
Larvae	4,87	0,54	95,52	17,91	0,00	0,00	0,00	0,00	0,58	2,33	4,33	0,00	0,00	0,00	0,00	0,00
Ostracoda	0,00	0,00	0,00	5,47	0,76	0,00	4,90	4,90	39,09	14,59	293,67	4,33	1651,13	3,26	3039,11	62,67
Total	**265,34**	**34,11**	**575,12**	**215,42**	**458,41**	**57,40**	**1397,01**	**127,50**	**787,66**	**189,62**	**1236,72**	**119,78**	**10069,87**	**162,44**	**18418,11**	**1068,87**

	P200	P350	P500	P650	P800	P950	P1100	P1250
Amphipoda	37,36	181,59	196,35	742,09	326,15	286,45	2948,03	5508,46
Isopoda	0,54	9,95	30,96	190,70	198,37	231,62	1694,19	1952,00
Cumacea	2,71	65,17	0,00	193,97	97,44	411,28	3552,77	6896,39
Tanaidacea	0,00	0,00	0,00	0,00	3,50	7,94	26,09	92,30
Mysidacea	64,44	113,43	125,36	304,57	74,68	59,89	152,00	406,81
Euphausiacea	49,82	49,25	22,66	0,00	5,83	0,00	0,00	12,53
Leptostraca	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,70
Copepoda	103,43	179,10	107,99	67,56	179,70	52,67	133,08	870,60
Chaetognata	35,20	73,13	30,96	15,26	32,67	3,61	21,53	121,93
Pycnogonda	0,54	0,00	0,76	0,54	2,33	0,72	50,23	518,48
Larvae	5,42	113,43	0,00	0,00	2,92	4,33	0,00	0,00
Ostracoda	0,00	5,47	0,76	9,81	53,68	298,00	1654,39	3101,78
Total	**299,45**	**790,54**	**515,80**	**1524,50**	**977,28**	**1356,50**	**10232,31**	**19486,99**

Absolute densities (ind. 100 m^{-2}) for the different hyperbenthic taxa sampled at the eight stations at Meriadzek Terrace (M200-M1250). Densities are given for each net sample (L= lower net, 0-50 cm; U= upper net, 50-100 cm) and per station (*i.e.* sum of both nets) (M200-M1250). Total density per net sample and per station is also indicated.

	M200L	M200U	M350L	M350U	M500L	M500U	M650L	M650U	M800L	M800U	M950L	M950U	M1100L	M1100U	M1250L	M1250U
Amphipoda	541,18	1,98	580,47	3,51	629,38	15,30	122,72	7,44	294,59	20,61	149,12	187,96	231,50	5,56	260,14	2,84
Isopoda	58,48	0,50	17,55	0,00	119,10	2,19	92,97	0,93	115,04	3,32	82,08	63,28	68,82	0,00	163,74	1,42
Cumacea	19,33	0,00	33,35	0,00	91,78	1,64	343,98	13,95	232,75	11,30	141,60	139,09	294,76	0,70	141,06	0,71
Tanaidacea	0,00	0,00	0,00	0,00	0,00	0,00	0,93	0,00	12,63	1,33	4,39	6,27	1,39	0,00	8,51	0,00
Mysidacea	1105,15	5,45	342,31	0,59	850,10	1,64	82,74	10,23	33,25	7,31	60,15	43,23	25,03	2,78	24,10	1,42
Euphausiacea	3,47	10,41	241,08	349,33	245,85	118,01	7,44	3,72	3,32	11,30	0,00	0,00	0,00	45,19	2,13	2,13
Leptostraca	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,25	0,00	0,00	0,00	0,00	0,00
Copepoda	592,72	53,52	281,46	149,21	431,60	421,77	204,53	195,23	27,26	210,14	14,41	85,84	19,47	428,24	64,50	17,01
Chaetognata	10,90	1,98	32,18	12,87	25,13	18,03	18,59	19,52	0,66	13,30	0,00	5,01	2,78	44,49	12,76	2,84
Pycnogonda	1,49	0,00	0,00	0,00	9,29	0,00	1,86	0,00	39,90	1,33	13,78	1,25	36,15	0,00	17,01	0,00
Larvae	124,39	8,92	107,67	11,70	91,24	0,00	21,38	0,00	7,98	3,32	7,52	8,77	9,73	3,48	4,25	0,71
Ostracoda	1,98	1,49	19,90	0,59	47,53	6,56	14,87	17,66	12,63	3,99	40,72	53,88	16,68	22,94	11,34	3,54
Polychaeta juv.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	18,62	0,00	65,79	33,21	47,97	0,00	26,94	0,71
Total	**2459,09**	**84,25**	**1655,97**	**527,80**	**2541,00**	**585,12**	**912,01**	**268,67**	**798,65**	**287,28**	**580,80**	**627,79**	**754,28**	**553,37**	**736,48**	**33,32**

	M200	M350	M500	M650	M800	M950	M1100	M1250
Amphipoda	543,16	583,98	644,67	130,15	315,21	337,08	237,06	262,98
Isopoda	58,97	17,55	121,29	93,90	118,37	145,36	68,82	165,16
Cumacea	19,33	33,35	93,42	357,92	244,05	280,69	295,45	141,77
Tanaidacea	0,00	0,00	0,00	0,93	13,96	10,65	1,39	8,51
Mysidacea	1110,60	342,90	851,74	92,97	40,56	103,38	27,81	25,52
Euphausiacea	13,88	590,41	363,86	11,16	14,63	0,00	45,19	4,25
Leptostraca	0,00	0,00	0,00	0,00	0,00	1,25	0,00	0,00
Copepoda	646,24	430,67	853,37	399,76	237,40	100,25	447,70	81,52
Chaetognata	12,89	45,06	43,16	38,12	13,96	5,01	47,27	15,59
Pycnogonda	1,49	0,00	9,29	1,86	41,23	15,04	36,15	17,01
Larvae	133,31	119,37	91,24	21,38	11,30	16,29	13,21	4,96
Ostracoda	3,47	20,48	54,09	32,54	16,62	94,61	39,63	14,89
Polychaeta juv.	0,00	0,00	0,00	0,00	18,62	98,99	47,97	27,64
Total	**2543,34**	**2183,77**	**3126,13**	**1180,68**	**1085,93**	**1208,59**	**1307,65**	**769,79**

Appendix 2

Amphipoda species list of all species sampled at the two study sites Porcupine Seabight and Meriadzek Terrace.

- **Phylum Arthropoda**
  - **Subphylum Crustacea**
    - **Classis Malacostraca**
      - **Subclassis Eumalacostraca**
        - **Superordo Peracarida**
          - **Ordo Amphipoda**
            - **Subordo Caprellidea**
              - **Familia Caprellidae**
                - *Parvipalpus capillaceus* (Chevreux,1887)
                - *Phtisica marina* (Slabber, 1769)
            - **Subordo Gammaridea**
              - **Familia Acanthonotozomatidae**
                - *Iphimedia obesa* (Rathke, 1843)
              - **Familia Ampeliscidae**
                - *Ampelisca aequicornis* (Bruzelius, 1859)
                - *Ampelisca brevicornis* (Costa, 1853)
                - *Ampelisca diadema* (Costa, 1853)
                - *Ampelisca eschrichtii* (Kroyer, 1846)
                - *Ampelisca gibba* (Sars, 1882)
                - *Ampelisca macrocephala* (Lilljeborg, 1852)
                - *Ampelisca spinipes* (Boeck, 1861)
                - *Ampelisca tenuicornis* (Lilljeborg, 1855)
                - *Ampelisca typica* (Bate, 1856)
                - *Byblis gaimardi* (Kroyer, 1846)
                - *Byblis guerni* (Chevreux, 1888)
                - *Haploops setosa* (Boeck, 1871)
                - *Haploops tubicola* (Lilljeborg, 1855)
              - **Familia Amphilochidae**
                - *Amphilochoides boecki* (Sars, 1892)
                - *Paramphilochoides intermedius* (Scott, 1896)
                - *Peltocoxa brevirostris* (Scott & Scott, 1893)
              - **Familia Aoridae**
                - *Lembos longipes* (Stebbing, 1895)
                - *Lembos websteri* (Bate, 1857)
                - *Lembos* species 1
              - **Familia Argissidae**
                - *Argissa hamatipes* (Norman, 1869)
              - **Familia Corophidae**
                - *Cerapus* species 1
                - *Chevreuxius grandimanus* (Bonnier, 1869)
                - *Corophium* species 1
                - *Siphonoecetes striatus* (Myers and Mcgrath, 1979)
                - *Unciola planipes* (Norman, 1867)
              - **Familia Cressidae**
                - *Cressa dubia* (Bate, 1857)
              - **Familia Dexaminidae**
                - *Atylus smithi* (Boeck, 1871)
                - *Atylus* species 1
                - *Dexamine spinosa* (Montagu,1813)
                - *Dexaminidae* species 1
              - **Familia Epimeriidae**
                - *Epimeria cornigera* (Fabricius, 1779)
                - *Epimeria parasitica* (Sars, 1858)

- **Phylum Arthropoda**
  - **Subphylum Crustacea**
    - **Classis Malacostraca**
      - **Subclassis Eumalacostraca**
        - **Superordo Peracarida**
          - **Ordo Amphipoda**
            - **Subordo Gammaridea**
              - **Familia Eusiridae**
                - *Apherusa bispinosa* (Bate, 1857)
                - *Apherusa ovalipes* (Norman & Scott, 1906)
                - *Apherusa* species 1
                - *Eusirus longipes* (Boeck, 1861)
                - *Haliragoides* species 1
                - *Rhachotropis caeca* (Ledoyer, 1977)
                - *Rhachotropis glabra* (Ledoyer, 1977)
                - *Rhachotropis gracilis* (Bonnier, 1896)
                - *Rhachotropis grimaldii* (Chevreux, 1888)
                - *Rhachotropis inermis* (Ledoyer, 1977)
                - *Rhachotropis integricauda* (Carausu, 1948)
                - *Rhachotropis rostrata* (Bonnier, 1896)
              - **Familia Gammaridae**
                - *Gammarellus homari* (Fabricius, 1779)
              - **Familia Haustoriidae**
                - *Bathyporeia pelagica* (Bate, 1856)
              - **Familia Ischyroceridae**
                - *Ericthonius hunteri* (G.O Sars, 1894)
                - *Ischyroceridae* species 1
              - **Familia Isaeidae**
                - *Gammaropsis maculata* (Johnston, 1828)
                - *Gammaropsis palmata* (Stebbing & Robertson, 1891)
                - *Megamphopus cornutus* (Norman, 1869)
                - *Isaeidae* species 1
              - **Familia Lafystiopsidae**
                - *Lafystiopsis* aff. planifrons
              - **Familia Lepechinellidae**
                - *Lepechinella manco* (Barnard, 1973)
                - *Lepechinella* species 1
              - **Familia Leocothoidae**
                - *Leucothoe liljeborgii* (Boeck, 1861)
              - **Familia Lilljeborgiidae**
                - *Lilljeborgia fissicornis* (Sars 1870)
                - *Lilljeborgia macronyx* (Sars, 1894)

Phylum Arthropoda
  Subphylum Crustacea
    Classis Malacostraca
      Subclassis Eumalacostraca
        Superordo Peracarida
          Ordo Amphipoda
            Subordo Gammaridea
              Familia Lysianassidae
                Acidostoma sarsi (Lincoln, 1979)
                Ambasia atlantica (Milne-Edwards, 1830)
                Anonyx liljeborgi (Boeck, 1871)
                Aristias neglectus (Hansen, 1887)
                Bathyamaryllis haswelli (Stebbing, 1888)
                Euonyx chelatus (Norman, 1867)
                Hippomedon denticulatus (Bate, 1857)
                Ichnopus spinicornis (Boeck, 1861)
                Lepidepecreum clypeatum (Ruffo & Schiecke, 1977)
                Lepidepecreum longicorne (Bate & Westwood, 1861)
                Lepidepecreum aff. umbo
                Lysianassa plumosa (Boeck, 1871)
                Metambasia faeroensis (Stephensen, 1923)
                Orchomene humilis (Costa, 1853)
                Orchomene pectinatus (Sars, 1882)
                Orchomenella nana (Kroyer, 1846)
                Paracentromedon crenulatus (Chevreux, 1900)
                Scopelocheirus hopei (Costa, 1851)
                Sophrosyne robertsoni (Stebbing & Robertson, 1891)
                Socarnes crenulatus (Chevreux, 1911)
                Tmetonyx cicada (Fabricius, 1780)
                Tmetonyx similis (Sars, 1891)
                Trischizostoma nicaeense (Costa, 1853)
                Tryphosella horingi (Boeck, 1871)
                Tryphosella insignis (Chevreux, 1935)
                Tryphosella nanoides (Liljeborg, 1865)
                Tryphosella species 1
                Tryphosites alleni (Sexton 1911)
                Tryphosites longipes (Bate & Westwood, 1861)
              Familia Melitidae
                Cheirocratus intermedius (Sars, 1894)
                Eriopsia elongata (Bruzelius, 1859)
                Maera othonis (Milne-Edwards, 1830)
                Melita gladiosa (Bate, 1862)
                Melita obtusata (Montagu, 1813)
              Familia Melphidippidae
                Megaluropus agilis (Hoek, 1889)
                Melphidippa goesi (Stebbing, 1899)
                Melphidippa macrura (Sars, 1894)
                Melphidipella macra (Norman, 1869)

Phylum Arthropoda
  Subphylum Crustacea
    Classis Malacostraca
      Subclassis Eumalacostraca
        Superordo Peracarida
          Ordo Amphipoda
            Subordo Gammaridea
              Familia Oedicerotidae
                Bathymedon acutifrons (Bonnier, 1896)
                Bathymedon longimanus (Boeck, 1871)
                Bathymedon longirostris (Jaume, Cartes & Sorbe, 1998)
                Bathymedon monoculodiformes (Ledoyer, 1983)
                Bathymedon saussurei (Boeck, 1871)
                Bathymedon species 1
                Monoculodes packardi (Boeck, 1871)
                Monoculodes species 1
                Oediceropsis brevicornis (Lilljeborg, 1865)
                Perioculodes longimanus (Bate & Westwood, 1868)
                Pontocrates altamarinus (Bate & Westwood, 1862)
                Synchelidium haplocheles (Grube, 1864)
                Synchelidium maculatum (Stebbing, 1906)
                Westwoodilla caecula (Bate, 1857)
              Familia Pardaliscidae
                Halice walkeri (Ledoyer, 1973)
                Halicoides anomalus (Walker, 1893)
                Nicippe tumida (Bruzelius, 1859)
                Pardalisca mediterranea (Bellan-Santini, 1984)
              Familia Phoxocephalidae
                Paraphoxus oculatus (Sars, 1879)
                Harpinia antennaria (Meinert, 1890)
                Harpinia crenulata (Boeck, 1871)
                Harpinia laevis (Sars, 1891)
                Harpinia pectinata (Sars, 1891)
                Harpinia truncata (Sars, 1892)
                Paraphoxus oculatus
              Familia Pleustidae
                Pleustidae species 1
                Pleustidae species 2
                Stenopleustes latipes (Sars, 1858)
                Stenopleustes malmgreni (Boeck, 1871)
              Familia Podoceridae
                Dyopedes monocanthus (Metzger, 1875)
                Laetmatophilus tuberculatus (Norman, 1869)
                Podoceridae species 1
              Familia Stegocephalidae
                Phippsia gibbosa (Sars, 1882)
                Stegocephaloides auratus (Sars, 1882)
                Stegocephalidae species 1

Phylum Arthropoda
  Subphylum Crustacea
    Classis Malacostraca
      Subclassis Eumalacostraca
        Superordo Peracarida
          Ordo Amphipoda
            Subordo Gammaridea
              Familia Stenothoidae
                Proboloides grandimanus (Bonnier, 1896)
                Stenothoe marina (Bate, 1856)
                Stenothoe richardi (Chevreux, 1895)
                Stenothoidae species 1
              Familia Stilidae
                Astyra abyssi (Boeck, 1871)
              Familia Synopiidae
                Bruzelia typica (Boeck, 1871)
                Ileraustroe species 1
                Syrrhoe affinis (Chevreux, 1908)
                Syrrhoites serratus (Sars, 1879)
                Syrrhoites walkeri (Bonnier, 1896)
              Familia Urothoidae
                Urothoe elegans (Bate, 1857)
                Urothoe marina (Bate, 1857)
                Carangolia aff. barnardi
            Subordo Hyperiidea
              Familia Hyperiidae
                Hyperia latissima (Bovallius, 1889)
                Hyperia schizogeneois (Stebbing, 1888)
                Parathemisto oblivia (Boval, 1889)
              Familia Phrosinidae
                Phrosina semilunata (Risso, 1882)
                Primno brevidens (Bowman, 1978)

Isopoda species list of all species sampled at the two study sites Porcupine Seabight and Meriadzek Terrace.

- **Phylum Arthropoda**
  - **Subphylum Crustacea**
    - **Classis Malacostraca**
      - **Subclassis Eumalacostraca**
        - **Superordo Peracarida**
          - **Ordo Isopoda**
            - **Subordo Gnathiidea**
              - **Familia Gnathiidae**
                - *Gnathia albescens* (Hansen, 1916)
                - *Gnathia oxyuraea* (Lilljeborg, 1855)
                - *Gnathia vorax* (Lucas, 1849)
            - **Subordo Anthuridea**
              - **Familia Paranthuridae**
                - *Leptanthura chardyi* (Negoescu, 1992)
                - *Leptanthura tenuis* (Sars, 1873)
              - **Familia Anthuridae**
                - *Anthuridae* species 1
            - **Subordo Flabellifera**
              - **Familia Aegidae**
                - *Aega* species 1
              - **Familia Cirolanidae**
                - *Eurydice grimaldii* (Dollfus, 1888)
                - *Metacirolana hanseni* (Bonnier, 1896)
                - *Natatolana borealis* (Lilljeborg, 1851)
                - *Natatolana caeca* (Dollfus, 1903)
              - **Familia Sphaeromatidae**
                - *Bathycopea typhlops* (Tattersall, 1905)
            - **Subordo Valvifera**
              - **Familia Arcturidae**
                - *Arcturella dilatata* (Sars, 1883)
                - *Astacilla intermedia* (Goodsir, 1841)
                - *Astacilla longicornis* (Sowerby, 1806)
                - *Astacilla pussila* (G.O. Sars, 1873)
                - *Astacilla* species 1
            - **Subordo Asellota**
              - **Familia Janiridae**
                - *Janira maculosa* (Leach, 1814)
              - **Familia Janirellidae**
                - *Janirella nanseni* (Bonnier, 1896)
              - **Familia Janiridae**
                - *Janiridae* species 1
              - **Familia Eurycopidae**
                - *Disconectes latirostris* (Sars, 1882)
                - *Munnopsurus atlanticus* (Bonnier, 1896)
                - *Tytthocope megalura* (Sars, 1872)
              - **Familia Ilyarachnidae**
                - *Aspidarachna longicornis* (G.O. Sars, 1899)
                - *Aspidarachna clypeata* (Chevreux, 1911)
                - *Bathybadistes hoplitis* (Hessler and Thistle, 1975)
                - *Ilyarachna longicornis* (G. O. Sars, 1864)
              - **Familia Munnidae**
                - *Munna limicola* (Sars, 1866)
              - **Familia Munnopsidae**
                - *Munnopsis beddardi* (Tattersall, 1905)
            - **Subordo Valvifera**
              - **Familia Ichnomesidae**
                - *Ischnomesus* species 1

Cumacea species list of all species sampled at the two study sites Porcupine Seabight and Meriadzek Terrace.

- **Phylum Arthropoda**
  - **Subphylum Crustacea**
    - **Classis Malacostraca**
      - **Subclassis Eumalacostraca**
        - **Superordo Peracarida**
          - **Ordo Cumacea**
            - **Familia Bodotriidae**
              - **Subfamilia Vaunthompsonia**
                - *Bathycuma brevirostris* (Bonnier, 1896)
              - **Subfamilia Bodotriinae**
                - *Cyclaspoides sarsi* (Bonnier, 1896)
              - **Subfamilia Vaunthompsonia**
                - *Vaunthompsonia cristata* (Bate, 1858)
              - **Subfamilia Bodotriinae**
                - *Cyclaspis longicaudata* (Sars, 1865)
                - *Iphinoe serrata* (Norman, 1867)
                - *Iphinoe tenella* (Sars, 1878)
            - **Familia Leuconidae**
              - *Leucon affinis* (Fage, 1951)
              - *Leucon longirostris* (Sars, 1871)
            - **Familia Nannastacidae**
              - *Campylaspis alba* (Hansen, 1920)
              - *Campylaspis glabra* (Sars, 1878)
              - *Campylaspis horridoides* (Stephensen, 1915)
              - *Campylaspis macrophthalma* (Sars, 1878)
              - *Campylaspis rostrata* (Calman, 1905)
              - *Campylaspis spinosa* (Calman, 1906)
              - *Campylaspis squamifera* (Fage, 1929)
              - *Campylaspis verrucosa* (Sars, 1866)
              - *Campylaspis vitrea* (Calman, 1906)
              - *Cumellopsis puritani* (Calman, 1906)
              - *Procampylaspis armata* (Bonnier, 1896)
              - *Procampylaspis bituberculata* (Hansen, 1920)
              - *Procampylaspis bonnieri* (Calman, 1906)
              - *Procampylaspis macronyx* (Hansen, 1920)
            - **Familia Ceratocumidae**
              - *Ceratocuma horrida* (Calman, 1905)
            - **Familia Lampropidae**
              - *Hemilamprops normani* (Bonnier, 1896)
              - *Hemilamprops uniplicata* (Kroyer 1846)
              - *Lamprops fasciata* (G. 0. Sars 1863)
              - *Paralamprops orbicularis* (Calman, 1905)
              - *Paralamprops* species 1
              - *Platysympus typicus* (Sars, 1870)
            - **Familia Diastylidae**
              - *Diastylis doryphora* (Fage, 1940)
              - *Diastylis laevis* (Norman, 1869)
              - *Diastylis rugosa* (Sars, 1865)
              - *Diastylis tumida* (Liljeborg, 1855)
              - *Diastyloides bacescoi* (Fage, 1940)
              - *Diastyloides biplicata* (Sars, 1865)
              - *Diastyloides serrata* (Sars, 1865)
              - *Leptostylis grandis* (Hansen, 1920)
              - *Leptostylis macrura* (Sars, 1870)
              - *Leptostylis villosa* (Sars, 1869)
              - *Makrokylindrus anomalus* (Bonnier, 1896)
              - *Makrokylindrus insignis* (Sars, 1871)
              - *Makrokylindrus josephinae* (Sars, 1871)
              - *Makrokylindrus longicaudatus* (Bonnier, 1896)
              - *Makrokylindrus longipes* (Sars, 1871)
              - *Makrokylindrus mystacinus* (Sars, 1887)

Mysidacea species list of all species sampled at the two study sites Porcupine Seabight and Meriadzek Terrace.

Phylum Arthropoda
  Subphylum Crustacea
    Classis Malacostraca
      Subclassis Eumalacostraca
        Superordo Peracarida
          Ordo Mysidacea
            Subordo Lophogastrida
              Familia Lophogastridae
                Lophogaster typicus (M. Sars, 1857)
              Familia Eucopidae
                Eucopia sculpticauda (Faxon, 1893)
                Eucopia unguiculata (Willemoes-Suhm, 1875)
            Subordo Mysida
              Familia Petalophthalmidae
                Hansenomysis fyllae (Hansen, 1887)
              Familia Mysidae
                Subfamilia Boreomysinae
                  Boreomysis arctica (Krøyer, 1861)
                  Boreomysis megalops (G.O. Sars, 1872)
                  Boreomysis microps (G.O. Sars, 1883)
                  Boreomysis tridens (G.O. Sars, 1870)
                Subfamilia Gastrosaccinae
                  Haplostylus normani (G.O. Sars, 1877)
                  Anchialina agilis (G.O. Sars, 1877)
                Subfamilia Mysinae
                  Amblyops abbreviata (G.O. Sars, 1869)
                  Amblyops kempi (Holt & Tattersall, 1905)
                  Dactylerythrops dactylops (Holt & Tattersall, 1905)
                  Erythrops neapolitana (Colosi, 1929)
                  Erythrops serrata (G.O. Sars, 1863)
                  Erythrops species 1
                  Hypererythrops serriventer (Holt & Tattersall, 1905)
                  Paramblyops rostrata (Holt & Tattersall, 1905)
                  Parapseudomma calloplura (Holt & Tattersall, 1906)
                  Parerythrops obesa (G.O. Sars, 1864)
                  Pseudomma affine (G.O. Sars, 1870)
                  Bathymysis helgae (W. Tattersall, 1907)
                  Leptomysis lingvura (G. O. Sars, 1866)
                  Mysideis insignis (G.O. Sars, 1864)
                  Mysidetes farrani (Holt & Tattersall, 1905)
                  Mysidopsis didelphys (Norman, 1863)

Tanaidacea species list of all species sampled at the two study sites Porcupine Seabight and Meriadzek Terrace.

Phylum Arthropoda
  Subphylum Crustacea
    Classis Malacostraca
      Subclassis Eumalacostraca
        Superordo Peracarida
          Ordo Tanaidacea
            Subordo Apseudomorpha
              Familia Apseudidae
                Apseudes grossimanus (Norman & Stebbing, 1886)
                Apseudes spinosus (M. Sars, 1858)
              Familia Sphyrapidae
                Sphyrapus species 1
            Subordo Tanaidomorpha
              Familia Leptognathiidae
                Typhlotanais aequiremis (Lilljeborg, 1864)
              Familia Paratanaidae
                Heterotanais species 1

Appendix 3

Absolute densities (ind. 100 m^{-2}) for all Amphipoda species sampled at the eight stations along the depth gradient at Porcupine Seabight (P200-P1250). Total density per station is also indicated. (continued)

	P200	P350	P500	P650	P800	P950	P1100	P1250
Phtisica marina	0,00	0,50	0,00	0,00	0,00	0,00	0,00	0,00
Iphimedia obesa	0,00	0,50	0,00	0,00	0,00	0,00	0,00	0,00
Ampelisca aequicornis	0,00	2,99	0,00	2,72	4,67	1,44	71,11	270,07
Ampelisca brevicornis	0,00	0,00	0,00	0,00	0,00	1,44	0,00	0,00
Ampelisca eschrichtii	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,70
Ampelisca gibba	0,00	0,00	0,00	8,72	17,50	33,19	1608,07	872,87
Ampelisca spinipes	0,00	0,00	0,00	0,00	0,58	0,00	0,00	0,00
Ampelisca tenuicornis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,70
Byblis gaimardi	0,00	0,00	0,00	22,34	2,92	0,00	0,00	0,00
Haploops setosa	0,00	0,00	0,00	108,97	9,92	0,72	0,00	7,98
Haploops tubicola	0,00	0,00	0,00	0,00	3,50	0,00	0,00	0,00
Amphilochoides boecki	0,54	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramphilochoides intermedius	0,00	0,50	0,00	0,00	0,00	0,00	0,00	0,00
Peltocoxa brevirostris	0,00	0,00	0,00	0,00	0,00	0,00	5,22	0,00
Lembos longipes	0,00	0,00	0,00	0,00	0,58	0,00	0,00	0,00
Lembos websteri	0,00	0,00	0,00	0,00	0,00	0,00	0,00	12,53
Argissa hamatipes	0,00	0,00	0,00	0,00	0,00	1,44	130,47	372,62
Cerapus species 1	0,00	0,00	0,00	0,00	0,00	0,72	0,00	0,00
Chevreuxius grandimanus	0,00	0,00	0,00	0,00	0,00	0,00	23,49	248,42
Siphonoecetes striatus	0,00	0,00	0,00	0,00	10,50	0,00	0,00	51,28
Unciola planipes	0,00	0,00	0,00	2,18	2,33	121,94	7,83	0,00
Cressa dubia	0,00	0,00	0,00	0,00	24,50	5,05	78,28	173,21
Atylus smithi	0,00	0,00	0,00	4,36	6,42	5,77	33,92	2,28
Epimeria cornigera	2,71	0,00	0,00	0,00	0,58	0,00	2,61	53,56
Epimeria parasitica	0,00	8,46	26,43	2,18	0,58	0,00	0,00	0,00
Eusirus longipes	0,54	1,00	0,00	3,27	1,17	0,72	2,61	161,81
Haliragoides species 1	0,00	0,00	0,00	0,00	0,58	0,00	0,00	2,28
Rhachotropis caeca	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00
Rhachotropis glabra	0,00	0,00	0,00	0,00	0,00	1,44	0,00	0,00
Rhachotropis gracilis	0,00	0,00	0,00	8,72	1,17	0,00	88,72	169,79
Rhachotropis grimaldii	0,00	3,48	30,21	2,72	0,00	0,00	0,00	1,14
Rhachotropis inermis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,14
Rhachotropis integricauda	9,75	11,94	0,00	0,00	0,00	0,00	0,00	0,00
Rhachotropis rostrata	0,00	0,00	1,51	1,63	0,00	0,72	50,88	149,28
Bathyporeia pelagica	0,54	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Ericthonius hunteri	0,00	0,00	0,00	10,90	1,75	0,00	0,00	0,00
Gammaropsis maculata	0,00	0,00	2,27	0,00	7,00	0,00	0,00	0,00
Gammaropsis palmata	0,00	0,00	0,00	215,76	44,93	0,00	0,00	2,28
Lepechinella manco	0,00	0,00	0,00	0,00	0,00	0,00	34,58	459,23
Lilljeborgia fissicornis	0,00	0,00	0,00	0,00	0,00	7,94	36,53	401,11
Acidostoma sarsi	0,00	1,99	0,76	0,00	0,58	0,00	0,00	0,00
Bathyamaryllis haswelli	0,00	0,00	0,00	0,54	0,00	0,00	0,00	207,39
Euonyx chelatus	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,14
Hippomedon denticulatus	0,00	5,97	3,78	2,72	0,00	0,00	0,00	5,70
Lepidepecreum clypeatum	0,00	0,00	0,00	0,00	0,00	0,00	18,92	47,86
Lysianassa plumosa	0,00	0,00	0,00	0,00	0,00	2,16	2,61	0,00
Metambasia faeroensis	0,00	0,00	0,00	0,00	0,00	0,00	8,48	31,91
Orchomene pectinatus	0,00	1,49	1,51	21,79	9,34	5,77	24,14	69,51
Orchomenella nana	0,00	2,49	0,00	0,00	0,58	0,00	0,00	0,00
Paracentromedon crenulatus	0,00	0,00	0,00	0,00	0,00	1,44	0,00	6,84
Scopelocheirus hopei	0,00	82,09	97,42	0,54	3,50	0,00	0,65	2,28
Sophrosyne robertsoni	0,00	0,00	0,00	0,00	0,00	0,00	2,61	0,00
Tmetonyx cicada	0,00	0,00	0,76	0,00	0,00	2,89	5,22	115,09
Tmetonyx similis	0,00	0,00	0,76	7,08	0,00	0,00	0,65	0,00
Trischizostoma nicaeense	0,00	1,99	0,00	0,00	0,00	0,00	0,00	0,00
Tryphosella horingi	0,00	0,00	0,00	0,00	0,00	2,89	10,44	177,77

(continued)

	P200	P350	P500	P650	P800	P950	P1100	P1250
Tryphosella insignis	0,00	0,00	0,00	0,00	5,83	20,20	153,31	339,58
Tryphosella nanoides	0,00	0,00	0,00	6,54	0,58	0,00	0,00	1,14
Tryphosites alleni	0,00	0,00	0,00	0,54	0,00	0,00	0,00	0,00
Tryphosites longipes	0,00	0,00	0,00	0,54	0,00	5,77	1,30	0,00
Melphidippa macrura	0,00	0,00	0,00	6,54	0,00	0,00	0,00	1,14
Melphidipella macra	5,42	0,00	0,00	0,00	1,17	0,00	0,00	0,00
Bathymedon acutifrons	0,00	1,49	0,00	0,00	0,00	0,00	8,48	9,12
Bathymedon longimanus	0,00	1,00	0,00	0,00	0,00	0,00	10,44	82,05
Bathymedon longirostris	0,00	0,00	0,00	0,00	0,00	0,00	10,44	2,28
Bathymedon monoculodiformes	0,00	0,50	0,00	0,00	0,00	0,00	10,44	3,42
Bathymedon saussurei	0,00	0,00	0,00	0,00	0,00	0,72	0,00	4,56
Bathymedon species 1	0,54	2,49	1,51	0,00	0,00	0,00	0,00	0,00
Pontocrates altamarinus	0,00	0,00	0,00	0,00	0,00	1,44	0,00	0,00
Synchelidium haplocheles	0,00	0,00	1,51	0,00	0,00	2,89	10,44	0,00
Synchelidium maculatum	0,00	0,00	0,00	2,18	0,00	0,00	0,00	0,00
Halicoides anomalus	0,00	0,00	0,00	0,00	0,00	0,00	0,65	44,44
Nicippe tumida	0,00	10,95	0,00	0,00	0,00	0,00	0,00	0,00
Pardalisca mediterranea	0,00	0,00	0,00	0,00	0,00	0,00	3,91	119,65
Harpinia antennaria	0,00	0,00	3,78	0,00	0,00	0,00	0,00	0,00
Harpinia crenulata	0,00	0,00	0,00	0,00	0,00	0,72	0,00	0,00
Harpinia laevis	0,00	0,00	0,00	0,00	0,00	0,72	0,00	0,00
Harpinia pectinata	0,00	0,00	0,00	10,90	13,42	4,33	127,86	183,46
Paraphoxus oculatus	0,00	0,00	0,00	13,62	9,34	0,00	0,00	0,00
Pleustidae species 1	0,00	0,00	0,00	0,00	0,00	0,00	2,61	22,79
Pleustidae species 2	0,00	0,00	0,00	0,00	0,58	0,72	0,00	0,00
Stenopleustes latipes	0,00	0,00	0,00	0,00	4,67	0,00	0,00	0,00
Stenopleustes malmgreni	0,00	0,00	0,00	21,79	1,17	0,00	0,00	0,00
Laetmatophilus tuberculatus	0,00	0,00	0,00	2,18	42,59	10,82	46,97	154,98
Podoceridae species 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,28
Stegocephaloides auratus	2,71	28,86	1,51	0,00	5,83	13,71	18,92	90,02
Proboloides grandimanus	0,00	0,50	0,00	21,25	4,67	1,44	0,00	0,00
Stenothoe marina	0,00	0,00	0,00	26,15	16,34	0,00	0,00	0,00
Stenothoidae species 1	0,00	0,00	0,76	0,00	4,67	0,00	0,00	0,00
Astyra abyssi	0,00	0,50	0,00	45,77	5,25	7,94	15,66	1,14
Bruzelia typica	0,00	0,00	0,00	0,00	0,00	6,49	57,41	19,37
Ileraustroe species 1	0,00	0,00	0,00	0,00	0,00	0,72	41,75	173,21
Syrrhoe affinis	0,00	1,49	13,59	27,79	0,00	0,72	15,66	9,12
Urothoe elegans	0,00	0,50	0,00	28,33	7,00	0,72	0,00	7,98
Carangolia aff. *barnardi*	0,00	0,00	0,76	2,72	3,50	0,00	0,00	7,98
Hyperia latissima	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,70
Parathemisto oblivia	13,54	2,99	3,02	1,09	7,00	2,89	3,26	7,98
Amphipoda indet.	1,08	3,98	4,53	96,98	37,34	5,77	160,48	125,35
Total	**37,36**	**181,59**	**196,35**	**742,09**	**326,15**	**286,45**	**2948,03**	**5508,46**

Absolute densities (ind. 100 m^{-2}) for all Isopoda species sampled at the eight stations along the depth gradient at Porcupine Seabight (P200-P1250). Total density per station is also indicated.

	P200	P350	P500	P650	P800	P950	P1100	P1250
Gnathia oxyuraea	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00
Gnathia vorax	0,00	0,00	0,00	0,00	0,00	0,00	5,22	22,79
Anthuridae species 1	0,00	0,00	0,00	0,00	3,50	0,00	1,96	52,42
Aega species 1	0,00	0,00	0,00	1,63	0,58	0,72	0,00	0,00
Eurydice grimaldii	0,00	0,00	0,00	5,45	0,58	0,72	0,00	0,00
Metacirolana hanseni	0,00	0,00	0,00	1,09	40,26	9,38	1508,26	1498,47
Natatolana borealis	0,00	1,49	30,96	0,00	14,59	92,36	17,61	0,00
Natatolana caeca	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,70
Bathycopea typhlops	0,00	0,50	0,00	16,89	12,84	46,18	147,43	43,30
Astacilla intermedia	0,00	1,00	0,00	69,20	54,84	29,58	5,22	0,00
Astacilla longicornis	0,00	0,00	0,00	34,87	21,59	44,74	5,22	0,00
Janiridae species 1	0,00	0,50	0,00	52,31	21,59	2,16	0,00	0,00
Disconectes latirostris	0,00	0,00	0,00	1,09	0,00	0,00	0,00	1,14
Munnopsurus atlanticus	0,00	0,00	0,00	0,00	0,00	1,44	0,00	0,00
Tytthocope megalura	0,00	0,00	0,00	0,00	1,17	0,00	0,00	1,14
Ilyarachna longicornis	0,00	5,47	0,00	0,00	9,92	2,16	3,26	59,26
Munna limicola	0,54	0,00	0,00	4,36	13,42	0,00	0,00	36,46
Munnopsis beddardi	0,00	0,00	0,00	0,00	0,00	0,72	0,00	46,72
Ischnomesus species 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	177,77
Isopoda indet.	0,00	0,00	0,00	3,81	3,50	1,45	0,00	6,83
Total	**0,54**	**9,95**	**30,96**	**190,70**	**198,37**	**231,62**	**1694,19**	**1952,00**

Absolute densities (ind. 100 m^{-2}) for all Cumacea species sampled at the eight stations along the depth gradient at Porcupine Seabight (P200-P1250). Total density per station is also indicated.

	P200	P350	P500	P650	P800	P950	P1100	P1250
Bathycuma brevirostris	0,00	0,00	0,00	0,00	0,00	0,00	20,88	0,00
Cyclaspoides sarsi	0,00	0,00	0,00	0,00	0,00	0,00	26,09	0,00
Vaunthompsonia cristata	0,00	0,00	0,00	0,00	0,00	0,00	36,53	28,49
Cyclaspis longicaudata	0,00	0,00	0,00	0,54	0,00	15,87	340,53	758,92
Leucon affinis	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,28
Campylaspis alba	0,00	0,00	0,00	0,00	0,00	0,00	0,00	6,84
Campylaspis glabra	0,00	15,92	0,00	0,00	0,00	16,60	116,77	140,16
Campylaspis horridoides	0,00	0,00	0,00	0,00	0,00	10,10	62,63	94,58
Campylaspis macrophthalma	0,00	4,98	0,00	0,54	21,00	70,71	1,30	33,05
Campylaspis rostrata	0,00	0,00	0,00	0,00	4,67	23,81	761,96	2130,91
Campylaspis spinosa	0,00	0,00	0,00	0,00	0,00	0,00	0,00	15,95
Campylaspis squamifera	0,00	0,00	0,00	0,00	0,00	0,00	0,00	56,98
Campylaspis verrucosa	0,00	0,00	0,00	0,54	0,00	33,19	17,61	83,19
Campylaspis vitrea	0,00	0,00	0,00	0,00	0,00	0,00	20,88	4,56
Cumellopsis puritani	0,00	0,00	0,00	0,00	0,00	0,00	448,83	347,55
Procamylaspis bituberculata	0,00	0,00	0,00	0,00	0,00	0,00	0,00	56,98
Procampylaspis bonnieri	0,00	0,00	0,00	0,00	0,00	0,00	0,00	74,07
Ceratocuma horrida	0,00	0,00	0,00	0,00	0,00	0,00	0,00	182,32
Hemilamprops normani	0,00	0,00	0,00	0,00	0,00	0,00	668,02	245,00
Hemilamprops uniplicata	0,00	1,00	0,00	192,33	67,10	194,82	368,58	414,79
Paralamprops species 1	0,00	0,00	0,00	0,00	0,00	3,61	165,05	177,77
Platysympus typicus	0,00	0,00	0,00	0,00	0,58	2,89	109,60	252,97
Diastylis doryphora	0,00	0,00	0,00	0,00	0,00	0,00	5,22	5,70
Diastylis tumida	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00
Diastyloides bacescoi	0,00	0,50	0,00	0,00	0,00	0,00	0,00	0,00
Diastyloides biplicata	0,54	0,50	0,00	0,00	0,00	0,00	0,00	0,00
Diastyloides serrata	0,00	0,00	0,00	0,00	0,00	0,00	36,53	908,20
Leptostylis macrura	0,00	0,00	0,00	0,00	0,00	0,00	5,22	0,00
Leptostylis villosa	1,08	39,80	0,00	0,00	0,00	0,00	26,09	5,70
Makrokylindrus insignis	0,00	0,00	0,00	0,00	1,75	0,00	0,00	0,00
Makrokylindrus josephinae	0,00	0,00	0,00	0,00	0,00	0,00	161,79	0,00
Makrokylindrus longicaudatus	0,00	0,00	0,00	0,00	0,00	0,00	5,22	0,00
Makrokylindrus longipes	0,00	0,00	0,00	0,00	1,75	29,58	78,28	586,85
Makrokylindrus mystacinus	0,00	0,00	0,00	0,00	0,00	0,00	31,31	0,00
Cumacea indet.	1,09	1,49	0,00	0,00	0,59	10,10	37,84	282,60
Total	**2,71**	**65,17**	**0,00**	**193,97**	**97,44**	**411,28**	**3552,77**	**6896,39**

Absolute densities (ind. 100 m^{-2}) for all Mysidacea species sampled at the eight stations along the depth gradient at Porcupine Seabight (P200-P1250). Total density per station is also indicated.

	P200	P350	P500	P650	P800	P950	P1100	P1250
Lophogaster typicus	0,54	3,48	0,00	0,00	0,00	0,00	0,00	0,00
Boreomysis megalops	0,00	2,49	0,00	0,00	0,00	0,00	0,00	0,00
Boreomysis tridens	0,00	0,00	0,00	0,00	0,00	0,72	7,83	70,65
Amblyops abbreviata	0,00	0,00	3,02	0,00	3,50	3,61	0,00	0,00
Amblyops kempi	0,00	0,00	0,00	0,00	0,00	0,00	0,00	13,67
Erythrops neapolitana	9,75	1,49	0,00	0,00	8,75	0,00	0,00	0,00
Erythrops serrata	31,41	30,85	1,51	0,00	0,00	0,00	0,00	0,00
Hypererythrops serriventer	0,00	13,43	0,00	0,00	0,00	0,00	0,00	0,00
Paramblyops rostrata	0,00	0,00	52,11	2,18	0,00	0,72	42,40	194,86
Parerythrops obesa	0,00	0,00	0,00	1,63	8,17	0,00	0,00	0,00
Pseudomma affine	0,00	11,44	57,40	206,50	17,50	30,30	39,14	43,30
Bathymysis helgae	0,00	0,00	0,00	0,00	0,00	0,00	0,00	5,70
Leptomysis lingvura	13,54	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Mysidetes farrani	0,00	1,99	0,00	0,00	0,00	0,00	0,00	0,00
Mysidopsis didelphys	6,50	44,78	0,00	0,00	0,00	0,00	0,00	0,00
Mysidacea indet.	2,71	3,48	11,32	94,26	36,76	24,53	62,63	78,63
Total	**64,44**	**113,43**	**125,36**	**304,57**	**74,68**	**59,89**	**152,00**	**406,81**

Absolute densities (ind. 100 m^{-2}) for all Tanaidacea species sampled at the eight stations along the depth gradient at Porcupine Seabight (P200-P1250). Total density per station is also indicated.

	P200	P350	P500	P650	P800	P950	P1100	P1250
Apseudes spinosus	0,00	0,00	0,00	0,00	0,00	5,77	4,57	37,60
Typhlotanais aequiremis	0,00	0,00	0,00	0,00	3,50	2,16	21,53	54,70
Total	**0,00**	**0,00**	**0,00**	**0,00**	**3,50**	**7,94**	**26,09**	**92,30**

Absolute densities (ind. 100 m^{-2}) for all Amphipoda species sampled at the eight stations along the depth gradient at Meriadzek Terrace (M200-M1250). Total density per station is also indicated. (continued)

	M200	**M350**	**M500**	**M650**	**M800**	**M950**	**M1100**	**M1250**
Parvipalpus capillaceus	0,00	0,00	0,00	0,00	0,66	0,00	0,00	0,00
Ampelisca aequicornis	3,96	11,70	0,00	1,86	3,32	0,63	4,87	23,39
Ampelisca brevicornis	0,00	0,00	0,55	0,00	0,00	0,00	0,00	0,00
Ampelisca diadema	0,00	0,00	0,00	0,00	3,32	0,00	0,00	0,00
Ampelisca gibba	0,00	4,68	49,72	2,79	3,32	6,89	2,09	4,25
Ampelisca macrocephala	0,00	0,00	0,00	0,00	21,28	9,40	1,39	0,00
Ampelisca spinipes	0,00	9,36	0,00	0,00	0,00	5,64	0,70	0,00
Ampelisca typica	0,00	4,68	0,00	0,00	0,00	0,00	0,00	0,00
Byblis gaimardi	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Byblis guerni	0,00	0,00	0,00	0,00	7,31	3,13	0,00	0,00
Haploops setosa	0,00	0,00	0,00	0,00	2,66	0,63	0,00	0,00
Amphilochoides boecki	3,96	16,38	8,74	0,00	0,00	0,00	0,00	0,00
Lembos longipes	35,68	42,13	21,85	9,30	18,62	0,00	0,70	0,00
Lembos species 1	0,00	0,00	0,00	0,00	0,66	14,41	0,00	7,09
Argissa hamatipes	0,00	0,00	0,00	0,00	7,98	5,64	2,78	6,38
Cerapus species 1	0,00	0,00	0,00	0,00	41,89	0,00	1,39	2,13
Chevreuxius grandimanus	0,00	0,00	0,00	1,86	0,00	3,76	0,70	1,42
Corophium species 1	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Siphonoecetes striatus	0,00	145,12	28,41	12,09	0,00	0,00	0,00	0,00
Unciola planipes	0,00	0,00	0,00	8,37	0,00	0,00	0,00	0,00
Cressa dubia	0,00	0,00	0,00	0,00	2,66	7,52	5,56	23,39
Atylus smithi	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,42
Atylus species 1	0,50	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Dexamine spinosa	0,00	0,00	0,00	0,00	0,00	0,00	0,70	0,00
Dexaminidae species 1	0,00	0,00	0,00	0,93	0,00	0,00	0,00	0,00
Epimeria cornigera	1,98	2,34	0,00	0,00	0,00	0,00	0,00	0,71
Epimeria parasitica	0,00	25,75	8,74	0,00	0,00	0,00	0,00	0,00
Apherusa bispinosa	5,95	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Apherusa ovalipes	0,00	4,68	2,19	0,00	0,00	0,00	0,00	0,00
Apherusa species 1	0,00	0,00	0,00	0,00	0,00	1,25	0,00	0,00
Eusirus longipes	15,86	2,34	4,37	0,00	2,66	8,14	4,87	1,42
Haliragoides species 1	0,00	0,00	0,00	3,72	0,00	0,00	1,39	4,25
Rachotropis glabra	0,00	0,00	0,00	0,93	0,00	3,76	0,00	0,00
Rachotropis gracilis	0,00	0,00	0,00	0,00	0,00	1,88	0,00	7,09
Rachotropis grimaldii	0,00	72,56	13,11	0,00	1,33	1,25	0,00	0,00
Rachotropis inermis	0,00	4,68	126,75	3,72	5,32	10,65	4,87	0,00
Rachotropis integricauda	57,49	18,72	0,00	0,00	0,00	0,00	0,00	0,00
Rachotropis rostrata	0,00	0,00	1,09	5,58	2,66	2,51	0,00	0,00
Gammarellus homari	0,00	0,00	0,00	0,00	0,00	0,00	0,70	0,00
Ischyroceridae species 1	0,00	0,00	0,00	0,93	0,00	0,00	0,00	0,00
Gammaropsis maculata	3,96	2,34	0,00	2,79	1,33	0,00	0,70	0,00
Megamphopus cornutus	35,68	4,68	4,37	2,79	5,98	0,00	0,00	0,00
Isaeidae species 1	0,00	0,00	0,00	0,00	0,00	1,25	0,00	7,09
Lafystiopsis aff. *planifrons*	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Lepechinella manco	0,00	0,00	9,29	0,93	5,98	4,39	3,48	9,92
Lepechinella species 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,71
Leucothoe liljeborgii	0,50	7,02	0,00	0,00	0,00	0,00	0,00	0,00
Lilljeborgia fissicornis	0,00	0,00	0,00	1,86	26,60	58,89	35,45	43,95
Lilljeborgia macronyx	0,00	0,00	0,00	0,00	2,66	0,00	0,00	0,00
Acidostoma sarsi	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Ambasia atlantica	0,00	0,00	2,19	0,00	0,66	1,25	2,78	0,00
Anonyx liljeborgi	0,00	0,00	0,55	0,00	0,00	0,00	0,00	0,00
Aristias neglectus	0,00	0,00	0,00	0,00	0,00	0,63	2,09	0,00
Bathyamaryllis haswelli	0,00	0,00	0,00	0,00	0,00	6,27	34,76	23,39
Euonyx chelatus	0,00	0,00	0,00	0,00	0,00	0,00	1,39	0,71
Hippomedon denticulatus	0,00	4,68	39,34	0,93	0,00	0,00	0,00	1,42
Ichnopus spinicornis	0,00	0,00	0,55	0,00	0,00	0,63	0,00	0,00
Lepidepecreum clypeatum	1,98	0,00	0,00	0,00	0,66	1,25	0,70	0,71
Lepidepecreum longicorne	1,98	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Lepidepecreum aff. *umbo*	0,00	0,00	0,00	0,00	0,00	0,00	2,78	2,13

(continued)

	M200	M350	M500	M650	M800	M950	M1100	M1250
Lysianassa plumosa	0,00	0,00	0,00	0,00	2,66	3,13	0,00	0,00
Metambasia faeroensis	0,00	0,00	0,00	0,00	0,00	0,63	1,39	12,05
Orchomene humilis	0,00	1,17	6,56	0,00	0,00	4,39	0,00	0,00
Orchomene pectinatus	0,00	0,00	2,19	0,00	0,00	0,63	0,00	0,00
Orchomenella nana	29,74	0,00	0,00	1,86	0,00	0,63	0,70	0,00
Paracentromedon crenulatus	0,00	0,00	0,00	0,00	0,00	1,25	0,00	0,00
Scopelocheirus hopei	0,00	0,00	0,00	0,00	0,66	1,25	0,00	0,00
Sophrosyne robertsoni	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Socarnes crenulatus	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Tmetonyx similis	0,00	0,00	0,00	0,00	0,00	0,00	1,39	0,00
Tryphosella horingi	0,00	0,00	0,00	0,00	0,66	2,51	2,78	0,00
Tryphosella insignis	0,00	0,00	0,00	0,00	0,00	1,88	8,34	0,00
Tryphosella nanoides	0,00	0,00	0,00	0,00	0,00	0,00	4,87	0,00
Tryphosella species 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,71
Tryphosites alleni	0,00	0,00	10,93	0,00	2,66	0,00	0,00	0,00
Tryphosites longipes	0,00	37,45	31,14	5,58	0,00	0,00	0,00	0,00
Cheirocratus intermedius	1,98	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Eriopsia elongata	0,00	0,00	0,00	0,00	3,32	0,00	0,00	0,00
Maera othonis	7,93	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Melita gladiosa	87,22	11,70	45,89	0,00	0,00	0,00	0,00	0,00
Melita obtusata	0,50	0,00	2,19	0,00	0,00	0,00	0,00	0,00
Megaluropus agilis	0,00	0,00	0,00	0,00	0,00	1,25	0,00	0,00
Melphidippa goesi	0,00	0,00	0,00	7,44	10,64	0,00	0,00	0,00
Melphidippa macrura	0,00	0,00	0,00	0,00	0,00	0,00	0,70	6,38
Melphidipella macra	150,66	2,34	8,74	0,00	0,00	0,63	0,00	0,00
Bathymedon acutifrons	0,00	0,00	0,00	0,00	7,98	0,63	0,00	0,00
Bathymedon longimanus	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Bathymedon monoculodiformes	0,00	0,00	0,00	0,00	14,63	11,90	0,00	1,42
Bathymedon species 1	3,96	0,00	0,00	0,93	0,00	0,00	1,39	0,00
Monoculodes packardi	0,00	0,00	0,00	1,86	0,00	0,63	1,39	0,00
Monoculodes species 1	3,96	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Oediceropsis brevicornis	0,00	0,00	7,10	0,00	0,00	0,00	0,00	4,96
Perioculodes longimanus	0,00	2,34	4,37	0,00	0,00	0,00	0,00	0,00
Pontocrates altamarinus	5,95	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Synchelidium maculatum	0,00	0,00	0,00	11,16	2,66	0,00	0,70	0,00
Westwoodilla caecula	11,89	28,09	39,34	0,93	0,00	0,00	0,00	0,00
Halice walkeri	0,00	7,02	0,00	0,00	0,00	0,00	0,00	0,00
Halicoides anomalus	0,00	0,00	0,00	0,00	0,66	1,88	4,17	0,00
Nicippe tumida	0,00	0,00	4,37	0,00	10,64	5,01	8,34	0,00
Pardalisca mediterranea	0,00	0,00	0,00	0,00	0,00	0,00	1,39	0,71
Paraphoxus oculatus	0,00	0,00	0,00	0,00	0,00	6,27	1,39	0,00
Harpinia antennaria	0,00	0,00	2,19	0,00	2,66	0,00	0,00	0,00
Harpinia laevis	0,00	0,00	0,00	0,93	0,00	0,00	0,00	0,00
Harpinia truncata	0,00	0,00	0,00	0,00	1,33	0,00	0,00	0,00
Stenopleustes malmgreni	0,00	0,00	0,00	0,00	2,66	0,00	0,00	0,00
Dyopedes monocanthus	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,42
Laetmatophilus tuberculatus	0,00	0,00	0,00	0,93	0,00	3,13	0,70	0,00
Phippsia gibbosa	0,00	0,00	2,19	2,79	0,00	0,00	0,00	0,00
Stegocephaloides auratus	3,96	15,21	9,29	5,58	3,99	19,42	14,60	17,72
Stegocephalidae species 1	0,00	0,00	0,00	0,00	0,00	0,00	4,87	0,00
Proboloides grandimanus	0,00	0,00	0,00	0,00	15,96	0,00	0,00	1,42
Stenothoe richardi	0,00	0,00	0,00	0,00	2,66	0,00	0,00	0,00
Stenothoidae species 1	0,00	0,00	0,00	0,00	0,00	0,00	0,70	0,71
Astyra abyssi	0,00	0,00	0,00	1,86	2,66	0,00	0,00	2,13
Bruzelia typica	0,00	0,00	2,73	5,58	2,66	8,14	0,00	0,00
Ileraustroe species 1	0,00	0,00	0,00	0,00	0,00	2,51	19,47	18,43
Syrrhoe affinis	0,00	4,68	73,76	4,65	0,00	0,00	0,00	0,00
Syrrhoites serratus	0,00	0,00	0,00	0,00	0,00	0,00	4,87	7,80
Syrrhoites walkeri	0,00	0,00	0,00	0,93	5,32	21,30	2,78	0,00
Urothoe elegans	0,00	0,00	6,56	0,00	0,00	0,00	0,00	0,00
Urothoe marina	0,00	0,00	2,19	0,00	0,00	0,00	0,00	0,00
Carangolia aff. *barnardi*	1,98	0,00	0,00	0,00	21,28	12,53	0,70	0,71

(continued)

	M200	M350	M500	M650	M800	M950	M1100	M1250
Hyperia schizogeneois	0,00	0,59	0,00	0,00	0,00	0,00	0,00	0,00
Parathemisto oblivia	0,00	0,00	1,09	0,00	0,00	0,00	2,09	0,00
Phrosina semilunata	0,00	0,00	0,00	0,00	0,00	0,00	0,70	0,00
Primno brevidens	0,00	0,00	0,00	0,93	0,00	0,00	0,00	0,00
Amphipoda indet.	63,93	89,53	60,09	14,87	27,27	59,52	29,89	13,47
Total	**543,16**	**583,98**	**644,67**	**130,15**	**315,21**	**337,08**	**237,06**	**262,98**

Absolute densities (ind. 100 m^{-2}) for all Isopoda species sampled at the eight stations along the depth gradient at Meriadzek Terrace (M200-M1250). Total density per station is also indicated.

	M200	M350	M500	M650	M800	M950	M1100	M1250
Gnathia albescens	0,00	0,00	0,00	0,00	0,00	1,88	2,09	0,00
Gnathia oxyuraea	4,46	5,27	0,55	0,00	0,00	0,00	0,00	0,00
Leptanthura chardyi	0,00	0,00	0,00	0,00	0,00	0,63	1,39	2,13
Leptanthura tenuis	0,00	0,00	0,00	0,00	0,00	1,25	0,00	0,00
Anthuridae species 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,71
Aega species 1	0,99	0,59	1,09	0,00	0,66	0,00	0,00	0,00
Eurydice grimaldii	0,99	0,59	1,09	0,00	13,96	3,76	0,00	0,00
Metacirolana hanseni	0,00	0,00	0,00	0,00	7,98	34,46	0,00	41,82
Natatolana borealis	0,00	1,76	102,71	6,51	0,66	0,00	0,00	0,00
Natatolana caeca	0,00	0,00	0,00	0,00	2,66	13,16	0,00	0,00
Bathycopea typhlops	0,00	0,00	4,37	33,47	13,30	24,43	47,27	15,59
Arcturella dilatata	0,50	2,34	0,00	1,86	0,00	0,00	0,00	0,00
Astacilla intermedia	0,50	0,59	0,00	5,58	0,00	0,00	0,00	0,00
Astacilla longicornis	0,00	0,00	0,00	0,00	0,66	0,00	0,00	0,00
Astacilla pussila	0,50	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Astacilla species 1	0,00	0,00	1,64	4,65	0,66	0,63	0,00	0,00
Janira maculosa	0,00	1,76	0,00	0,00	0,66	2,51	0,00	0,00
Janirella nanseni	0,00	0,00	0,00	0,00	0,00	5,64	5,56	55,29
Disconectes latirostris	47,08	2,93	6,56	3,72	14,63	3,76	1,39	1,42
Munnopsurus atlanticus	0,50	0,00	0,00	1,86	0,00	11,90	1,39	5,67
Tytthocope megalura	0,00	0,00	0,00	0,93	3,32	1,88	4,87	9,21
Aspidarachna longicornis	0,00	0,00	0,00	0,00	0,00	2,51	0,00	0,00
Aspidarachna clypeata	0,00	0,00	0,00	0,00	3,32	2,51	0,00	0,00
Bathybadistes hoplitis	0,00	0,00	0,00	0,00	5,32	0,63	0,00	0,00
Ilyarachna longicornis	0,00	0,00	0,55	34,40	38,57	25,69	2,09	24,81
Munna limicola	0,00	0,00	0,00	0,00	0,00	3,13	0,00	0,00
Munnopsis beddardi	0,00	0,00	0,00	0,93	11,30	0,63	0,70	0,71
Isopoda indet.	3,46	1,75	2,74	0,00	0,67	4,39	2,08	7,80
Total	**58,97**	**17,55**	**121,29**	**93,90**	**118,37**	**145,36**	**68,82**	**165,16**

Absolute densities (ind. 100 m^{-2}) for all Cumacea species sampled at the eight stations along the depth gradient at Meriadzek Terrace (M200-M1250). Total density per station is also indicated.

	M200	M350	M500	M650	M800	M950	M1100	M1250
Vaunthompsonia cristata	0,00	0,00	0,00	0,00	6,65	3,13	1,39	0,00
Cyclaspis longicaudata	0,99	0,00	3,82	17,66	12,63	17,54	4,17	0,00
Iphinoe serrata	0,50	5,27	0,00	0,00	0,66	0,00	0,00	0,00
Iphinoe tenella	0,50	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Leucon longirostris	0,00	0,00	0,00	0,00	0,00	1,88	0,00	0,00
Campylaspis glabra	0,00	0,00	0,55	13,95	14,63	13,16	9,73	6,38
Campylaspis horridoides	0,00	0,00	0,00	0,00	1,33	3,76	3,48	1,42
Campylaspis macrophthalma	0,00	0,00	0,00	0,00	0,00	0,00	1,39	0,00
Campylaspis rostrata	0,00	0,00	0,00	2,79	35,24	25,69	4,17	0,00
Campylaspis squamifera	0,00	0,00	0,00	0,93	1,99	1,25	0,00	3,54
Campylaspis verrucosa	0,00	0,00	0,00	0,00	0,66	0,00	0,00	0,71
Campylaspis vitrea	0,00	0,00	0,00	0,00	0,66	0,00	0,00	0,00
Cumellopsis puritani	0,00	0,00	0,00	0,00	0,00	4,39	4,87	2,13
Procampylaspis armata	0,00	0,59	3,82	3,72	0,00	4,39	0,00	0,00
Procampylaspis bituberculata	0,00	0,00	0,00	0,00	0,00	0,63	5,56	0,00
Procampylaspis bonnieri	0,00	0,00	0,00	0,00	0,00	0,00	2,09	0,71
Procampylaspis macronyx	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Ceratocuma horrida	0,00	0,00	0,00	0,00	0,00	56,39	132,09	70,88
Hemilamprops normani	0,99	12,87	26,22	3,72	76,47	67,04	35,45	21,97
Hemilamprops uniplicata	6,94	5,27	15,84	156,18	17,29	19,42	14,60	0,00
Lamprops fasciata	0,99	0,00	2,73	98,55	0,66	0,63	2,78	0,71
Paralamprops orbicularis	0,00	0,00	0,00	4,65	3,99	1,88	4,17	0,00
Platysympus typicus	0,00	0,00	0,00	7,44	4,65	10,65	17,38	13,47
Diastylis laevis	0,00	0,00	0,00	0,00	0,00	0,63	0,00	0,00
Diastylis rugosa	0,00	0,59	1,09	0,00	0,00	0,00	0,00	0,00
Diastylis tumida	0,00	0,00	0,00	0,00	4,65	11,28	1,39	1,42
Diastyloides bacescoi	4,96	2,93	21,85	22,31	0,66	0,00	0,00	0,00
Leptostylis grandis	0,00	0,00	0,00	0,00	0,00	0,00	0,70	0,00
Leptostylis macrura	0,00	0,00	7,10	4,65	6,65	1,88	1,39	0,00
Makrokylindrus anomalus	0,00	0,00	2,19	0,00	0,00	0,00	0,00	0,00
Makrokylindrus josephina	0,00	0,00	0,00	1,86	26,60	13,16	35,45	7,09
Makrokylindrus longipes	0,00	0,00	0,00	0,00	19,28	8,77	6,26	2,13
Makrokylindrus mystacinus	0,00	0,00	2,19	4,65	1,33	0,00	0,00	0,00
Cumacea indet.	3,47	5,85	6,01	14,87	7,31	12,53	6,95	9,22
Total	**19,33**	**33,35**	**93,42**	**357,92**	**244,05**	**280,69**	**295,45**	**141,77**

Absolute densities (ind. 100 m^{-2}) for all Mysidacea species sampled at the eight stations along the depth gradient at Meriadzek Terrace (M200-M1250). Total density per station is also indicated.

	M200	M350	M500	M650	M800	M950	M1100	M1250
Eucopia sculpticauda	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,71
Eucopia unguiculata	0,00	0,00	0,00	0,93	0,00	0,00	1,39	0,71
Hansenomysis fyllae	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,42
Boreomysis arctica	0,00	0,00	0,00	3,72	0,66	0,00	0,00	0,00
Boreomysis microps	0,00	9,36	2,19	0,00	0,00	0,00	0,70	0,00
Boreomysis tridens	0,00	0,00	0,00	0,00	0,00	0,00	0,70	0,00
Gastrosaccus normani	0,50	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Anchialina agilis	0,99	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Amblyops abbreviata	0,00	0,00	34,97	1,86	0,00	0,00	0,70	0,00
Dactylerythrops dactylops	0,00	0,00	2,19	0,00	0,00	0,00	0,00	0,00
Erythrops neapolitana	868,26	65,54	6,56	0,00	0,00	0,00	0,00	0,00
Erythrops species 1	0,00	0,00	0,00	0,00	0,66	0,00	0,00	0,00
Hypererythrops serriventer	43,61	65,54	4,37	0,00	0,00	0,00	0,00	0,00
Paramblyops rostrata	0,00	0,00	0,00	0,00	0,00	15,66	8,34	16,30
Parapseudomma calloplura	0,00	0,00	0,00	0,93	0,00	0,63	0,00	0,00
Parerythrops obesa	63,43	4,68	2,19	0,00	0,00	0,00	0,00	0,00
Pseudomma affine	7,43	23,41	479,68	29,75	20,61	14,41	7,65	0,71
Mysideis insignis	22,30	0,59	2,19	0,00	0,00	0,00	0,00	0,00
Mysidopsis didelphys	6,94	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Mysidacea indet.	97,13	173,79	317,42	55,78	18,62	72,68	8,34	5,67
Total	**1110,60**	**342,90**	**851,74**	**92,97**	**40,56**	**103,38**	**27,81**	**25,52**

Absolute densities (ind. 100 m^{-2}) for all Tanaidacea species sampled at the eight stations along the depth gradient at Meriadzek Terrace (M200-M1250). Total density per station is also indicated.

	M200	M350	M500	M650	M800	M950	M1100	M1250
Apseudes grossimanus	0,00	0,00	0,00	0,93	0,66	0,00	0,00	0,00
Apseudes spinosus	0,00	0,00	0,00	0,00	5,98	1,25	0,70	0,00
Sphyrapus species 1	0,00	0,00	0,00	0,00	3,32	7,52	0,70	0,71
Typhlotanais aequiremis	0,00	0,00	0,00	0,00	1,99	1,88	0,00	5,67
Heterotanais species 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,13
Tanaidacea indet.	0,00	0,00	0,00	0,00	1,99	0,00	0,00	0,00
Total	**0,00**	**0,00**	**0,00**	**0,93**	**13,96**	**10,65**	**1,39**	**8,51**

Appendix 4

Result file of Draftsman plot (pairwise scatter plot) illustrating correlation between certain environmental variables (correlation > 0.95)

Variable	Variable	Correlation
mud	median grain size	-0.965
mud	sorting coefficient	0.886
mud	depth	0.900
mud	temperature	-0.898
mud	salinity	0.262
mud	dissolved oxygen	-0.813
mud	density	0.974
mud	chla (µg)	-0.742
median grain size	sorting coefficient	-0.774
median grain size	depth	-0.856
median grain size	temperature	0.927
median grain size	salinity	-0.158
median grain size	dissolved oxygen	0.667
median grain size	density	-0.962
median grain size	chla (µg)	0.663
sorting coefficient	depth	0.765
sorting coefficient	temperature	-0.686
sorting coefficient	salinity	0.472
sorting coefficient	dissolved oxygen	-0.826
sorting coefficient	density	0.826
sorting coefficient	chla (µg)	-0.777
depth	temperature	-0.903
depth	salinity	0.075
depth	dissolved oxygen	-0.859
depth	density	0.946
depth	chla (µg)	-0.725
temperature	salinity	0.149
temperature	dissolved oxygen	0.626
temperature	density	-0.958
temperature	chla (µg)	0.777
salinity	dissolved oxygen	-0.474
salinity	density	0.135
salinity	chla (µg)	0.159
dissolved oxygen	density	-0.792
dissolved oxygen	chla (µg)	0.556
density	chla (µg)	-0.741

Appendix 5

Relative abundance of the ten most abundant Peracarida species per station along the depth gradient at Porcupine Seabight (P200-P1250). The order each species belong to is indicated: M= Mysidacea, A= Amphipoda, I= Isopoda, C=Cumacea.

		P200			P350
Erythrops serrata	M	31,35	*Scopelocheirus hopei*	A	22,73
Leptomysis lingvura	M	13,51	*Mysidopsis didelphys*	M	12,40
Parathemisto oblivia	A	13,51	*Leptostylis villosa*	C	11,02
Rhachotropis integricauda	A	9,73	*Erythrops serrata*	M	8,54
Erythrops neapolitana	M	9,73	*Stegocephaloides auratus*	A	7,99
Mysidopsis didelphys	M	6,49	*Campylaspis glabra*	C	4,41
Melphidipella macra	A	5,41	*Hypererythrops serriventer*	M	3,72
Epimeria cornigera	A	2,70	*Rhachotropis integricauda*	A	3,31
Stegocephaloides auratus	A	2,70	*Pseudomma affine*	M	3,17
Leptostylis villosa	C	1,08	*Nicippe tumida*	A	3,03
		P500			**P650**
Scopelocheirus hopei	A	28,92	*Gammaropsis palmata*	A	17,45
Pseudomma affine	M	17,04	*Pseudomma affine*	M	16,70
Paramblyops rostrata	M	15,47	*Hemilamprops uniplicata*	C	15,56
Natatolana borealis	I	9,19	*Haploops setosa*	A	8,81
Rhachotropis grimaldii	A	8,97	*Astacilla intermedia*	I	5,60
Epimeria parasitica	A	7,85	Janiridae species 1	I	4,23
Syrrhoe affinis	A	4,04	*Astyra abyssi*	A	3,70
Hippomedon denticulatus	A	1,12	*Astacilla longicornis*	I	2,82
Harpinia antennaria	A	1,12	*Urothoe elegans*	A	2,29
Parathemisto oblivia	A	0,90	*Syrrhoe affinis*	A	2,25
		P800			**P950**
Hemilamprops uniplicata	C	10,79	*Hemilamprops uniplicata*	C	20,39
Astacilla intermedia	I	8,82	*Unciola planipes*	A	12,76
Gammaropsis palmata	A	7,22	*Natatolana borealis*	I	9,67
Laetmatophilus tuberculatus	A	6,85	*Campylaspis macrophthalma*	C	7,40
Metacirolana hanseni	I	6,47	*Bathycopea typhlops*	I	4,83
Cressa dubia	A	3,94	*Astacilla longicornis*	I	4,68
Astacilla longicornis	I	3,47	*Ampelisca gibba*	A	3,47
Janiridae species 1	I	3,47	*Campylaspis verrucosa*	C	3,47
Campylaspis macrophthalma	C	3,38	*Pseudomma affine*	M	3,17
Ampelisca gibba	A	2,81	*Makrokylindrus longipes*	C	3,10
		P1100			**P1250**
Ampelisca gibba	A	19,82	*Campylaspis rostrata*	C	14,84
Metacirolana hanseni	I	18,59	*Metacirolana hanseni*	I	10,43
Campylaspis rostrata	C	9,39	*Diastyloides serrata*	C	6,32
Hemilamprops normani	C	8,23	*Ampelisca gibba*	A	6,08
Cumellopsis puritani	C	5,53	*Cyclaspis longicaudata*	C	5,28
Hemilamprops uniplicata	C	4,54	*Makrokylindrus longipes*	C	4,09
Cyclaspis longicaudata	C	4,20	*Lepechinella manco*	A	3,20
Paralamprops species 1	C	2,03	*Hemilamprops uniplicata*	C	2,89
Makrokylindrus josephinae	C	1,99	*Lilljeborgia fissicornis*	A	2,79
Tryphosella insignis	A	1,89	*Argissa hamatipes*	A	2,59

Relative abundance of the ten most abundant Peracarida species per station along the depth gradient at Meriadzek Terrace (M200-M1250). The order each species belong to is indicated: M= Mysidacea, A= Amphipoda, I= Isopoda, C=Cumacea.

		M200			M350
Erythrops neapolitana	M	55,51	*Siphonoecetes striatus*	A	20,53
Melphidipella macra	A	9,63	*Rachotropis grimaldii*	A	10,26
Melita gladiosa	A	5,58	*Erythrops neapolitana*	M	9,27
Parerythrops obesa	M	4,06	*Hypererythrops serriventer*	M	9,27
Rachotropis integricauda	A	3,68	*Lembos longipes*	A	5,96
Disconectes latirostris	I	3,01	*Tryphosites longipes*	A	5,30
Hypererythrops serriventer	M	2,79	*Westwoodilla caecula*	A	3,97
Lembos longipes	A	2,28	*Epimeria parasitica*	A	3,64
Megamphopus cornutus	A	2,28	*Pseudomma affine*	M	3,31
Orchomenella nana	A	1,90	*Rachotropis integricauda*	A	2,65
		M500			**M650**
Pseudomma affine	M	36,21	*Hemilamprops uniplicata*	C	26,46
Rachotropis inermis	A	9,57	*Lamprops fasciata*	C	16,69
Natatolana borealis	I	7,75	*Ilyarachna longicornis*	I	5,83
Syrrhoe affinis	A	5,57	*Bathycopea typhlops*	I	5,67
Ampelisca gibba	A	3,75	*Pseudomma affine*	M	5,04
Melita gladiosa	A	3,46	*Diastyloides bacescoi*	C	3,78
Hippomedon denticulatus	A	2,97	*Cyclaspis longicaudata*	C	2,99
Westwoodilla caecula	A	2,97	*Campylaspis glabra*	C	2,36
Amblyops abbreviata	M	2,64	*Siphonoecetes striatus*	A	2,05
Tryphosites longipes	A	2,35	*Synchelidium maculatum*	A	1,89
		M800			**M950**
Hemilamprops normani	C	11,31	*Hemilamprops normani*	C	9,21
Cerapus species 1	A	6,19	*Lilljeborgia fissicornis*	A	8,09
Ilyarachna longicornis	I	5,70	*Ceratocuma horrida*	C	7,75
Campylaspis rostrata	C	5,21	*Metacirolana hanseni*	I	4,73
Lilljeborgia fissicornis	A	3,93	*Ilyarachna longicornis*	I	3,53
Makrokylindrus josephina	C	3,93	*Campylaspis rostrata*	C	3,53
Ampelisca macrocephala	A	3,15	*Bathycopea typhlops*	I	3,36
Carangolia aff. *barnardi*	A	3,15	*Syrrhoites walkeri*	A	2,93
Pseudomma affine	M	3,05	*Stegocephaloides auratus*	A	2,67
Makrokylindrus longipes	C	2,85	*Hemilamprops uniplicata*	C	2,67
		M1100			**M1250**
Ceratocuma horrida	C	22,65	*Ceratocuma horrida*	C	12,48
Bathycopea typhlops	I	8,10	*Janirella nanseni*	I	9,74
Lilljeborgia fissicornis	A	6,08	*Lilljeborgia fissicornis*	A	7,74
Hemilamprops normani	C	6,08	*Metacirolana hanseni*	I	7,37
Makrokylindrus josephina	C	6,08	*Ilyarachna longicornis*	I	4,37
Bathyamaryllis haswelli	A	5,96	*Ampelisca aequicornis*	A	4,12
Ileraustroe species 1	A	3,34	*Cressa dubia*	A	4,12
Platysympus typicus	C	2,98	*Bathyamaryllis haswelli*	A	4,12
Stegocephaloides auratus	A	2,50	*Hemilamprops normani*	C	3,87
Hemilamprops uniplicata	C	2,50	*Ileraustroe* species 1	A	3,25