UNIVERSITY OF SOUTHAMPTON

Macrobenthic Ecology of the West Shetland Slope

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ABSTRACT

FACULTY OF SCIENCE
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by

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An unusual and complex hydrographic regime in the Faeroe-Shetland Channel makes it one of the best-studied oceanographic provinces in the world. However, few benthic ecological studies of the region have been undertaken since the early 1880s. The present study examines the influence of a number of environmental variables on macrobenthic faunal distribution on the West Shetland Slope.

Macrobenthic samples were collected by corer and grab along a depth transect in 1996 and 1998. The macrofauna studied were retained on 500 μm and 250 μm sieves enabling comparisons to be made between samples taken using these two sieve sizes.

The addition of the 250 μm-to-500 μm size fraction to the >500 μm size fraction resulted in an increase in species diversity (31% at the 150 m station) and species richness (38% at the 800 m station). Faunal abundance was also seen to increase by an average of 40% per station when combining the smaller size fraction. The results also illustrated that water temperature appears to be the major environmental variable controlling benthic macrofaunal distribution (especially in terms of standing stock), polychaete species diversity, feeding modes and restriction of polychaete species to specific temperature bands. Other environmental variables such as sediment grain size and total organic carbon also influenced macrofaunal distribution although to a lesser degree. The level of taxonomic resolution required was investigated and the conclusion drawn was that to achieve adequate discrimination between stations for this area, the macrofauna should be identified to species level.

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4 Studies in benthic macrofaunal ecology I: Standing stock of the West Shetland Slope

For Mum, Dad and Hari

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"As we descend deeper and deeper....inhabitants become fewer and fewer, indicating our approach towards an abyss....it is in the exploration of this vast deep-sea region that the finest field for submarine discoveries yet remains."

Edward Forbes (1815 – 1854)

GENERAL INTRODUCTION

1.1. THE DEEP SEA

More is known, in general, regarding the mapping of the human genome compared to the 70% of the Earth's surface that is covered by water, most of which lies below 2000 m. As it is so remote and inaccessible, this environment and the organisms living there are not as well known as those found in shallow seas.

The oceans can be divided into five mainly depth-related zones: the continental shelf, the continental slope, the continental rise, the abyssal plain and the trenches (Anikouchine and Sternberg, 1973). The continental shelf generally ends at a depth of about 200 m; however at high southern latitudes, the shelf edge may be found at a depth of approximately 500 m owing to the weight of the ice-cap. On the continental shelf, terraces or benches occur, the deepest occurring in the Antarctic and the widest in the Arctic (Kennett, 1982).

The continental slope is indicated by an increase in the topographical gradient and occurs from a depth of about 200 m to between 1500 m and 3500 m. The continental slope tends to be the boundary between the continental crust and the oceanic crust (Brown *et al.*, 1989). The slope is also the main continental margin that may be active, as off the west coast of the Americas, or passive as in the Northeast Atlantic. The slope region is a narrow zone generally less than 200 km wide. It has a thin sediment cover owing to its highly dynamic environment. The continental rise is a wedge-shaped sedimentary province between the slope and ocean basins and is between 100 km and 1000 km wide (Kennett, 1982). Submarine canyons cut through the continental rise, and can act as channels, transporting sediments towards the abyssal plains, although in the present day this is greatly reduced. Canyons may extend upwards and incise both the continental slope and shelf (Kennett, 1982), as with the Scripps Canyon that starts at a depth of 50 m. Sediment settles at the base of these canyons on the rise because of a reduction in current speed (Stow, 1986).

Abyssal plains extend from the continental rise at depths between 3000 m and 6000 m deep, and act like huge sediment traps in accumulating a thick mantle of mainly biogenic sediment particles. The abyssal plains of the Atlantic are generally flatter compared to those in the Pacific because of the large input of sediment derived from the continental areas by turbidity currents (Brown *et al.*, 1989) and higher surface production giving rise to biogenic deposits. The Pacific Ocean receives less sediment

as fewer rivers drain into it and also because it is bordered by trenches that trap the majority of the sediment (Kennett, 1982). The abyssal plains of the Pacific Ocean are predominantly covered by pelagic sediment rather than continental-derived sediment (Brown *et al.*, 1989).

Mid-ocean ridges separate the abyssal plains. An example of this is the Mid-Atlantic ridge separating the Madeira Abyssal Plain on the eastern side of the Atlantic from the Sohm Abyssal Plain on the western side (Holcombe, 1977). The mid-ocean ridges are also known as constructive margins, as this is where new oceanic lithosphere is formed. The flanks are symmetrical about the axis and the sediment coverage increases with increasing distance from the ridge crest (Kennett, 1982).

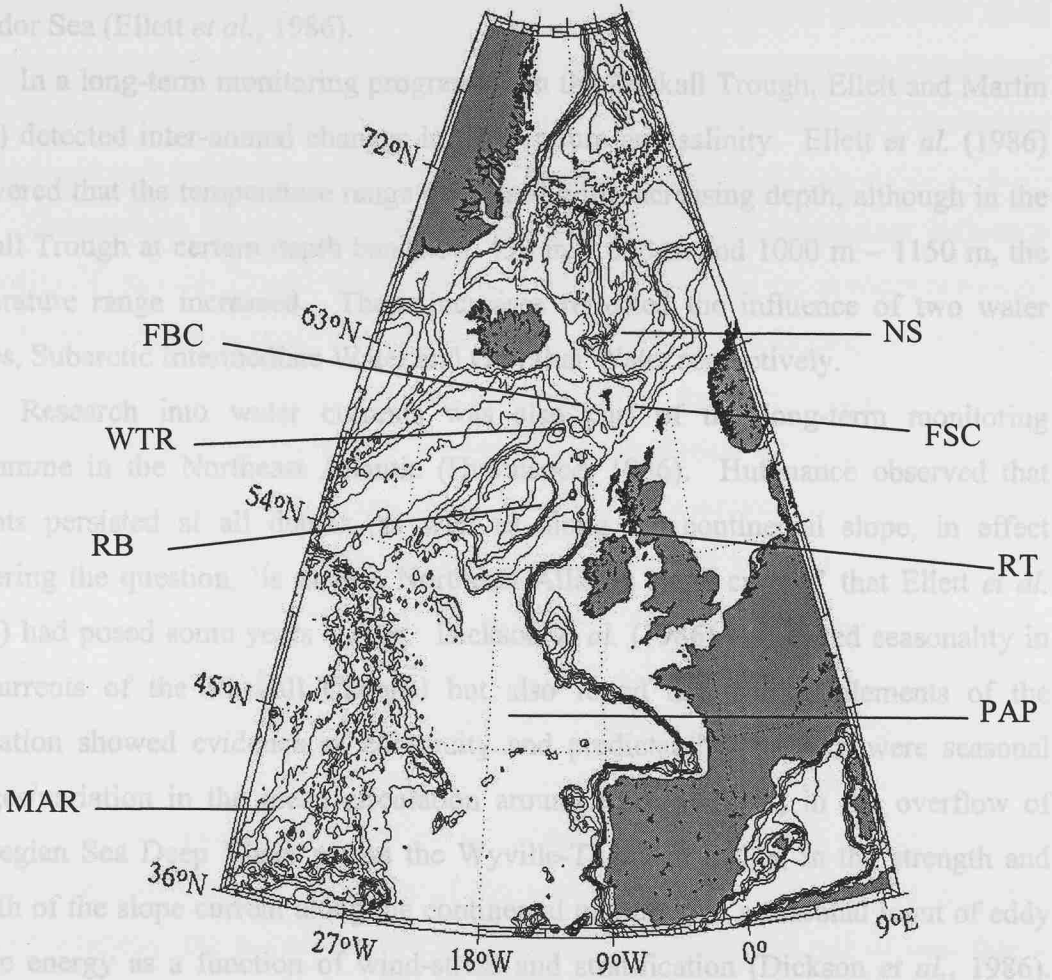
Marginal trenches are troughs that run almost parallel and adjacent to the continental margins. Below these trenches are subduction zones where the oceanic plate is consumed at a rate that is similar, but not the same, as that of plate formation at the spreading centres (Press and Siever, 1986).

1.2. THE PHYSICAL ENVIRONMENT OF THE NORTHEAST ATLANTIC

1.2.1. Topography and Hydrography

In their benchmark studies of the seabed areas of the deep Northeast Atlantic, Roberts *et al.* (1979) argued that the usual steady transition from land to ocean is absent. The Northeast Atlantic has a number of anomalous shallow plateaux such as the Rockall Plateau (in reality a micro-continent) and deep troughs such as the Rockall Trough (Figure 1.1) (Roberts *et al.*, 1979). The Mid-Atlantic Ridge system forms a western border to the Northeast Atlantic. The main abyssal plain in the Northeast Atlantic is the Porcupine Abyssal Plain at approximately 4800 m depth. There are also semi-isolated deep-sea basins such as the Norwegian Basin (Hansen and Østerhus, 2000) separated at depth from the Northeast Atlantic Ocean by the Scotland-Faeroes-Iceland-Greenland sill or the Wyville-Thomson Ridge. Water from the Norwegian Sea enters the North Atlantic via the Denmark Strait and the Faeroe-Shetland Channel (Figure 1.1).

Figure 1.1. A Transverse Mercator Projection of the Northeast Atlantic and surrounding regions.



PAP – Porcupine Abyssal Plain

RT – Rockall Trough

FSC – Faeroe-Shetland Channel

NS – Norwegian Sea

FBC – Faeroe-Bank Channel

WTR – Wyville-Thomson Ridge

RB – Rockall Bank

MAR – Mid Atlantic Ridge

The hydrography of the water masses in the Atlantic, and in particular the Rockall Trough, has been well studied over the past 35 years (Currie, 1986). In the Rockall Trough the water masses can be divided into an upper and a lower layer (Ellett *et al.*, 1986). The upper layer mainly consists of water derived from the western Atlantic (Iselin, 1939; Sverdrup *et al.*, 1942), whilst the lower layer originates from the Labrador Sea (Ellett *et al.*, 1986).

In a long-term monitoring programme in the Rockall Trough, Ellett and Martin (1973) detected inter-annual changes in temperature and salinity. Ellett *et al.* (1986) discovered that the temperature range decreased with increasing depth, although in the Rockall Trough at certain depth bands i.e. 450 m – 650 m and 1000 m – 1150 m, the temperature range increased. These increases reflected the influence of two water masses, Subarctic Intermediate Water and Gibraltar Water respectively.

Research into water currents was also part of the long-term monitoring programme in the Northeast Atlantic (Huthnance, 1986). Huthnance observed that currents persisted at all depths, as well as along the continental slope, in effect answering the question, 'is there a Northeast Atlantic slope current' that Ellett *et al.* (1979) had posed some years earlier. Dickson *et al.* (1986) also noted seasonality in the currents of the Rockall Channel but also found that certain elements of the circulation showed evidence of continuity and predictability. There were seasonal changes/variation in the mean circulation around Rockall Bank; in the overflow of Norwegian Sea Deep Water across the Wyville-Thomson Ridge; in the strength and breadth of the slope current along the continental margin; and a seasonal input of eddy kinetic energy as a function of wind-stress and stratification (Dickson *et al.*, 1986). Long-term changes in the temperature and salinity of the Trough were also noted (Ellett *et al.*, 1986). Between 1927 and 1931 the surface water temperature was low, but salinity relatively high; this was thought to be as a result of deeper winter mixing. However, the period encompassing 1972 to 1976 saw a sharp decline in salinity values (Ellett *et al.*, 1986; Belkin *et al.*, 1998). This period is now known as the 'Great Salinity Anomaly' of the 1970s and is thought to have occurred because of a general widespread freshening of the North Atlantic (Brewer *et al.*, 1983; Roemmich and Wunsch, 1984; Ellett *et al.*, 1986; Dickson *et al.*, 1988). The Great Salinity Anomaly of the 1970s was not a unique phenomenon. Retrospective analyses have shown that a large salinity anomaly appears to be almost a regular phenomenon at the decadal scale (Myers *et al.*, 1989; Ellett and Blindheim, 1992; Drinkwater, 1994; Belkin *et al.*, 1998).

1.2.2. Circulation

The oceans were once thought to be a static body of water and one in which the temperature at any depth and location would be the same. The difference in temperature between near surface water and bottom water was first discovered in 1791 (Warren, 1981). Count Von Rumford, in 1797, suggested that this deep water must develop in cold regions of the world and sink under the warmer waters (Mann and Lazier, 1991). Von Rumford and subsequent authors proposed the idea of a convective circulation, or as it is known today, the thermohaline circulation.

Temperature, salinity and processes that may alter these parameters, influence the density of seawater (Sverdrup *et al.*, 1942). Most of the deep dense water is formed at high latitudes and was originally near surface water (Mann and Lazier, 1991). It is at these high latitudes that intense cooling, evaporation or freezing occurs (Sverdrup *et al.*, 1942). This in turn leads to a greater depth penetration by vertical convection currents until the density throughout the water column is relatively constant (Sverdrup *et al.*, 1942). If the process continues and the surface water is becoming still denser, then as long as the body of water is continuous with other areas, the deep dense water will spread to these regions. If denser water already exists in these areas, then the new inflow of water will form an intermediate layer. Continuation of this process leads to the cold, but less dense, water being pushed towards the surface at low latitudes. The actual rate of movement is small, 10^{-5}cm s^{-1} (Mann and Lazier, 1991). However, it has an important effect on the structure of the ocean. Over time a balance has been achieved whereby, the downward diffusion of heat is equal to the rate of heat that is being moved back up by the upward motion in the water (Mann and Lazier, 1991). The balance between advection and diffusion with respect to the vertical flow of heat, leads to their being two layers; a warm upper layer that is separated by a permanent thermocline from a cold lower layer.

Eddy motions in moving water masses are now known to occur throughout the oceans. Eddies result in lower-amplitude current variations at the scale of tens to hundreds of kilometres. Eddies tend to be barotropic and interact with one another owing to the sheer number of them in the ocean (Robinson, 1983). The eddies associated with narrow boundary flows, such as the Gulf Stream (Mann and Lazier, 1991), tend to have high current and energy levels compared to those found in remote areas such as the Southeast Pacific. It is thought that eddies may be responsible for the

transient upwelling events that stimulate the primary productivity of surface waters to a far greater extent than their long-term average values of upward water movement would suggest (Mann and Lazier, 1991).

1.2.3. Seabed currents

Heezen and Hollister (1971) suggested that asymmetric sand ripples and deep scour crescents, seen in photographs taken of the seafloor in the western Atlantic and Pacific, were as a result of strong bottom currents. Lonsdale and Hollister (1979) made similar observations in the Rockall Trough area. Heezen and Hollister (1971) also inferred that ripple marks are a continuation of a smaller form of sediment waves found on the seafloor. Deep scour crescents, found only around large rocks, and drifts of sediment in the lee of small obstacles, were thought to be caused by moderate currents (Heezen and Hollister, 1971; Lonsdale and Hollister, 1979). The strength of currents mentioned above are part of a much larger, deep and dynamic current known as the boundary current that is known to be well developed in the North Atlantic (Heezen and Hollister, 1971).

1.3. BIOLOGICAL OBSERVATIONS IN THE NORTHEAST ATLANTIC

The existence of fauna in deep-sea sediments in the Northeast Atlantic has been known since the *Lightning* and *Porcupine* expeditions in 1868 – 1870 (Thomson, 1873). The Scottish Association for Marine Science (formerly the Scottish Marine Biological Association) began long-term temporal studies on deep-water faunal populations of the Rockall Trough and adjacent areas in the early 1970s. Since 1973, Gage (1986) has sampled the Rockall Trough area to map the distribution of megafauna with respect to bathymetry and hydrography. The focus has mainly been on two permanent stations (2200 m and 2900 m depth) where studies of population processes such as reproduction and growth have been addressed from long-term sample time series (Tyler, 1986). Echinoderms have dominated the study of the biogeography of megafauna of this region, as they are generally predominant in bottom trawlings. It was found that echinoids and holothurians have a greater degree of depth-related zonation in comparison to ophiuroids and asteroids (Gage, 1986).

Megafauna of the Rockall Trough (Gage, 1986) was found to be similar to that of the Bay of Biscay (Le Danois, 1948) and of the Porcupine Seabight (Sibuet, 1977). The main controls on the distribution of the benthos are i) winter mixing to a depth of 600 m especially in the Rockall Trough (Ellett and Martin, 1973) and ii) the depth of development of the seasonal thermocline (Gage, 1986).

The Southampton Oceanography Centre (formerly the Institute of Oceanographic Sciences Deacon Laboratory) undertook extensive surveys of the benthic biology in the Porcupine Seabight and the adjoining Abyssal Plain (Rice *et al.*, 1986; 1991; 1994). The most interesting discovery was of a seasonal deposition of surface-derived phytodetritus on the seabed with evidence for subsequent re-suspension of the material (Billett *et al.*, 1983; Lampitt, 1985). However, Thurston *et al.* (1998) found that there was no evidence of seasonal or temporal changes with regards to abundance, biomass and taxonomic structure of the megafauna. The macrofauna however, do appear to react to deposition of phytodetrial material. High quantity and quality of deposited material may induce an increase in metabolic rates as well as an increase in biomass (Pfannkuche *et al.*, 1999). There is also now known to be seasonal reproduction in the deep-sea (Tyler, 1986).

A study of deep-sea polychaete assemblages from bathymetric transects in the Northeast Atlantic region was undertaken by Paterson (1993). On the Hebridean slope, species richness increased with depth to a maximum between 1000 m and 1400 m thereafter decreasing with depth. Paterson also determined that the species equitability pattern on the upper slopes between 400 m and 600 m appeared to reflect the greater disturbance caused by currents, compared to the deeper stations.

1.4. GENERAL INTRODUCTION TO THE FAEROE-SHETLAND CHANNEL

The Faeroe-Shetland Channel has been well studied for over 100 years. Observations undertaken in the Channel have found an unusual and highly dynamic physical environment. This has been attributed to the hydrography of the Channel resulting from the confluence and conduits for five bodies of water (Dooley *et al.*, 1984). The Channel is extremely important in the exchange of water between the Atlantic and Norwegian basins. Constraining, but not blocking, this exchange is a partly submerged topographic high, which includes Iceland and the Faeroe Islands, which is collectively known as the Greenland-Scotland Ridge. The exchange of water

across this Ridge is fundamentally important for the oceanic areas situated to the north and is partly responsible for the relatively mild climate of Northwest Europe (Mowatt *et al.*, 1997). The Faeroe-Shetland Channel also plays a major role in the global thermohaline circulation (Hansen and Østerhus, 2000).

Two main agents drive the exchange of water across the Greenland-Scotland Ridge. The first is thought to be wind stress affecting the properties of water flowing into, and the distribution of the water in the Arctic Mediterranean. The Arctic Mediterranean comprises the Arctic Ocean, the Barents Sea, the Norwegian Sea, the Iceland Sea and the Greenland Sea (Hansen and Østerhus, 2000). The second is the pressure gradient, which is established by the thermohaline process in the Arctic Mediterranean. There are thought to be three processes: open ocean convection, frontal sinking and shelf convection, which are thought to contribute to the thermohaline forcing (Hansen and Østerhus, 2000). Horizontal pressure and density gradients are set up, which then drive the overflow systems.

1.4.1. Sediments and geology of the Faeroe-Shetland Channel

The Faeroe-Shetland Channel lies between the continental shelf of Scotland and the Faeroese Plateau. To the Northeast the Channel is connected to the Norwegian Sea (Figure 1.1), whilst to the Southwest, it is connected to the Atlantic across the Wyville-Thomson Ridge and through the Faeroe Bank Channel (Turrell *et al.*, 1999). The Faeroe-Shetland Channel is a rift basin that was thought to have formed during the early Mesozoic (Hitchen and Ritchie, 1986). During the late Pleistocene large quantities of glaciogenic material were deposited on the continental slope (Stoker, 1995). Large areas of the seabed (<200 m to 500 m) have plough marks caused by icebergs drifting westwards from what are now the Scottish Highlands during the last ice age. The Channel ranges in depth from approximately 100 m on the continental shelf to over 1500 m in the deepest part. The Wyville-Thomson Ridge has a sill depth of 600 m to 650 m (Ellett and Roberts, 1973) and acts to prevent outflow of cold water from the Faeroe-Shetland Channel into the Rockall Trough (Ellett, 1988). Occasionally water overflows over the Wyville-Thomson Ridge (Ellett and Roberts, 1973; Swift, 1984) and enters the Rockall Trough through the Ymir Channel. The Faeroe Bank Channel, an extension of the Faeroe-Shetland Channel, has a sill depth of 850 m and

serves as an outflow of water from the Channel into the Rockall Trough (Saunders, 1990), as well as into the Iceland Basin (Hansen and Østerhus, 2000).

The sediment types and features found on the West Shetland slope vary with depth. The outer continental shelf (120 m - 200 m) is characterised by 32 main sediment facies (Masson, in press). The two main facies consist of streaks and patches of sand overlying the gravel substratum or are dominated by what are thought to be iceberg plough marks, some of which are overlain by sand (Stoker *et al*, 1993; Masson *et al.*, 1997). Iceberg plough marks dominate the water depths of <200 m to 500 m, many of which have been filled with younger sediments. The region between 500 m and 850 m depth has been classed as the sediment wave zone. Two types have been found, mud waves at shallow water depths e.g. 500 m and sand waves at greater water depths e.g. 800 m (Stoker *et al.*, 1993; Masson *et al.*, 1997). Well-sorted fine sand characterises the 850 m to 1000 m region. The fine sand is several tens of centimetres deep, suggesting that this is a sandy contourite sheet (Masson, in press). Contourite sheets are extensive low-relief accumulations that form part of abyssal basins, or cover parts of the continental margin (Faugères and Stow, 1993). Below 1000 m the sediments are mainly comprised of fine-grained sediments. However, there are many large boulders and stones in this depth range that are of glacial origin.

1.4.2. Hydrography of the Faeroe-Shetland Channel

The Faeroe-Shetland Channel is of historical importance as the area where it was first realised that topography may play an important part in thermal stratification of the ocean (Thomson, 1873).

Until the cruise of the *Lightning* in 1869, it was assumed that the temperature of deep-ocean water remained at a constant 4 °C. The theory was based on the surmise that salt water, like fresh water, has a maximum density at 4 °C (Rice, 1986). However, as early as 1883, Depretz had observed sea temperatures at great depth, which were below the freezing point of fresh water (Thomson, 1873). The Royal Navy made H.M.S. *Lightning* available to C. Wyville Thomson and W. B. Carpenter for a cruise to the northwest of Scotland in 1868 to see whether life existed at great depths. While in the Faeroe-Bank Channel and Faeroe-Shetland Channel, Thomson and Carpenter found that dredgings from depths greater than 300 fathoms (548.4 m) contained a great diversity of fauna, even though this seemed rather sparse in numbers (Thomson, 1873).

It was whilst on this cruise that they made the startling discovery that the deep water was not of a uniform temperature. Deep water sampled south of Tørshavn in the Faeroe Islands was between 0.5 °C and 1.1 °C, whilst water of a similar depth a few hundred kilometres to the south had a temperature of 6.4 °C (Adams, 1995). This was validated by similar results obtained by work carried out on H.M.S. *Porcupine* (Rice, 1986).

The 4 °C theory was clearly contradicted by Thomson and Carpenter's discovery of two bodies of water lying very close together, one warm and the other about 8 °C cooler (Deacon, 1977). Although they hypothesised the existence of a submarine ridge separating the two bodies of water, the idea was resisted as scientists thought the area had been sufficiently well sounded to have detected any topographical high (Deacon, 1977). Thomson then asked for further help from the British Admiralty. He wanted to know if a bathymetric high was controlling the distribution of warm and cold water in the Channel (Adams, 1995). This led to the *Knight Errant*, a paddle steamer, and H.M.S. *Triton* being made available for work in the Faeroe-Shetland Channel in 1880 and 1882 respectively. Lead-line soundings taken on board the *Knight Errant* confirmed that there was indeed a ridge located to the South of the Channel. Thomson and Tizard reasoned that the temperature distribution that occurs in the Faeroe-Shetland Channel must be governed by a topographic high that linked the Faeroes with Shetland (Deacon, 1977). This ridge would prevent the flow of cold Arctic water through the Channel and into the Rockall Trough. However, it is now known that Arctic water does exit to the Atlantic via the Faeroe Bank Channel and also occasionally as an overflow into the northern Rockall Trough (Belkin *et al.*, 1998).

An anonymous report written regarding the expeditions on H.M.S. *Lightning* and *Porcupine* showed, *"that in the channel* [of] *from 600 to 700 fathoms depth which lies between the North of Scotland, the Orkney and Shetland Islands, and the Færoes, there is an upper stratum of which the temperature is considerably higher than the normal of the latitude; whilst there is stratum occupying the lower half of this channel, of which the temperature ranges as low as from 32° to 29.5°* [Fahrenheit]*; and a stratum of intermixture lying between these two in which the temperature rapidly falls as much as 15° in 100 fathoms "* (Anon, 1871 cited in Deacon, 1977).

At the surface there is a Northeast flow of warm, saline water, which separates from the North Atlantic current, flowing through the Faeroe-Shetland Channel, and entering the Nordic Seas. Once in the Nordic Seas two processes cool the warm upper

water; i) the cold atmosphere leads to a transfer of heat from the water (Worthington, 1970), ii) lateral mixing with polar waters (Ellett and Roberts, 1973). This causes the density gradient between the water masses to diminish. Norwegian Sea Deep Water is produced by the formation of vertical convective cells (McCartney and Talley, 1984). At mid-bathyal depths in the Faeroe-Shetland Channel, there is a south-westerly flow of cold water from the Norwegian Sea. Surface water flows in a north-easterly direction over the upper slope and West Shetland Shelf (Emson *et al.*, 1994). Coriolis force affects the pycnocline that forms in the Faeroe-Shetland Channel (Saunders, 1990). Saunders (1990) found that towards the Faeroe shelf the pycnocline tended to slope upwards, although Schlichtholz and Jankowski (1993) found that in some years the pycnocline was almost horizontal.

Up to the early 1980s, four principal water masses had been distinguished in the Faeroe-Shetland Channel (Martin, 1988). These were North Atlantic Water (NAW); Modified North Atlantic Water (MNAW); Arctic Intermediate/North Icelandic Winter Water (AI/NIW) and Norwegian Sea Deep Water (NSDW), or what is now known as Faeroe-Shetland Channel Bottom Water (FSCBW) (Figure 1.2). In the Faeroe-Shetland Channel, the flow from the Atlantic and that of the Faeroe current converge (Hansen, 1985). In both these currents, the upper layers consist mainly of Modified North Atlantic Water (MNAW). It was only when temperature and salinity measurements were made in 1981 that an anomaly was found. It was then realised that there was a fifth water mass that had not been previously detected (Martin, 1993). This water mass is what is now known as Norwegian Sea Arctic Intermediate Water (NSAIW). Prior to 1960, NSAIW was evident as a salinity minimum. The period 1960-1980, however, saw this minimum disappear. In the 1980s this minimum re-appeared.

1.4.2.1. North Atlantic Water (NAW)

NAW occupies the surface (0 – 300 m) layer of the Channel. It is a warm and saline water mass (Figure 1.3) that originates south of the Rockall Trough. It flows northwards though the Faeroe-Shetland Channel and is confined to the Scottish slopes (Figure 1.2) (Hill and Mitchelson-Jacob, 1993).

1.4.2.2. Modified North Atlantic Water (MNAW)

MNAW occupies the rest of the surface (0 – 400 m) layer of the Channel and covers a greater area in comparison to NAW (Dooley and Meincke, 1981). It is colder

and less saline in comparison to NAW (Figure 1.3). This indicates that its path to the Faeroe-Shetland Channel is more northerly than that of NAW. It flows to the North around the Faeroe Islands (Figure 1.2) in an anticyclonic direction (Becker and Hansen, 1988).

1.4.2.3. Arctic Intermediate/North Icelandic Winter Water (AI/NIW)

AI/NIW lies directly below MNAW, occupying a depth of 300 m – 600 m. It is formed from a combination of two water masses, Arctic Intermediate Water and North Icelandic Winter Water that are mixed on the Iceland- Faeroe Ridge (Dooley *et al.*, 1984). The East Icelandic Current brings AI/NIW to the North of the Faeroes (Meincke, 1978), then circulates clockwise round the Faeroese plateau before arriving in the Faeroe-Shetland Channel. AI/NIW is mainly found on the Faeroese side of the Channel (Figure 1.3); on the Scottish side it is found between 550 m and 600 m. Most of the AI/NIW is re-circulated in the Faeroe-Shetland Channel and little escapes (Becker and Hansen, 1988). The range of temperature and salinity values of this water mass is quite considerable (Figure 1.3 and Table 1.1).

1.4.2.4. Norwegian Sea Arctic Intermediate Water (NSAIW)

NSAIW is the second intermediate water mass found in the Faeroe-Shetland Channel. However, it is found slightly deeper than AI/NIW, occupying a depth range of 600 m - 800 m (Figure 1.4). NSAIW was only discovered in the early 1980s (Martin, 1988; Martin, 1993) owing to the presence of a salinity minimum on a temperature-salinity diagram at a temperature of almost zero and salinity of 34.89 (Mowatt *et al.*, 1997). In the previous twenty years, the intermediate waters had salinity values that were greater than those of the bottom water (Turrell *et al.*, 1999). Like the AI/NIW, NSAIW is found to be much shallower on the Scottish slope and occasionally does not reach the slope at all (Turrell *et al.*, 1999). This sloping up of deep water towards the Faeroes is a result of the Coriolis force (Schlichtholz and Jankowski, 1993). NSAIW originates as surface water in the Greenland and Iceland seas (Blindheim, 1990). It becomes intermediate water owing to subduction at the Arctic front. It flows South between the NSDW and the warmer saline waters from the Atlantic (Blindheim, 1990).

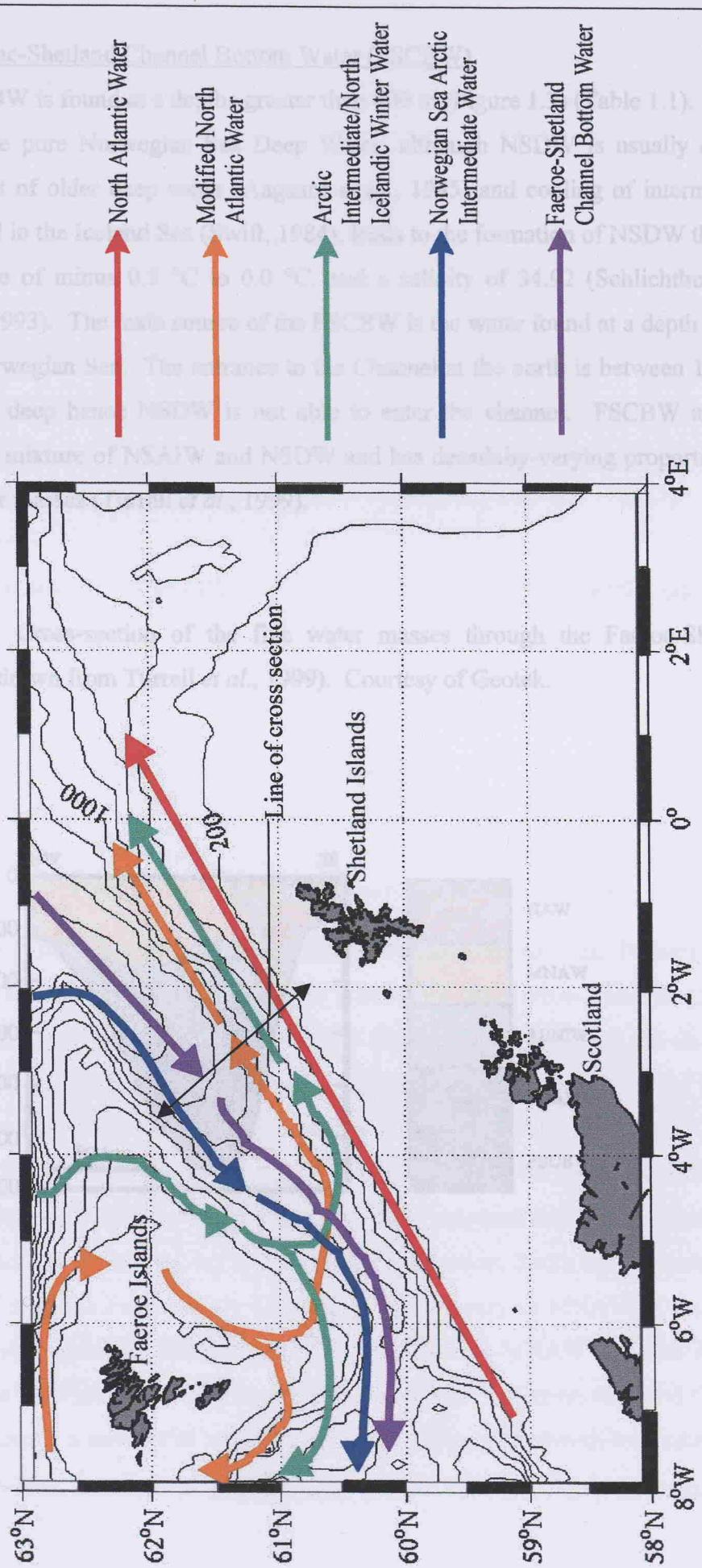


Figure 1.2. Summary of the flow of water masses to the North and West of Scotland. Warm North Atlantic Water flowing in a north-easterly direction, colder Norwegian Sea Water flowing in a south-westerly direction (re-drawn from Turrell *et al.*, 1999).

1.4.2.5. Faeroe-Shetland Channel Bottom Water (FSCBW)

FSCBW is found at a depths greater than 600 m (Figure 1.3) (Table 1.1). It was thought to be pure Norwegian Sea Deep Water, although NSDW is usually colder. Displacement of older deep water (Aagaard *et al.*, 1985) and cooling of intermediate water formed in the Iceland Sea (Swift, 1984), leads to the formation of NSDW that has a temperature of minus 0.5 °C to 0.0 °C, and a salinity of 34.92 (Schlichtholz and Jankowski, 1993). The main source of the FSCBW is the water found at a depth of 800 m in the Norwegian Sea. The entrance to the Channel at the north is between 1500 m and 2000 m deep hence NSDW is not able to enter the channel. FSCBW actually consists of a mixture of NSAIW and NSDW and has decadally-varying proportions of the two water masses (Turrell *et al.*, 1999).

Figure 1.3. Cross-section of the five water masses through the Faeroe-Shetland Channel (re-drawn from Turrell *et al.*, 1999). Courtesy of Geotek.

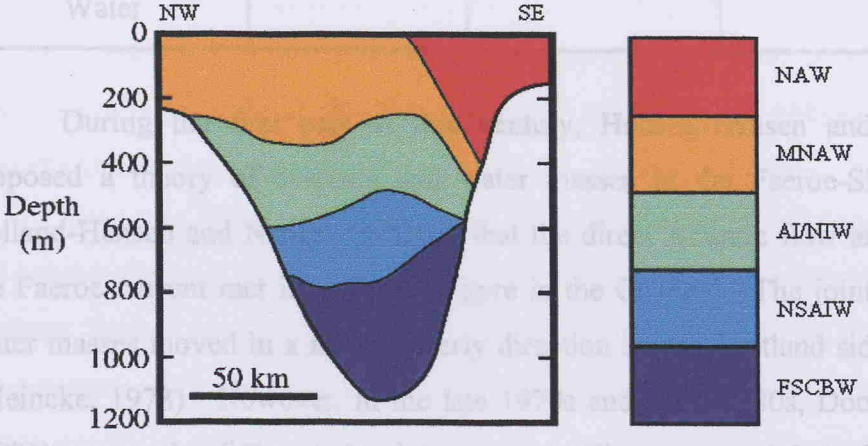


Table 1.1. Properties of the water masses found in the Faeroe-Shetland Channel.

Water Mass	Abbreviation	Temperature °C	Salinity	Depth (m)
Surface				
North Atlantic Water	NAW	>9	35.25 – 35.35	0 – 300
Modified North Atlantic Water	MNAW	6.5 – 9	35.1 –35.3	0 – 400
Intermediate				
Arctic Intermediate/North Icelandic Winter Water	AI/NIW	1 – 4	34.76 – 34.99	300 –600
Norwegian Sea Arctic Intermediate Water	NSAIW	0 – 2	34.89 – 34.90	600 – 800
Deep				
Faeroe-Shetland Channel Bottom Water	FSCBW	-0.5	34.92	>600

During the first part of this century, Helland-Hansen and Nansen (1909) proposed a theory of currents and water masses in the Faeroe-Shetland Channel. Helland-Hansen and Nansen believed that the direct Atlantic flow and the flow from the Faeroe current met in a cyclonic gyre in the Channel. The joint flow of the two water masses moved in a north-easterly direction on the Shetland side of the Channel (Meincke, 1978). However, in the late 1970s and early 1980s, Dooley and Meincke (1981) proposed a different circulatory pattern. They proposed that of the upper part of the Faeroe current about half moved in a westerly direction, South of the Faeroes, and then flowed over the Faeroe Bank Channel. The discovery of MNAW in the Faeroe Bank Channel supported Dooley and Meincke's theory, as MNAW was also found to be present in the Faeroe-Shetland Channel. However, in the Faeroe-Shetland Channel, the upper water is a mixture of MNAW and Arctic Intermediate/North Icelandic Winter (AI/NIW), whilst the upper part of the Faeroe Bank Channel consists of almost pure

MNAW (Hansen, 1985). The original description of the circulation scheme in the Faeroe-Shetland Channel by Helland-Hansen and Nansen in 1909 is now generally accepted.

It is only at depth that the convergence zone of the two water masses containing MNAW becomes apparent. As depth increases, the percentage of AI/NIW present also increases, and a definite front appears as shown on temperature/salinity charts. The dominance of a particular water mass can affect the temperature front quite considerably (Hansen 1985). Hansen (1985) reported that the East Icelandic current was the prevailing current. However, a year later this was no longer the case, the current was weaker, and the front, which had been located at a depth of 400 m the previous year, was more diffuse and had moved further to the East.

1.5. THE INFLUENCE OF TEMPERATURE ON BENTHIC FAUNA

Benthic communities are influenced by many physical and chemical factors including oxygen concentration (Svarda and Botjet, 1991), current intensity (Warwick and Uncles, 1980), tidal variation (Gould and McKee, 1973), sediment type (Rhoads, 1974) and salinity (Rosenberg and Moller, 1979). The effect of temperature, however, is often neglected in ecological studies. This was a concern voiced by Hedgpeth (1957), " *For some reason ecologists have not as yet paid as much attention to the temperature as a factor in the major divisions of the oceans, although it is of primary concern to biogeography.*"

However, the first investigations of the biogeography of benthic invertebrates did suggest that one of the main factors influencing distribution was temperature. Many workers have suggested that faunal depth-related distribution is a result of the temperature structure of the oceans, and that the boundaries between the zoogeographical regions follow underwater ridges and other elevations (Vinogradova, 1959). This theory was supported by findings from the Danish '*Galathea*' expedition (Wolff, 1962; Millar, 1970). There have been many conflicting arguments with regards to definition of faunal zones. Since species tend to have depth-related distributions, thought to be dependent on the special hydrodynamic and ecological features of each geographical region (Menzies *et al.*, 1973) it is difficult to outline specific faunal regions. In fact, Menzies (1965) implied that the abyssal fauna was located at different depths in different parts of the world.

From Le Danois studying the vertical distribution of the benthos off the coast of France, to the Russian workers investigating the zoogeographic regions of deep-sea populations (Sokolova, 1972), there were a number of common themes to these investigations. These implied that biological distributions were aligned with latitudinal climatic belts (Carney *et al.*, 1983) and that temperature was the prime factor influencing faunal distribution (Westerberg, 1990). Horizontal distribution circles the globe in latitudinal bands, which follow the isotherms (Carney *et al.*, 1983). The temperature gradient that occurs geographically is quite shallow thus many species are widespread horizontally.

Molander (1930) was one of the first to introduce temperature as a factor in the classification of communities. This concept was used by Glémarec (1973) who was able to isolate three communities, based on sediment type and faunal zonation, on the North Gascony continental shelf. Glémarec found that he was able to define each étage (def. tier.)* by the variation in temperature between the surface water and the near-bottom water. Glémarec (1973) also argued that near bottom thermal stability was of great physical importance in determining the composition of benthic communities.

Ekman (1953) noted how fauna, characteristic of the deep-sea to abyssal depths, could also be found in relatively shallow polar seas. Thus it is difficult to put an upper limit on the boundary between deep-sea fauna and shallow water fauna (Ekman, 1953). The Antarctic continent is a good example where there may be no apparent difference between the fauna found in deeper waters and those found at shallower depths (Menzies *et al.*, 1973). Fauna of the continental shelf bathed by polar seas is similar to the fauna found in bathyal zones (Menzies *et al.*, 1973). Ekman used the term Equatorial Submergence to describe this trend. Studies carried out on submarine caves have found they share several ecological features with deep-sea habitats e.g. light is absent which leads to no photosynthetic production, flux of organic matter is low (Ott and Svoboda, 1967; Reiswig, 1981; Fichez, 1990). Recently, Vacelet *et al.* (1994) discovered hexactinellid sponges inhabiting a Mediterranean marine cave. The fauna of the cave strikingly resembled the fauna of the deep Mediterranean Sea, which included a family of deep-sea invertebrates. The water temperature in the cave was

* (See Glémarec, 1973 for reasons why étage has not been translated into English)

cold and had smaller fluctuations in temperature in comparison to external water (Vacelet *et al.*, 1994).

The greatest vertical changes in temperature, salinity and oxygen concentration occur within the top 1000 m of the ocean. Theoretically, the effects of these factors on faunal distribution should be restricted to these depths and above (Carney *et al.*, 1983). However, increased knowledge of the effect of pressure on the metabolic reactions of the fauna, has led to the belief that below 1000 m, physical factors can still influence faunal zonation (Siebenaller and Somero, 1978).

Interest in faunal zonation grew prior to the Second World War. Le Danois (1948) was the first to suggest that the vertical zonation of benthic fauna was related to variations in physiography and sediment type at different depths. As technology advanced, other physical factors were found to influence faunal distributions in the deep sea. One in particular was the link between specific water masses and the benthic fauna found in those regions (Marshall, 1979). For example, species of *Ophiocten* were thought to be closely related to the hydrography of the main water masses in the North Atlantic (Paterson *et al.*, 1982). Tyler and Zibrowius (1992) interpreted that the vertical zonation of suspension feeders corresponded with water mass structure on the steep slopes to the west of the Goban Spur and Porcupine Bank. However, other factors that are not intrinsic properties of the water mass itself such as currents and suspended material may be the real controlling factors.

1.6. INVESTIGATIONS UNDERTAKEN IN THE FAEROE-SHETLAND CHANNEL

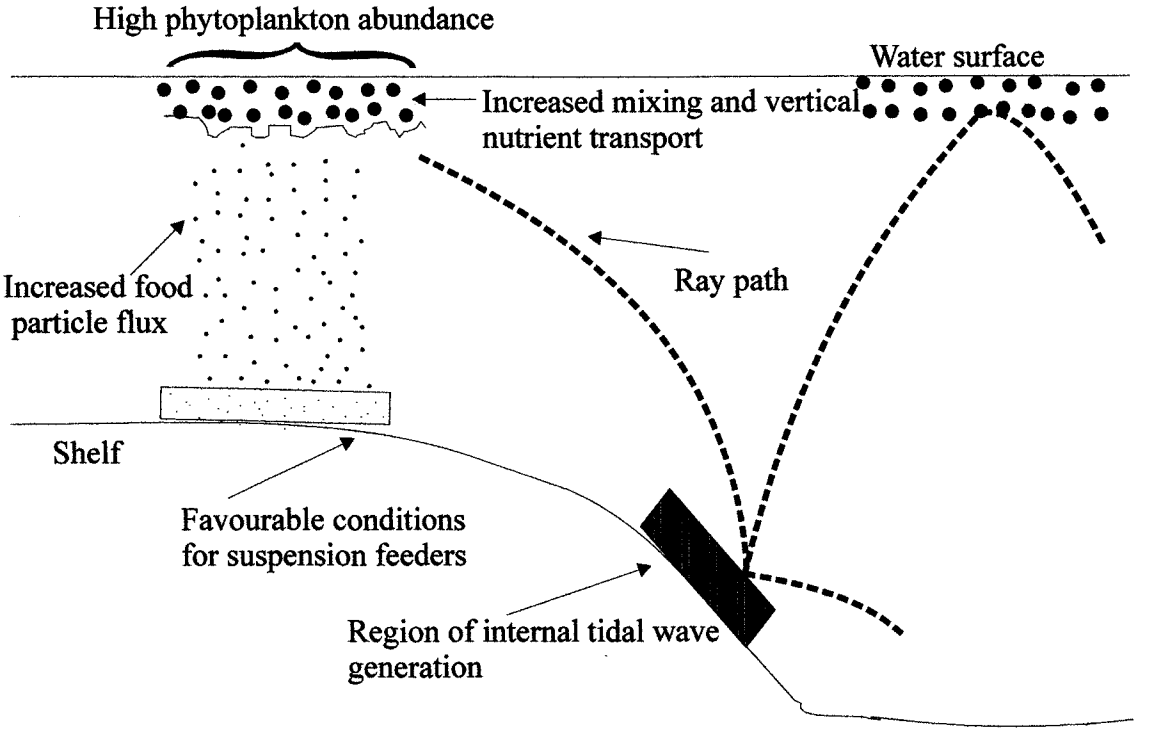
The Aberdeen Marine Laboratory in Scotland has maintained a programme of sampling along two hydrographic sections in the Faeroe-Shetland Channel. This work was started by H. N. Dickson on board HMS *Jackal* in 1893 (Adams, 1995). Dickson took water casts along the two sections now known as the Fair Isle-Munken line and the Nolso-Flugga line. These stations have been regularly sampled, approximately three times a year since the beginning of the 1900s except during World War II, and a period at the beginning of the 1980s (Turrell *et al.*, 1996). This established sampling regime has provided detailed information about long-term changes of temperature and salinity occurring in the Channel. An example of this is the re-appearance of the Norwegian Sea/Arctic Intermediate Water in the Channel (see page 15).

The Nordic Council for Marine Biology established a benthic faunal sampling programme around the Faeroes known as the Benthic BIOlogy of the FARoe islands (BIOFAR) programme. Emson *et al.*, (1994) studied the distribution of bathyal ophiuroids around the Faeroe Islands. They found that many of the ophiuroids were 'warm water' species, thus originating from the North Atlantic Surface Water. The 'cold water' species, of which few individuals were found, occur in waters that originate from the Norwegian Sea and flow South through the Faeroe-Shetland Channel as a cold current (Mortensen, 1927; 1933). There are transitional zones instead of sharply demarcated vertical distribution boundaries (Madsen, 1961). One species of ophiuroid, *Ophiacantha bidentata*, appears to have two varieties; one found in warm water and the other in cold water (Mortensen, 1927; Emson *et al.*, 1994). Evidence for this separation comes about from the reproductive biology of the two forms. *Ophiacantha fraterna*, the warm water variety, is found to be a protandric hermaphrodite, whereas *O. bidentata*, the cold water variety, is dioecious (Tyler and Gage, 1982). From the data available, it appears that the Faeroes straddle a major biogeographic boundary (Emson *et al.*, 1994).

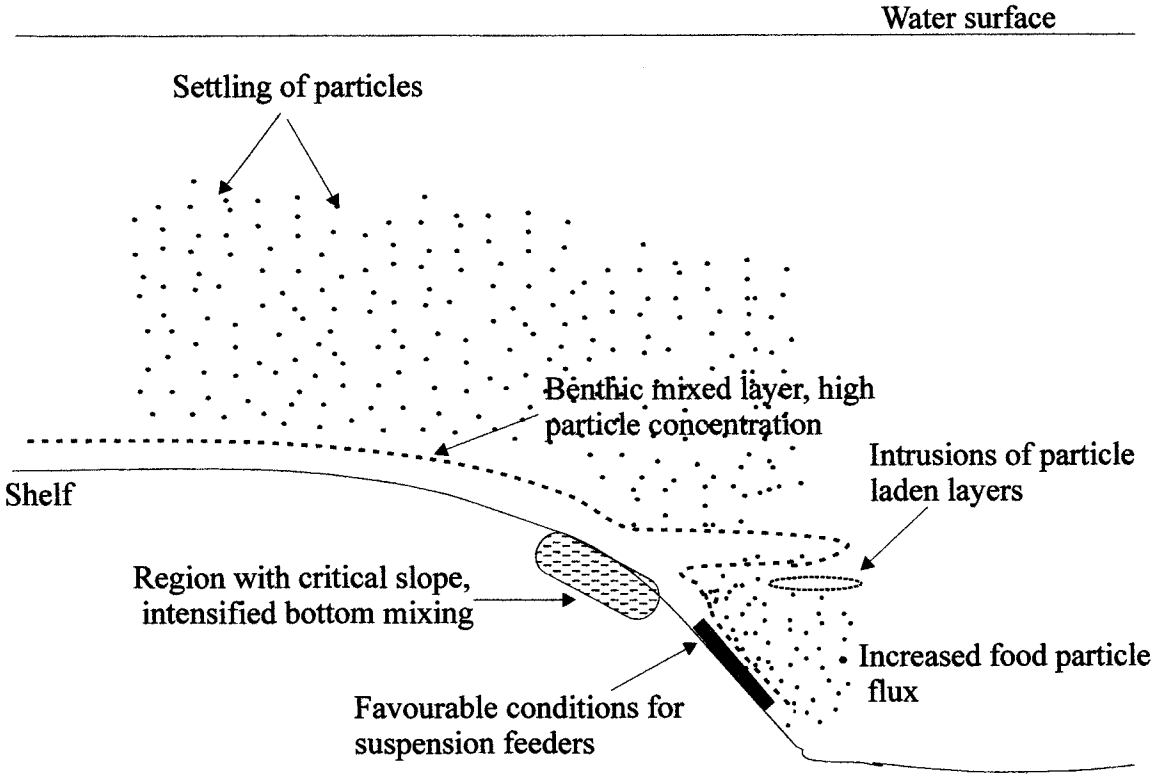
Within the BIOFAR programme, Klitgaard *et al.* (1995) described the characteristics, distribution and possible causes for aggregations of large sponges around the Faeroe Island shelf and slope region. They concluded that areas with *ostur*, (defined as a restricted area where large demospongid sponges are extremely common) were to be found in narrow bands close to, and parallel to, the shelf break in many places. These zones were North, South, East and West of the Faeroes and Northeast and Southeast along the Faeroe bank. Westerberg (1990) and Nørrevang *et al.* (1994) found that areas on the Southeast shelf, which had large aggregations of *ostur*, were mainly covered by warm (6.5 °C - 7.9 °C) Atlantic water. However, on the northern and western shelf slopes, although large clusters of *ostur* were found, the water mass was a mixture of cooler (5.0 °C - 6.8 °C) NI/AIW and Atlantic water. In regions where the water temperature was less than 5 °C, few specimens of the five main large sponge species were found. A second factor that is thought to affect the distribution of the benthic fauna, such as sponges, is the propagation of internal tidal waves (Klitgaard *et al.*, 1995). Internal waves are propagated along ray paths (Figure 1.4a) determined by stratification, with one wave deflected towards and one away from the shelf once the initial wave comes up against the slope (Frederiksen *et al.*, 1992).

Figures 1.2a,b. Two mechanisms for the increase in food particle flux to the benthos (re-drawn from Klitgaard et al. 1995)

1.2a. Increased particle flux at the shelf edge as a result of propagation of internal waves



1.2b. Increase in particle flux as a result of an intensification of bottom water mixing in areas with a critical slope



Where the returning waves reach the thermocline, vertical mixing is enhanced, thus creating two nutrient rich bands either side of the shelf break (Klitgaard *et al.*, 1995). This process is also thought to occur on the Faeroes shelf. The increase in detrital flux is thought to encourage development of sponge and cold-water coral populations. In deeper water areas on the slope an increase in the intensity of the local mixing leads to particle re-suspension (Figure 1.4b) (Wunsch, 1968; Cacchione and Wunsch, 1974).

Tongue-like extrusions containing particles form because of the formation of horizontal density gradients between the benthic mixed layer and the stratified water (Dickson and McCave, 1986; Thorpe *et al.*, 1990). The decrease in turbulence leads to particles falling out of suspension, thus enhancing the conditions for filter feeders further down slope. However, the nutritional value of these re-suspended particles to the benthic filter feeders depends on its quality of organic matter (Thomsen and van Weering, 1998).

1.7 BACKGROUND TO SAMPLING BY THE OIL/GAS INDUSTRY IN THE FAEROE-SHETLAND CHANNEL

The decision to survey and sample the seabed to the Northwest of Scotland (Atlantic Frontier region) arose at the time when discussions for the U. K. 16th round of oil licensing were being held (Hugget and Francis, 2000). Exploration of the continental shelf to the North of Scotland began in the 1970s, the first well being drilled in 1972 and Clair, the first field located in 1977. In 1992, BP discovered the Foinaven field to the Southwest of the Clair field. Baseline environmental data were required from the Atlantic Frontier region. However, the unusual hydrographic conditions posed problems in meeting existing survey protocols (Hugget and Francis, 2000). The Atlantic Frontier Environmental Network (AFEN), a consortium of 22 oil and gas companies, the Joint Nature Conservation Committee (JNCC), the Fisheries Research Services (FRS) and the Department of Trade and Industry (DTI) commissioned surveys of the Atlantic Frontier in 1996 and 1998. The aim was to describe the benthic environment of the Atlantic Margin. A regional seabed survey was identified as the means of providing the data required. This seabed survey design constituted mapping the seabed by using sidescan sonar followed by seabed sediment sampling. The main aim was to provide a baseline environmental assessment of seabed

areas in deep water on the continental margin, licensed for oil and gas exploration. This activity is furthest advanced in the Faeroe-Shetland Channel.

The survey conducted in 1996 was based on a stratified random sampling design (Cochran, 1953; Green, 1979; Bett, 1997), whilst the 1998 study, although similar, was mainly to collect samples specifically from deep water areas in the 17th round tranches to the North and West of Scotland (Bett, 1999). Emphasis was placed on assessing the range of variation throughout the region and not to concentrate sampling effort on any specific location (Bett, 1997; 1999).

A secondary objective was to sample along a depth-related transect at one location on the West Shetland Slope (Bett, 1997). The present study is based on the samples obtained along this transect.

1.8 STUDY AIMS

The principal aim of this study was to investigate the effects of a suite of environmental parameters on the benthic fauna along a depth gradient. A variety of uni- and multivariate analyses were used in an attempt to determine which specific or suite of environmental parameters had the most impact on influencing faunal abundance, biomass, diversity and composition. Other aims included

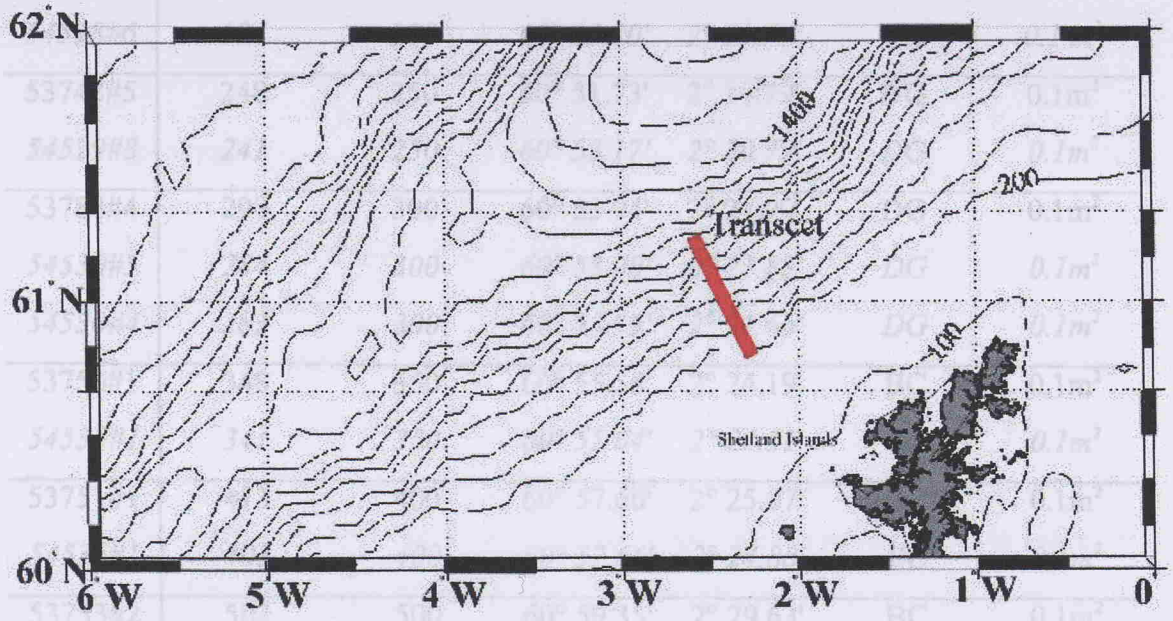
- determining which species were dominant,
- whether there were changes in species dominance with increasing depth and
- were these changes actually depth related or related to other environmental variables.

MATERIALS AND METHODS

2.1 STUDY AREA

Samples were collected along a depth transect on the West Shetland Slope (Figure 2.1) during R.R.S. *Charles Darwin* cruise 101C leg 2 in July 1996 (Bett, 1997; 2000) and cruise 112C in May 1998 (Bett, 1999; 2000). Fifteen stations were sampled at depths ranging from 150 m to 1000 m (Table 2.1).

Figure 2.1. The bathymetric transect that was sampled in 1996 and 1998



2.2 SAMPLING APPARATUS

Three pieces of sampling apparatus were used: a Megacorer, based on a concept similar to that of a multiple corer (see Barnett *et al.*, 1984), a modified USNEL Box core (Hessler and Jumars, 1974) and a Day grab (Holme and McIntyre, 1984). The three different sampling devices were used to cope with varying sediment types. The Megacorer was used in preference to the Box core, as the Megacorer is designed to minimise disturbance of sediments at the sediment water interface (Bett *et al.*, 1994). The Megacorer was used at the deeper stations where the sediment was very fine, the Box core for intermediate depths, as it can penetrate further into the sediment compared to the Megacorer, and the Day grab for the shallowest stations containing mainly sand-sized particles not retained by the Megacorer or Box core.

Table 2.1. Station list for Day grab (DG), Box corer (BC) and Megacorer (MC) deployments along the bathymetric transect in the Faeroe-Shetland Channel. Normal text indicates stations worked in 1996, whilst stations worked in 1998 are italicised.

Station	Actual depth (m)	Target depth (m)	Position N	Position W	Equipment	Area Sampled
53746#4	133	150	60° 49.45'	2° 20.01'	DG	0.1 m^2
54527#3	*126*	*150*	*60° 49.36'*	*2° 20.01'*	*DG*	*0.1 m^2*
53747#6	202	200	60° 52.36'	2° 19.58'	DG	0.1 m^2
54528#6	*194*	*200*	*60° 52.30'*	*2° 19.56'*	*DG*	*0.1 m^2*
53748#5	248	250	60° 51.73'	2° 20.79'	DG	0.1m^2
54529#8	*241*	*250*	*60° 53.17'*	*2° 20.72'*	*DG*	*0.1m^2*
53784#4	290	300	60° 53.94'	2° 21.90'	DG	0.1m^2
54530#3	*284*	*300*	*60° 53.90'*	*2° 21.88'*	*DG*	*0.1m^2*
54530#4	*283*	*300*	*60° 53.95'*	*2° 21.66'*	*DG*	*0.1m^2*
53750#1	348	350	60° 55.58'	2° 24.19'	BC	0.1m^2
54535#1	*341*	*350*	*60° 55.64'*	*2° 24.11'*	*BC*	*0.1m^2*
53751#1	413	400	60° 57.66'	2° 25.07'	BC	0.1m^2
54536#1	*403*	*400*	*60° 57.66'*	*2° 24.88'*	*BC*	*0.1m^2*
53753#2	502	500	60° 59.35'	2° 29.63'	BC	0.1m^2
54538#4	*492*	*500*	*60° 59.43'*	*2° 29.21'*	*BC*	*0.1m^2*
53764#2	552	550	61° 09.74'	2° 31.90'	MC	0.063m^2
54539#1	*539*	*550*	*61° 01.21'*	*2° 30.82'*	*MC*	*0.039m^2*
54539#2	*539*	*550*	*61° 00.96'*	*2° 31.52'*	*MC*	*0.024m^2*
53767#2	601	600	61° 25.53'	2° 33.97'	MC	0.063m^2
54540#1	*588*	*600*	*61° 02.74'*	*2° 33.89'*	MC	*0.008m^2*
54540#2	*590*	*600*	*61° 02.93'*	*2° 34.09'*	*MC*	*0.055m^2*
53765#2	650	650	61° 45.48'	2° 36.79'	MC	0.063m^2
54541#1	*638*	*650*	*61° 04.49'*	*2° 36.81'*	*MC*	*0.063m^2*
53766#2	709	700	61° 55.68'	2° 40.95'	MC	0.063m^2
54542#1	*695*	*700*	*61° 05.54'*	*2° 40.96'*	*MC*	*0.063m^2*

.....continued

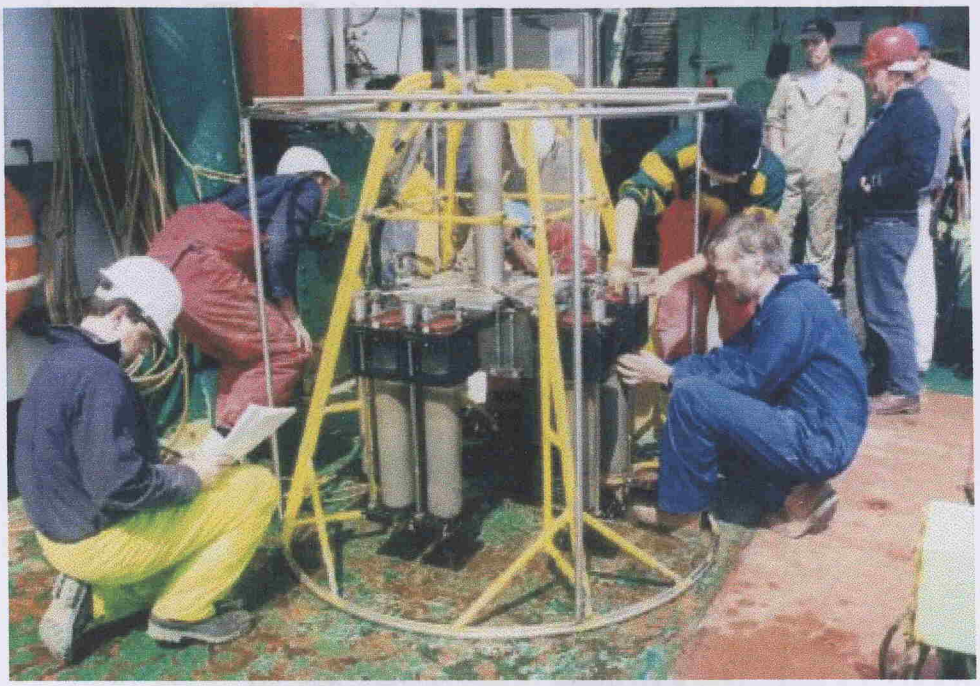
.....continued

Station	Actual depth (m)	Target depth (m)	Position N	Position W	Equipment	Area Sampled
53769#1	804	800	61° 08.03'	2° 41.77'	MC	0.063m^2
54543#1	*790*	*800*	*61° 08.11'*	*2° 41.67'*	*MC*	*0.063m^2*
53770#2	919	900	61° 09.59'	2° 44.02'	MC	0.063m^2
54544#1	*918*	*900*	61° 09.75'	*2° 44.49'*	*MC*	*0.063m^2*
53771#2	998	1000	61° 10.51'	2° 45.28'	MC	0.063m^2
54545#1	*985*	*1000*	*61° 10.49'*	*2° 45.94'*	*MC*	*0.063m^2*

2.2.1. Megacorer

The Megacorer (Figure 2.2) is equipped with up to 12 cores, each with an internal diameter of 10 cm. For a biological sample, eight cores were pooled to give a total sample size of 0.063 m^2. Occasionally less than eight full cores were recovered from an individual deployment. In these situations, the full cores were removed and kept and the Megacorer was re-deployed. If eight cores were not collected from the second deployment, the best cores from the two deployments were pooled to make up the full complement of eight required. For the macrofaunal samples, each core length was measured and any descriptive notes of the sediment surface and profile, visible through the transparent walls of the tube were recorded. To accept an individual core, the following criteria had to be met: i) that the core was greater than 10 cm in length; ii) that the surface of the core was essentially level, and iii) that the sediment water interface was intact. Once accepted, the overlying water was siphoned off and retained with the 0-5 cm sample. The cores were extruded by using a plunger from below (Figure 2.3) and sectioned into two horizons, 0-5 cm and 5-10 cm.

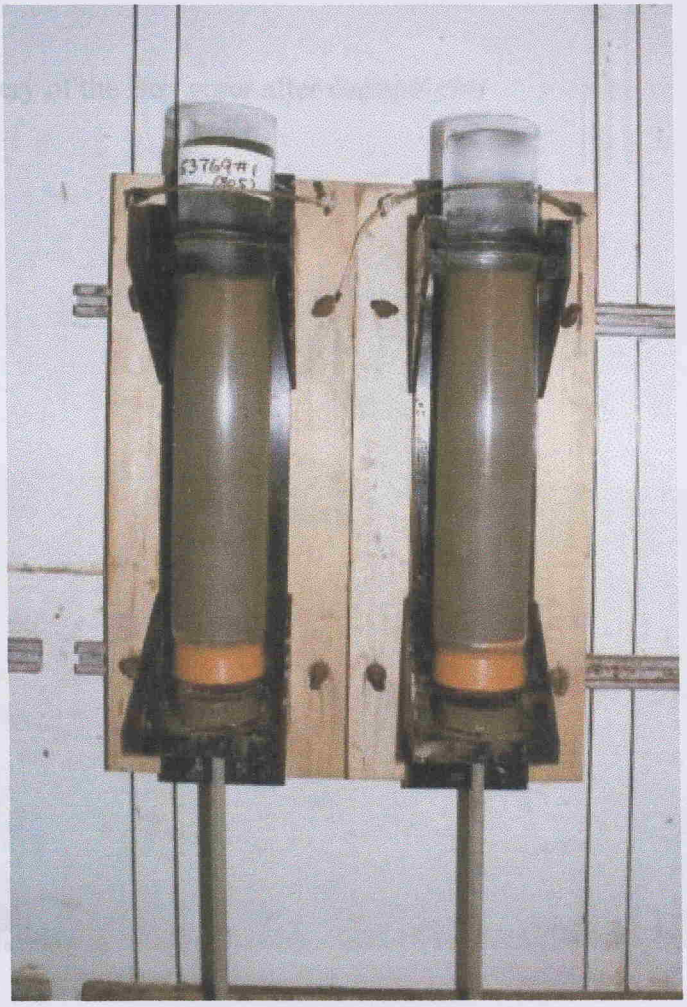
Figure 2.2. Notes and measurements of cores being made prior to removal from the Megacore frame



Each fraction was washed through stacked 500 µm and 250 µm sieve meshes. This was to enable a link to be formed between protocols employed in deep-sea and shallow water studies (Bachelet, 1990; Gage and Tyler, 1991; SCOR, 1994). The four resultant fractions (0-5 cm, 500 µm; 0-5 cm, 250 µm; 5-10 cm, 500 µm; 5-10 cm, 250 µm) were preserved in 10% borax buffered formalin in filtered seawater.

Cores used to obtain samples for hydrocarbon analysis were collected by extruding the core into a metal collar. The top 2 cm horizon was sectioned off, the samples were stored in pre-cleaned glass pots and frozen at –20 °C. Samples for particle size analysis were collected in the same way as for hydrocarbon analysis. However, samples were extruded into a polycarbonate collar and sectioned at the 5 cm horizon. Samples were preserved, in polythene bags, and frozen at –20 °C. Samples for heavy metal analysis were collected in the same way as for particle size analysis but cores were sectioned at the 2 cm horizon. Samples were stored in pre-cleaned polycarbonate pots and once again frozen at –20 °C.

Figure 2.3. Cores affixed to the wall ready for extraction by using the plunger below (photograph courtesy of Brian Bett)



2.2.2. Box corer

Cores from the Box corer (Figure 2.4) were accepted on criteria similar to those used for accepting a mega core. Metal inserts (Figure 2.5) were used to divide up the box core as sub-samples for biology, geology and chemistry were taken from the same core.

It had been decided by the contracting parties that an area of $0.1m^2$ would be used for the biological sample, thus allowing both biological and geological samples to be taken from the same Box core. The overlying water in the sub-core was siphoned off and passed through a 250 μm sieve, and later added to the 0-5 cm fraction. The surface of the sub-core was examined and notes made on any features or fauna found.

of the Box core was removed and the $0.1m^2$ area was sectioned into the 0-5 cm and 5-10 cm fractions. As for the Megacorer, the fractions were sieved through the 500 µm and 250 µm stacked sieve meshes. The four resultant fractions were dealt with in the same way as samples collected from the Megacorer.

Figure 2.4. Recovery of the Box corer after deployment

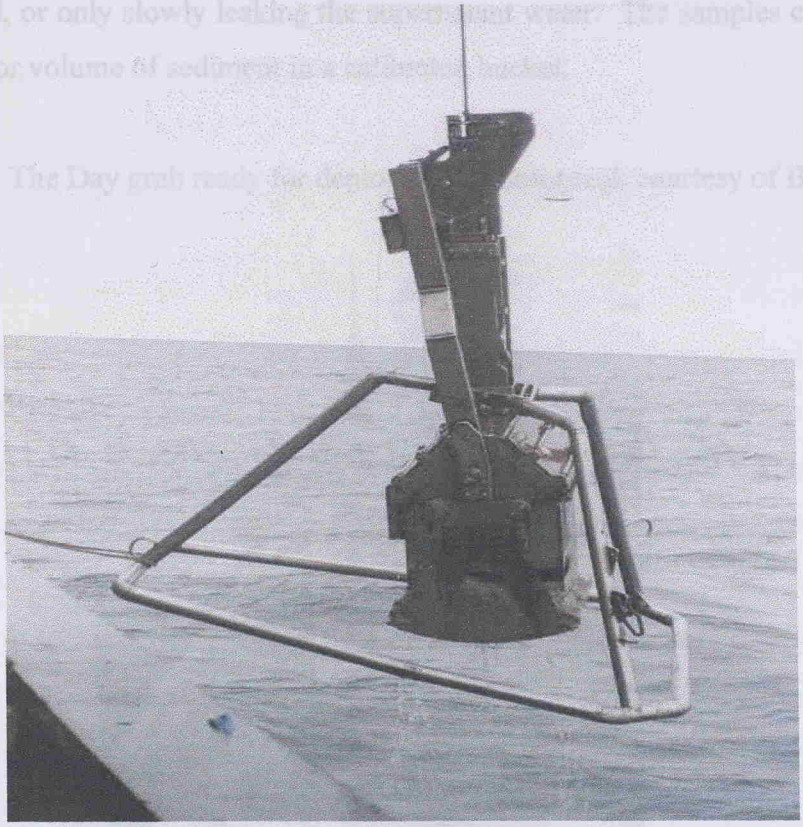
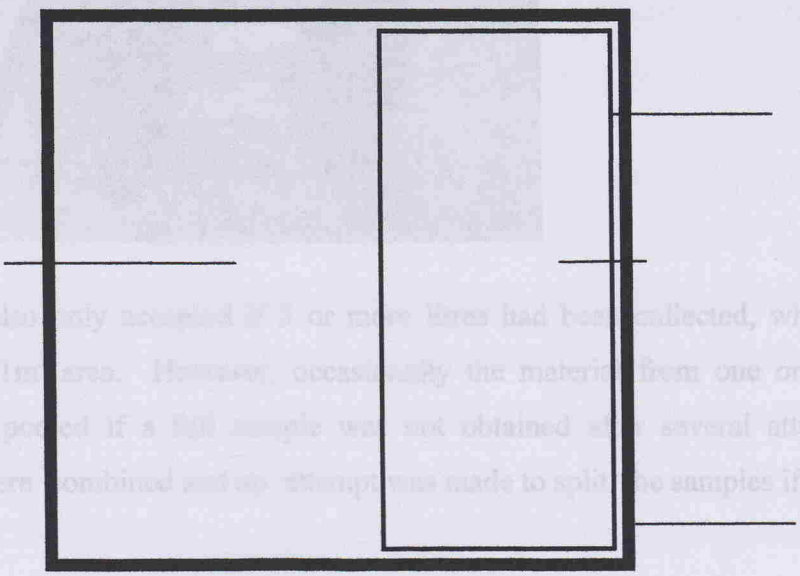


Figure 2.5. Plan of inserts used for separation of macrobenthic and chemical samples in the Box corer.



Samples for hydrocarbon, particle size and heavy metal analyses were collected and stored in the same way as for the Megacorer.

2.2.3. Day grab

The contents of the Day grab (Figure 2.6) were only accepted if the grab was fully closed, or only slowly leaking the supernatant water. The samples collected were measured for volume of sediment in a calibrated bucket.

Figure 2.6. The Day grab ready for deployment (photograph courtesy of Brian Bett)

The sample was also only accepted if 5 or more litres had been collected, which is equivalent to a $0.1m^2$ area. However, occasionally the material from one or more deployments was pooled if a full sample was not obtained after several attempts. Whole samples were combined and no attempt was made to split the samples if there

was more than 5 litres in total. The grab is likely to fail if coarse stones are caught in the jaws, thus causing loss of sediment (Tyler and Shackley, 1978). The samples were elutriated through two stacked sieves of mesh size 500 μm and 250 μm. The two fractions were preserved in the same way as samples collected from the Box corer and Megacorer. The particle size, hydrocarbon and heavy metal samples were collected in a similar manner as for the Box corer and Megacorer.

2.3. LABORATORY METHODS

2.3.1 Macrobenthos sorting

The >500 μm size fraction was sorted by the environmental consultancy group, Cordah Ltd. of Edinburgh, formerly OPRU Environmental Science and Interpretation (OPRU), Pembroke (Baker, 1998). The 250 μm-to-500 μm size fraction was sorted by myself. Prior to sorting, every sample had 1g l^{-1} of Rose Bengal added, to aid in the sorting of specimens. Each sample was thoroughly washed to remove any traces of formalin and fine particles and then stored in a mixture of 70% ethanol and 1% glycol.

Two techniques were used to sort the macrofauna depending on the size fraction. The >500 μm size fraction was sorted using the following technique:
Each sample was sub-sampled. The sub-sample was evenly distributed on a flooded white tray and sorted using an illuminated bench magnifier (Baker, 1998; Bett, 2000). The original sample was continuously sub-sampled until none of the original fraction remained. The fauna was separated into five major groups: annelids, molluscs, crustaceans, echinoderms and others. The various taxa from each sample were counted and stored in vials containing 70-80% alcohol. Approximately 10% of the samples were re-sorted as a quality control check.

The 250 μm-to-500 μm size fraction was sorted using a flotation technique. The sample was re-washed and small fractions were added to a solution of Ludox™ (colloidal silica). The mixture was gently stirred and left to settle for approximately 20 minutes. This technique is generally used for meiofauna (McIntyre and Warwick, 1984). However, the organisms in the 250 μm-to-500 μm fraction were sufficiently small for this flotation technique to be used successfully. The Ludox plus macrofauna was gently poured through a 250 μm sieve ensuring that the sediment remained in the

pot. The Ludox was collected and re-used, and the macrofauna gently rinsed and poured onto a sorting tray. The process was repeated until no more macrofauna appeared in three consecutive extractions. Five residue samples were re-sorted as a quality control check. The macrofauna was sorted using a WILD M5 binocular microscope (12 x 10 mag.) and once again separated into five major groups. Nematodes, harpacticoid copepods and ostracods were not counted (even though large numbers were retained on the 250 μm sieve) as they are regarded as part of the taxonomic meiofauna (Sanders *et al.*, 1965; Hessler and Jumars, 1974; Desbruyères *et al.*, 1980; Gage and Tyler, 1991). Often only fragments of animals were present in the sample. In these cases only those fragments with a recognisable anterior end were counted. All identifiable fragments were removed to give complete values of biomass for each taxonomic group. Unidentifiable fragments were removed and labelled as 'Residue'.

2.3.2. Taxonomic Identification

The macrofauna was identified to species level or putative species level where possible. Table 2.2 indicates which groups have been identified to which taxonomic level. The group labelled 'Others' has not been identified at all.

Table 2.2. Level of taxonomic identification (Ph. – Phylum; Or. – Order; F. – Family; G. - Genus; Sp. – Species; X – identified; — - not identified)

	>500 μm					250 μm to 500 μm				
	Ph.	Or.	F.	G.	Sp.	Ph.	Or.	F.	G.	Sp.
Polychaetes	X	—	X	X	X	X	—	X	X	X
Crustaceans	X	X	X	X	X	X	X	—	—	—
Molluscs	X	—	X	X	X	X	—	—	—	—
Echinoderms	X	—	X	X	X	X	—	X	X	X

Specialists at Cordah Ltd. identified the >500 μm fraction fauna collected in 1996, whilst the rest of the taxonomic identification has been mainly carried out by

myself. However, some expert help has been sought for specific phyla and families (Table 2.3).

To aid in identification, some specimens were temporarily mounted in glycol and viewed under a WILD M20 compound microscope. Additional features were revealed using an ethanolic solution of methyl green, a non-permanent stain.

Table 2.3. People involved in the taxonomy of the fauna. Italicised names indicate the person(s) who identified the group to species level.

Major Groups	**Specific Families**	**Name of identifying person(s)**
Polychaetes		Bhavani Narayanaswamy
	Cirratulidae	*Mary Petersen*
	Glyceridae	*Brendan O'Connor*
	Paraonidae	*John Hartley*
	Pholoidae	*Mary Petersen*
	Syllidae	*Peter Garwood*
Crustaceans	Amphipoda	*Bhavani Narayanaswamy, Linda Robb*
Molluscs		*Shelagh Smith*
Echinoderms		Bhavani Narayanaswamy, *John Gage*

2.3.3. Biomass measurements

Blotted wet weight biomass was measured using a Sartorius BP221S balance with a sensitivity of ± 1mg. Blotted wet weight was used to ensure comparability with the 1996 >500 μm data collected by Cordah. Where possible specimens were removed from tubes, although in some instances this was not practical, especially for small, fragile organisms. Individual biomass values were measured for single large specimens.

THE PHYSIO-CHEMICAL AND GEOLOGICAL ENVIRONMENT OF THE WEST SHETLAND SLOPE

3.1. INTRODUCTION

3.1.1. Environmental Setting

The Faeroe-Shetland Channel lies between the Scottish continental shelf and Faeroese plateau. Studies undertaken in the Channel have found an unusual and highly dynamic physical environment. This has been attributed to the convergence and flow regimes of the water masses in this confined trough (Dooley and Meincke, 1981; Hansen, 1985; Turrell *et al.*, 1999).

The Channel is extremely important in the exchange of water between the Atlantic and Arctic basins. Constraining, but not blocking this exchange is a partly submerged topographic high, which includes Iceland and the Faeroe Islands, which is collectively known as the Greenland-Scotland Ridge. The exchange of water across the Ridge is fundamentally important for the oceanic areas situated to the North and is partly responsible for the relatively mild climate of Northwest Europe (Mowatt *et al.*, 1997). The Faeroe-Shetland Channel also plays a major role in the global thermohaline circulation (Hansen and Østerhus, 2000).

3.1.2. Geological Setting

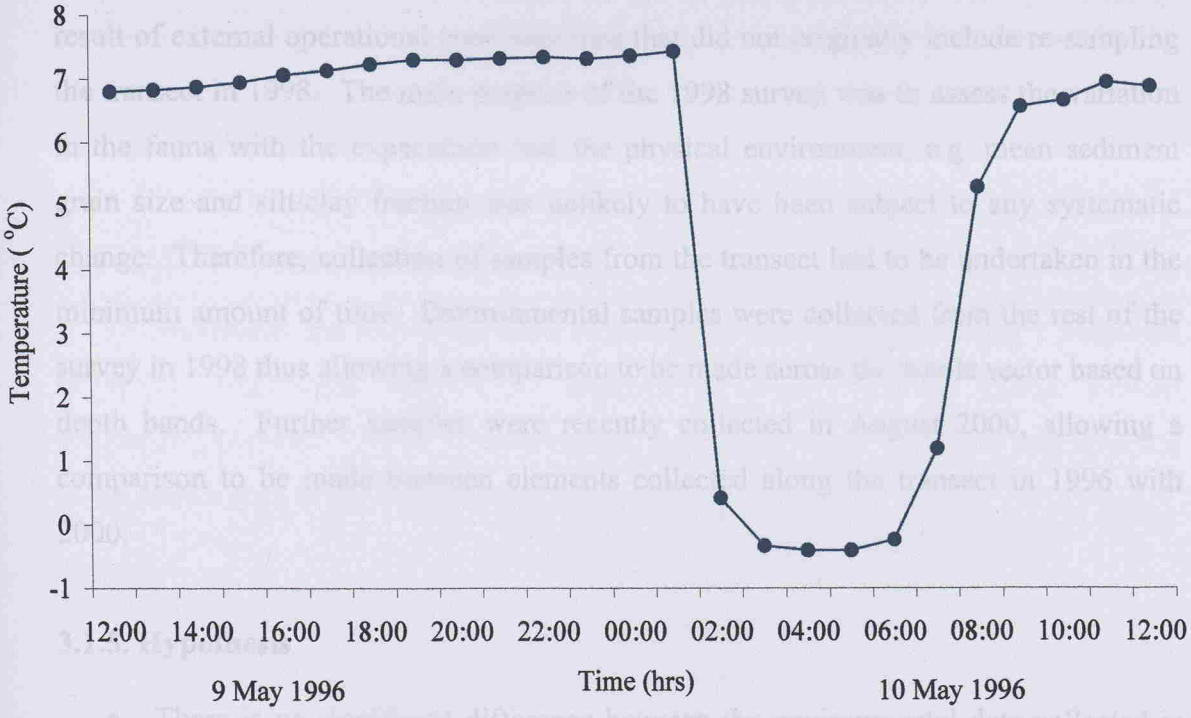
The seafloor of the Faeroe-Shetland Channel was characterised by TOBI sidescan sonar survey in conjunction with seabed still photographs. There is great variation of sediment types and features within the Channel (Masson, 2000) and these vary distinctly with depth. Between 300 m and 400 m iceberg ploughmarks are the dominant feature, whilst between 500 m and 800 m, sand and mud waves dominate the seabed (Stoker *et al.*, 1993; Masson *et al.*, 1997).

3.1.3. Hydrography

Water temperature in the Channel is known to vary quite considerably at nominally intermediate, 350 m to 650 m, depths. Recordings of temperature and salinity of the Faeroe-Shetland Channel have been carried out for over 100 years (Turrell, 1996). Temperature range can change dramatically as recorded by a current meter located at a depth of 550 m ten months prior to the survey (Bett, 2000). A

sudden drop in temperature of 7 °C in the space of one hour was recorded for four to five hours (Figure 3.1) (Bett, 2000). Internal tides are thought to be responsible for this rapid change as they can cause intermediate waters to move vertically by as much as 100 m during a six hour period (Bullough *et al.*, 1998).

Figure 3.1. Recorded change in water temperature at 550 m depth in the Faeroe-Shetland Channel in May 1996. This was one of 15 such observations in a ten-month period. (Unpublished data courtesy of B. J. Bett and J. P. Hartley).



3.1.4. Environmental variables

Other environmental variables of interest measured are, total organic carbon, total hydrocarbon and barium to see if and how they may influence the faunal distribution. As elsewhere in the deep-sea, total organic carbon is known to decrease with increasing depth in the Faeroe-Shetland Channel (Bett, 2000). Organic carbon in the deep-sea is thought to have a direct influence on the distribution of the macrofauna. As depth increases the amount of organic carbon decreases therefore leading to a decrease in macrofaunal abundance (Vinogradova, 1962; Belyaev, 1966).

The oil industry has been operating in the Channel since the mid 1970s with the

discovery of the Clair oil field (Ferguson, 1997). Some 150 wells had been drilled before the first survey in 1996. Barium sulphate is a naturally occurring material in marine sediments and is almost always a major constituent of drilling muds. Therefore, well-used barite, which has a small particle size of 4.5 μm, is small enough to be used as a tracer to detect the presence of hydrocarbons (Hartley, 1996).

The main focus of this chapter is to determine the influence of environmental variables on the benthic macrofauna. Although biological samples were collected in 1996 and 1998, environmental samples were only collected in 1996. This was as a result of external operational considerations that did not originally include re-sampling the transect in 1998. The main purpose of the 1998 survey was to assess the variation in the fauna with the expectation that the physical environment, e.g. mean sediment grain size and silt/clay fraction was unlikely to have been subject to any systematic change. Therefore, collection of samples from the transect had to be undertaken in the minimum amount of time. Environmental samples were collected from the rest of the survey in 1998 thus allowing a comparison to be made across the whole sector based on depth bands. Further samples were recently collected in August 2000, allowing a comparison to be made between elements collected along the transect in 1996 with 2000.

3.1.5. Hypothesis

- There is no significant difference between the environmental data collected in 1996 and 1998 along the transect.

3.2. MATERIALS AND METHODS

3.2.1. Geological, Physical and Chemical Analysis

Two commercial companies, Cordah Ltd. and Environment and Resource Technology Ltd. (ERT) Edinburgh, carried out analysis of the seabed samples. Elemental analyses (not looked at in this study) and the 1996 >500 μm macrobenthic fraction analysis were carried out by Cordah Ltd. Hydrocarbon, nitrogen, total organic carbon analyses and sediment characterisation was carried out by ERT. A brief outline of standard methodologies used in these analyses follows based on reports written by ERT and Cordah Ltd (see Baker, 1997; McDougall, 1997; Smith, 1997; Bett, 2000). Further statistical analyses of these data was undertaken by myself (section 3.2.3.).

3.2.1.1. Water temperature

Maximum and minimum water temperature were measured using a Falmouth Scientific Instruments Micro-CTD attached to TOBI (Towed Ocean Bottom Instrument) (Masson, 1997). Measurements were made every 4 seconds and recorded in the header data of the sidescan data string.

3.2.1.2. Sediment characterisation

Particle size analysis was carried out on samples of oven-dried sediment (McManus, 1988). Organic matter was removed from the samples by addition of 30% hydrogen peroxide followed by re-suspension in a 0.6% solution of sodium hexametaphosphate (Calgon). The mixture was left to stand for at least two hours (McDougall, 1997; Bett, 2000) before being sieved through a 63 μm mesh to enable separation of the sand from the silt/clay fraction. Sands were fractioned using a Wentworth series of analytical sieves (63 μm – 4000 μm). The remaining silt/clay was fractionated either by pipette analysis or using a Coulter counter (McManus, 1988). Pipette analysis was undertaken where the fraction accounted for 5% or more of the total sample weight. Coulter Counter analysis was undertaken if the silt/clay fraction accounted for 10% or more of the total sample weight.

Sediment organic matter and calcium carbonate were also determined. Organic matter constitutes material containing other elements apart from carbon such as

nitrogen, oxygen, hydrogen, etc. Inorganic carbon was removed from a pre-dried amount of sediment by adding an excess of hydrochloric acid. The residual sediment was washed and dried to a constant weight before being placed in a muffle furnace for two hours at 600 °C (McDougall, 1997; Bett, 2000). Difference in weight pre- and post combustion allows for determination of organic matter and carbonate.

3.2.1.3. Total Organic Carbon and Nitrogen

Samples used for total organic carbon and nitrogen analyses were pre-treated by adding hydrochloric acid followed by grinding to less than 63 μm. Using a Leeman CE440 elemental analyser, the material was air dried and combusted in an atmosphere of oxygen at 1000 °C (McDougall, 1997; Bett, 2000).

3.2.1.4. Hydrocarbon analyses

Sediment samples were thawed before being homogenised and accurately weighed in 250 ml conical flasks. A solution of known aliphatic and aromatic standards were added to the sediment along with methanol and mixed. Dichloromethane was added and the sample mixed again (McDougall, 1997; Bett, 2000). A silica gel column was used to remove polar materials. Aromatic hydrocarbons were analysed by gas chromatography-mass spectrometry.

3.2.2. Standardisation of data

Most potential contaminants are associated with small grain size as there is a higher surface area. To take into account the natural increase in barium with decreasing sediment grain size, barium was standardised against a non-reactive metal, in this instance aluminium (Loring and Rantala, 1992). Aluminium is also related to grain size and therefore may be used as a proxy for sediment grain size.

3.2.3. Statistical Analysis

3.2.3.1. Analysis of Variance (ANOVA)

As a result of *a priori* assumptions of data normality made when using parametric statistics, data were log transformed prior to ANOVA being undertaken, the

exception being mean sediment grain size as it is already in a logarithmic format. Analysis of Variance was carried out using Minitab (v.12). The data was tested for normality after the transformation had been applied. The data used for ANOVA are based on samples collected through out the entire surveys in both 1996 and 1998 and not from the transect.

3.2.3.2. Spearman Rank Correlation Coefficient

Spearman rank correlation was applied to the 1996 environmental transect results to test for an association between two variables.

Spearman Rank Correlation (Siegel and Castellan, 1998)

$$r_s = 1 - \left(\frac{6 \sum d^2}{n(n^2 - 1)} \right)$$

r_s = Spearman Rank Coefficient

Σd^2 = the sum of the differences squared

n = the number of observations

3.3. RESULTS

3.3.1. Background

Analysis of variance was calculated on certain environmental variables collected in the Faeroe-Shetland Channel in 1996 and 1998 (Table 3.1). This was undertaken to see whether data from the transect in 1996 could justifiably be used as a model for 1998, the null hypothesis being that the environmental data have not changed significantly between the two years. It was not possible to do equal depth increments in the two years, as the depths did not always exactly match (see appendix I).

Table 3.1. A two-factor analysis of variance without replication of the environmental variables in the Faeroe-Shetland Channel in 1996 and 1998 separated into 20 depth bands (200 m – 1488 m). Degrees of freedom = 39, $\alpha = 0.05$

Environmental variable	**F-value**	**p-value**
Total hydrocarbon	1.04	0.46
Mean sediment grain size	1.10	0.38
Total Organic Carbon	1.17	0.32
Silt/clay	1.50	0.10
Ba	0.94	0.54
MgO	0.95	0.56
Al_2O_3	1.04	0.46

These data satisfied the criteria for use of parametric statistics in that the data was tested for normality after the transformation had taken place. The results show that there was no significant difference in the environmental variables tested in the 1996 AFEN survey with those from the 1998 AFEN survey.

At the time of writing elemental results from 2000 have just been made available allowing a comparison of transect results from 1996 with 2000 (table 3.2). Barium and aluminium oxide were the two variables compared as barium can be used as a tracer for contaminants and aluminium as a proxy for sediment grain size.

Table 3.2. A two-factor analysis of variance without replication of the barium and aluminium down the depth transect in the Faeroe-Shetland Channel in 1996 and 2000 separated into 15 depth bands (150 m – 1000 m). Degrees of freedom = 29, $\alpha = 0.05$

Environmental variable	F-value	p-value
Barium	0.94	0.57
Al_2O_3	1.00	0.49

3.3.2. Physical Variables

3.3.2.1. Hydrography

The temperature of the water column varied with depth, as did the temporal range of temperatures at each depth (Figure 3.2) (Masson, 1997; B. J. Bett, pers. comm.). At shallow depths (100 m – 250 m) the temperature range was 2.2 °C, but at shallow/intermediate depths (300 m – 550 m) the range became much greater (6.63 °C) (Figure 3.2). The minimum temperature recorded exhibited the greatest change between 250 m and 400 m whilst the maximum temperature showed a relatively steady decline with depth. At depths greater than 750 m, the difference between minimum and maximum temperatures recorded was almost negligible. The temperature at intermediate depths also changed rapidly (see page 34, Figure 3.1). Such a scale of variability is unknown elsewhere in the deep-sea except at hydrothermal vents (Tunnicliffe, 1991).

3.3.2.2. Sediment analysis

The sediments in the Channel ranged from coarse sand found at the 150 m station to very fine sand at the 1000 m station (Table 3.3). The mean grain size also varied with depth from –0.03 Φ (s.d. 1.76 Φ) at 150 m to 3.48 Φ (s.d. 1.42 Φ) at 800 m (for an explanation of Φ, see Page, 1955) (Figure 3.3). The highest standard deviation was found at the 550 m station (±2.96) and the smallest at the 900 m station (±0.52). The general trend seen was finer sediment with increased depth. However, exceptions to this were at the 250 m and 550 m stations where the sediment changed to coarse sand. Thus the range of grain size was found to be quite variable at all depths (Bett, 1997). From the shallowest station to mid depth stations (650 m) the sediment consisted of shelly sands and slightly pebbly sands. However, from 650 m to 1000 m

depth the composition changed to mixed and muddy sands (Graham *et al.*, 1996).

The percentage of silt/clay found at each station generally increased with depth (Figure 3.4). However, below 700 m there was a sharp decrease in the silt/clay fraction.

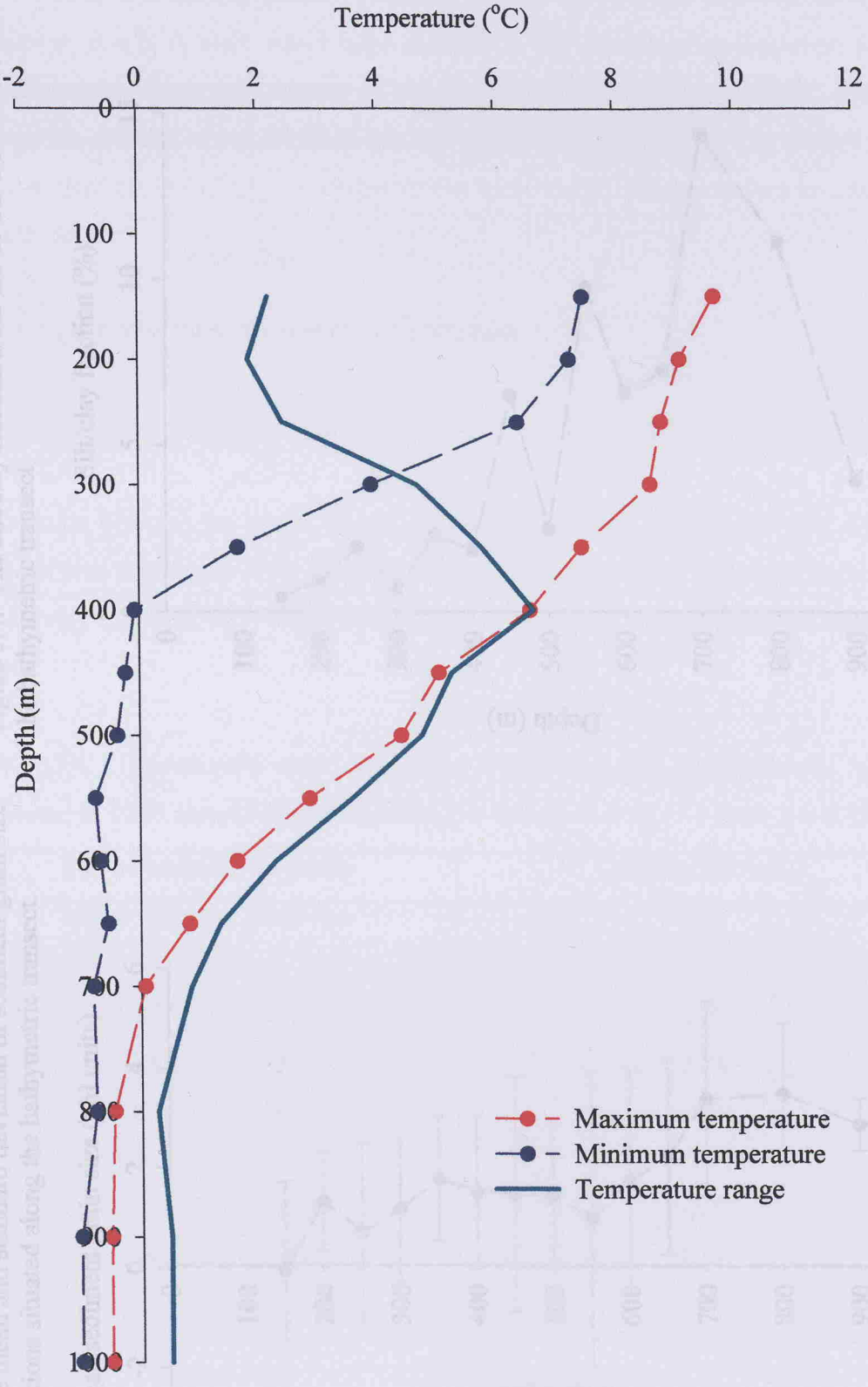
3.3.2.3. Total organic carbon and organic content

The overall pattern for total organic carbon was very variable (Figure 3.5). It appeared not to be strongly linked with increasing depth, although there was a slightly higher total organic carbon content at greater depths. Organic content generally appeared to show an increase with increasing depth, the highest value being recorded at 550 m (Figure 3.5).

Table 3.3. Characteristics of sediments found along the bathymetric transect in the Faeroe-Shetland Channel.

Actual depth (m)	Wentworth Scale	Sorting	Standard Deviation (Φ)	Skewness (Φ)
133	Very coarse sand	Moderate	1.76	-0.06
202	Medium sand	Good	1.0	-0.35
248	Coarse sand	Moderate	1.76	-0.31
290	Medium sand	Good	1.44	-1.06
348	Medium sand	Good	1.24	-1.42
413	Medium sand	Moderate	1.55	-1.25
454	Medium sand	Poor	2.35	0.86
502	Medium sand	Good	1.42	-0.74
552	Coarse sand	Very poor	2.96	0.73
601	Medium sand	Poor	2.25	0.20
650	Fine sand	Moderate	1.97	0.04
709	Very fine sand	Moderate	1.94	1.05
804	Very fine sand	Good	1.42	2.36
919	Fine sand	Very good	0.52	0.53
998	Very fine sand	Good	1.19	3.31

Figure 3.2. The maximum (red line), minimum (blue line) and therefore range of temperatures (green line) encountered in the deep water to the West of Shetland.



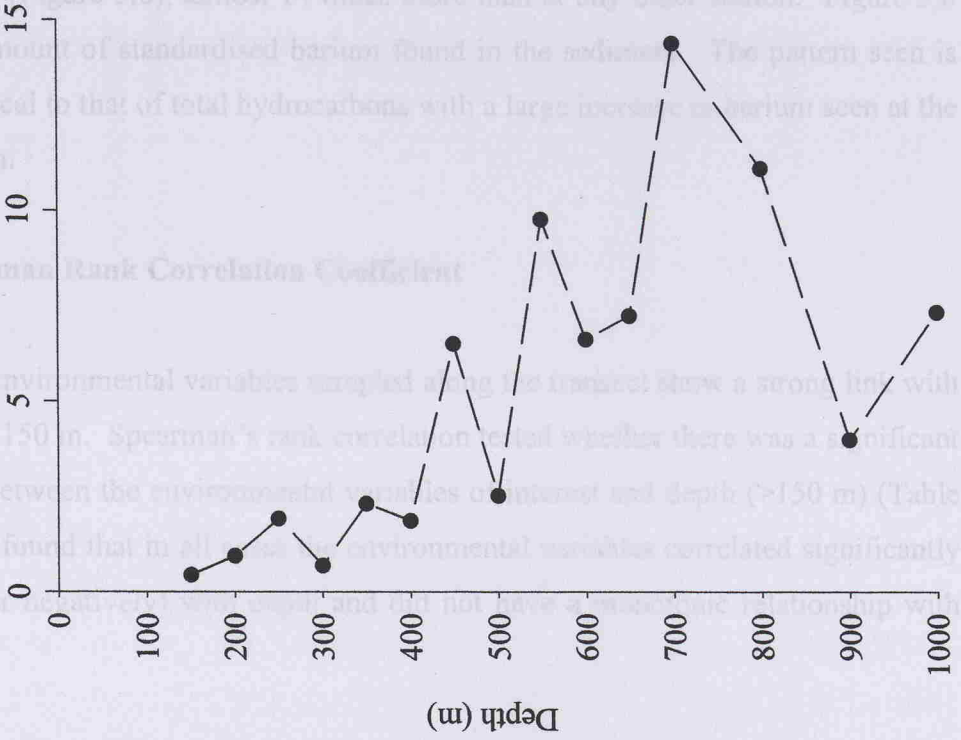


Figure 3.4. The silt/clay fraction from the 15 stations situated along the bathymetric transect

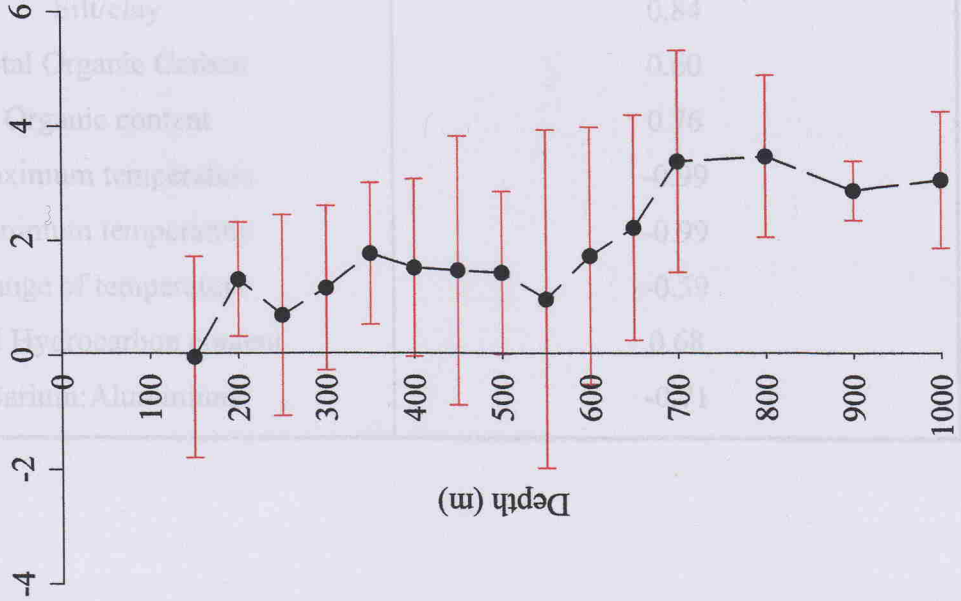


Figure 3.3. The mean and standard deviation of sediment grain size from the 15 stations situated along the bathymetric transect.

3.3.2.4. Total hydrocarbon and barium content

Total hydrocarbon content generally showed little change with increasing depth. However, at 650 m there was a large increase in the amount of hydrocarbon found in the sediment (Figure 3.6), almost 14 times more than at any other station. Figure 3.6 shows the amount of standardised barium found in the sediment. The pattern seen is almost identical to that of total hydrocarbons with a large increase in barium seen at the 650 m station.

3.3.3. Spearman Rank Correlation Coefficient

The environmental variables sampled along the transect show a strong link with depth below 150 m. Spearman's rank correlation tested whether there was a significant correlation between the environmental variables of interest and depth (>150 m) (Table 3.4). It was found that in all cases the environmental variables correlated significantly (positively or negatively) with depth and did not have a monotonic relationship with depth.

Table 3.4. Spearman's rank correlation values for the environmental variables collected in 1996 correlated with depth below 150 m. $n = 15$, $\alpha = 0.05$; $r_s = 0.521$.

Environmental Variable	Correlation value
Mean sediment grain size	0.83
Silt/clay	0.84
Total Organic Carbon	0.60
Organic content	0.76
Maximum temperature	-0.99
Minimum temperature	-0.99
Range of temperature	-0.59
Total Hydrocarbon content	0.68
Barium:Aluminium	-0.71

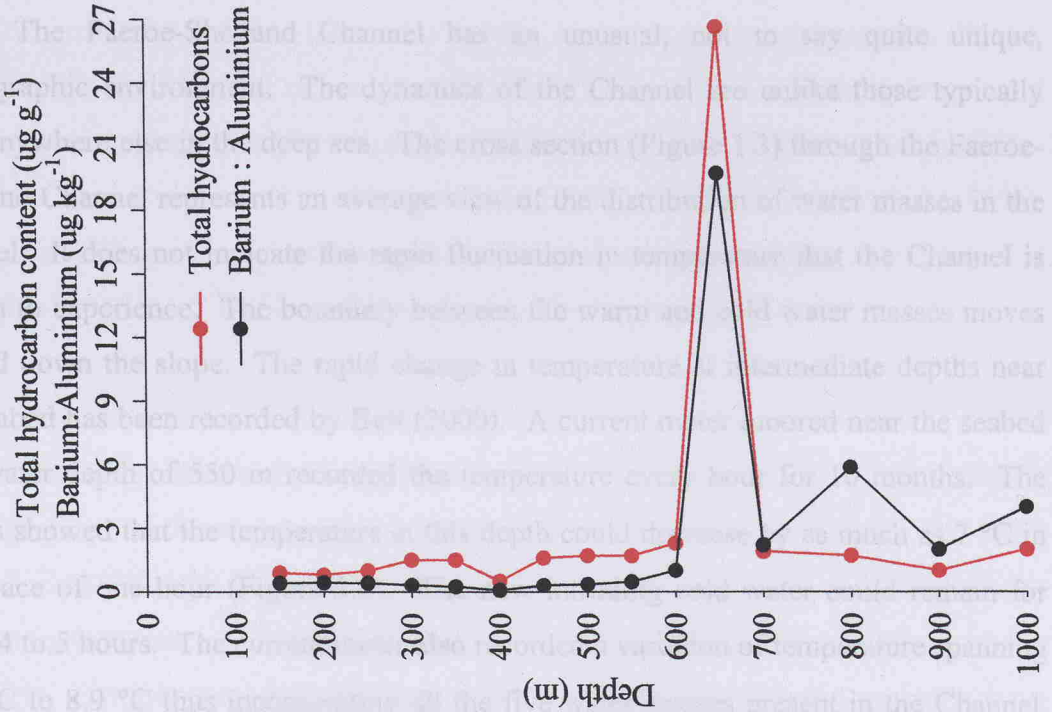


Figure 3.6. The amount of total hydrocarbons and barium collected from the 15 stations situated along the bathymetric transect.

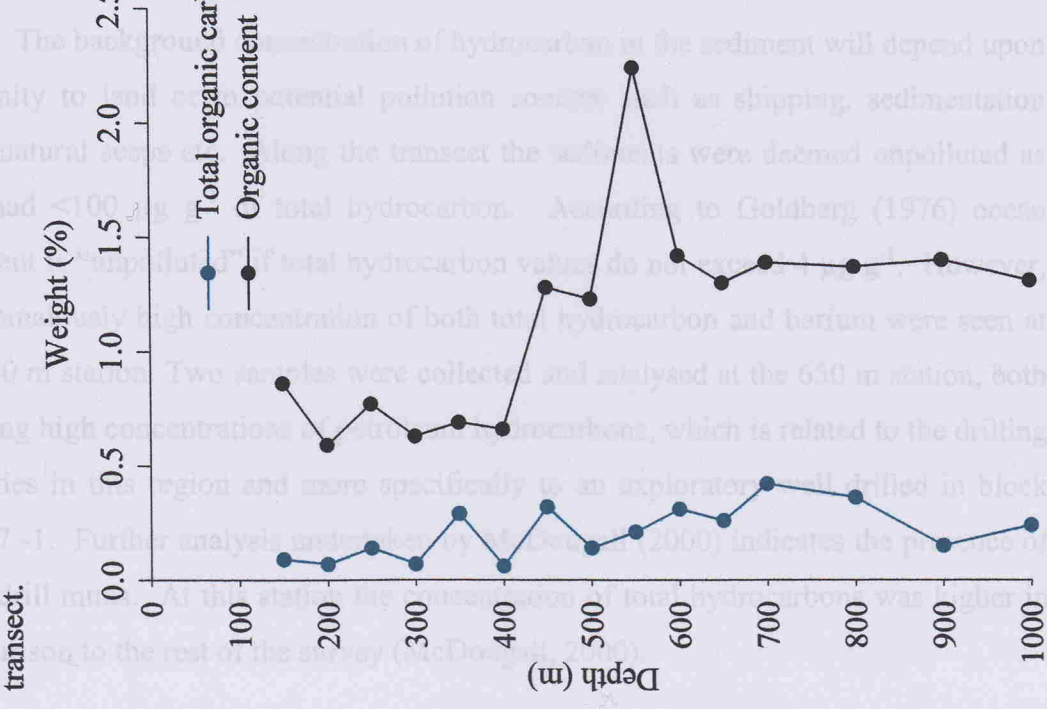


Figure 3.5. The percentage of total organic carbon and organic content collected from the 15 stations situated along the bathymetric transect.

3.4. DISCUSSION

3.4.1. Physical environment of the Faeroe-Shetland Channel

The Faeroe-Shetland Channel has an unusual, not to say quite unique, hydrographic environment. The dynamics of the Channel are unlike those typically seen anywhere else in the deep sea. The cross section (Figure 1.3) through the Faeroe-Shetland Channel represents an average view of the distribution of water masses in the channel. It does not indicate the rapid fluctuation in temperature that the Channel is known to experience. The boundary between the warm and cold water masses moves up and down the slope. The rapid change in temperature at intermediate depths near the seabed has been recorded by Bett (2000). A current meter moored near the seabed at a water depth of 550 m recorded the temperature every hour for 10 months. The results showed that the temperature at this depth could decrease by as much as 7 °C in the space of one hour (Figure 3.1). The new intruding cold water could remain for some 4 to 5 hours. The current meter also recorded a variation of temperature spanning -0.8 °C to 8.9 °C thus incorporating all the five water masses present in the Channel. This rapid change in temperature is thought to be as a result of internal waves at the boundary between warm and cold water. Sherwin (1991) suggested that this was generated by the flow of water from the North Atlantic over the Wyville-Thomson Ridge. Increased total organic matter at these intermediate depths is also thought to be a result of internal waves.

The background concentration of hydrocarbon in the sediment will depend upon proximity to land or to potential pollution sources such as shipping, sedimentation rates, natural seeps etc. Along the transect the sediments were deemed unpolluted as they had <100 $\mu g\ g^{-1}$ of total hydrocarbon. According to Goldberg (1976) ocean sediment is "unpolluted" if total hydrocarbon values do not exceed 4 $\mu g\ g^{-1}$. However, an anomalously high concentration of both total hydrocarbon and barium were seen at the 650 m station. Two samples were collected and analysed at the 650 m station, both showing high concentrations of petroleum hydrocarbons, which is related to the drilling activities in this region and more specifically to an exploratory well drilled in block 214/27 -1. Further analysis undertaken by McDougall (2000) indicates the presence of fresh drill muds. At this station the concentration of total hydrocarbons was higher in comparison to the rest of the survey (McDougall, 2000).

Drill cuttings constitute a suspension of solids such as clays, barite, small cuttings etc. in a liquid, such as water or oil, or liquid emulsion that contains chemical additives (Hudgins, 1994). Initially a hydrocarbon such as diesel fuel was used as a drill mud, followed by synthesised lubricants made from products such as ethylene when the toxicity of diesel to the marine benthic environment became apparent (Breuer *et al.*, 2000). However, the new synthesised muds, consisting of carbon, hydrogen and oxygen atoms, were also found to have a high toxicity and their biodegradation properties were similar to that of the mineral oils they had replaced (Hudgins, 1994). At present drilling mud content is regulated and the use of lubrication only allowed if difficulties occur such as the drill stem sticking (Breuer *et al.*, 2000).

The results have shown that there is no significant difference in the environmental variables collected in 1996 and 1998 from the survey area, nor was there any significant difference in barium or aluminium oxide sampled down the study transect in 1996 and 2000 leading to the hypothesis, that there is no significant difference between environmental data from 1996 and 1999, being accepted. Therefore, environmental data collected in 1996 in this instance may be used as a proxy for the 1998 data.

STUDIES IN BENTHIC MACROFAUNAL ECOLOGY I: STANDING STOCK OF THE WEST SHETLAND SLOPE

4.1. INTRODUCTION

4.1.1. Quantitative deep-sea benthic sampling

Russian workers undertook the first quantitative assessment of deep-sea benthic fauna in 1949 (Zenkevitch, 1965), even though qualitative deep-sea benthic samples had been collected for at least a century prior to this date. Soon after the Russian expeditions, the Danish '*Galathea*' expedition collected quantitative samples using a Peterson grab off the West coast of Africa (Spärck, 1956). Russian scientists led the sampling in the deep sea in the 1950s, particularly in the Antarctic, Indian and Pacific Oceans (Vinogradova, 1962 and references therein). Quantitative data generated by this work suggested that as depth and distance from land increased the quantity of macrofauna decreased (Vinogradova, 1962) and that the main controlling factor was the dependence of the benthic fauna on available food resources (Belyaev, 1966).

Work undertaken by American scientists along the Gay Head-Bermuda transect was the first instance of benthic sampling conducted on a smaller scale. Previous investigations of deep-sea benthic fauna tended to be of a world wide-ranging nature and so covering large geographic areas albeit with small samples. Sanders *et al.* (1965) collected semi-quantitative samples using a modified anchor dredge, which was designed to dig to a given depth, in order to study the open ocean benthic communities in some detail.

The results obtained by Sanders and colleagues along the Gay Head-Bermuda transect generally agreed with those of the Russians. However, because Sanders *et al.* obtained such high population densities, they tested the possibility that they had abnormally high values by sampling at comparable stations along the coast of South America. It was here that Sanders (1969) found that his results were comparable to those collected in the North Atlantic. The trend of an exponential decline in abundance with increasing depth is also seen with biomass (Rowe and Menzel, 1971; Rowe *et al.*, 1974; Haedrich and Rowe, 1978). Rowe (1983) illustrated this trend in a compilation of biomass values plotted for 709 samples collected around the world.

There are differing views as to whether abundance or biomass values are a more accurate way of determining faunal existence. Rowe (1983) felt that biomass was a more meaningful measure than the number of animals per unit area. However, biomass measurements can be more variable as they can be affected by the relatively rare

appearance of large-bodied animals (Gage, 1977). The preferred measurement may differ from study to study. However, if a 250 μm mesh is used to collect the fauna as well as 500 μm, the fauna from the smaller sieve ought to have little effect on the overall total biomass, even though many more individuals are retained by the smaller sieve.

Most Box core designs are generally based on the 'Kastengriefer' designed by Reineck (Reineck, 1963). The style of Box corer often used nowadays initially underwent several modifications by Bouma and Marshall (1964) and then again by Rosfelder and Marshall (1967) in conjunction with the United States Naval Electronics Laboratory (USNEL) (Hessler and Jumars, 1974). The USNEL box corer for sampling deep-sea macrobenthos was first used in the early 1970s (Hessler and Jumars, 1974). This device is designed to sample a precise area for a full depth bite. Additionally, samples could be recovered relatively intact compared to a grab or dredge (Hessler and Sanders, 1967) and the assumption was that the effect of a bow wave would be minimal (McIntyre, 1971). However, Box cores are now thought to create a bow-wave on their approach to the sediment and the rapid penetration of the Box core in to the sediment can result in small, light macrofauna being blown away (see Bett, 1994).

More recently a multiple corer has been widely adopted (Barnett *et al.*, 1984) as it is able to collect undisturbed sediment cores. The multiple corer is able to recover larger amounts of phytodetritus from the same site as compared to a Box corer (Thiel *et al.*, 1988/1989). Bett *et al.* (1994) found that the density of meiofauna in the multiple corer could be up to 50% greater in comparison to the Box corer. A similar conclusion was also reached when sample comparison was undertaken on samples collected in the AFEN 1996 and 1998 surveys. The faunal density in a Box corer was found to be between 48% and 68% of the corresponding Megacorer samples (Bett and Gage, 2000). Bett also suggested that the Box corer may influence faunal composition because the descending bow wave blows some of the smaller, lighter fauna aside.

4.1.2. Hypotheses

- Standing stock of the Faeroe-Shetland Channel conforms to traditional deep-sea expectation whereby an exponential decline in standing stock is seen with increasing water depth.

- The distribution and biomass of the fauna is predominantly controlled by a suite of depth-related environmental variables. Historically, in the deep-sea, depth and organic input have been deemed the most important variables influencing faunal distribution and biomass.

4.2. ANALYTICAL METHODS

4.2.1. Statistical analyses

Owing to the nature of the data, i.e. lack of replicate samples, the use of rank statistical tests was deemed to be more appropriate for some of the analyses undertaken. A range of univariate and multivariate statistical analyses has been used to determine the relationship between the environmental parameters and the fauna.

1) Spearman Rank Correlation Coefficient
2) Partial Correlation Coefficient
3) Canonical Correspondence Analysis (CCA)

Spearman's Rank and Partial Correlation coefficients were calculated using Minitab v.12.0, and CCA was performed using CANOCO v.4.0 (ter Braak and Smilaeur, 1998). All analyses were performed on P.C. using Windows 95.

4.2.2. Univariate Analyses

4.2.2.1. Spearman Rank Correlation Coefficient and Partial Correlation Coefficient

See Analytical Methods section Chapter 3, page 38 for methods detailing Spearman's rank correlation.

There is often more than one variable to be taken into account and simple correlation fails to take into consideration the interactions of any of the other variables. "*Partial Correlation solves this problem as it considers the correlation between each pair of variables while holding constant the value of each of the other variables*" (Zar, 1984).

Partial Correlation Coefficient (Zar, 1984)

$$s_{r_{ik}} = \sqrt{\frac{1 - r_{ik}^2}{n - M}}$$

r_{ik} = the correlation between two variables

M = total number of variables in multiple correlation

n = number of observations

4.2.3. Multivariate analyses

4.2.3.1. Cluster analysis

Initially multivariate analysis was applied to untransformed data, however very abundant species heavily influenced the analysis and therefore it was deemed necessary to fourth root transform the biological data. Transformations are performed in order to increase the influence of rare fauna, or to weight the respective contributions of rare and common species in the multivariate representations (Clarke and Warwick, 1994). Clustering was undertaken using the Cluster programme in PRIMER, and proceeds from a ranked similarity matrix formulated using the Bray Curtis similarity coefficient (Bray and Curtis, 1957). To classify the stations based on faunal groupings, the similarity matrix is subject to hierarchical, agglomerative classification, employing group average sorting (Lance and Williams, 1967). Hierarchical dendrograms are plotted from the results of the analysis.

4.2.3.2. Non-metric multidimensional scaling and ordination

Clustering such as Bray-Curtis can be misleading where there is a gradient in the community structure across sample sites, e.g. water depth, sediment grain size (Clarke and Warwick, 1994). Anomalies occurring at the lowest combinatorial level may also obscure true affinities between sites. Ordination can avoid this as it simplifies the data set and makes a representation of samples in an *s*-dimensional coordinate frame. Using the similarity matrices constructed by the Bray Curtis similarity coefficient, non-metric multidimensional scaling analysis (MDS ordination) (Shepard, 1962; Kruskal, 1964) was undertaken. Kruskal's stress formula (Kruskal and Wish, 1978) measures the goodness-of-fit in the MDS ordination plots. There is no unique solution for an MDS ordination therefore either repeating the process several times or increasing the number of random starts to ensure the lowest stress value.

4.2.3.3. Canonical Correspondence Analysis

Canonical correspondence analysis (CCA) was chosen over programmes such as BIOENV found in the PRIMER package, as the results from CCA can be tested statistically using a Monte Carlo test. BIOENV does not have the facility to do this.

Canonical correspondence analysis was undertaken using Canonical Community Ordination (CANOCO) (v. 4) and in these analyses the biological data

were fourth root transformed. CANOCO is an extension of DECORANA (Detrended Correspondence Analysis) (Hill, 1979). This analysis allows one to test statistically whether species distributions are related to environmental variables (ter Braak and Verdonschot, 1995). The statistical significance of the relationship between the species and the whole suite of environmental variables given the co-variables can be tested by using a Monte Carlo permutation test (Manly, 1991; ter Braak, 1992). A Monte Carlo permutation test repeatedly shuffles (permutates) the samples. The number of environmental variables related to the species data is tested at the 5% significance level. Eigenvalues are also presented and these measure the total amount of variance seen, whilst the canonical eigenvalue measures the variance with respect to the environmental variables used (ter Braak and Smilaeur, 1998). From this it can be determined whether the environmental variables used explain the majority of the variance seen (ter Braak and Smilaeur, 1998). Insights into the structure of biological communities and into the impact of environmental disturbances on the biological assemblages are provided by ordination analysis in conjunction with CANOCO.

4.3. RESULTS

To test if the standing stock of the West Shetland Slope declined exponentially with depth, macrofaunal abundance and biomass was measured at each station along the depth transect. Macrofaunal abundance and biomass was also analysed with respect to the data collected from the suite of environmental variables measured.

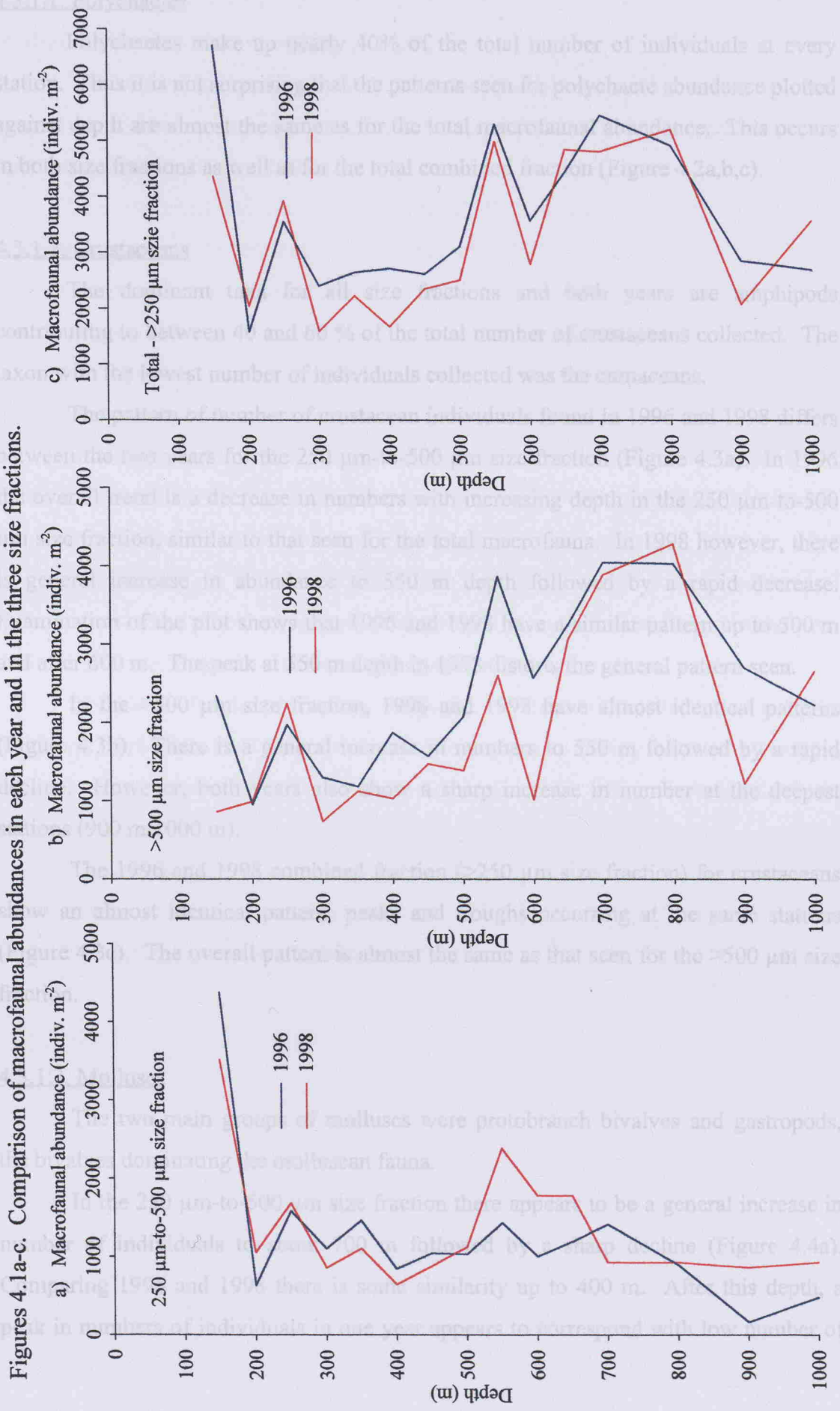
4.3.1. Macrofaunal abundance

Results from 1996 and 1998 for the 250 μm-to-500 μm size fraction are quite similar (Figure 4.1a). The general trend seen with this fraction is an overall decrease in individual abundance with increasing depth. However, this is interrupted with a peak at 550 m in 1998.

With the >500 μm size fractions, plots of abundance for the two years are almost identical (Figure 4.1b). The results from 1998 however, are almost consistently lower than for 1996, particularly noticeable at the following depths; 550 m, 600 m and 900 m. In this fraction there is a general increase in abundance with increasing depth. The pattern seen here is almost the reverse to the one seen with the smaller fraction.

Looking at the two size fractions more specifically, similarities and differences become more apparent. Both the 250 μm-to-500 μm size fraction and the >500 μm size fraction show an increase in abundance with increasing depth to around 600 m. After this point the larger fraction continues to show an increase whilst the smaller fraction decreases in abundance with depth.

By combining the two fractions one can see how much of an impact each fraction contributes to the total (Figure 4.1c). High numbers of individuals were found at relatively shallow (150 m) stations and again at intermediate-deep (550 m-700 m) stations. These major peaks corresponded to those seen in each of the individual size fractions. Once again 1996 and 1998 exhibit a similar pattern.



Figures 4.1a-c. Comparison of macrofaunal abundances in each year and in the three size fractions.

4.3.1.1. Polychaetes

Polychaetes make up nearly 40% of the total number of individuals at every station. Thus it is not surprising that the patterns seen for polychaete abundance plotted against depth are almost the same as for the total macrofaunal abundance. This occurs in both size fractions as well as for the total combined fraction (Figure 4.2a,b,c).

4.3.1.2. Crustaceans

The dominant taxa for all size fractions and both years are amphipods contributing to between 40 and 60 % of the total number of crustaceans collected. The taxon with the lowest number of individuals collected was the cumaceans.

The pattern of number of crustacean individuals found in 1996 and 1998 differs between the two years for the 250 μm-to-500 μm size fraction (Figure 4.3a). In 1996 the overall trend is a decrease in numbers with increasing depth in the 250 μm-to-500 μm size fraction, similar to that seen for the total macrofauna. In 1998 however, there is general increase in abundance to 550 m depth followed by a rapid decrease. Examination of the plot shows that 1996 and 1998 have a similar pattern up to 500 m and after 600 m. The peak at 550 m depth in 1998 distorts the general pattern seen.

In the >500 μm size fraction, 1996 and 1998 have almost identical patterns (Figure 4.3b). There is a general increase in numbers to 550 m followed by a rapid decline. However, both years also show a sharp increase in number at the deepest stations (900 m/1000 m).

The 1996 and 1998 combined fraction (>250 μm size fraction) for crustaceans show an almost identical pattern, peaks and troughs occurring at the same stations (Figure 4.3c). The overall pattern is almost the same as that seen for the >500 μm size fraction.

4.3.1.3. Molluscs

The two main groups of molluscs were protobranch bivalves and gastropods, the bivalves dominating the molluscan fauna.

In the 250 μm-to-500 μm size fraction there appears to be a general increase in number of individuals to about 700 m followed by a sharp decline (Figure 4.4a). Comparing 1996 and 1998 there is some similarity up to 400 m. After this depth, a peak in numbers of individuals in one year appears to correspond with low number of

individuals in the other year. In both years two main peaks are noticeable, one at 300 m, the other between 600 m and 700 m depth.

The larger fraction shows much greater similarity between the two years. The general trend is an increase in abundance to intermediate-deep (700 m) depths followed by a sharp decrease (Figure 4.4b).

The combined fractions for 1996 and 1998 show a similar pattern to the two separate fractions, with peaks at 300 m as well as at 700 m. The overall picture is one of increasing molluscan abundance with increasing depth to 700 m followed by a rapid decline (Figure 4.4c).

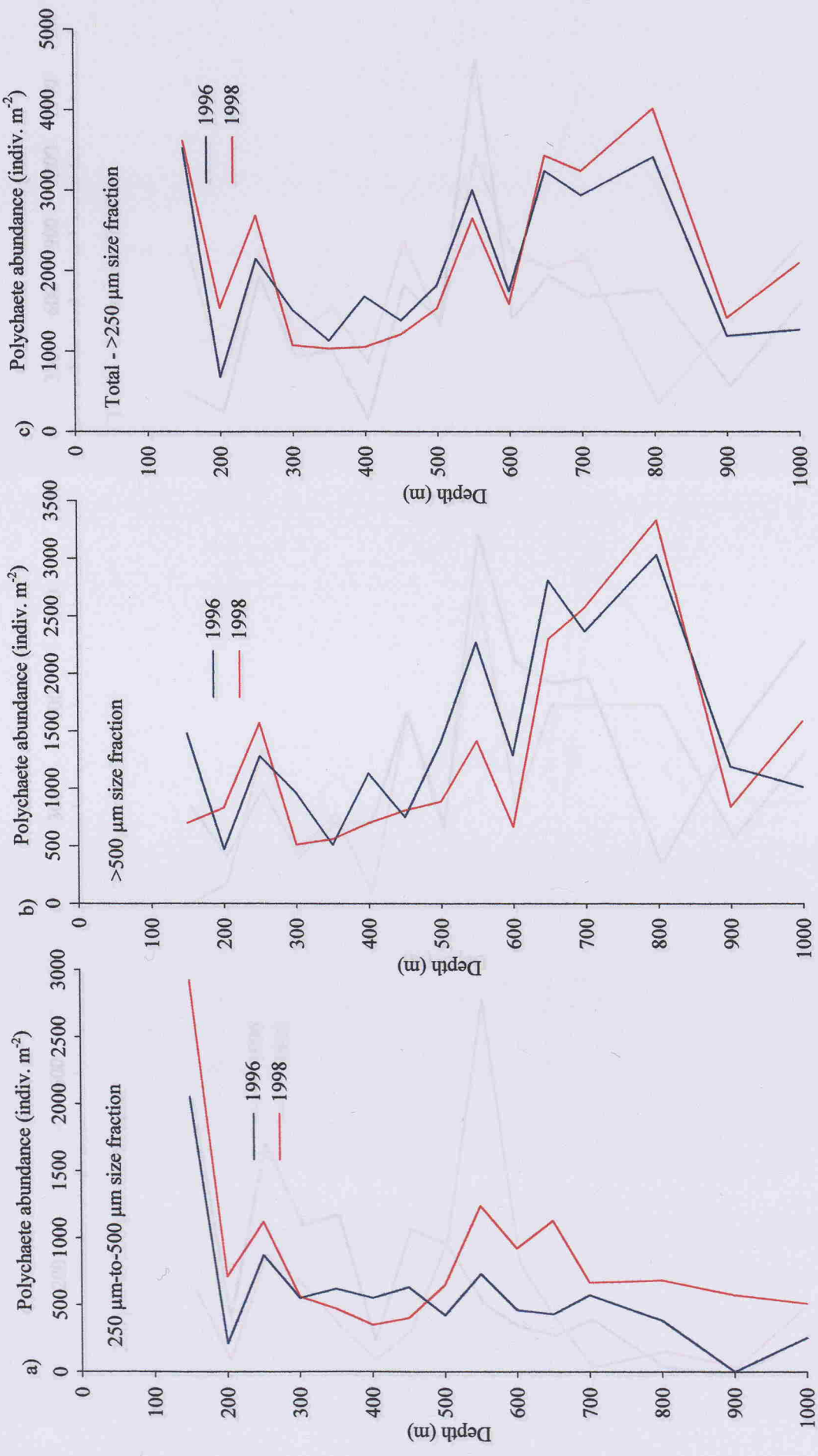
4.3.1.4. Echinoderms

The dominant taxon within this phylum was the Ophiuroidea accounting for between 50% and 80% of the total number of individuals. The class Ophiolepidae had the greatest number of individuals.

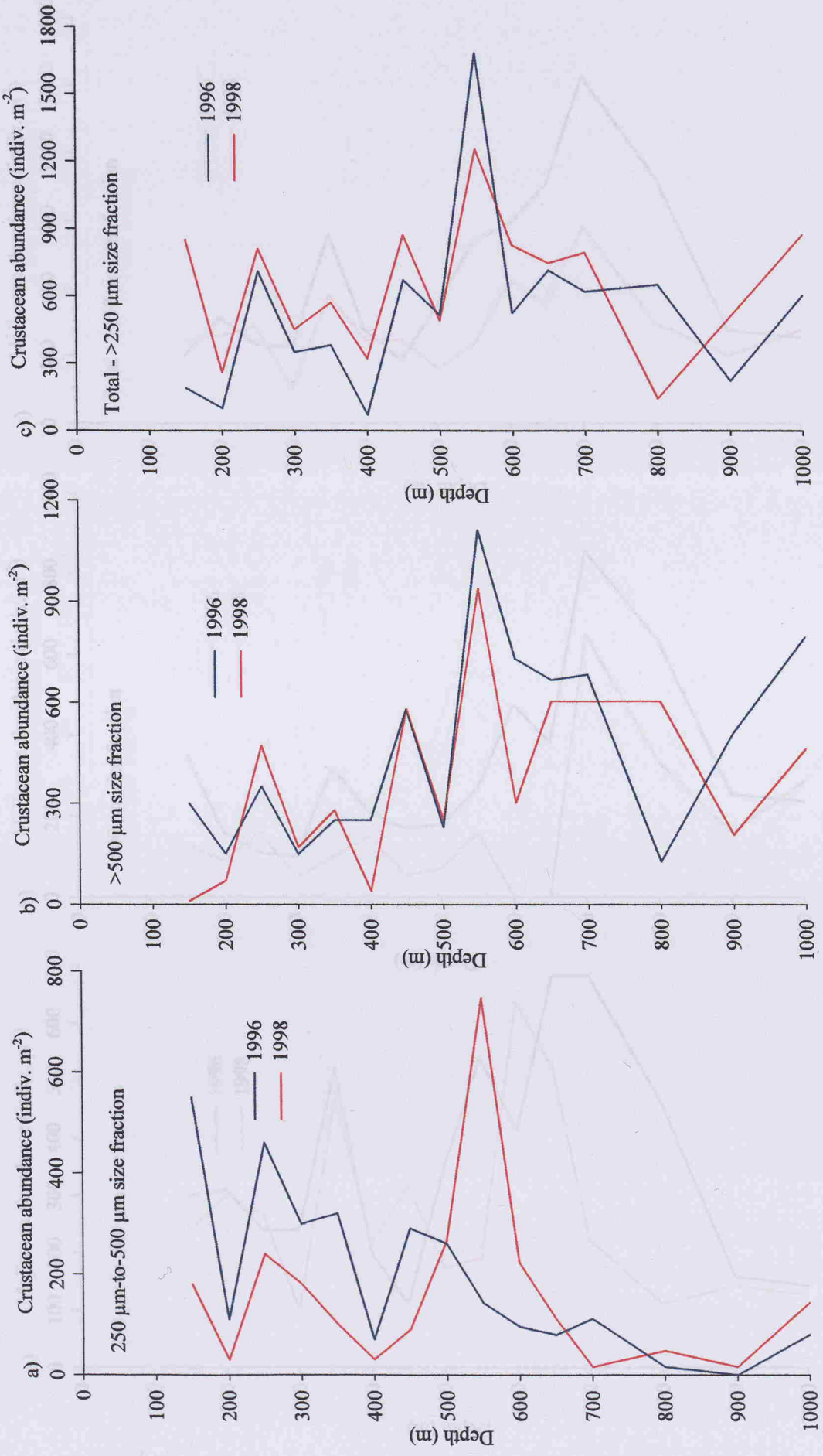
The trend seen in the 250 μm-to-500 μm size fraction is high numbers of individuals at the shallowest station followed by a general decline (Figure 4.5a). No echinoderms were found at five hundred metres and deeper.

The pattern for the >500 μm size fraction is very variable when comparing the results of 1996 with 1998 (Figure 4.5b). 1996 shows an overall decline in numbers with increasing depth, whilst the converse is true for 1998. Only between 350 m and 600 m are the results for the two years similar.

Combining the two fractions together, the trend is a general decrease in number of individuals with increasing depth for both years (Figure 4.5c). Results from 1996 and 1998 are similar to a depth of 600 m.

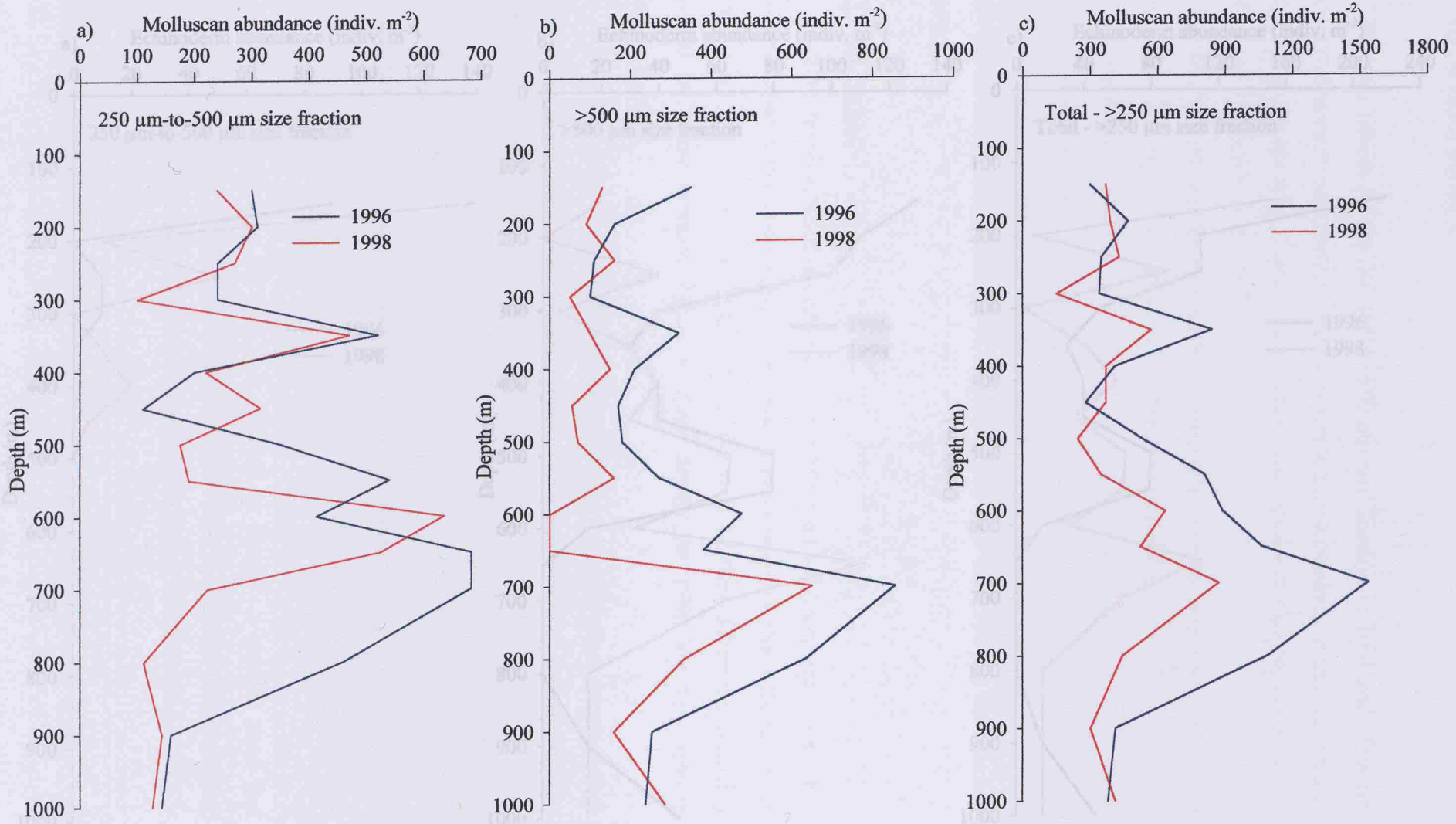


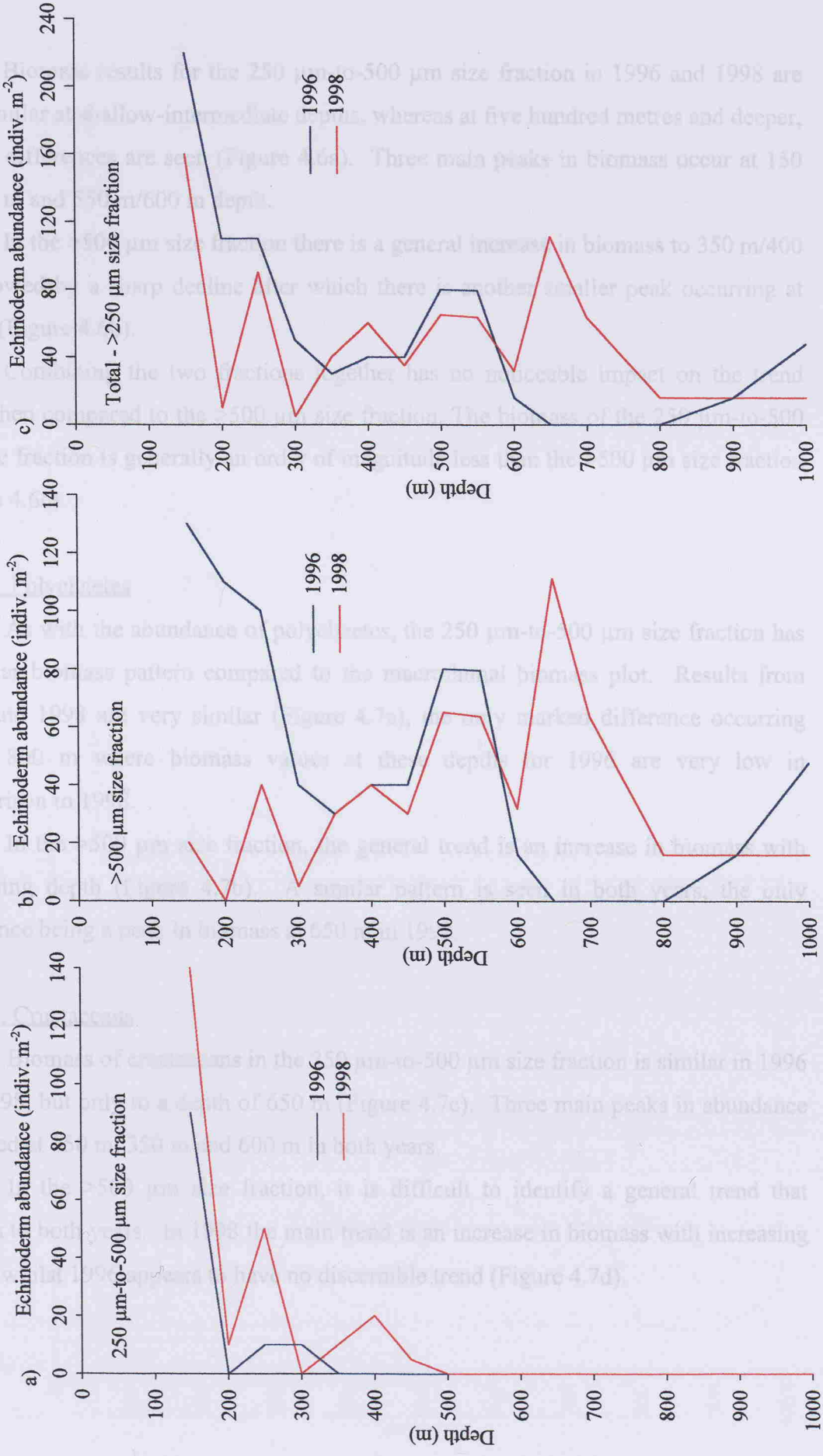
Figures 4.2a-c. Comparison of polychaete abundance in each year and in the three size fractions.



Figures 4.3a-c. Comparison of crustacean abundance in each year and in the three size fractions.

Figures 4.4a-c. Comparison of molluscan abundance in each year and in the three size fractions.





Figures 4.5a-c. Comparison of echinoderm abundance in each year and in the three size fractions.

4.3.2. Macrofaunal biomass

Biomass results for the 250 µm-to-500 µm size fraction in 1996 and 1998 are very similar at shallow-intermediate depths, whereas at five hundred metres and deeper, greater differences are seen (Figure 4.6a). Three main peaks in biomass occur at 150 m, 350 m and 550 m/600 m depth.

In the >500 µm size fraction there is a general increase in biomass to 350 m/400 m followed by a sharp decline after which there is another smaller peak occurring at 700 m (Figure 4.6b).

Combining the two fractions together has no noticeable impact on the trend seen when compared to the >500 µm size fraction. The biomass of the 250 µm-to-500 µm size fraction is generally an order of magnitude less than the >500 µm size fraction (Figure 4.6c).

4.3.2.1. Polychaetes

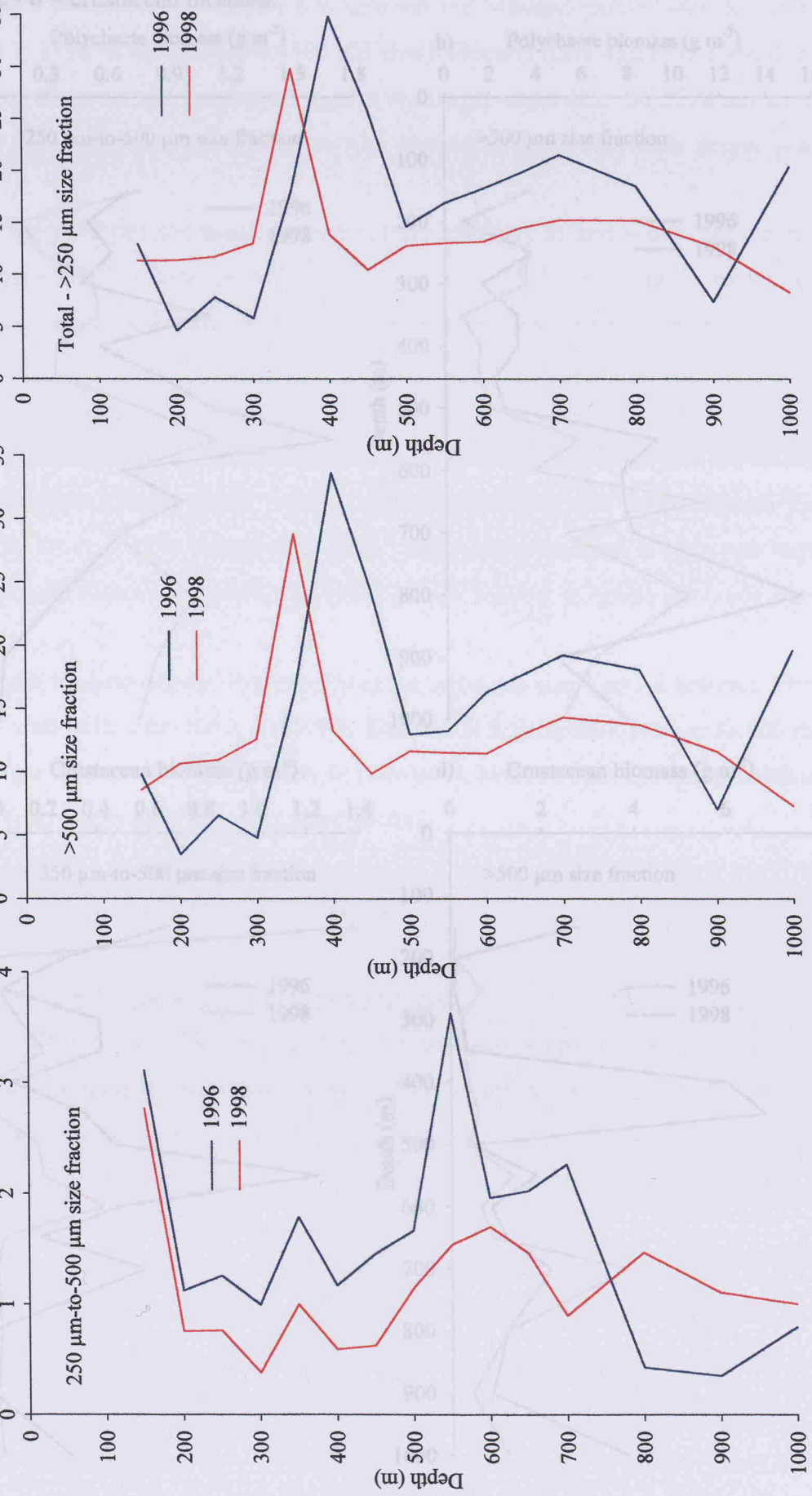
As with the abundance of polychaetes, the 250 µm-to-500 µm size fraction has a similar biomass pattern compared to the macrofaunal biomass plot. Results from 1996 and 1998 are very similar (Figure 4.7a), the only marked difference occurring below 800 m where biomass values at these depths for 1996 are very low in comparison to 1998.

In the >500 µm size fraction, the general trend is an increase in biomass with increasing depth (Figure 4.7b). A similar pattern is seen in both years, the only difference being a peak in biomass at 650 m in 1998.

4.3.2.2. Crustaceans

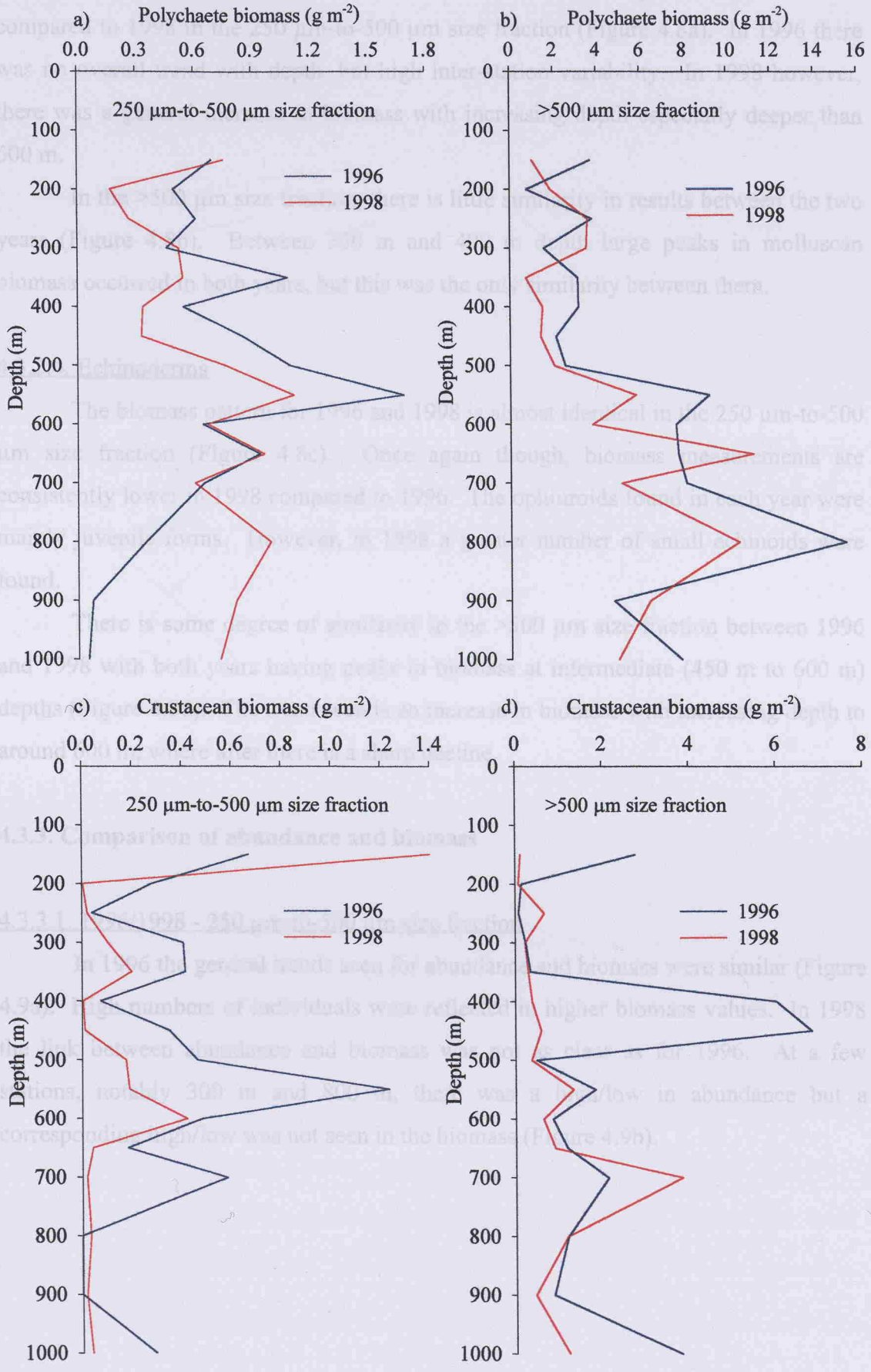
Biomass of crustaceans in the 250 µm-to-500 µm size fraction is similar in 1996 and 1998, but only to a depth of 650 m (Figure 4.7c). Three main peaks in abundance occurred at 150 m, 350 m and 600 m in both years.

In the >500 µm size fraction, it is difficult to identify a general trend that applies to both years. In 1998 the main trend is an increase in biomass with increasing depth, whilst 1996 appears to have no discernible trend (Figure 4.7d).



Figures 4.6a-c. Comparison of macrofaunal wet weight biomass in each year and in the three size fractions.

Figures 4.7a-d. Comparison of polychaete and crustacean wet weight biomass in each year and in the 250 µm-to-500 µm and >500 µm size fraction. a - b = polychaete biomass, c - d = crustacean biomass.



4.3.2.3. Molluscs

There are almost no similarities between the biomass pattern seen for 1996 compared to 1998 in the 250 μm-to-500 μm size fraction (Figure 4.8a). In 1996 there was no overall trend with depth, but high inter-station variability. In 1998 however, there was a general increase in biomass with increasing depth especially deeper than 600 m.

In the >500 μm size fraction, there is little similarity in results between the two years (Figure 4.8b). Between 350 m and 400 m depth large peaks in molluscan biomass occurred in both years, but this was the only similarity between them.

4.3.2.4. Echinoderms

The biomass pattern for 1996 and 1998 is almost identical in the 250 μm-to-500 μm size fraction (Figure 4.8c). Once again though, biomass measurements are consistently lower in 1998 compared to 1996. The ophiuroids found in each year were mainly juvenile forms. However, in 1998 a greater number of small echinoids were found.

There is some degree of similarity in the >500 μm size fraction between 1996 and 1998 with both years having peaks in biomass at intermediate (450 m to 600 m) depths (Figure 4.8d). The trend seen is an increase in biomass with increasing depth to around 600 m, where after there is a sharp decline.

4.3.3. Comparison of abundance and biomass

4.3.3.1. 1996/1998 - 250 μm-to-500 μm size fraction

In 1996 the general trends seen for abundance and biomass were similar (Figure 4.9a). High numbers of individuals were reflected in higher biomass values. In 1998 the link between abundance and biomass was not as clear as for 1996. At a few stations, notably 300 m and 800 m, there was a high/low in abundance but a corresponding high/low was not seen in the biomass (Figure 4.9b).

Figures 4.8a-d. Comparison of molluscan and echinoderm wet weight biomass in each year and in the 250 µm-to-500 µm and >500 µm size fraction. a - b = molluscan biomass, c - d = echinoderm biomass.

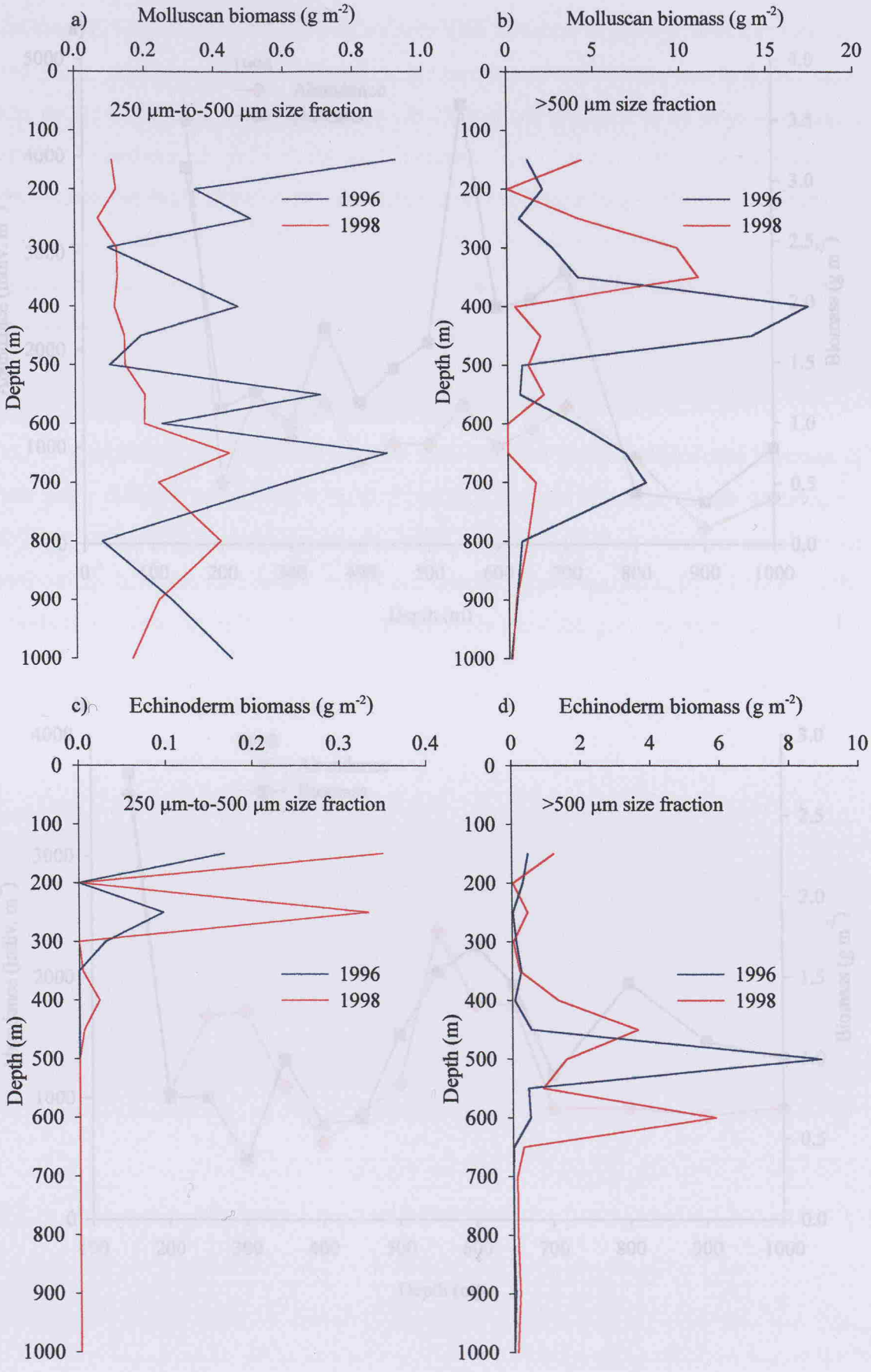
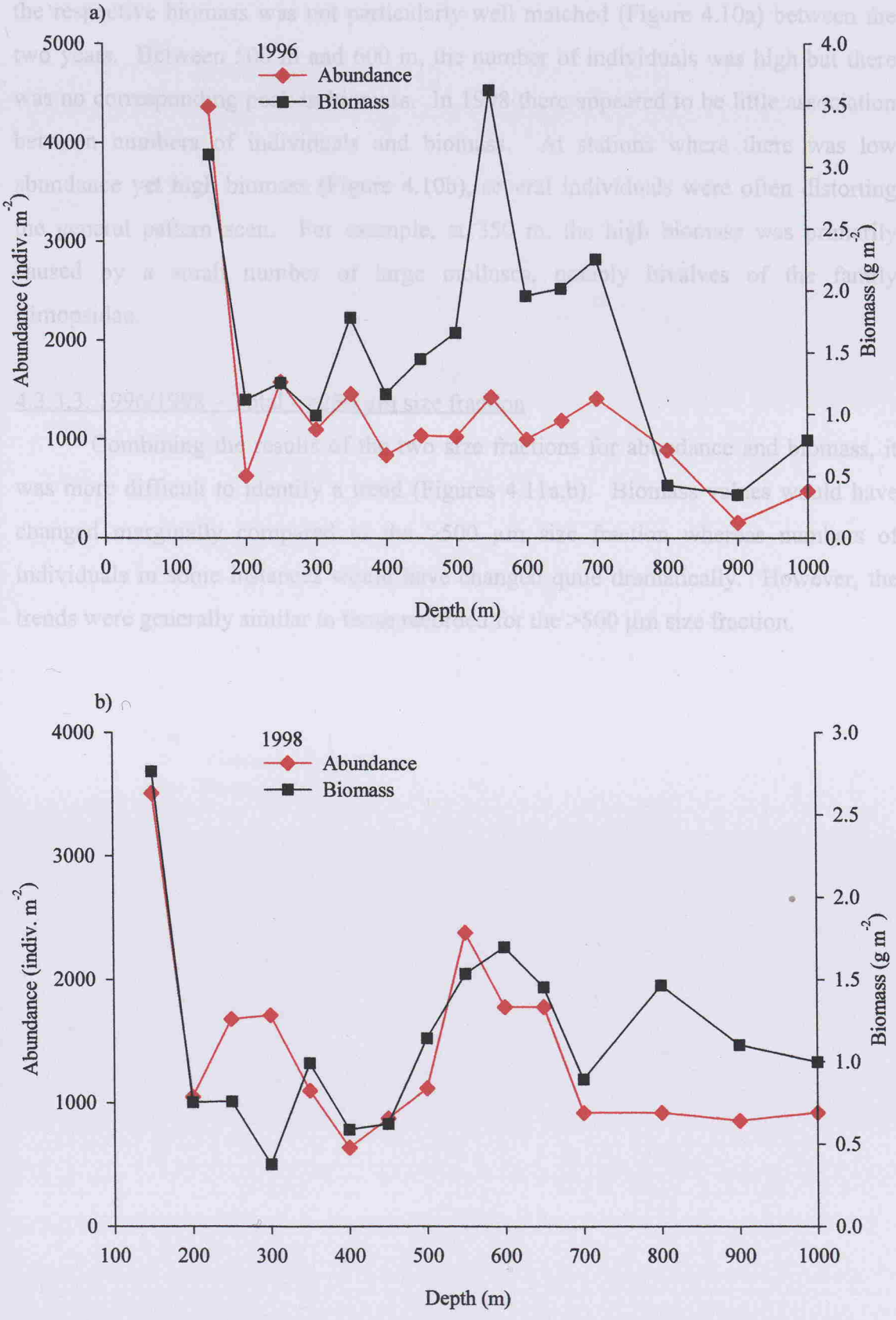


Figure 4.9a,b. Comparison of the distribution of faunal abundance and biomass in the 250 µm-to-500 µm size fraction for 1996 and 1998.



4.3.3.2. 1996/1998 - >500 µm size fraction

In contrast to the 250 µm-to-500 µm size fraction the number of individuals and the respective biomass was not particularly well matched (Figure 4.10a) between the two years. Between 500 m and 600 m, the number of individuals was high but there was no corresponding peak in biomass. In 1998 there appeared to be little association between numbers of individuals and biomass. At stations where there was low abundance yet high biomass (Figure 4.10b), several individuals were often distorting the general pattern seen. For example, at 350 m, the high biomass was primarily caused by a small number of large molluscs, notably bivalves of the family Limopsidae.

4.3.3.3. 1996/1998 – Total - >250 µm size fraction

Combining the results of the two size fractions for abundance and biomass, it was more difficult to identify a trend (Figures 4.11a,b). Biomass values would have changed marginally compared to the >500 µm size fraction whereas numbers of individuals in some instances would have changed quite dramatically. However, the trends were generally similar to those recorded for the >500 µm size fraction.

Figure 4.10a,b. Comparison of the distribution of faunal abundance and biomass in the >500 µm size fraction for 1996 and 1998.

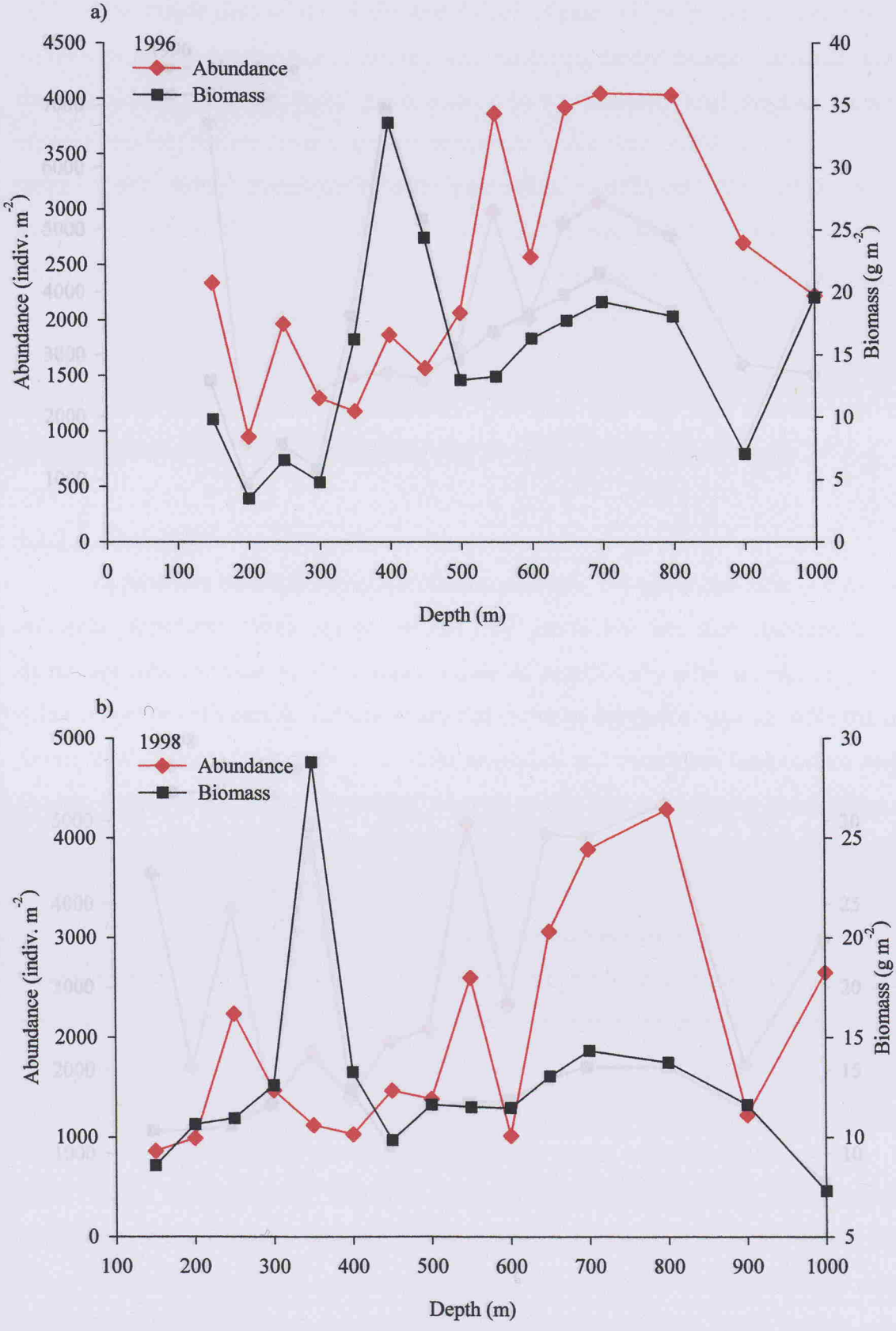
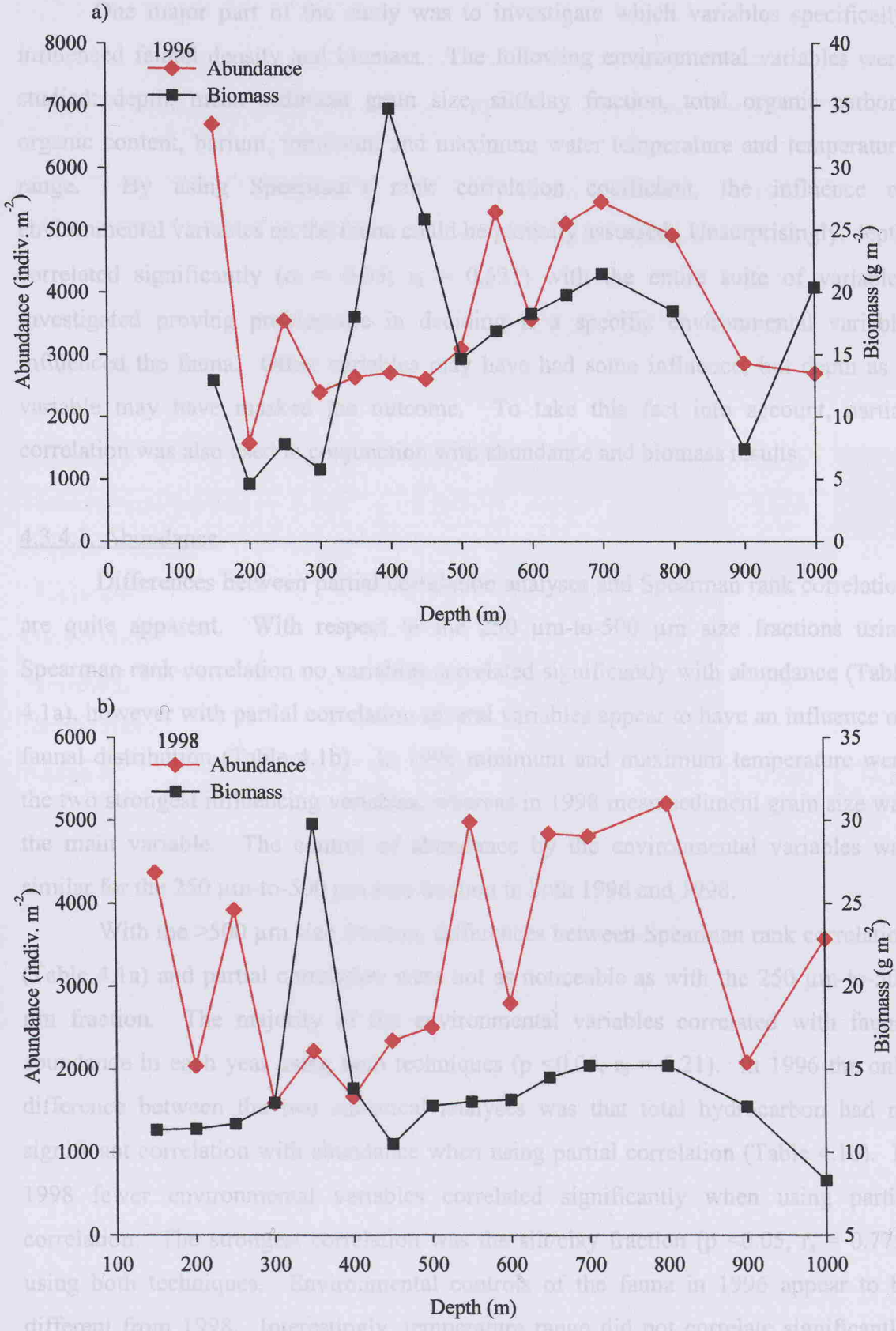


Figure 4.11a,b. Comparison of the distribution of faunal abundance and biomass in the Total - >250 µm size fraction for 1996 and 1998.



4.3.4. Spearman Rank Correlation Coefficient and Partial Correlation

One major part of the study was to investigate which variables specifically influenced faunal density and biomass. The following environmental variables were studied: depth, mean sediment grain size, silt/clay fraction, total organic carbon, organic content, barium, minimum and maximum water temperature and temperature range. By using Spearman's rank correlation coefficient, the influence of environmental variables on the fauna could be partially assessed. Unsurprisingly, depth correlated significantly ($\alpha = 0.05$; $r_s = 0.521$) with the entire suite of variables investigated proving problematic in deciding if a specific environmental variable influenced the fauna. Other variables may have had some influence, but depth as a variable may have masked the outcome. To take this fact into account, partial correlation was also used in conjunction with abundance and biomass results.

4.3.4.1. Abundance

Differences between partial correlation analyses and Spearman rank correlation are quite apparent. With respect to the 250 μm-to-500 μm size fractions using Spearman rank correlation no variables correlated significantly with abundance (Table 4.1a), however with partial correlation several variables appear to have an influence on faunal distribution (Table 4.1b). In 1996 minimum and maximum temperature were the two strongest influencing variables, whereas in 1998 mean sediment grain size was the main variable. The control of abundance by the environmental variables was similar for the 250 μm-to-500 μm size fraction in both 1996 and 1998.

With the >500 μm size fraction, differences between Spearman rank correlation (Table 4.1a) and partial correlation were not as noticeable as with the 250 μm-to-500 μm fraction. The majority of the environmental variables correlated with faunal abundance in each year using both techniques ($p < 0.05$, $r_s = 5.21$). In 1996 the only difference between the two statistical analyses was that total hydrocarbon had no significant correlation with abundance when using partial correlation (Table 4.1b). In 1998 fewer environmental variables correlated significantly when using partial correlation. The strongest correlation was the silt/clay fraction ($p < 0.05$, $r_s = 0.775$) using both techniques. Environmental controls of the fauna in 1996 appear to be different from 1998. Interestingly, temperature range did not correlate significantly.

However, when it was held constant and abundance correlated with the remaining variables all, with the exception of barium, correlated significantly.

Table 4.1a. Spearman rank correlation values for abundance in the three fractions and both years. n = 15, $\alpha = 0.05$, $r_s = 0.521$. Significant correlation values are shaded in grey.

	1996	1998	1996	1998	1996	1998
	250 µm-to-500 µm	250 µm-to-500 µm	>500 µm	>500 µm	Total - >250 µm	Total - >250 µm
Depth	-0.504	-0.253	0.679	0.686	0.251	0.200
Mean sediment grain size	-0.496	-0.484	0.446	0.589	0.084	0.075
Silt/clay	-0.143	0.023	0.754	0.775	0.450	0.554
Total organic carbon	0.088	0.111	-0.164	0.673	0.360	0.540
Organic content	-0.100	0.242	0.839	0.557	0.604	-0.315
Maximum temperature	0.506	0.257	-0.685	-0.677	-0.255	-0.204
Minimum temperature	0.456	0.239	-0.702	-0.692	-0.283	-0.222
Range of temperature	0.331	0.120	-0.620	-0.463	-0.370	-0.315
Total hydrocarbon	0.005	0.267	0.571	0.596	0.351	0.777
Barium	-0.236	0.052	0.750	0.639	0.475	0.479

The difference in results between Spearman rank correlation and partial correlation for the total - >250 µm size fraction in 1996 are almost negligible. In 1998 however, several variables, in particular silt/clay and organic content, appear to have a strong effect on the fauna (Table 4.1b).

Table 4.1b. Abundance partial correlation results for the three fractions: indicating total number of times an environmental variable had a significant correlation; n = 12, $p<0.05$, $r_s = 0.532$

	250 µm-to-500 µm		>500 µm		Total - >250 µm	
	1996	1998	1996	1998	1996	1998
Depth	3	2	1	1	0	1
Mean sediment grain size	3	4	0	0	0	0
Silt/clay	3	1	4	8	1	4
Total organic carbon	3	1	0	1	0	2
Organic content	0	3	8	0	4	3
Maximum temperature	4	2	3	1	3	1
Minimum temperature	4	2	4	1	0	1
Range of temperature	0	0	2	0	0	1
Total hydrocarbon	1	3	0	0	0	0
Barium	0	0	2	0	0	0

4.3.4.2. Biomass

None of the environmental variables were correlated with the biomass of the 250 µm-to-500 µm size fraction when using Spearman's rank correlation (Table 4.2a). However, with partial correlation several variables appeared to correlate with the biomass. In 1996 all but temperature range correlated with biomass (Table 4.2b) whereas in 1998 only organic content showed a significant correlation with both Spearman's rank correlation ($p = 0.05$, $r_s = 0.643$) and partial correlation.

In the >500 µm size fraction few variables appeared to correlate with faunal biomass when using Spearman's rank correlation (Table 4.2a). However, partial correlation had more variables significantly correlating with biomass (Table 4.2b). In 1996 the silt/clay fraction was the variable that correlated most often, whereas in 1998 it was mean sediment grain size.

Table 4.2a. Spearman rank correlation values for biomass in the three fractions and both years. n = 15, α = 0.05, r_s = 0.521. Significant correlation values are shaded in grey.

	1996	1998	1996	1998	1996	1998
	250 µm-to-500 µm	250 µm-to-500 µm	>500 µm	>500 µm	Total - >250 µm	Total - >250 µm
Depth	-0.239	0.293	0.499	0.189	0.446	0.221
Mean sediment grain size	-0.336	0.064	0.574	0.461	0.525	0.450
Silt/clay	0.125	0.346	0.556	0.239	0.546	0.368
Total organic carbon	0.199	0.315	0.044	0.254	0.521	0.386
Organic content	0.232	0.643	0.319	-0.011	0.289	0.073
Maximum temperature	0.243	-0.295	-0.484	-0.202	-0.431	-0.231
Minimum temperature	0.179	-0.277	-0.470	-0.195	-0.420	-0.220
Range of temperature	0.282	-0.402	0.037	0.123	0.095	0.073
Total hydrocarbon	0.280	0.434	0.383	0.111	0.408	0.278
Barium	0.095	-0.020	-0.061	0.504	0.071	0.073

Combining the two fractions together for each year there is no difference in the results compared to the >500 µm size fraction results for both Spearman's rank and partial correlation.

Table 4.2b. Biomass partial correlation results for the three fractions: indicating number of times an environmental variable had a significant correlation; n = 12, $p<0.05$, $r_s = 0.532$

	250 µm-to-500 µm		>500 µm		Total - >250 µm	
	1996	1998	1996	1998	1996	1998
Depth	3	0	1	1	1	0
Mean sediment grain size	3	0	1	2	1	1
Silt/clay	3	0	2	0	2	0
Total organic carbon	1	0	1	0	1	0
Organic content	3	5	0	0	0	0
Maximum temperature	3	0	1	0	1	0
Minimum temperature	2	0	1	0	1	0
Range of temperature	0	0	0	0	0	0
Total hydrocarbon	3	0	0	0	0	0
Barium	0	0	0	0	0	0

4.3.5. Canonical Correspondence Analysis

Initially Bray-Curtis dendrograms and multi-dimensional scaling ordination plots were used to identify similarities/difference between stations. However, whilst MDS allows phyla and environmental variables to be superimposed, no formal statistical significance test can be ascribed to it. Using canonical correspondence analysis, fauna, environmental variables and stations can all be plotted on one ordination diagram.

Initially, depth was left in the analyses as a variable. However, when using the Monte Carlo significance test it was seen that depth strongly influenced the fauna i.e. depth accounted for over 50% of the variance. By removing depth from the analyses, the effect of the remaining variables could be seen on the fauna and the stations. In some ordination plots various environmental variables were removed, as they were found to be co-linear.

4.3.5.1. Abundance

The CCA ordination plots for the 250 µm-to500 µm size fraction for both 1996

and 1998 indicate that temperature is the main variable influencing the faunal community (Figure 4.12a,b). In both years, the echinoderms were strongly related to the maximum temperature gradient. Temperature also accounts for most of the variability seen with regards to the fauna when using the Monte Carlo permutation test (Table 4.3).

Looking specifically at the ordination plots it is noticeable that the eigenvectors do not take into account all the variability that is seen. In the 250 μm-to-500 μm 1996 ordination plot a circle drawn round a group of stations and fauna indicates that there is no environmental variable influencing them. In 1998, however, there are two stations, 150 m and 800 m, which lie diagonally opposite and no eigenvector takes into account their position on the ordination plot.

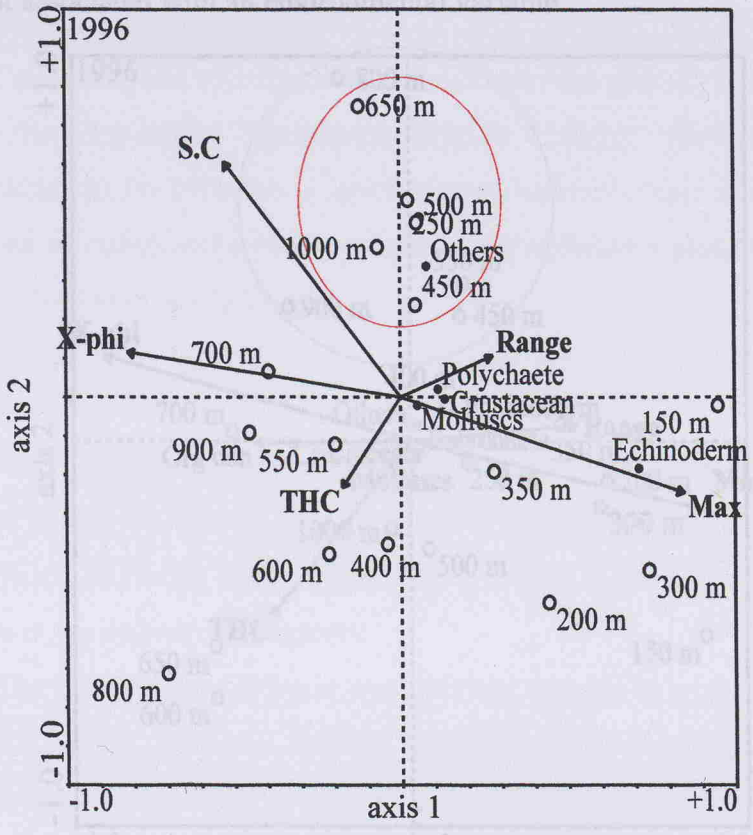
Table 4.3. Results from the Monte Carlo permutation test analysing influence of environmental variables on faunal abundance. Variance of variables accepted at 0.05 significance level. (Min = Minimum temperature, Max = Maximum temperature, X-phi = mean sediment grain size).

Size fraction/year	Unconstrained eigenvalue	Canonical eigenvalue	Variance of variable	Variable
250 μm-to-500μm 1996	0.142	0.112	0.06	Min
250 μm-to-500μm 1998	0.107	0.075	0.05	Max
>500μm 1996	0.036	0.031	0.02	X-phi
>500μm 1998	0.071	0.046	(0.01) (0.01)	Min & Max
Total - >250 μm 1996	0.039	0.033	0.02	X-phi
Total - >250 μm 1998	0.044	0.022	0.01	Min

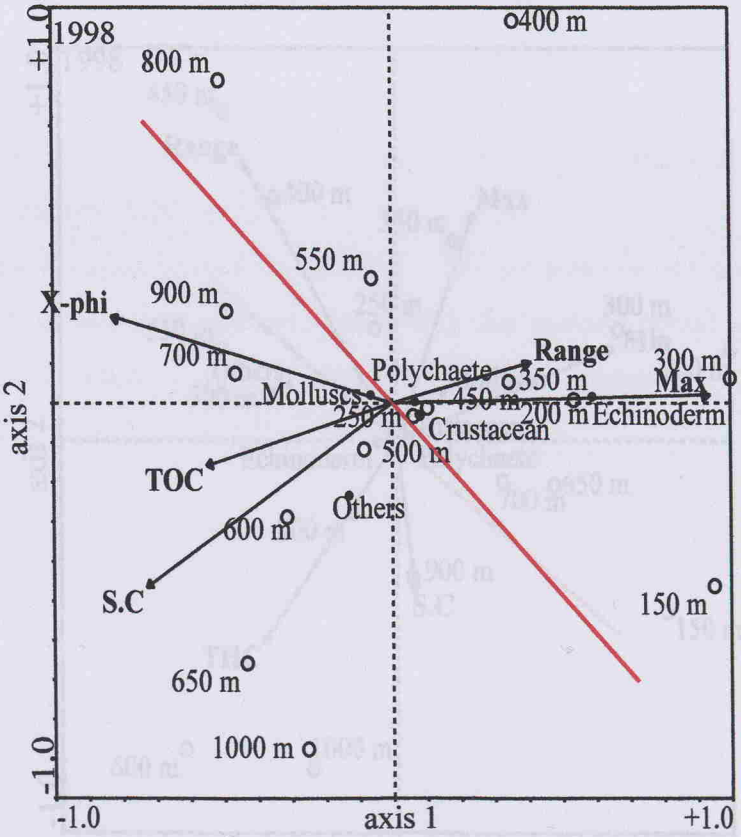
In the 1996 >500 μm size fraction the fauna appear to lie close to the temperature variable (Figure 4.13a), however, the results from the Monte Carlo test suggests that mean sediment grain size is the variable influencing the fauna most strongly. For 1998 however, there appears to be a less well-defined environmental variable influencing the fauna (Figure 4.13b), although from the Monte Carlo test, temperature is closely related to faunal community variation.

Figures 4.12a,b. CCA ordination plots of phyla abundance, stations and environmental variables for the 250 µm-to-500 µm size fraction in 1996 and 1998. Max = maximum temperature, range = temperature range, X-phi = mean sediment grain size, S.C = silt/clay, THC = total hydrocarbons. o = station, • = fauna, ⟶ = environmental variable. The red circle and line indicates a group of stations not associated with an environmental variable.

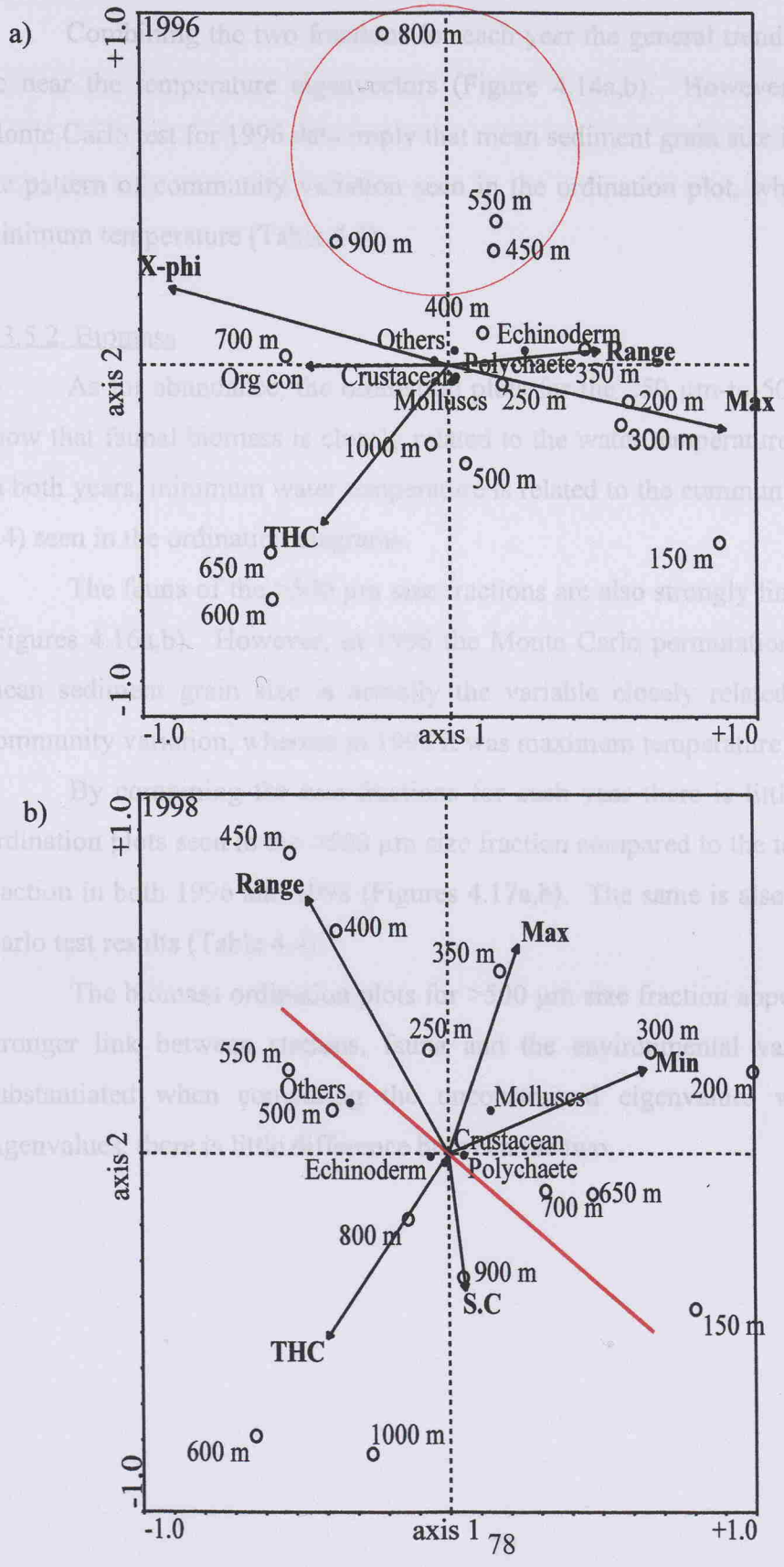
a)



b)



Figures 4.13a,b. CCA ordination plots of phyla abundance, stations and environmental variables for the >500 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, S.C = silt/clay, Org con = organic content, THC = total hydrocarbons. • = station, o = fauna, ⟶ = environmental variable. The red circle and line indicates a group of stations not associated with an environmental variable



The ordination plot for the >500 μm size fraction in 1996 suggests that most variability is accounted for by the environmental variables, and this is substantiated by the small difference, 0.005, between the unconstrained and canonical eigenvalues (Table 4.3). In 1998, the 150 m and 550 m stations lie diagonally opposite one another as seen in the small size fraction.

Combining the two fractions for each year the general trend is for the fauna to lie near the temperature eigenvectors (Figure 4.14a,b). However, results from the Monte Carlo test for 1996 data imply that mean sediment grain size is closely related to the pattern of community variation seen in the ordination plot, whereas in 1998 it is minimum temperature (Table 4.3).

4.3.5.2. Biomass

As for abundance, the ordination plots for the 250 μm-to-500 μm size fraction show that faunal biomass is closely related to the water temperature (Figures 4.15a,b). In both years, minimum water temperature is related to the community variation (Table 4.4) seen in the ordination diagrams.

The fauna of the >500 μm size fractions are also strongly linked to temperature (Figures 4.16a,b). However, in 1996 the Monte Carlo permutation test suggests that mean sediment grain size is actually the variable closely related to the pattern of community variation, whereas in 1998 it was maximum temperature (Table 4.4).

By combining the two fractions for each year there is little difference in the ordination plots seen in the >500 μm size fraction compared to the total - >250 μm size fraction in both 1996 and 1998 (Figures 4.17a,b). The same is also true for the Monte Carlo test results (Table 4.4).

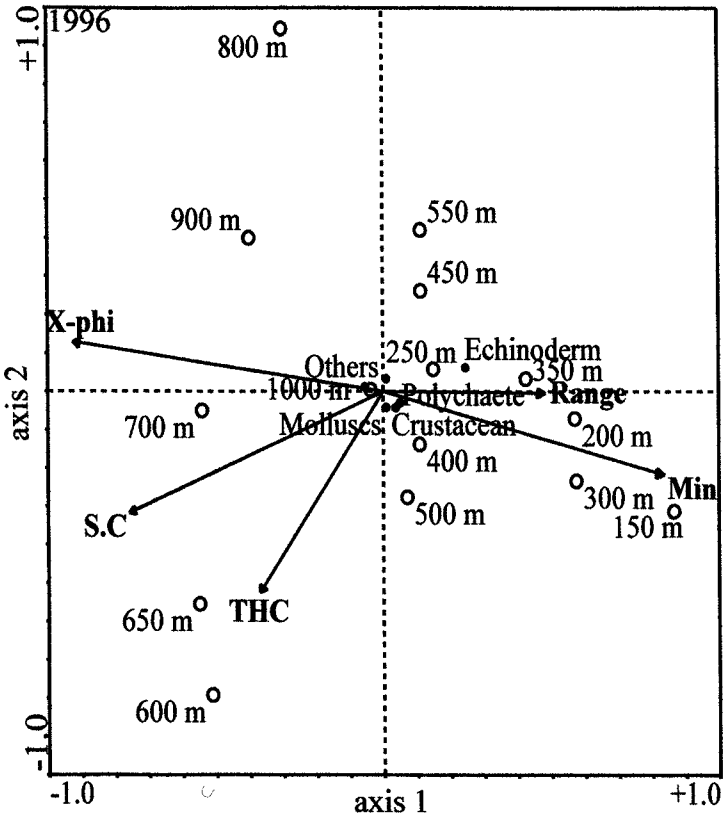
The biomass ordination plots for >500 μm size fraction appear to show a much stronger link between stations, fauna and the environmental variables and this is substantiated when comparing the unconstrained eigenvalues with the canonical eigenvalues, there is little difference between the two.

Table 4.4. Results from the Monte Carlo permutation test analysing influence of environmental variables on faunal biomass. Variance of variable accepted at 0.05 significance level. (Min = Minimum temperature, Max = Maximum temperature, X-phi = mean sediment grain size).

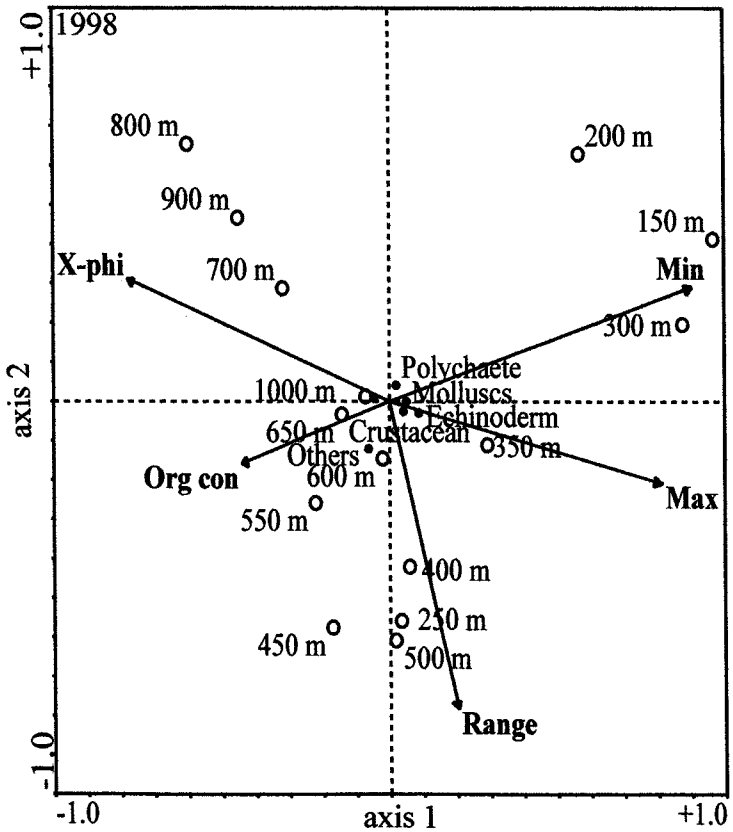
Size fraction/year	**Unconstrained eigenvalue**	**Canonical eigenvalue**	**Variance of variable**	**Variable**
250µm-to-500µm 1996	0.067	0.053	0.01	Min
250µm-to-500µm 1998	0.039	0.029	0.02	Min
>500µm 1996	0.032	0.023	0.01	X-phi
>500µm 1998	0.034	0.029	0.02	Max
Total - >250 µm 1996	0.031	0.023	0.01	X-phi
Total - >250 µm 1998	0.028	0.023	0.02	Max

Figures 4.14a ,b. CCA ordination plots of phyla abundance, stations and environmental variables for the total - >250 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, S/C = silt:clay, Org con = organic content, THC = total hydrocarbons. o = station, • = fauna, ⟶ = environmental variable

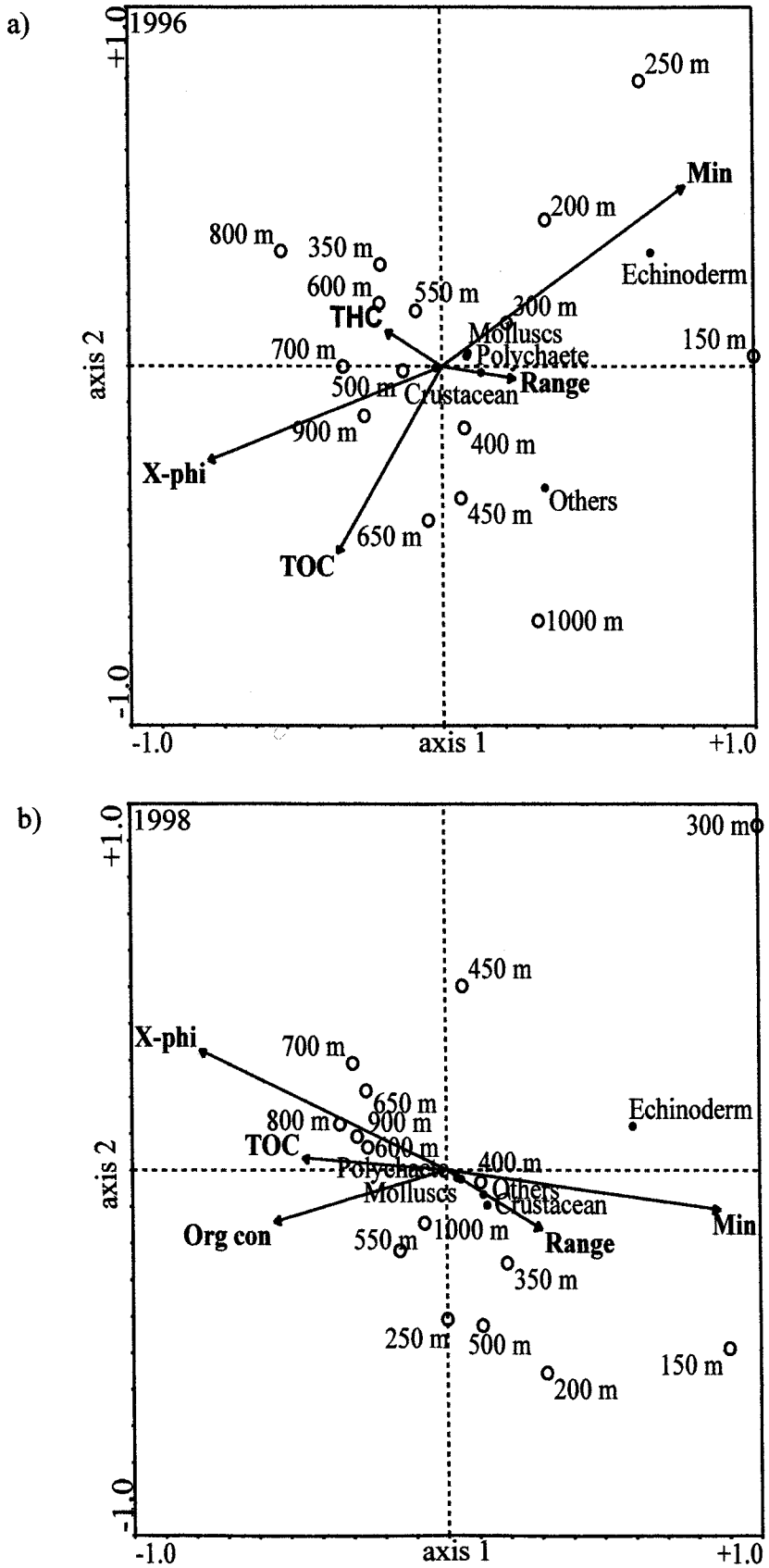
a)



b)

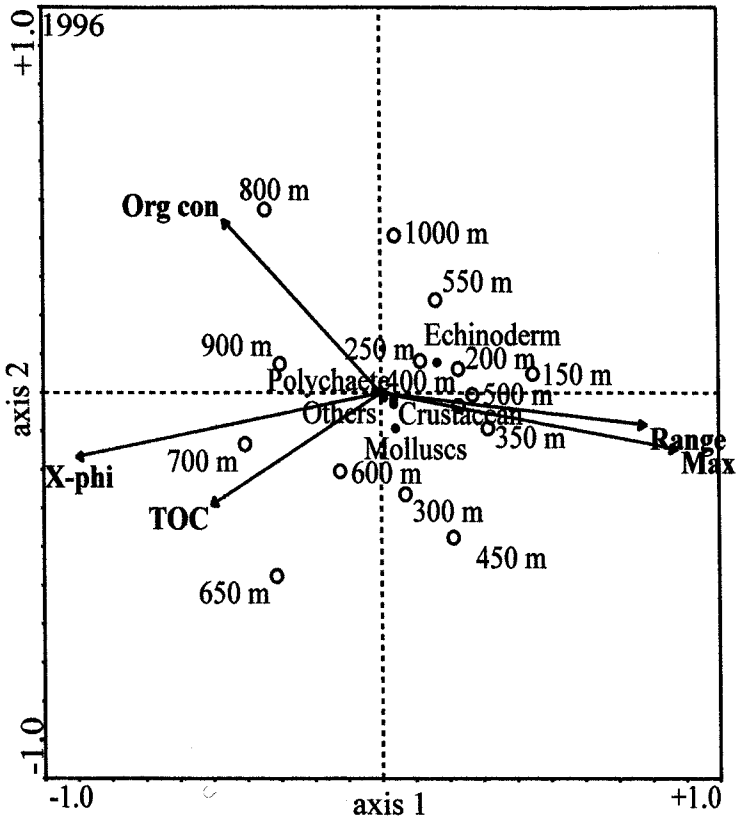


Figures 4.15a,b. CCA ordination plots of phyla biomass, stations and environmental variables for the 250 µm-to-500 µm size fraction in 1996 and 1998. Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content, TOC = total organic carbon, THC = total hydrocarbons. o = station, • = fauna, ⟶ = environmental variable

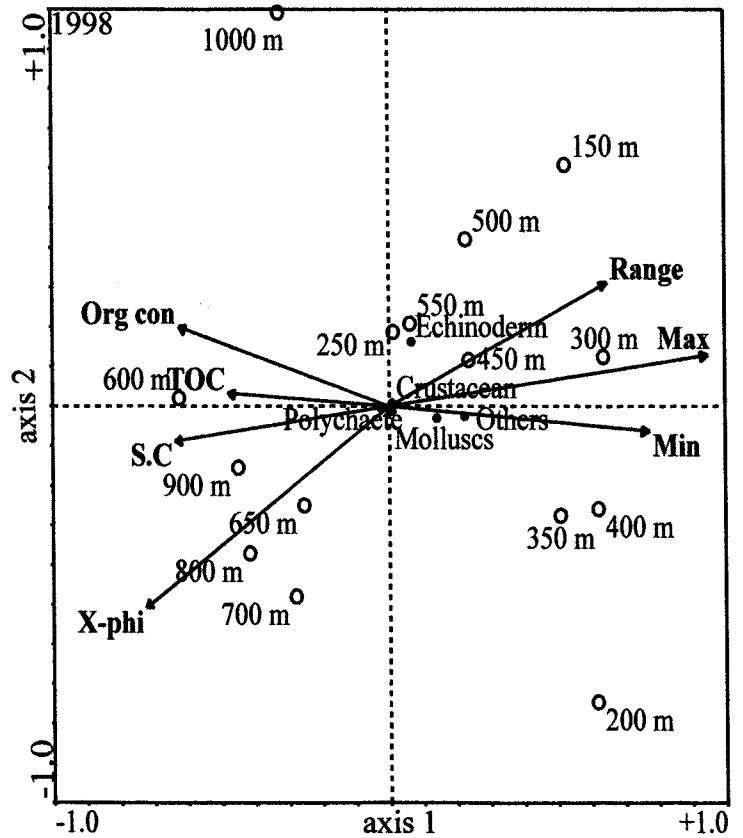


Figures 4.16a,b. CCA ordination plots of phyla biomass, stations and environmental variables for the >500 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content, TOC = total organic carbon, S.C = silt/clay. o = station, • = fauna, ⟶ = environmental variable

a)

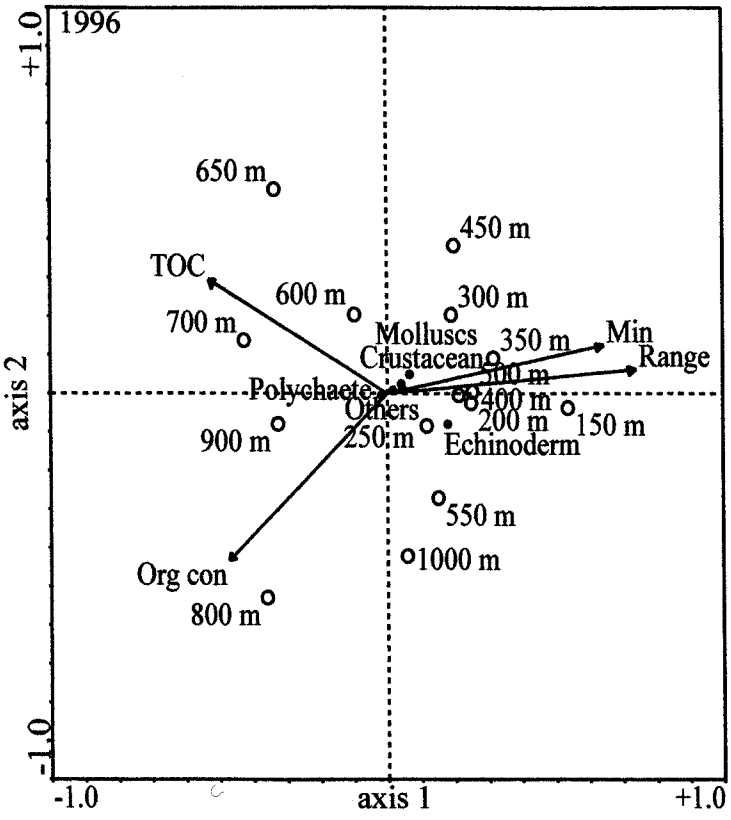


b)

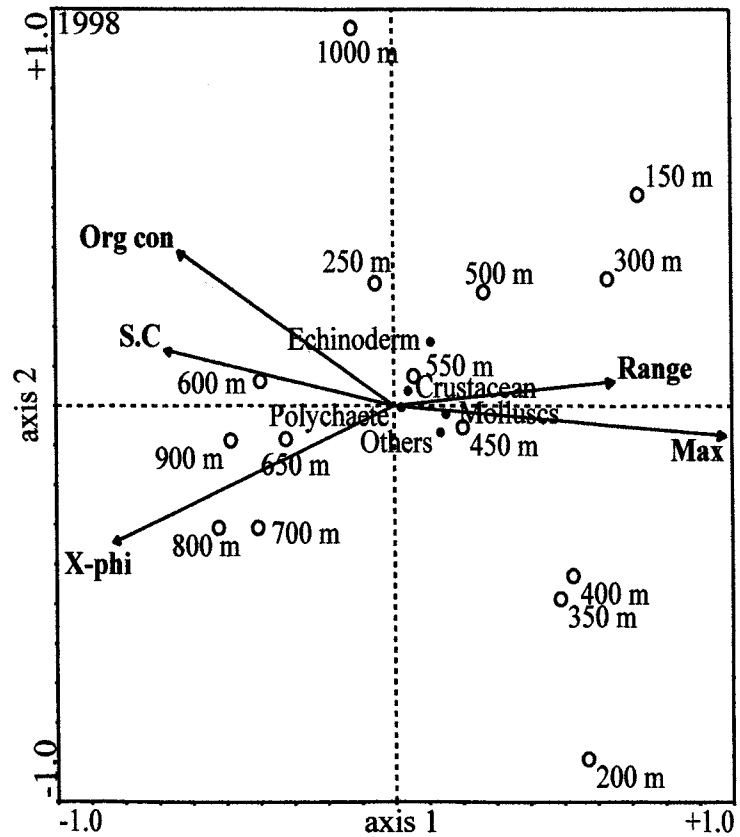


Figures 4.17a,b. CCA ordination plots of phyla biomass, stations and environmental variables for the Total - >250 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content, TOC = total organic carbon, S.C = silt/clay. o = station, • = fauna, ⟶ = environmental variable

a)



b)



4.4. DISCUSSION

4.4.1. Faunal abundance and biomass

On a global basis the general expectation is for deep-sea macrofaunal abundance and biomass to decline with increasing depth (Vinogradova, 1962; Rowe and Menzel, 1971; Rowe, 1983). This same pattern is seen on a more local scale in the Northeast Atlantic (Heip *et al.*, 1996). Biomass tends to exhibit a much stronger exponential decline with increasing depth (Rowe, 1983; Gage and Tyler, 1991) in comparison to abundance, which does not decline as rapidly (Gage *et al.*, 2000). On the Hebridean slope, a decline in abundance and biomass with depth was seen below 1000 m, however, between 600 m and 1000 m a maximum in biomass was observed (Gage *et al.*, 2000). The decline is thought to correspond with the attenuated supply of organic matter, for as depth increases the material in the water column has an increased possibility of being intercepted by mid-water animals (Sibuet *et al.*, 1989). However, variations on this general trend have been found regarding both biomass and abundance. Jumars and Gallagher (1982) found major differences in abundance from samples at similar depths but different geographical locations, as did Rowe (1983), who compared biomass values from similar depths from different regions. Large differences in faunal density were also seen at three sites situated at a similar depth although only 150 km apart (Schaff *et al.*, 1992; DeMaster *et al.*, 1994). Local differences in organic flux may result in differences between sites, but the general trend still stands.

In this study a general decline in abundance with increasing depth is seen in the 250 μm-to-500 μm size fraction, yet the >500 μm size fraction and the total - >250 μm size fraction both show an overall increase in abundance with increasing depth. In the Arctic Eurasian Basin decreasing macrofaunal abundance (>500 μm) was correlated significantly with depth (Kröncke *et al.*, 2000), the reverse of that seen in the Faeroe-Shetland Channel. Biomass in all three fractions tends to peak at intermediate depths (350 m to 600 m) along the transect in the Faeroe-Shetland Channel. In the >500 μm size fraction this increase was a result of several large molluscs skewing the biomass data. Contrastingly, in the 250 μm-to-500 μm size fraction the peak in biomass was caused by polychaetes. The marked peak in mollusc biomass at intermediate depths was also seen in the 1996 Atlantic Frontier Environmental Network (AFEN) survey

area (Bett, 2000). In the survey this peak corresponds with a decrease in polychaete biomass, which is also seen along the transect. The molluscs in this depth band (300 m to 400 m) are mainly suspension-feeding limopsids. Correlating molluscan biomass with the suite of environmental variables, it was found that there was a significant association between biomass in 1996 and barium normalised to aluminium. However, in 1998, molluscan biomass showed significant correlations with the majority of the environmental variables examined, the exceptions being total organic carbon and barium, although peaks in biomass also seemed to be linked to slight peaks in total organic carbon, silt/clay fraction and a large increase in the temperature range. That there was only one significant correlation between molluscan biomass and environmental variables in 1996, and several in 1998, may possibly be because the analyses are based on environmental data collected only in 1996 (see Chapter 3).

Spearman's rank correlation implies that only abundance of the >500 μm size fraction is significantly related with depth. However, the AFEN 1996 survey conducted in the rest of the Faeroe-Shetland Channel showed a non-significant relationship between abundance/biomass and depth (Bett, 2000). Care, however, must be taken when comparing these results as the 250 μm-to-500 μm size fraction, although collected, was not processed, therefore the results from the AFEN 1996 survey are based upon the >500 μm size fraction. The 250 μm-to-500 μm size fraction in the present study must therefore have a relatively strong influence in determining the interaction between the fauna and depth and also the other environmental variables that have been used. This becomes apparent when comparing the significance values of the >500 μm fraction with the total - >250 μm size fraction. Partial correlation was useful in determining which environmental variables may be influencing the distribution of the fauna and this coincided with the most significant Spearman's rank correlation. It also suggested that with regards to the 250 μm-to-500 μm size fraction, depth was possibly acting as a co-variable and masking the effect of the other environmental variables on the fauna. As seen in this region, depth is not the main variable controlling faunal abundance or biomass.

Rowe (1983) argued that benthic biomass was a more relevant measure in marine studies than abundance per unit area. This was based on work undertaken by Rowe and Menzel (1971), which showed that organic carbon weight, dry weight and even wet weight were all better indicators of ecological conditions. Sanders *et al.* (1965) argued that in a small sample area the presence or absence of a large, rare,

sporadically distributed animal could increase the total biomass between 2 and 50 times. Therefore because of this variation, comparing samples of biomass between different regions was questionable and comparing numbers of individuals was more reliable (Sanders *et al.*, 1965). However, in a study such as the present where a 250 μm mesh has also been used, both faunal abundance and biomass are equally important, a view proposed by Paul and Menzies (1974) in their studies of high arctic benthos.

Specific peaks and troughs seen in abundance/biomass plots may sometimes be explained by a similar pattern seen with respect to the environmental variables. Generally both the 250 μm-to-500 μm size fraction and the >500 μm size fraction show peaks in faunal abundance that correspond to relatively coarse sediment, although, in the larger fraction, a large peak at 800 m also happens to coincide with very fine sediment. The >500 μm and total - >250 μm size fractions also show a generally similar response to temperature. Where the water temperature is relatively high, or the temperature range is greatest, faunal abundance is quite low and vice-versa. The peaks in faunal abundance noted at 550 m and 700 m along the transect are also seen in the rest of the survey results (Bett, 2000). Russell *et al.* (1999) studied the labile organic matter taken from sediment samples collected along the transect. These authors found that the sediments were more enriched with labile organic matter at intermediate depths. Bett (2000) has suggested that the peaks in macrofaunal abundance at intermediate depths seen in the AFEN 1996 survey may correspond with the organically enriched sediment.

In their studies of Arctic benthos, Paul and Menzies (1974) found that whilst polychaetes comprised 42% of the total number of individuals they only accounted for 5% of the total biomass. Along the study transect in the Faeroe-Shetland Channel, polychaetes dominated the faunal abundance in all size fractions and in both years (Table 4.5), contributing between 33% and 83% of the total. The second most abundant taxon depended on the size fraction. For the 250 μm-to 500-μm size fraction, molluscs were more dominant (6% - 57%) than crustaceans, whereas in the >500 μm and total - >250 μm size fractions crustaceans were the more dominant (1% - 35%). However, unlike the results from the Arctic (Paul and Menzies, 1974) polychaetes also dominated faunal biomass ranging from 42% to 86% of the total biomass. Molluscs were the second most dominant and contributed between 15% and 58% of the total biomass. The results from the survey of the Faeroe-Shetland Channel found that at all depths polychaetes also numerically dominated the fauna (64% - 81%) whereas

biomass was more variable. On the upper slope and shelf, polychaetes contributed 20% to 40% of the total biomass; molluscs contributed 20% to 60%, whereas on the lower slope and on the channel floor, polychaetes contributed 60% to 80% of the total biomass (Bett, 2000).

Along the OMEX (Ocean Margin EXchange Programme) transect Heip *et al.* (1996) found that crustaceans became relatively more abundant in the community as water depth increased, the highest abundances being found at mid-slope depths. Although a direct comparison cannot be undertaken with the present study as stations along the Faeroe-Shetland Channel transect do not go as deep as the OMEX transect and a 500 μm sieve was used, similarities can be seen. Crustaceans were generally found to have a major peak in abundance in the >500 μm size fraction at a depth of 550 m in both 1996 and 1998. This was also seen in the 250 μm-to-500 μm size fraction collected in 1998.

Overall, the AFEN survey in 1996 found that crustaceans had a higher average faunal composition (43.6%) than the polychaetes (36.5%). Very similar results were also found in the Faeroe-Shetland Channel survey in 1998 as well as in the Rockall Trough: polychaetes 35.8% and 35.7%; crustaceans 41.1% and 40.3% respectively (Bett, 2000). However, these results differ somewhat from the transect results whereby polychaetes dominate the fauna overall (Table 4.5).

Table 4.5. Percentage composition of the five major groups in the 250 μm-to-500 μm, >500 μm and total - >250 μm size fractions in 1996 and 1998.

	250 μm-to-500 μm		**>500 μm**		**Total - >250 μm**	
	1996	**1998**	**1996**	**1998**	**1996**	**1998**
Polychaetes	50.5%	63.2%	60.2%	67.6%	57.1%	65.9%
Crustaceans	16.7%	11.9%	18.8%	19.6%	18.2%	16.4%
Molluscs	31.0%	19.8%	12.9%	8.6%	18.7%	13.1%
Echinoderms	0.7%	1.2%	1.9%	2.0%	1.6%	1.7%
Others	1.1%	3.9%	6.2%	2.2%	4.6%	2.9%

At the highest taxonomic level, it is very difficult to determine whether a specific environmental variable is having an effect on a particular group. Similarity dendrograms from the Bray-Curtis analysis and multi-dimensional scaling ordination

were not included as it was clear from the analyses that the level of phyla did not reveal much information. The stress levels also associated with the MDS plots were generally >0.1 suggesting that the representation was not so useful. There was no distinct separation into different depth or temperature bands, which is not surprising as one would expect to find the majority of the major phyla at all depths. Separation into different depth or temperature bands would be more likely seen once the fauna has been separated into genera or species (putative species) level.

Using CCA ordination plots, it was seen that echinoderms generally aligned themselves with a temperature eigenvector when using either abundance or biomass data. Molluscan abundance and biomass were also found to be generally associated with a temperature eigenvector, usually minimum temperature. However, there was found to be no significant correlation between abundance and temperature ($n = 15$, $\alpha = 0.05$, $r_s = 0.521$) when using Spearman's rank correlation, but there was a significant correlation between biomass and temperature. Polychaetes and crustaceans appear not to be strongly linked with any specific parameter as they are generally found at the centre of the ordination plots (ter Braak, 1987; ter Braak and Verdonschot, 1995). Although the suggestion is that no particular environmental variable influences the distribution of the polychaetes and crustaceans, this may be because species within each group are strongly linked to different variables.

From the data presented here in the current study, the hypothesis stating that standing stock of the Faeroe-Shetland Channel conforms to deep-sea expectations of an exponential decline with increasing depth must be rejected. However, these data show that standing stock is predominantly controlled by a suite of depth-related variables allowing this second hypothesis to be accepted.

STUDIES IN BENTHIC MACROFAUNAL ECOLOGY II: FAUNAL DIVERSITY OF THE WEST SHETLAND SLOPE

5.1. INTRODUCTION

5.1.1. Diversity

In the past, theories addressing the high deep-sea species diversity tend to assume that the environment of the deep-sea is more stable than the shallow water environment (Rex, 1983). In fact, until relatively recently, it was still believed that species richness and diversity in shallow water environments were much greater in comparison to the deep sea (Marshall, 1979). However, the supposedly tranquil deep-sea environment is known to be affected by strong currents causing scouring and rippling (e.g. Heezen and Hollister, 1971), benthic storms and fluctuations in the flow of deep currents (e.g. Dickson *et al.*, 1982).

Species richness varies both bathymetrically (*beta* diversity) as well as regionally (*gamma* diversity) within the deep-sea although the actual causes of the diversity gradients are far from understood. A number of suggestions have been put forward ranging from spatio-temporal heterogeneity to food availability and predation. These factors, as well as the physical effects on the environment are thought to play an important role with regards to structuring the community.

Grassle and Maciolek's detailed study of macrofauna from box core samples from the New Jersey-Delaware slope confirms the expectation that deep bathyal environments have high macrofaunal species richness (Grassle and Maciolek, 1992). Sanders (1968; 1969) found that overall diversity increased with depth down the continental slope. More specifically, Hessler and Jumars (1974) found that diversity for bivalves was found to increase with depth along the Gay Head-Bermuda transect. Generally, it is assumed that in the deep-sea a parabolic curve fits the relationship between species diversity and depth (Rex, 1981, 1983; Svavarsson *et al.*, 1990; Paterson and Lambshead, 1995) although slightly tenuously in some cases. Diversity increases, reaching a maximum at intermediate/bathyal depths before decreasing (Rex, 1981; Maciolek *et al.*, 1987a,b; Paterson and Lambshead 1995).

As water depth increases, availability of organic matter is known to decrease (Vinogradova, 1962; Belyaev, 1966). It is thought that between 1% and 3% of the total surface organic primary productivity reaches the deep-sea floor suggesting that particulate food availability is a limiting factor of benthic standing stock and diversity in the deep-sea. This is despite seasonal influxes (e.g. deposition of phytodetritus) as

well as periodic influxes (e.g. animal carcases) of organic matter. However, patchiness in organic input and sporadic small-scale disturbances are thought to be important in maintaining high species richness in the deep-sea (Gage and Tyler, 1991).

The diversity of the deep-sea fauna off the eastern United States was found to have a close relationship with sediment particle diversity. Etter and Grassle (1992) found that by holding silt diversity constant depth did not correlate significantly with species diversity. These authors suggested that it was the range in sediment particle size that played an important role in controlling the number of species found within a community. The bathymetric patterns were chiefly attributed to changes in sediment type with depth (Etter and Grassle, 1992).

Temperature is thought to be an important factor influencing species diversity, particularly with regard to amphipods and isopods in the Northern Seas (Svavarsson *et al.*, 1990; Svavarsson *et al.*, 1993).

Latitudinal gradients of species diversity were initially thought to be confined to terrestrial and coastal marine biota. However, when Rex *et al.* (1993) reviewed the diversity of deep-sea gastropods, bivalves and isopods, they found that there was a clear latitudinal diversity gradient in the North Atlantic and the Norwegian Sea. By restricting the analysis to bathyal depths, and then removing the depth variables by means of partial regression, Rex *et al.* (1993) found that the relationship between the diversity of these taxa and latitudinal gradients was highly significant. There is a general decline in diversity both on a local and regional scale towards the poles. The fauna in the northern hemisphere is thought to be recovering from the effect of glaciation (Dahl, 1976) that resulted in low diversity of the Norwegian Sea. Cronin and Raymo (1997) used ostracods to show that species diversity was depressed during glacial advances but recovered during interglacial phases. A high degree of endemism in amphipod (Dahl, 1979) and mollusc (Bouchet and Warén, 1979) species suggests that abyssal and deep bathyal fauna of the Norwegian Sea have a high degree of geographic isolation. The deep-water amphipods of the Norwegian Sea show a closer affinity with the Arctic and North Atlantic upper slope and shelf fauna than other deep-sea regions (Dahl, 1979), which suggests that the Norwegian Sea is in a 'recovery' phase.

5.1.2. Macrofaunal body size

A trend towards body-size miniaturisation has been recognised amongst deep-sea macrobenthos (Sanders *et al.*, 1965; Rowe, 1971; Rowe and Menzel, 1971). Sanders *et al.* (1965) observed that the macrofauna (>420 μm) appeared to decrease in size with increasing depth along the Gay Head-Bermuda transect. Rowe (1971) also found that body-size decreased with depth along two transects off Peru. It is possible to predict the standard metabolic rate of homeotherms and poikilotherms from fresh body mass and this shows that smaller sized organisms have a higher average metabolism per unit weight (Hemmingsen, 1960 cited in Peters, 1983). Several authors (see Thiel, 1975 and references therein) suggested that the small organisms were therefore relatively more important with regard to community metabolism than large organisms in the deep sea, dependent on density. As early as 1961, Madsen was concluding that there was an overall trend towards faunal dwarfism, which was related to food scarcity (Madsen, 1961). Thiel (1975) proposed that the deep-sea be termed a 'small-organism habitat'. However, Polloni *et al.* (1979) found no significant decrease in macrofaunal body size between 400 m and 3600 m depth in the northwestern Atlantic. As some taxa appear to move towards dwarfism, others attain relatively gigantic proportions. Wolff (1960; 1962) found that some species of isopod and tanaid showed increases in body size, whilst Jones (1969) and Knudsen (1970) found that species of cumacean and bivalve were larger than expected. Rex and Etter (1998) investigated the size of gastropods along a depth gradient and found that the gastropods actually increased in size with increasing depth. They suggested that increasing depth and decreasing nutrient input would favour larger sized molluscs because of metabolic and competitive advantages for both the adults and larvae. However, these results must be treated with some caution as only eight species of one taxon were studied (Rex and Etter, 1998). Generally, macrofaunal deposit feeders appear to head towards dwarfism, whilst gigantism appears to occur among opportunistic megafaunal scavengers.

5.1.2.1. Diversity indices

A huge variety of ecological diversity indices have been developed to answer a range of questions. Investigations into ecological diversity are often restricted to species richness, i.e. the number of specimens present (Magurran, 1988). However, the

relative abundances of species is usually to a greater or lesser extent incorporated into "diversity indices".

Diversity indices tend to be constructed in such a way as to be sensitive to a varying extent to changes in the size structure of the sample used. As previously mentioned, the concept of species diversity incorporates both species richness and evenness. However, it has been found that with use of a finer sieve species diversity decreases as the number of individuals of a species population increases, as does evenness (Gage *et al.*, in press). Finer sieves retaining more young individuals of a species population cause this decrease in evenness. These authors also found species richness increased with use of finer sieves because a greater number of small sized species were caught.

5.1.3. Hypotheses

The preceding account leads to several testable hypotheses. By incorporating the species collected in the 250 μm-to-500 μm size fraction with that of the >500 μm size fraction:

- species richness will increase in the total - >250 μm size fraction
- species diversity will increase in the total - >250 μm size fraction
- evenness will increase while dominance decreases in the total - >250 μm size fraction

- The main variables influencing the polychaete community are depth and organic matter.

5.2. ANALYTICAL METHODS

5.2.1. Diversity Indices

A variety of diversity indices are applied in this chapter in order to measure species richness, evenness, dominance and diversity. The dominant species at each station is also determined by using Rank-1 dominance.

5.2.1.1. Margalef diversity index (Clifford and Stephenson, 1975)

Margalef's diversity index is a measure of species richness. The formula is simply calculated from the number of species and the total number of individuals in the sample (Magurran, 1988).

$$D_{Mg} = \frac{(S-1)}{\log N}$$

S = number of species

N = total number of individuals summed over all S species

5.2.1.2. Shannon-Wiener diversity index (Pielou, 1975)

The Shannon diversity index is based on the sum of the proportional abundances of species. The underlying assumption of this index is that individuals are randomly sampled from an infinitely large population (Pielou, 1975). The Shannon index value usually falls between 1.5 and 3.5 and is rarely greater than 4.5 when using $\log_{10}$ (Margalef, 1972), although in the deep-sea this value often exceeds 5.0.

$$H' = -\sum_{i=1}^{s} (p_i \log p_i)$$

p_i = mean abundance of the i^{th} taxon / mean total abundance

5.2.1.3. Pielou's diversity index

Pielou's diversity index measures the evenness of a sample. It is derived from Shannon diversity where evenness is the ratio between the observed diversity value and the maximum possible diversity (Pielou, 1975). The evenness value is constrained between 0 and 1.0 whereby 1.0 represents a situation where all species are equally represented in the sample.

$$J' = \frac{H'}{LogS}$$

H' = Shannon diversity index

S = number of species

5.2.1.4. Simpson's dominance index (Simpson, 1949)

The Simpson's dominance index is the sum of the squared proportions of the total made up by individual species. This index is heavily weighted towards the most abundant species in the community hence making it less sensitive to rare species (May, 1975).

$$D = \sum pi^2$$

pi = the proportion of individuals in the *i*th species.

5.2.1.5. Rarefaction (Hurlbert, 1971)

The rarefaction technique was initially devised by Sanders (1968). However, Hurlbert (1971) subsequently modified Sanders' rarefaction formula so as to produce unbiased estimates. Rarefaction generates a curve of expected number of species ($E(S_n)$) versus the number of individuals. Generally the greater the diversity of the community, the more elevated the rarefaction curve. However, care must be taken when comparing $E(S_n)$ values, as samples may be of the same size, but the actual distribution of abundances amongst species may differ (Tipper, 1979; Gage and May, 1993), thus generating very different curves.

$$E(S_n) = \sum_i \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right]$$

E(S) = Expected number of species

n = standardised sample size

N = total number of individuals recorded

N_i = number of individuals in the ith species

5.2.1.6. Rank-1 dominance

Rank-1 dominance, similar to the Berger-Parker index, may be determined from the first point on a k-dominance curve, or in this instance was calculated by hand using the following formula:

$$K = \left(\frac{D_{sp}}{N} \right) \times 100$$

K = dominant species

D_{sp} = abundance of most dominant species

N = Total number of individuals

5.2.2. Species accumulation

Species accumulation curves, also known as "collectors curves" (e.g. Bett and Gage, 2000) are used as a method of detecting the rate at which new species, previously unrecorded, appear in the samples. The samples are generally arranged along an environmental gradient, e.g. depth so that areas of rapid changes in species composition can be detected. Species accumulation curves were calculated by determining the number of new species found at each station These were cumulatively added together for each station. To obtain the percentage total cumulation, the cumulative values were divided by the cumulative total number of species and multipled by 100. This was undertaken to determine where the greatest rate of change was occurring.

5.2.3. Geometric class abundances

Geometric class abundance can be used indirectly to determine the abundance of rare and non-rare species. Geometric abundance is calculated by the plots of the number of species represented by only 1 individual in the sample (class 1), 2 - 3 individuals (class 2), 4 - 7 individuals (class 3), 8 - 15 individuals (class 4) etc. (Gray and Pearson, 1982; Clarke and Warwick, 1994). The geometric class plots were determined by using the PRIMER package.

Rarefaction analysis was calculated using the rarefaction program in the BioDiversity Professional Beta version 2 (McAleece *et al.*, 1996). The remaining diversity indices with the exception of Rank-1 dominance were calculated using the PRIMER (Plymouth Routines in Multivariate Ecological Research) package. All formuale using logarithms are to the base e.

5.3. RESULTS

In order to test the hypotheses presented on page 93, the macrofauna retained on the two sieves were analysed and identified separately. This was done in order to determine if species in the 250 μm-to-500 μm size fraction influenced the diversity indices of the total size fraction

The suite of results presented here is based on polychaete species unless otherwise stated. Polychaetes dominate the macrofauna, between 42% and 83%, and were identified to species or putative species level where possible.

5.3.1. Polychaete Diversity Indices

5.3.1.1. 250 μm-to-500 μm size fraction

In both 1996 and 1998, the greatest number of species (30 in each size fraction) were found at the shallowest, 150 m, station, whilst the lowest were found at 900 m/1000 m. The total number of individuals found shows a similar pattern, the highest number being found at the shallowest station. Figures 5.1a-c shows the different diversity results obtained using Margalef, Pielou and Simpson's Dominance indices.

As is evident from Figure 5.1a highest species richness occurred at similar depths in both years, as did the lowest. However, low species evenness occurred at similar depths whilst high species evenness occurred at different depths (Figure 5.1b). Evenness tended to be relatively high at all stations, with exceptions at 150 m in 1996 and 200 m in 1998. The reverse was found to be true for Simpson's index (Figure 5.1c). In this size fraction there was spatial as well as inter-annual variability especially regarding the Shannon index. Variability was much lower with expected number of species ($E(S_n)$). Rank-1 dominance, which was used to identify which stations appeared to be dominated by one species (Figure 5.2a), showed little spatial or temporal variability down to a depth of 550 m, where-after variability increased. The highest number of expected species to be found was at the 450 m station in 1996 and 500 m station in 1998 (Figure 5.2b). The Shannon plots (Figure 5.2c) support these $E(S_n)$ results whereby the 450 m and 500 m stations had the greatest diversity. There are noticeable differences between the two years with respect to the position of the station's curves on the rarefaction plots as well as the curvature (Figures 5.3a,b), but generally the 150 m station and a mixture of intermediate stations form one group, the

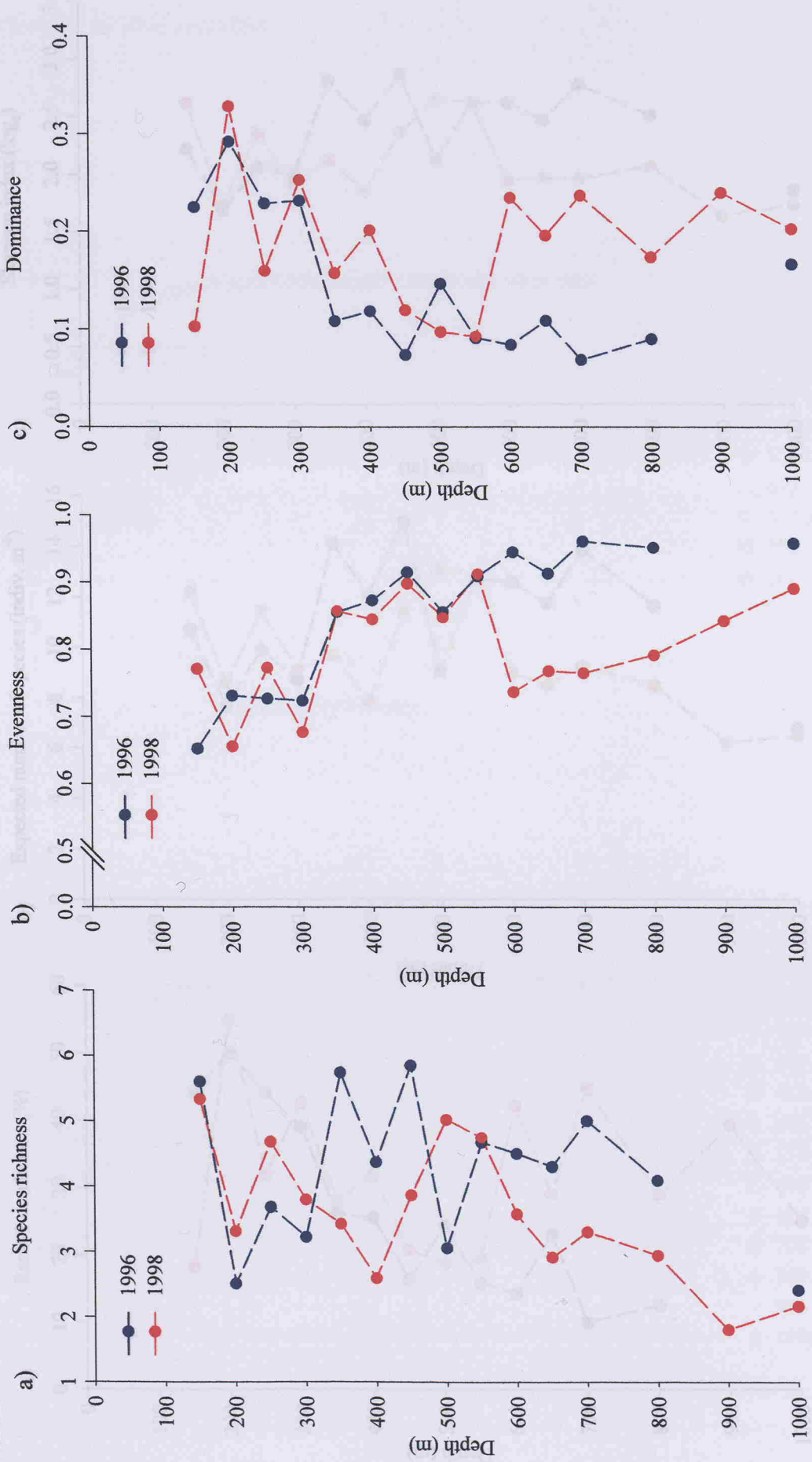
rest of the shallow/intermediate stations form a second group and the deepest stations tend to form a third group in the lower part of the plot. This suggests that the expected number of species to be found at the intermediate stations in a specific sample size is greater than at deeper stations.

5.3.1.2. >500 μm size fraction

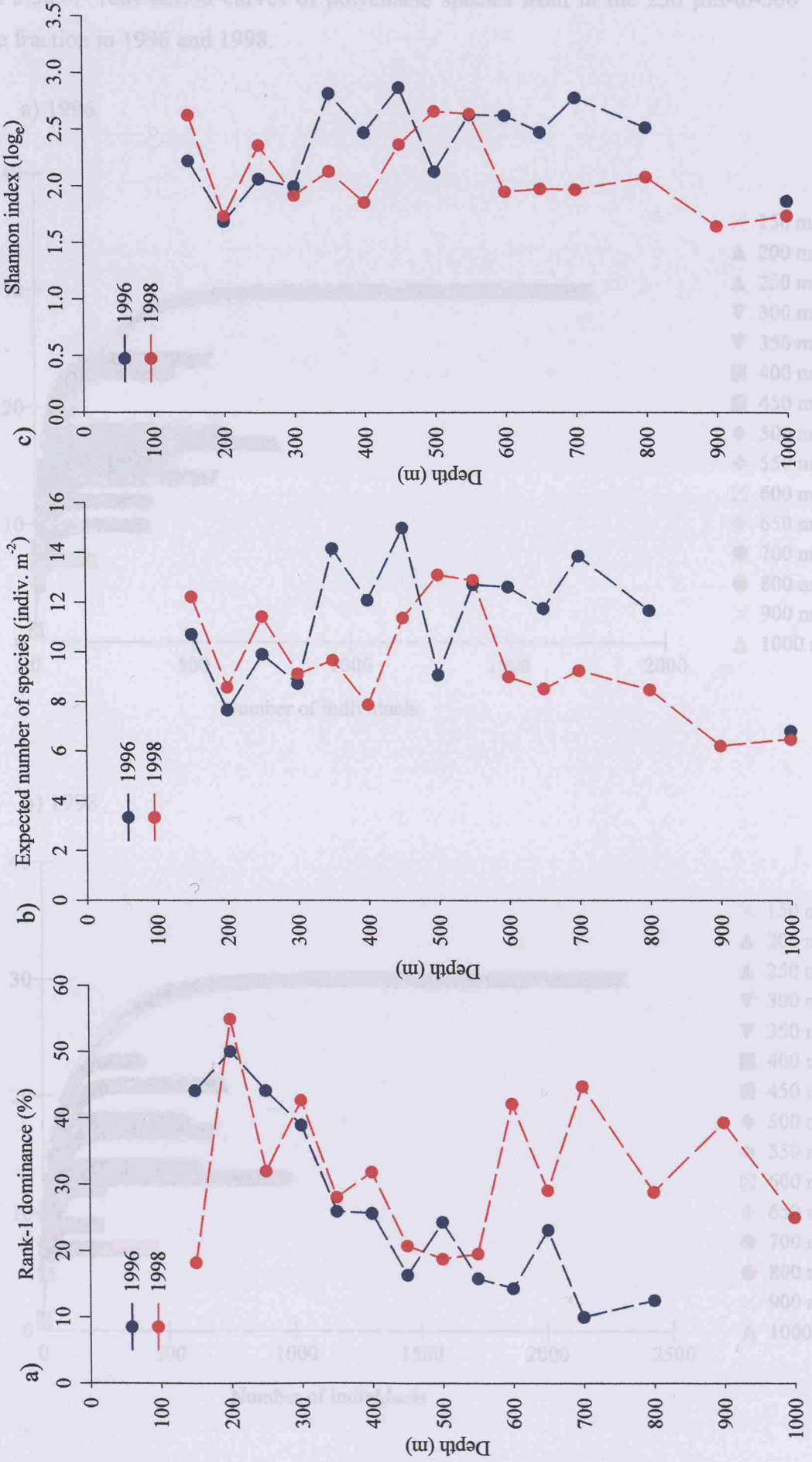
The greatest number of species in the >500 μm size fraction occurred at a depth of 150 m (46 species) in 1996, whereas in 1998 it was at 500 m (46 species also). However, the least number of species recorded occurred at 900 m depth in both years. The highest number of individuals were counted at a depth of 800 m in both 1996 and 1998, the least occurring at 250 m in 1996 and 350 m in 1998.

From the Margalef index it can be seen that the 150 m station (1996) and the 500 m station (1998) were found to have the highest species richness (Figure 5.4a). The 800 m/900 m stations were the least species rich in both years. The stations with the highest Pielou's evenness index were different in 1996 (450 m) and 1998 (350 m) whilst the 800 m station showed the lowest evenness in both years (Figure 5.4b). Generally species evenness was high throughout all the stations. The 800 m station had the greatest dominance in both years, whilst low dominance was seen at 150 m in 1996 and 500 m in 1998 (Figure 5.4c). Rank-1 dominance, in both years, shows an increase to around 800 m before decreasing (Figure 5.5a). *Paramphinome jeffreysi* generally dominated the deeper stations i.e. ≥600 m in both years. Both the plots of expected number of species and the Shannon index show a general decline with depth, which becomes more marked below 650 m (Figures 5.5b). However, at the 800 m station, more than 45% of the total numbers of individuals were found to be *Spiophanes kroyeri*. The stations with the greatest number of expected species are quite dissimilar in the two years (Figure 5.5c). In 1996 the 150 m and 550 m stations have the highest number of expected species whilst in 1998 it is the 450 m and 500 m stations.

The rarefaction plots (Figures 5.6a,b) are again dissimilar when comparing 1996 with 1998, although in both plots deeper stations are generally found towards the lower part of the plot. One similarity seen is at the 800 m station, in both years there is a long 'tail' possibly implying that there is a dominant species, which in this instance is *Spiophanes kroyeri*.

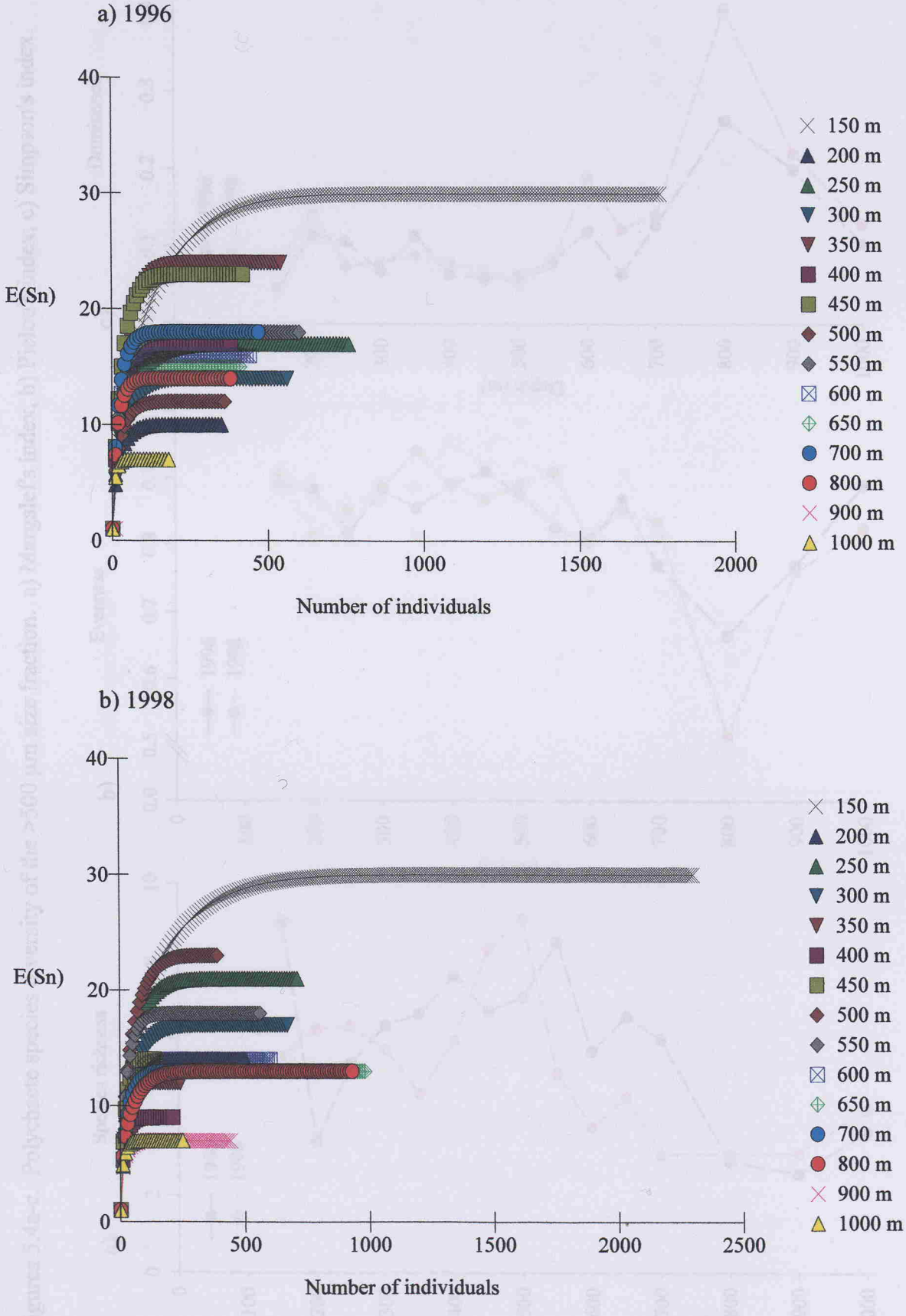


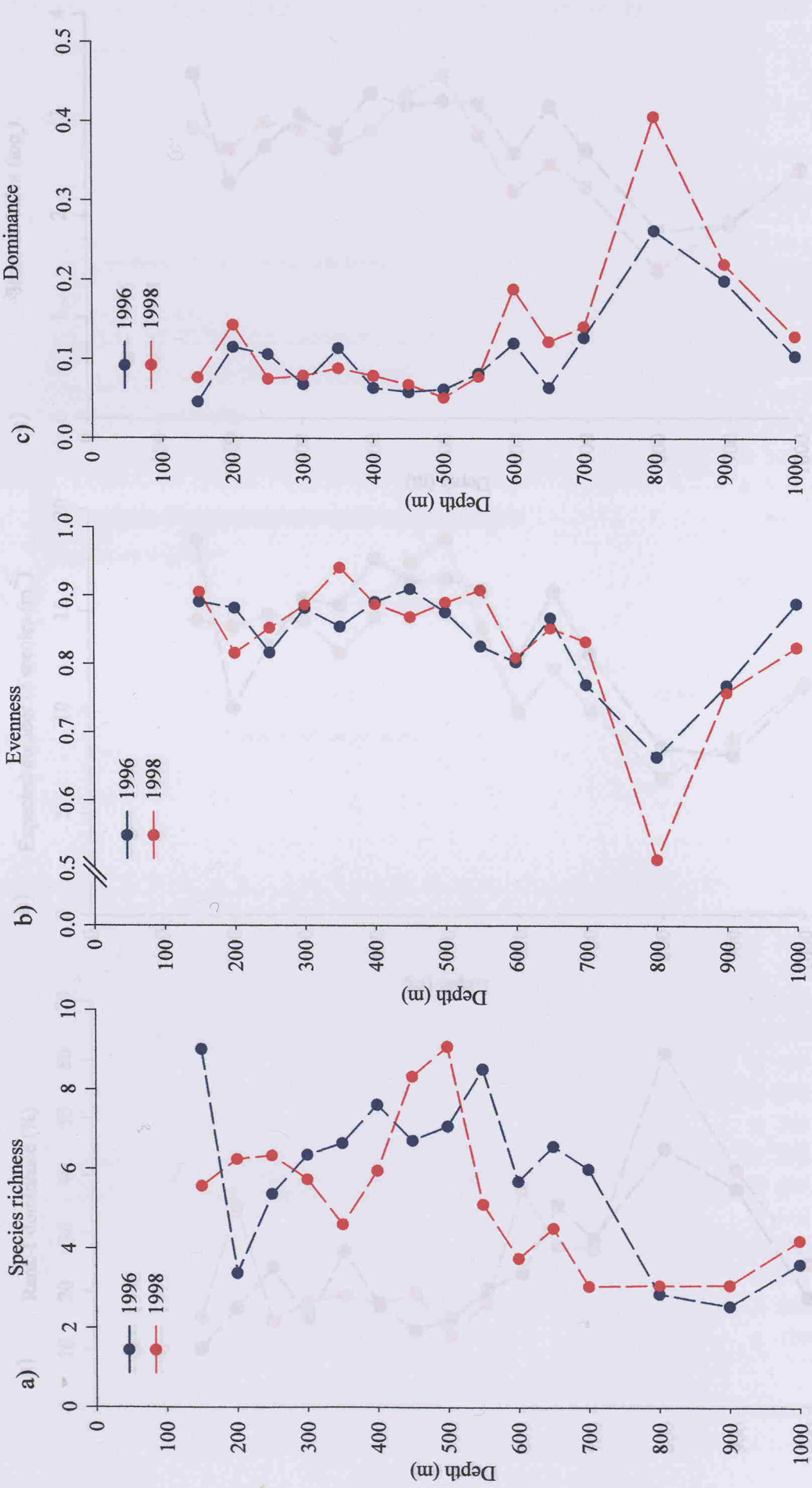
Figures 5.1a-c. Polychaete species diversity indices of the 250 µm-to-500 µm size fraction. a) Margalef's index, b) Pielou's index, c) Simpson's index.



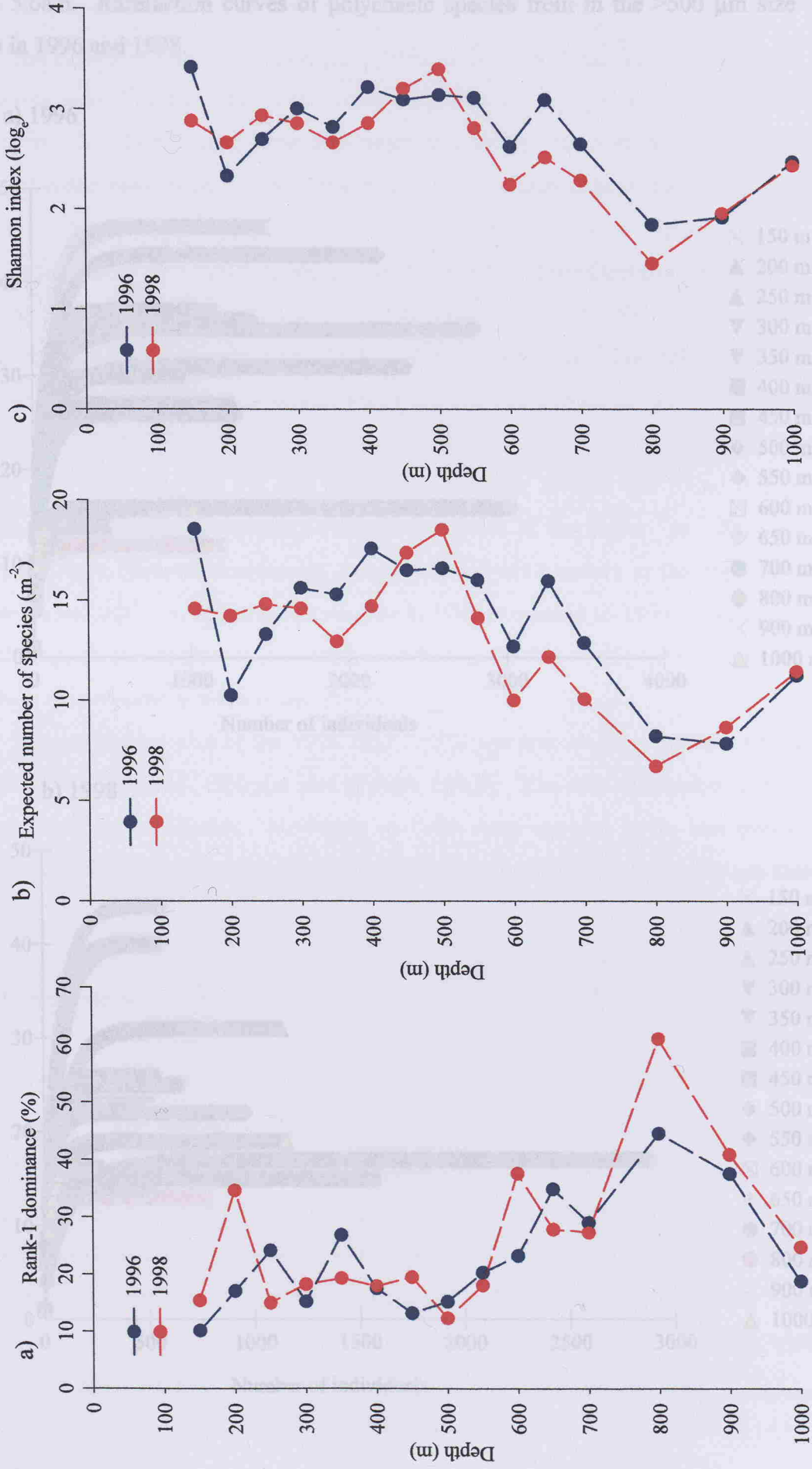
Figures 5.2a-c. Polychaete species diversity indices of the 250 µm-to-500 µm size fraction. a) rank-1 dominance, b) expected number of species, c) Shannon index.

Figures 5.3a,b. Rarefaction curves of polychaete species from in the 250 µm-to-500 µm size fraction in 1996 and 1998.



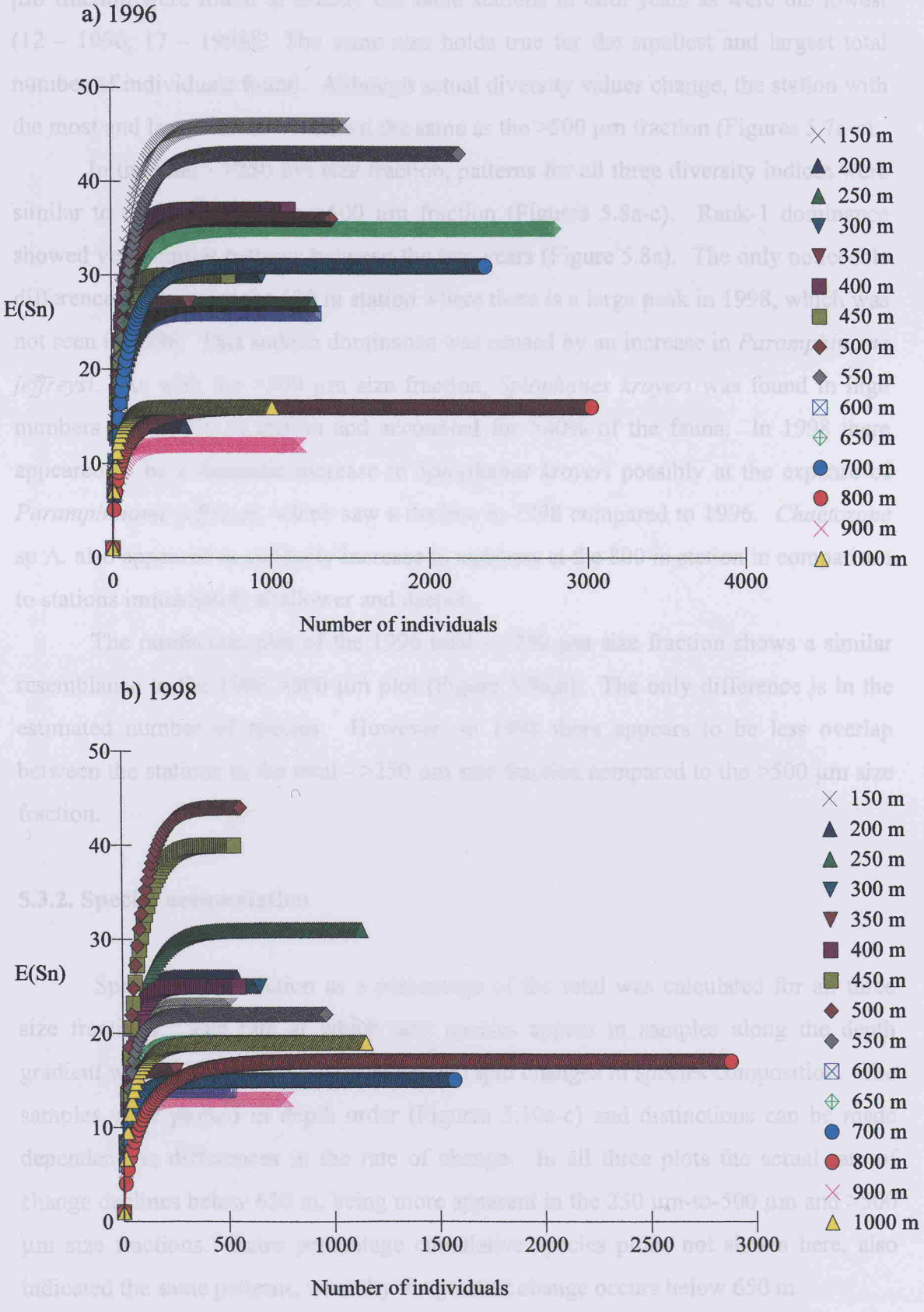


Figures 5.4a-c. Polychaete species diversity of the >500 µm size fraction. a) Margalef's index, b) Pielou's index, c) Simpson's index.



Figures 5.5a-c. Polychaete species diversity of the >500 µm size fraction. a) rank-1 dominance, b) expected number of species, c) Shannon index.

Figures 5.6a,b. Rarefaction curves of polychaete species from in the >500 µm size fraction in 1996 and 1998.



5.3.1.3. Total - >250 µm size fraction

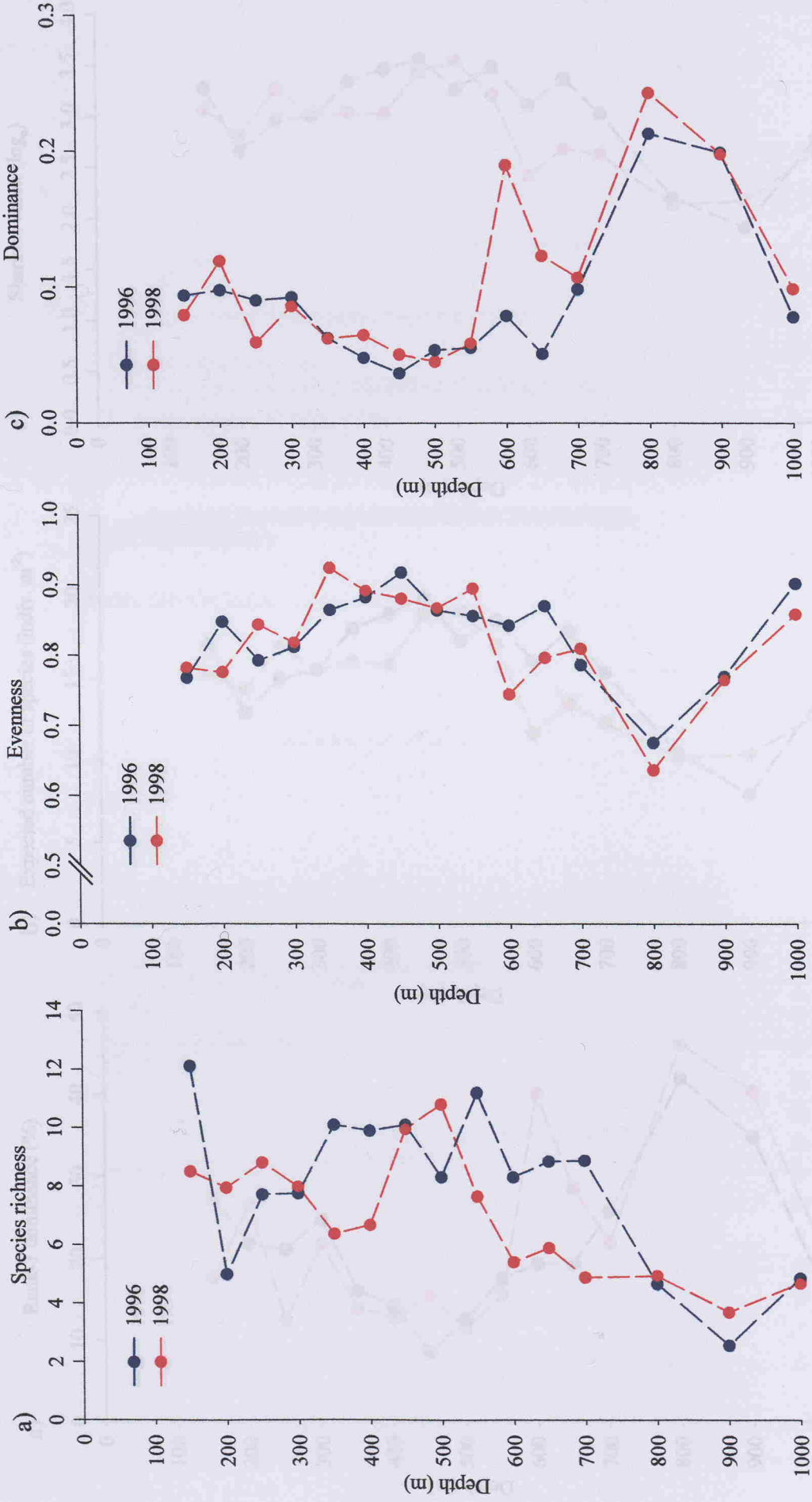
The highest number of species (72 – 1996, 61 – 1998) found in the total - >250 µm fraction were found at exactly the same stations in both years as were the lowest (12 – 1996, 17 – 1998). The same also holds true for the smallest and largest total number of individuals found. Although actual diversity values change, the station with the most and least values are almost the same as the >500 µm fraction (Figures 5.7a-c).

In the total - >250 µm size fraction, patterns for all three diversity indices were similar to those seen in the >500 µm fraction (Figures 5.8a-c). Rank-1 dominance showed very similar patterns between the two years (Figure 5.8a). The only noticeable difference was seen at the 600 m station where there is a large peak in 1998, which was not seen in 1996. This sudden dominance was caused by an increase in *Paramphinome jeffreysi*. As with the >500 µm size fraction, *Spiophanes kroyeri* was found in high numbers at the 800 m station and accounted for >40% of the fauna. In 1998 there appeared to be a dramatic increase in *Spiophanes kroyeri* possibly at the expense of *Paramphinome jeffreysi*, which saw a decline in 1998 compared to 1996. *Chaetozone* sp A. also appeared to suddenly increase in numbers at the 800 m station in comparison to stations immediately shallower and deeper.

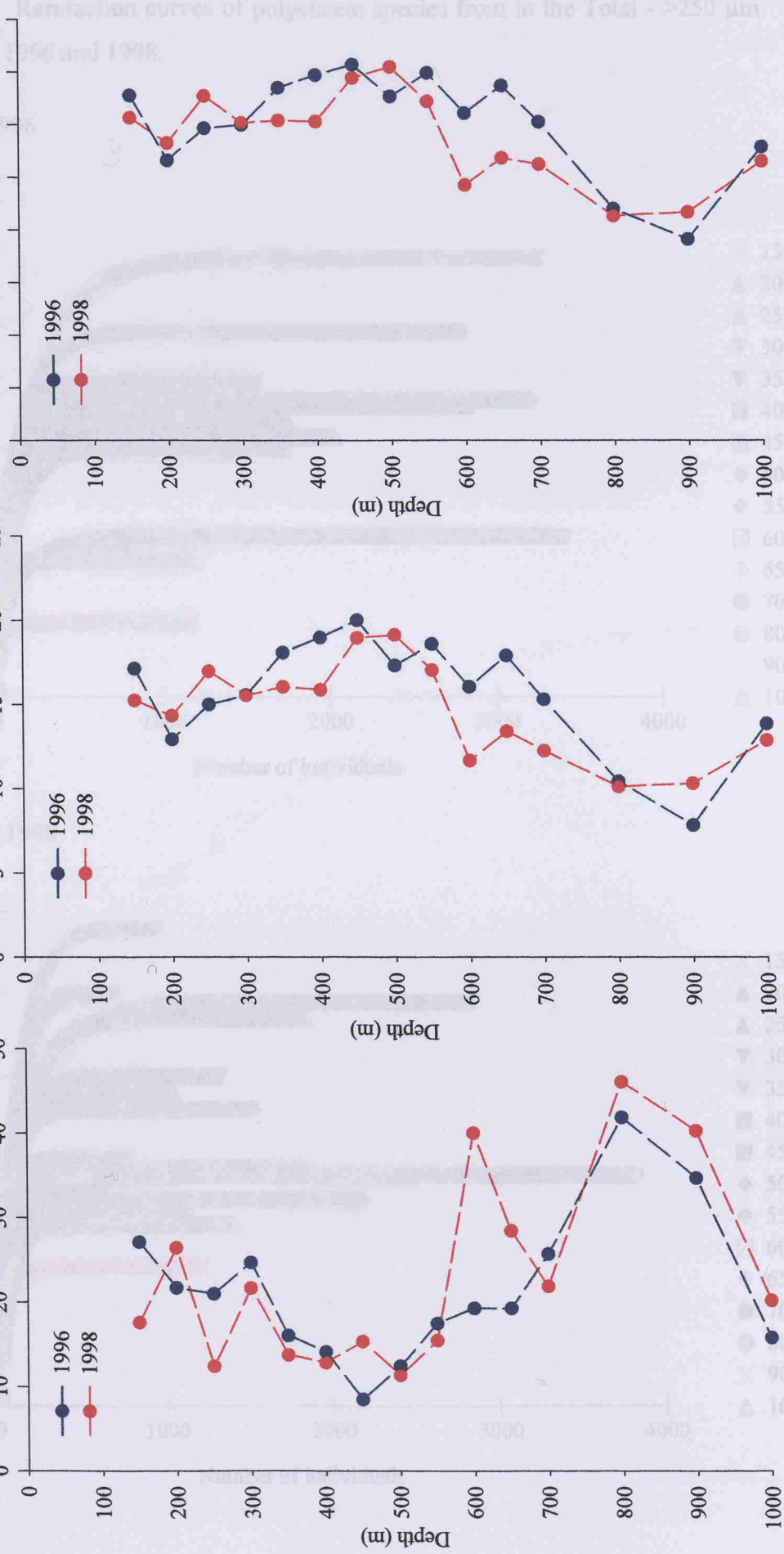
The rarefaction plot of the 1996 total - >250 µm size fraction shows a similar resemblance to the 1996 >500 µm plot (Figure 5.9a,b). The only difference is in the estimated number of species. However, in 1998 there appears to be less overlap between the stations in the total - >250 µm size fraction compared to the >500 µm size fraction.

5.3.2. Species accumulation

Species accumulation as a percentage of the total was calculated for all three size fractions. The rate at which new species appear in samples along the depth gradient was used as a method of detecting rapid changes in species composition. The samples were plotted in depth order (Figures 5.10a-c) and distinctions can be made dependent on differences in the rate of change. In all three plots the actual rate of change declines below 650 m, being more apparent in the 250 µm-to-500 µm and >500 µm size fractions. Retro percentage cumulative species plots, not shown here, also indicated the same patterns, whereby the greatest change occurs below 650 m.



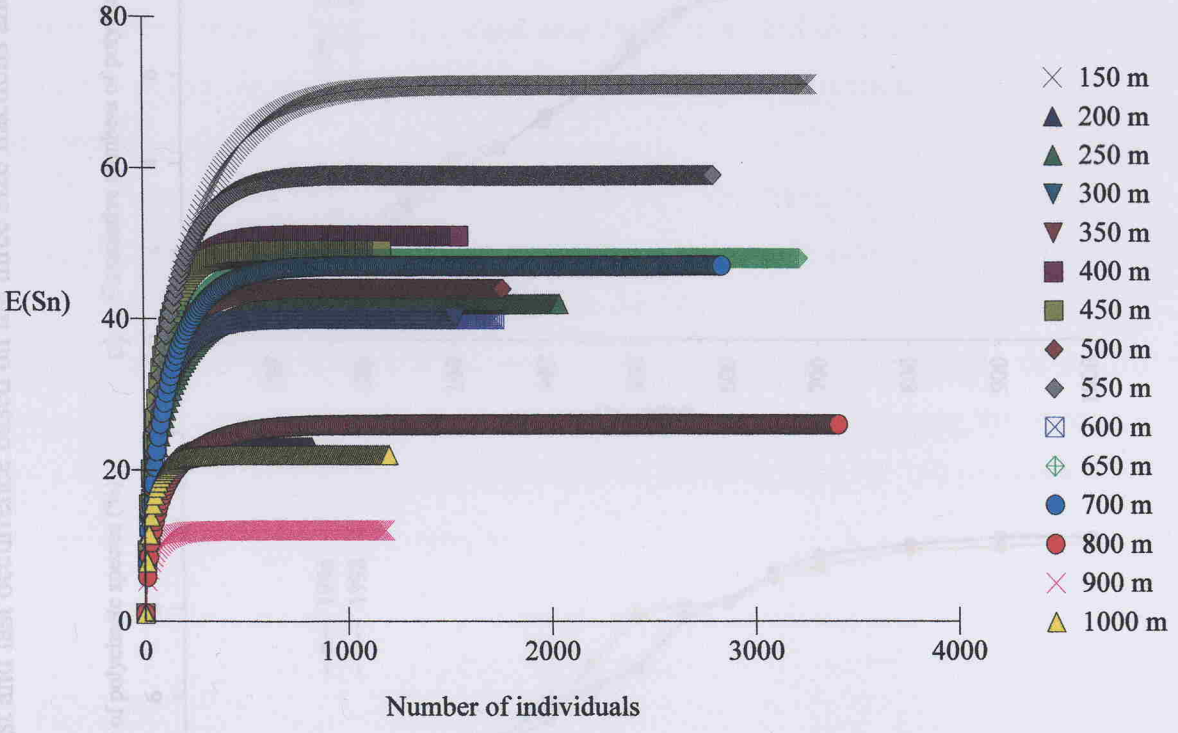
Figures 5.7a-c. Polychaete species diversity of the Total - >250 µm size fraction. a) Margalef's index, b) Pielou's index, c) Simpson's index.



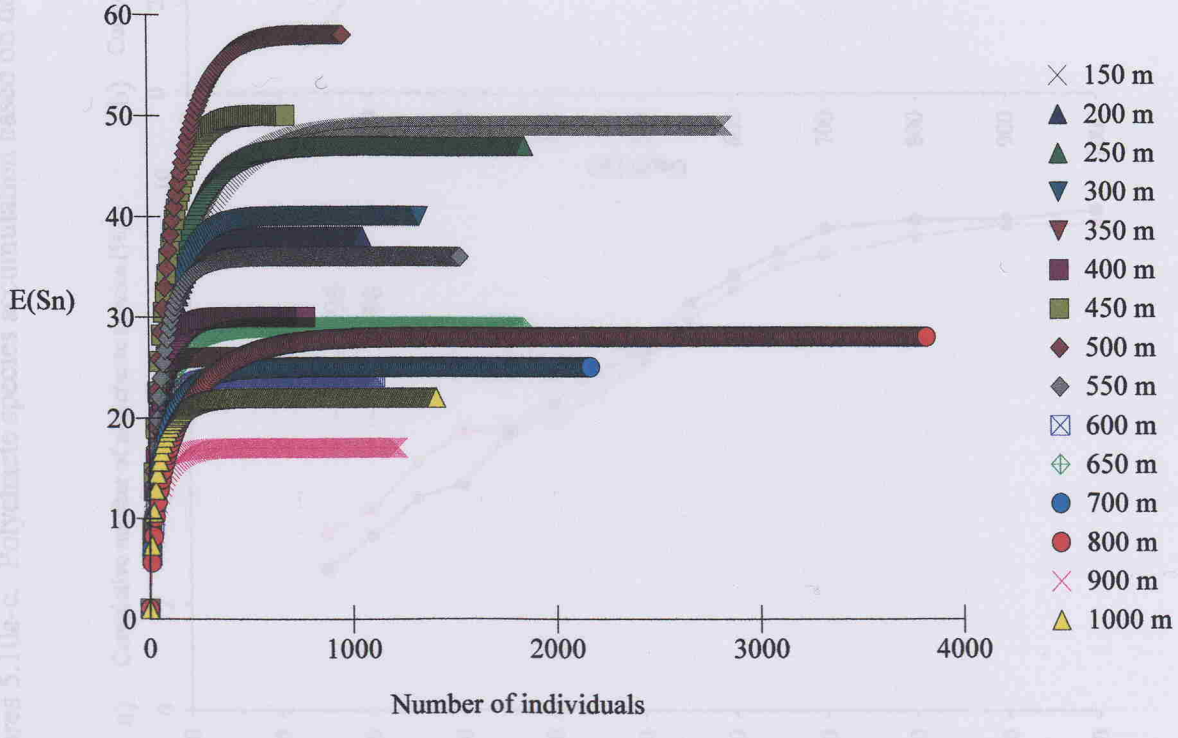
Figures 5.8a-c. Polychaete species diversity indices of the Total - >250 µm size fraction. a) rank-1 dominance, b) expected number of species, c) Shannon index.

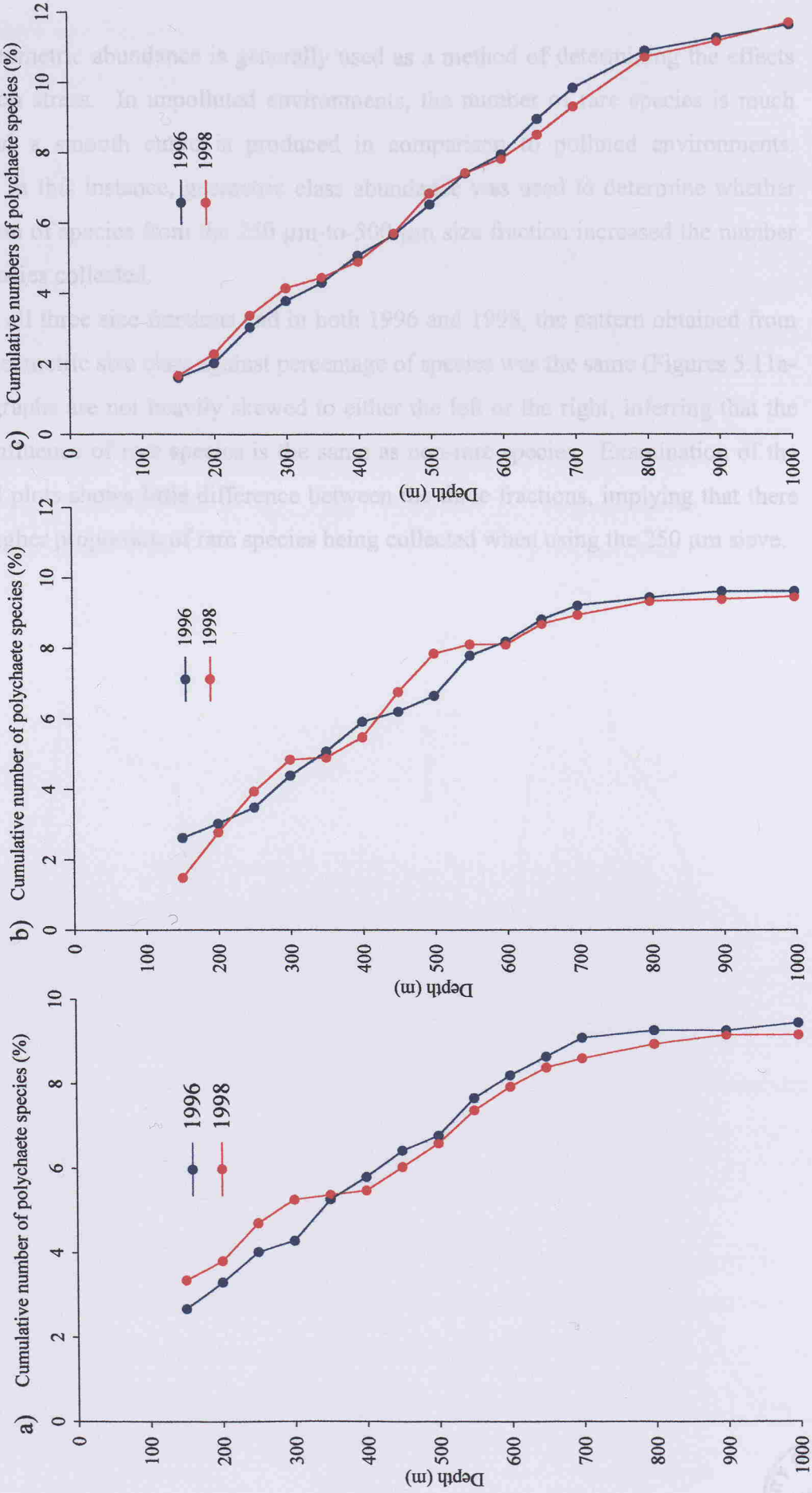
Figures 5.9a,b. Rarefaction curves of polychaete species from in the Total - >250 µm size fraction in 1996 and 1998.

a) 1996



b) 1998





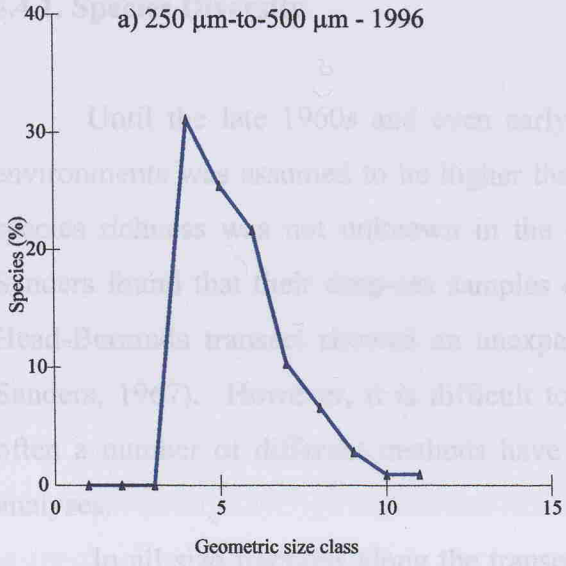
Figures 5.10a-c. Polychaete species accumulation based on depths of first and last occurrence based on the three size fractions and the two years.

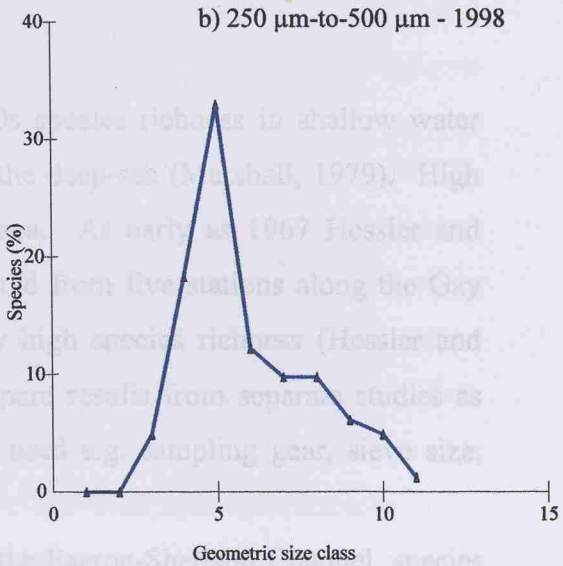
5.3.3. Geometric class abundances

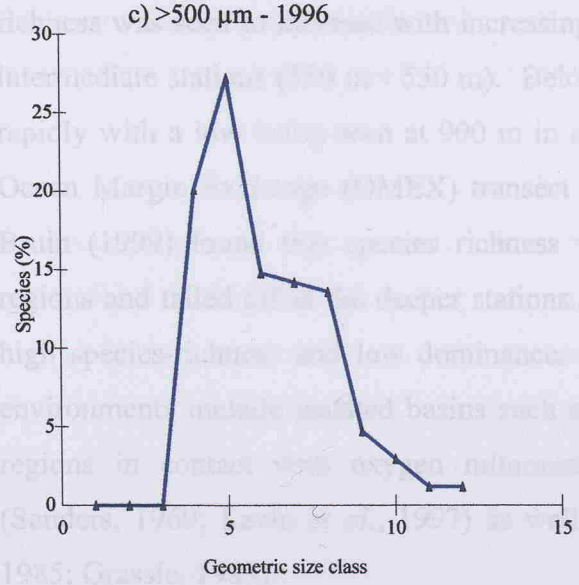
Geometric abundance is generally used as a method of determining the effects of pollution stress. In unpolluted environments, the number of rare species is much higher and a smooth curve is produced in comparison to polluted environments. However, in this instance, geometric class abundance was used to determine whether the addition of species from the 250 μm-to-500 μm size fraction increased the number of rare species collected.

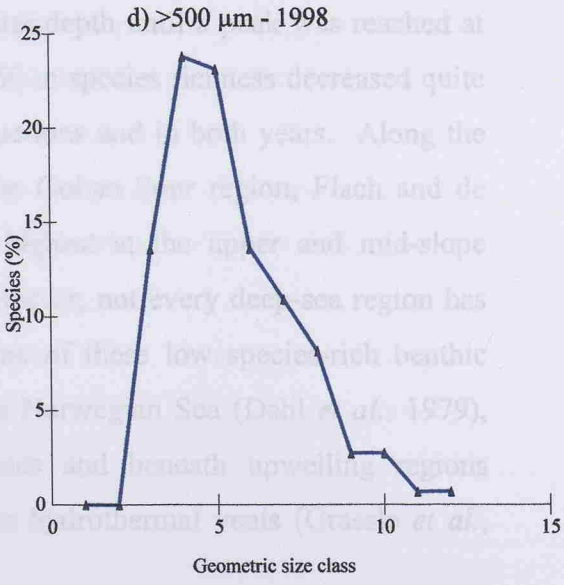
In all three size fractions and in both 1996 and 1998, the pattern obtained from plotting geometric size class against percentage of species was the same (Figures 5.11a-f). The graphs are not heavily skewed to either the left or the right, inferring that the relative influence of rare species is the same as non-rare species. Examination of the combined plots shows little difference between the three fractions, implying that there is not a higher proportion of rare species being collected when using the 250 μm sieve.

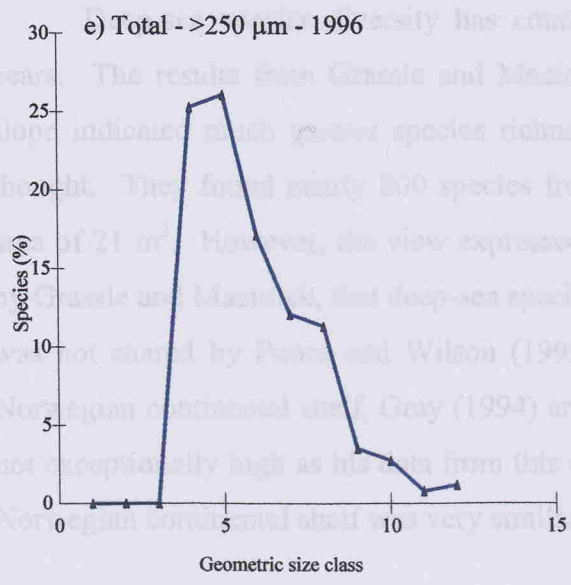
Figures 5.11a-f. Geometric class abundance plots of polychaete species in the two years and three size fractions.

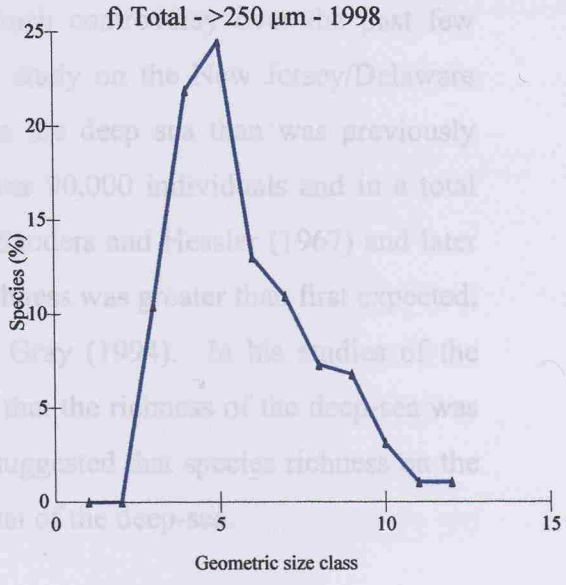












5.4. DISCUSSION

5.4.1. Species Diversity

Until the late 1960s and even early 1970s species richness in shallow water environments was assumed to be higher than in the deep-sea (Marshall, 1979). High species richness was not unknown in the deep-sea. As early as 1967 Hessler and Sanders found that their deep-sea samples collected from five stations along the Gay Head-Bermuda transect showed an unexpectedly high species richness (Hessler and Sanders, 1967). However, it is difficult to compare results from separate studies as often a number of different methods have been used e.g. sampling gear, sieve size, analyses.

In all size fractions along the transect in the Faeroe-Shetland Channel, species richness was seen to increase with increasing water depth until a peak was reached at intermediate stations (350 m - 550 m). Below 650 m species richness decreased quite rapidly with a low being seen at 900 m in all fractions and in both years. Along the Ocean Margin Exchange (OMEX) transect in the Goban Spur region, Flach and de Bruin (1999) found that species richness was highest at the upper and mid-slope regions and tailed off at the deeper stations. However, not every deep-sea region has high species-richness and low dominance. Some of these low species-rich benthic environments include isolated basins such as the Norwegian Sea (Dahl *et al.*, 1979), regions in contact with oxygen minimum zones and beneath upwelling regions (Sanders, 1969; Levin *et al.*, 1997) as well as at hydrothermal vents (Grassle *et al.*, 1985; Grassle, 1989).

Deep-sea species diversity has courted much controversy over the past few years. The results from Grassle and Maciolek's study on the New Jersey/Delaware slope indicated much greater species richness for the deep sea than was previously thought. They found nearly 800 species from over 90,000 individuals and in a total area of 21 m^2. However, the view expressed by Sanders and Hessler (1967) and later by Grassle and Maciolek, that deep-sea species richness was greater than first expected, was not shared by Poore and Wilson (1993) or Gray (1994). In his studies of the Norwegian continental shelf, Gray (1994) argued that the richness of the deep-sea was not exceptionally high as his data from this area suggested that species richness on the Norwegian continental shelf was very similar to that of the deep-sea.

In the present study, focusing on polychaetes, a peak in species diversity (using both $E(S_n)$ and the Shannon index) occurred at intermediate depths (450 m – 550 m) in all size fractions and in both years. In 1996, the 250 μm-to-500 μm size fraction had a peak in diversity at 450 m, whereas in the >500 μm and total - >250 μm size fractions the peak differed slightly depending on whether $E(S_n)$ or the Shannon index was being used. In 1998, all fractions showed a peak in species diversity at 500 m. Interestingly both the >500 μm and total - >250 μm size fractions had a higher species diversity at 150 m. However, peaks in species diversity from the Shannon index with depth were not as distinct as that seen when using $E(S_n)$. This is possibly because the Shannon index gives a value based on the data set used, whereas $E(S_n)$ is a prediction albeit based on real values. Greater variability was seen in the 250 μm-to-500 μm size fraction in both years, and differences between the two were also more apparent. The pronounced variability is not so strong in the >500 μm and total - >250 μm size fractions. The results of the Shannon index and expected number of species from the AFEN 1996 survey show similar trends with depth as seen along the study transect. The greatest diversity (based on all species) occurred at the 400 m to 500 m depth band (Bett, 2000). Using all the species from the present study in the >500 μm size fraction, the greatest diversity occurred at the 450 m to 550 m depth and, slightly different to the results from the AFEN 1996 survey.

On both sides of the Atlantic, species diversity $E(S_n)$, has been found to have a peak at mid slope depths with a decline both into shallower water and into the abyss (Rex, 1981, 1983; Paterson and Lambshead, 1995). Paterson and Lambshead (1995) utilised benthic samples collected from three cruises in the Rockall Trough. A diversity maxima occurred between 1400 m and 1800 m in the Rockall Trough, similar to results by Maciolek *et al.* (1987a,b) where they found that macrofaunal species diversity exhibited a peak at bathyal depth (1000 m to 2000 m) on the Northwest Atlantic slope. Rex (1983) and Etter and Grassle (1992) found that the macrofaunal diversity maxima occurred between 2000 m and 3000 m. All sets of results are quite different to the present study where a maximum was identified at 450 m to 550 m. Levin and Gage (1998) combined macrofaunal data from the Pacific and Indian Ocean as well as the Northeast Atlantic at depths ranging from 154 m to 3400 m. They found an exponential increase in diversity of the total macrofauna as well as for polychaetes. However, not all areas of the deep-sea exhibit bathymetric diversity patterns, Blake *et al.* (1985, 1987) in their study of biological processes on the South Atlantic slope and

rise did not find a bathymetric diversity pattern, suggesting that patterns vary from place to place.

The values of the diversity indices from the present study transect were correlated using Spearman rank correlation coefficient with the suite of environmental variables. The Shannon diversity results from the transect in 1998 showed a significant negative correlation with increasing water depth, whereas in 1996 no significant correlation was seen ($n = 15$, $\alpha = 0.05$, $r_s = 0.521$). The strongest correlations in both years were seen with mean sediment grain size (negative) and temperature range (positive). Etter and Grassle (1992) also found that species diversity did not correlate significantly with depth but did so with sediment particle diversity. These results are the opposite of those of Flach and de Bruin (1999) from the Goban Spur, where they found that species diversity positively correlated with increasing water depth.

In the AFEN 1996 survey, temperature range was recorded as having the strongest correlation (Bett, 2000). Plotting species diversity with temperature range, the peak in species diversity corresponds to the large temperature range seen at the same depths, stronger and clearer in 1998 than in 1996. The expected number of species and temperature range does not show quite as strong an association as seen with the Shannon diversity or with the expected number of species used in the AFEN 1996 survey (see Bett, 2000). This is probably as a result of the huge difference in the number of samples per station used in the Shannon diversity analysis, one sample per depth band along the transect as opposed to several stations per depth band in the 1996 AFEN survey. Having only one sample available per depth band/station does not provide any opportunity to test for small-scale variability caused by patchiness. Only by increasing the number of samples per depth band could the variability of the area be determined.

The expected number of species along the study transect in all size fractions in 1998 correlated most strongly with sediment grain size. However, using the Spearman rank correlation coefficient the results from 1996 (>500 μm and total - > 250 μm size fractions only) showed a significant correlation with temperature range ($n = 15$, $\alpha = 0.05$, $r_s = 0.521$). The second strongest associated environmental variable in 1998 was maximum temperature, for all size fractions. Etter and Grassle (1992) examined the relationship between species diversity ($E(S_n)$) and a number of environmental variables. They found that species diversity correlated most strongly with either sediment particle size diversity, or one of the sediment fractions, more specifically with silt diversity (silt

diversity based on 4 Φ fractions between 4 Φ and 8 Φ). Etter and Grassle's results appear to suggest that the majority of variability in species diversity, in the bathyal Northwest Atlantic can be attributed to changes in sediment characteristics (Etter and Grassle, 1992). Changes in sediment characteristics can be as a result of hydrodynamic regimes or burrowing organisms re-distributing the sediment. In this study however sediment grain size does not account for the majority of species variability, but temperature, whether it be maximum or range, appears to be the most important variable in determining species diversity.

In all size fractions and in both years, a general decline in diversity was seen below 500 m depth. However, below 800 m/900 m an increase in diversity is seen especially in the Shannon plots. The same pattern is also seen in the AFEN 1996 survey, a general decline below 500 m but followed by a slight increase between 900 m and 1100 m (Bett, 2000). This is seen more clearly on the expected number of species plot rather than the Shannon plot. However, results from the Rockall Trough appear to show a different pattern, macrofaunal species diversity seems to steadily increase with depth with a maximum occurring at about 1400 m (Gage *et al.*, in press), although it must be noted that there are no results below a water depth of 1800 m. Comparing diversity indices from similar depth values along the transect with the Rockall Trough, some similarities are seen. At the 400 m stations diversity was comparable; as the stations became deeper there was less similarity (see Gage *et al.*, in press).

In the rarefaction plots, stations generally separate into three groups that appear to comprise shallow-warm stations, intermediate stations and cold-deep stations, although there is a greater degree of mixing between the shallow-warm and intermediate stations. The distribution of the curves plotted indicate no clear depth trend, however, it is possible that the groupings of the stations are dependent upon the hydrography. The intermediate stations generally have higher curves than the cold-deep stations, implying a greater number of species per number of individuals.

5.4.1.1. Evenness and Dominance

Evenness was generally high at all stations (>0.5) resulting in dominance being relatively low (<0.25), the exception occurring at 800 m in the >500 μm size fraction in 1998 where there was high dominance and thus low evenness. The high Simpson's dominance value also corresponds with a high rank-1 dominance (≈ 61%), which is

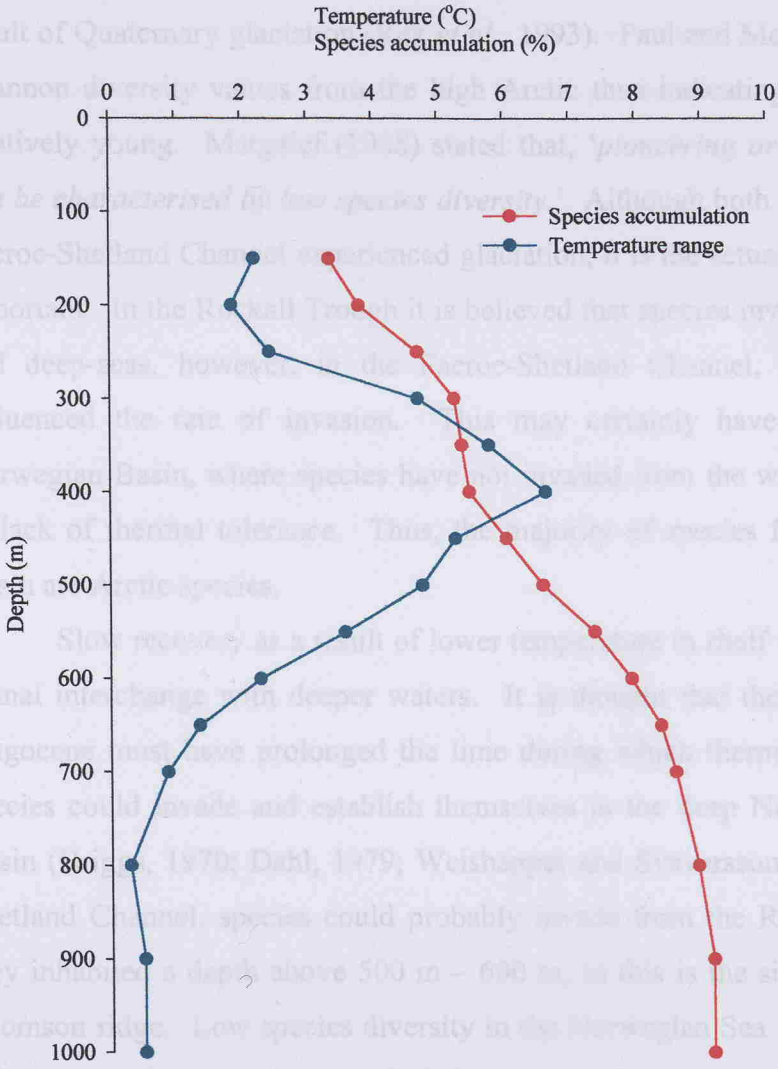
caused by an increase in the number of *Spiophanes kroyeri* present. In both the 1996 and 1998 >500 μm and total - >250 μm size fractions, the 800 m stations had the highest Simpson's index value, greatest rank-1 dominance and thus the lowest evenness. As to what caused a sudden increase in *Spiophanes kroyeri* at the possible expense of *Paramphinome jeffreysi* is unknown. There appears to be nothing unusual about the 800 m station chemically, physically or geologically, at least nothing detectable from the environmental data available; it is similar to the 900 m and 1000 m stations, all three occurring on a contourite sheet (see Chapter 6 – discussion). In both the AFEN 1996 and 1998 surveys, *S. kroyeri* dominates the 700 m - 800 m depth band, whilst there appears to be a corresponding decline in number of *P. jeffreysi* (Bett, 2000).

Combining the two size fractions, 250 μm-to-500 μm and >500 μm influences the total (>250 μm) evenness result. In 1996, evenness generally increased, but in 1998 a greater number of stations showed an overall decline in evenness. However, the same result was not seen in the Simpson's Dominance index. The 250 μm-to-500 μm size fraction appeared to have little influence on the total dominance even though dominance values in the smaller fraction were generally higher than in the larger fraction.

5.4.2. Species accumulation with depth

The plots of species accumulation show a marked change below 650 m depth. This was more noticeable in the 250 μm-to-500 μm and >500 μm size fractions as opposed to the Total - >250 μm size fraction. Figure 5.12 illustrates the plot of the 250 μm-to-500 μm size fraction with the temperature range superimposed. As can be seen below a depth of about 500 m the species accumulation curve is the mirror image of the temperature range curve. It is possible that where there is a rapid decline in the addition of new species, that this may mark a boundary between the water masses, in this instance intermediate and cold. Below about 650 m depth, the fauna will be subjected to permanently cold water. The change in species accumulation with depth curve was also seen in the 1996 AFEN results (see Bett, 2000). As depth increased species accumulation was high, although below 700 m the rate of species addition was relatively low.

Figure 5.12. Species accumulation of the 250 µm-to-500 µm size fraction with the temperature range superimposed on top.



5.4.3. The influence of the 250 µm sieve on the total result

Species diversity appears to increase when combining the 250 µm-to-500 µm fraction with the >500 µm fraction in both 1996 and 1998. However, the geometric abundance plots (see Figures 5.11a-f) did not suggest that the 250 µm-to-500 µm size fraction had a greater number of rare species as the graphs were not heavily skewed. Therefore, the influence of rare species was the same as non-rare species in both size

fractions the only difference being the species that are collected may be quite different (see Chapter 6 for composition).

It is highly likely however, that species diversity is not dependent upon depth or hydrography, but rather has been influenced by the evolutionary/geological timescale. Dahl (1979) suggested that in the Norwegian Basin, low species diversity might be a result of Quaternary glaciation (Rex *et al.*, 1993). Paul and Menzies (1974) found low Shannon diversity values from the high Arctic thus indicating that this ecosystem is relatively young. Margalef (1968) stated that, '*pioneering or immature communities can be characterised by low species diversity.*' Although both the Rockall Trough and Faeroe-Shetland Channel experienced glaciation, it is the actual rate of recovery that is important. In the Rockall Trough it is believed that species invaded from both shallow and deep-seas, however, in the Faeroe-Shetland Channel, temperature may have influenced the rate of invasion. This may certainly have been the case in the Norwegian Basin, where species have not invaded from the warmer deep-sea because of lack of thermal tolerance. Thus, the majority of species found in the Norwegian Basin are Arctic species.

Slow recovery as a result of lower temperature in shelf waters would instigate a faunal interchange with deeper waters. It is thought that the cold period during the Oligocene must have prolonged the time during which thermally tolerant shelf/slope species could invade and establish themselves in the deep Norwegian Sea and Polar Basin (Briggs, 1970; Dahl, 1979; Weishappel and Svavarsson, 1998). In the Faeroe-Shetland Channel, species could probably invade from the Rockall Trough provided they inhabited a depth above 500 m – 600 m, as this is the sill depth of the Wyville-Thomson ridge. Low species diversity in the Norwegian Sea would therefore have an effect on species situated at depths below 600 m in the Channel and this would explain why below 500 m species diversity tends to decline with depth.

The hypopsychral (temperature below 0 °C) environment and fauna of the Arctic has possibly only existed for the past 2 million years, implying that the Arctic has not yet achieved stability (Dunbar, 1968; Paul and Menzies, 1974). Even though the Arctic has a strong hydrographic connection with the Atlantic at the Greenland-Iceland-Faeroe Ridge, the deep Arctic fauna are characteristically endemic to this region and therefore can be distinguished from the Atlantic fauna (Menzies *et al.*, 1973). However, shallow water Arctic fauna have been found to be closely related to

both Atlantic and Pacific fauna, suggesting that species have been able to invade the Arctic to a certain degree but are only able to inhabit the upper, warmer waters.

Data from the present study leads to the acceptance of the hypothesis that by incorporating the 250 μm-to-500 μm size fraction with the >500 μm size fraction, species richness, species diversity and evenness show an overall increase while dominance decreases. However, the final hypothesis must be rejected, as it is temperature, and not depth and organic matter that influence the polychaete community on the West Shetland Slope.

STUDIES IN BENTHIC MACROFAUNAL ECOLOGY III: FAUNAL COMPOSITION OF THE WEST SHETLAND SLOPE

6.1. INTRODUCTION

6.1.1. Temperature

In the deep sea it is generally expected that there is a successive replacement of species with increasing depth. As other environmental variables, such as temperature and oxygen concentration change with depth, species may reach their upper/lower tolerance limit to the changes in these variables. Areas with a higher rate of change or replacement are thought to mark the position of zone boundaries (Carney *et al.*, 1983). Distribution of species may be regulated by the thermal tolerance that the species themselves show. The geographical range that a species inhabits, indicates that by natural selection this species has adapted to changes in the temperature of the environment (Levinton, 1982). Based on prior knowledge of the water mass structure of the Faeroe-Shetland Channel, it is likely that an 'ecotone' is formed. The ecotone would represent an overlapping boundary between the two communities, one in the warm and the other in the cold-water mass. An ecotone would contain species from both communities as well as some specialist edge species (Odum, 1971). The ecotone would be unlikely to contain competing/dominant species, as they would tend to exclude one another. The evolution of these species at the boundary may have resulted in an adaptation to one another (Whittaker, 1975).

6.1.2. Polychaete feeding modes

Fauchald and Jumars (1979) divided polychaetes into four groups dependent upon their feeding modes: filter feeders, carnivores, surface deposit and subsurface deposit feeders. Categorisation was interpreted from morphology, feeding behaviour as well as previously published experimental work (see Fauchald and Jumars, 1979). For example Ockelmann and Vahl (1970) and Dyal (1973) examined feeding in glycerids and polynoids. They found that these two predatory families would attack living prey, showing little interest in non-motile prey. Ockelmann and Vahl (1970) also found that *Glycera alba* would not attack its prey until a burrow had been constructed. Four groups can also be identified by using the Infaunal Trophic Index (ITI) (Word, 1979; 1980). Fauchald and Jumars (1979) further separated the feeding modes into feeding guilds, which were dependent upon feeding mode, sub-mode, morphological subgroup

and motility. Thus, "*the feeding guild of an organism may be defined as the set of relations among food particle size and composition, the mechanism involved in food intake and the motility patterns associated with feeding*" (Fauchald and Jumars, 1979). It may be difficult to determine the general feeding modes of polychaetes, in some families. For example species of Spionidae may show differing feeding modes in relation to the environment (Word, 1979; 1980; Mearns and Word 1982). Taghon and Greene (1992) undertook experimental work on two species of spionid, *Boccardia pugettensis* and *Pseudopolydora kempi japonica* and found that under certain conditions e.g. change in flow regime, these two species could change from being deposit feeders to suspension feeders. By switching between the two modes of feeding, the two spionid species can have greater access to the available food and so have been termed "interface feeders" (Taghon and Greene, 1992).

6.1.3. Hypotheses

- Water mass structure does not influence the distribution of individual species down the transect. Species will remain within a definite temperature band.
- Dominance of feeding modes does not change with depth. Environmental variables that change with depth e.g. mean sediment grain size do not influence the feeding modes of polychaetes.

6.2. ANALYTICAL METHODS

6.2.1. Feeding modes

Determination of polychaete feeding modes is usually undertaken using either classification from the Infaunal Trophic Index (ITI UK) (Wrc plc, 1992) based on work undertaken by Word (1979), or groupings suggested by Fauchald and Jumars (1979). In the present study neither was used, as the distribution of polychaetes was visualised more easily when categorising the feeding types into filter, deposit (combining surface and sub-surface deposit feeders) and predatory feeders. This simplified categorisation of feeding modes was based on the ITI. However, care must be taken as the divisions used here may not apply to the families in different locations or under different environmental conditions. Additionally, polychaete families are often speciose and their dietary plasticity (Fauchald and Jumars, 1979) makes it difficult to determine whether a family was truly predatory or whether it had species that could sometimes feed as a surface deposit feeder.

6.2.2. Multi-variate analysis

6.2.2.1. Cluster analysis

See Analytical Methods section in Chapter 4, page 52.

6.2.2.2. Non-metric multidimensional scaling and ordination

See Analytical Methods section in Chapter 4, page 52.

6.2.2.3. Canonical Correspondence Analysis

See Analytical Methods section in Chapter 4, page 52.

6.3. RESULTS

To test the hypotheses on page 122, the distribution of species within each temperature band was determined in order to establish if a species dominated, or was restricted, to a particular temperature band. The distribution of polychaete feeding modes was also analysed in relation to the suite of environmental variables to determine if these had any influence on the feeding modes observed.

6.3.1. Polychaete distribution with respect to temperature bands

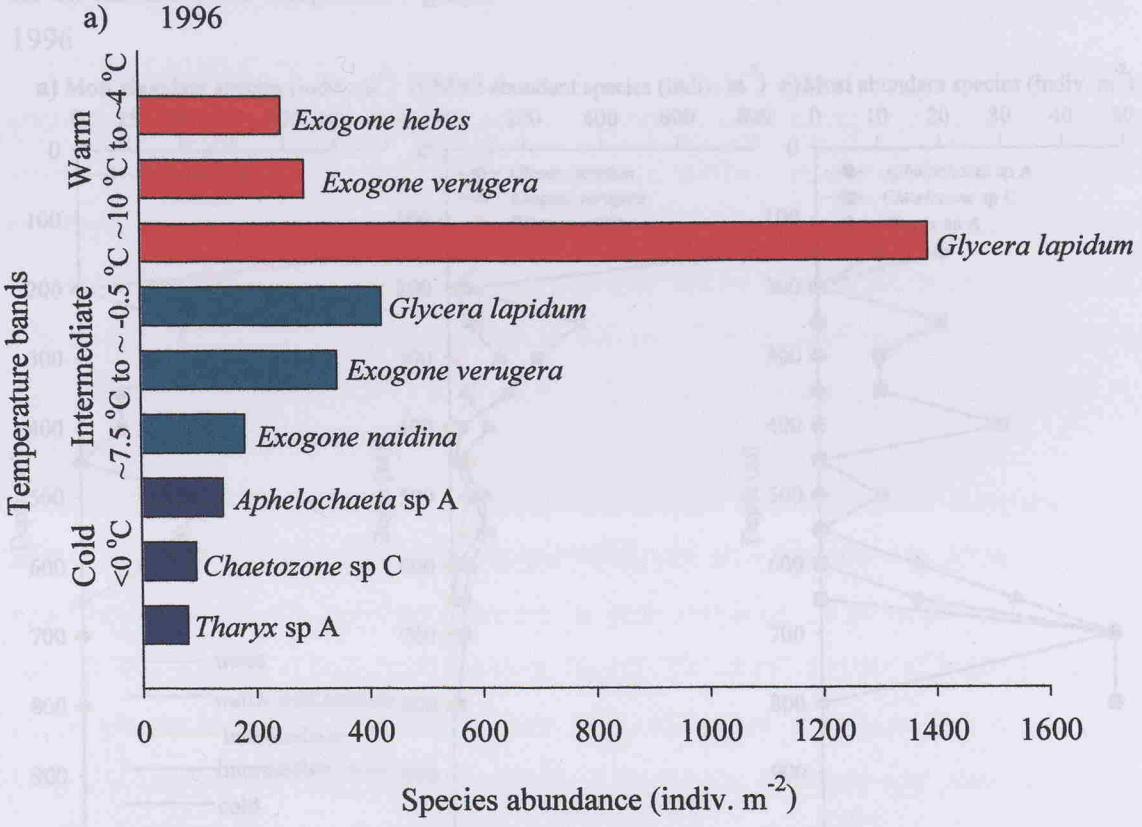
From the results obtained, there appears to be a strong relationship between temperature and faunal distribution. Three temperature bands were determined from the physical data: a warm band (~10 °C to ~4 °C) consisting of stations between 150 m and 300 m; an intermediate band (~7.5 °C to –0.5 °C) of stations between 350 m and 650 m, and finally a cold band (0 °C) consisting of stations situated below 700 m. These station bands are based upon similar groups used by Bett (2000) from TOBI results where the minimum temperature for the warm stations remained above zero, while maximum temperature for the cold stations did not exceed zero. The rest of the analysis in the section is based upon this separation.

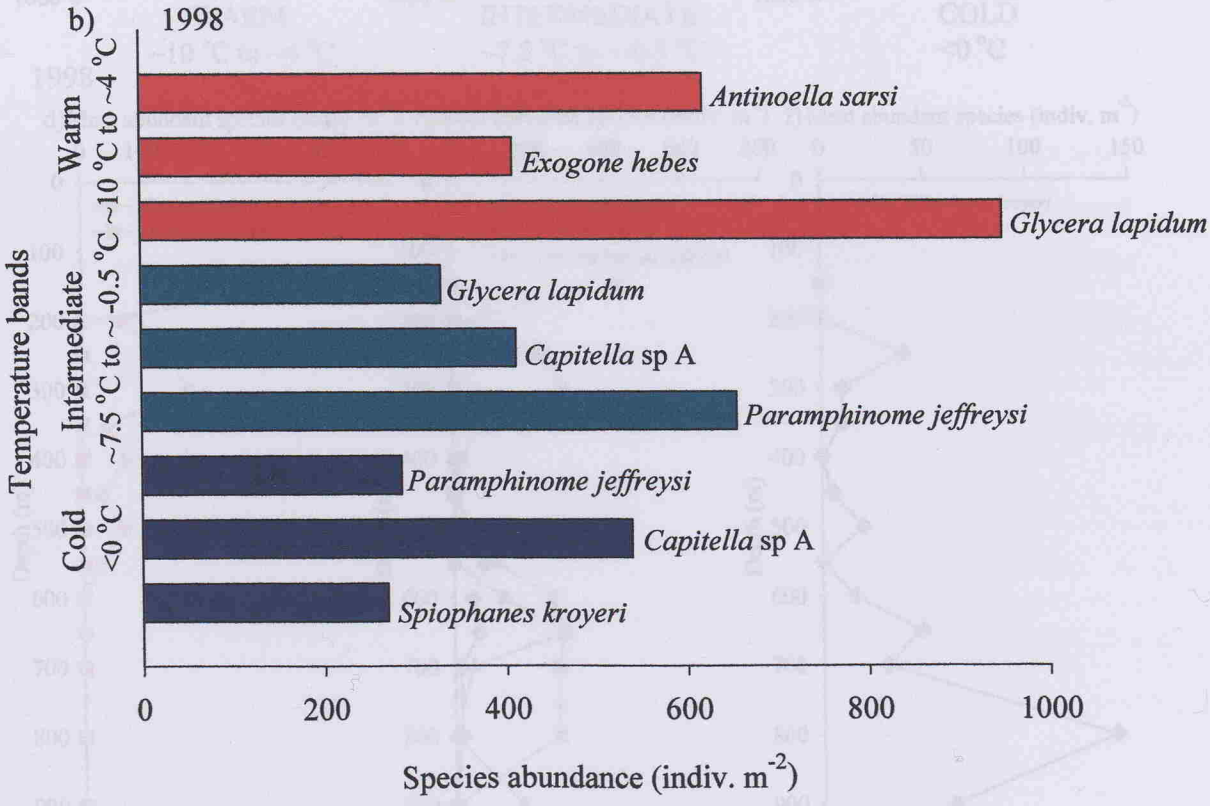
Two types of simple plot were constructed. The first was based on the three most abundant species in each temperature band, and the second shows the distribution of these species with depth.

6.3.1.1. 250 µm-to-500 µm size fraction

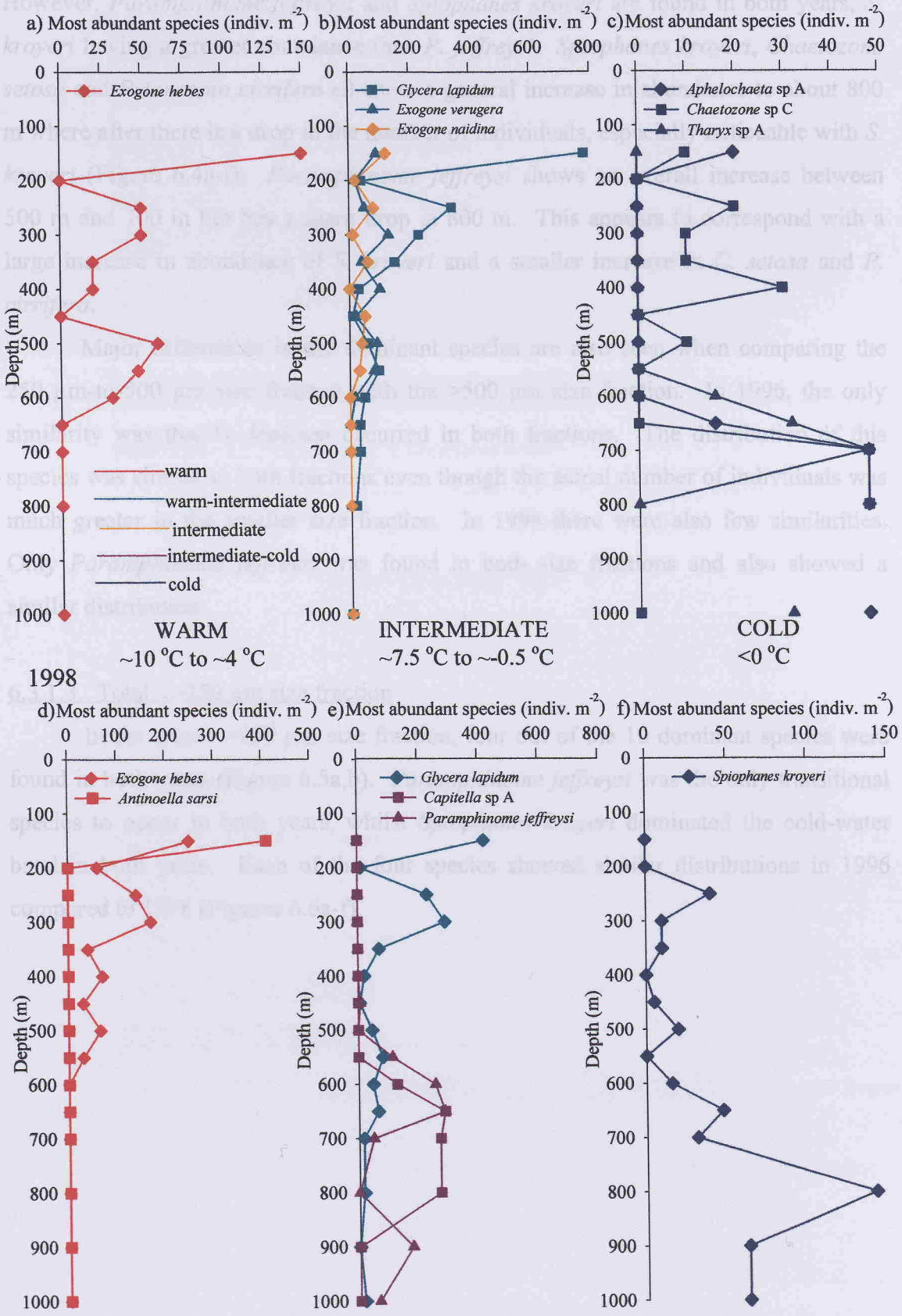
The three most abundant species in each temperature band in the 250 µm-to-500 µm size fraction in 1996 are quite different to those in 1998 (Figure 6.1a,b). The distribution of three species, *Exogone hebes* and *Glycera lapidum* in the warm temperature band and *Chaetozone* sp. C. in the cold temperature band, were the only ones that could be compared in the two years (Figures 6.2a-f). Overall *E. hebes* and *G. lapidum* showed very similar patterns whilst *Chaetozone* sp. C. was quite different. In 1996 there appears to be no dominant intermediate-cold water transitional species as seen in 1998 i.e. *Paramphinome jeffreysi*. The term transitional species has been applied to species that are found in relatively high numbers in the warm-intermediate or intermediate-cold temperature band.

Figures 6.1a,b. Vertical distribution of the three most abundant polychaete species in each temperature band in the 250 µm-to-500 µm size fraction. Warm = red, Intermediate = green, Cold = blue.





Figures 6.2a-f. Distribution of the most abundant polychaete species in each temperature band with depth in the 250 µm-to-500 µm size fraction. Species that are considered transitional species i.e. inhabit the boundary of two temperature bands have been plotted on the intermediate temperature graph.



6.3.1.2. >500 µm size fraction

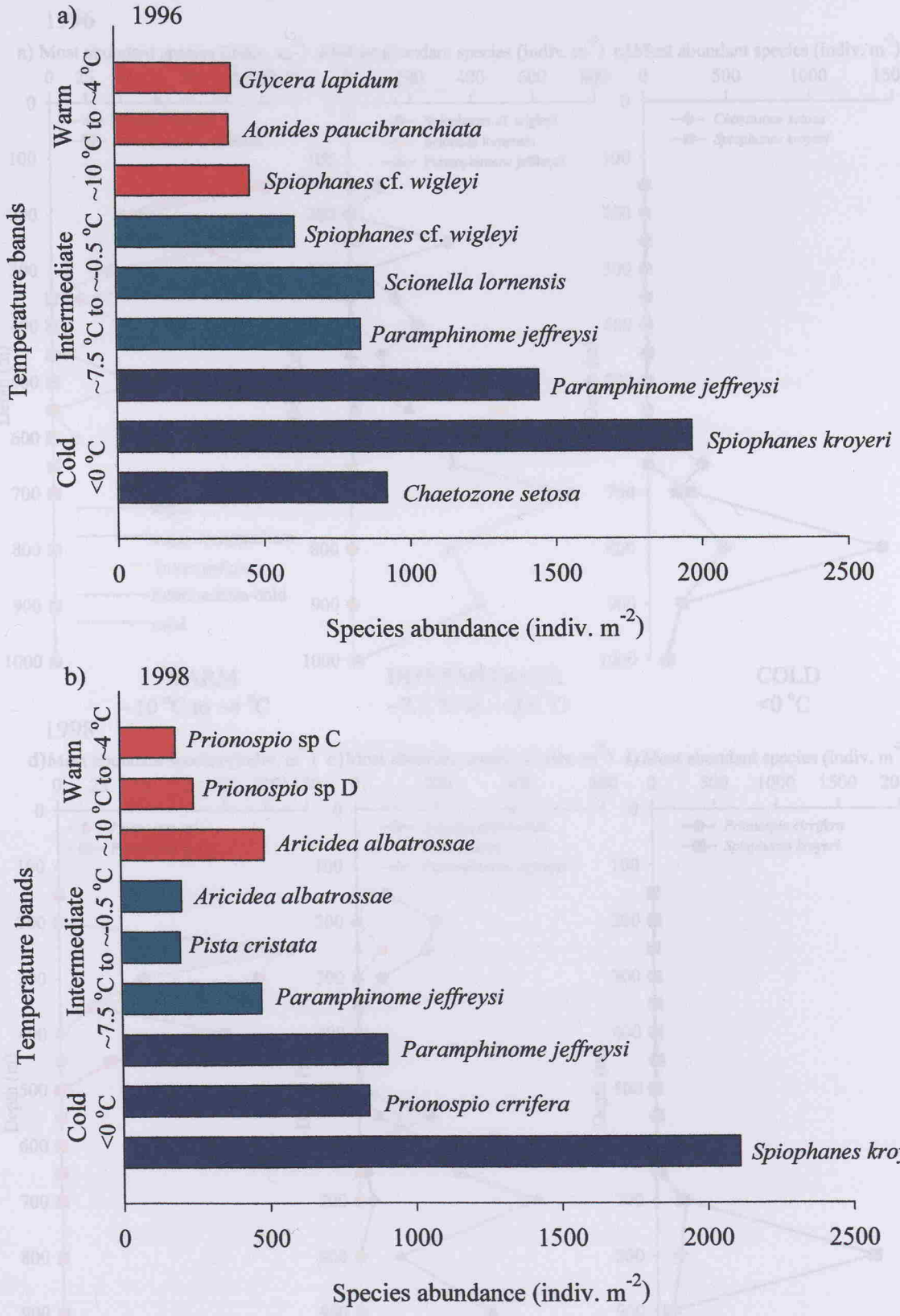
The >500 µm size fraction has notable differences between 1996 and 1998. In the warm temperature band there are no similar dominant species (Figure 6.3a,b). However, *Paramphinome jeffreysi* and *Spiophanes kroyeri* are found in both years, *S. kroyeri* having a greater abundance than *P. jeffreysi*. *Spiophanes kroyeri*, *Chaetozone setosa* and *Prionospio cirrifera* all show a general increase in abundance to about 800 m where after there is a drop in the number of individuals, especially noticeable with *S. kroyeri* (Figure 6.4a-f). *Paramphinome jeffreysi* shows an overall increase between 500 m and 700 m but has a sharp drop at 800 m. This appears to correspond with a large increase in abundance of *S. kroyeri* and a smaller increase in *C. setosa* and *P. cirrifera*.

Major differences in the dominant species are also seen when comparing the 250 µm-to-500 µm size fraction with the >500 µm size fraction. In 1996, the only similarity was that *G. lapidum* occurred in both fractions. The distribution of this species was similar in both fractions even though the actual number of individuals was much greater in the smaller size fraction. In 1998 there were also few similarities. Only *Paramphinome jeffreysi* was found in both size fractions and also showed a similar distribution.

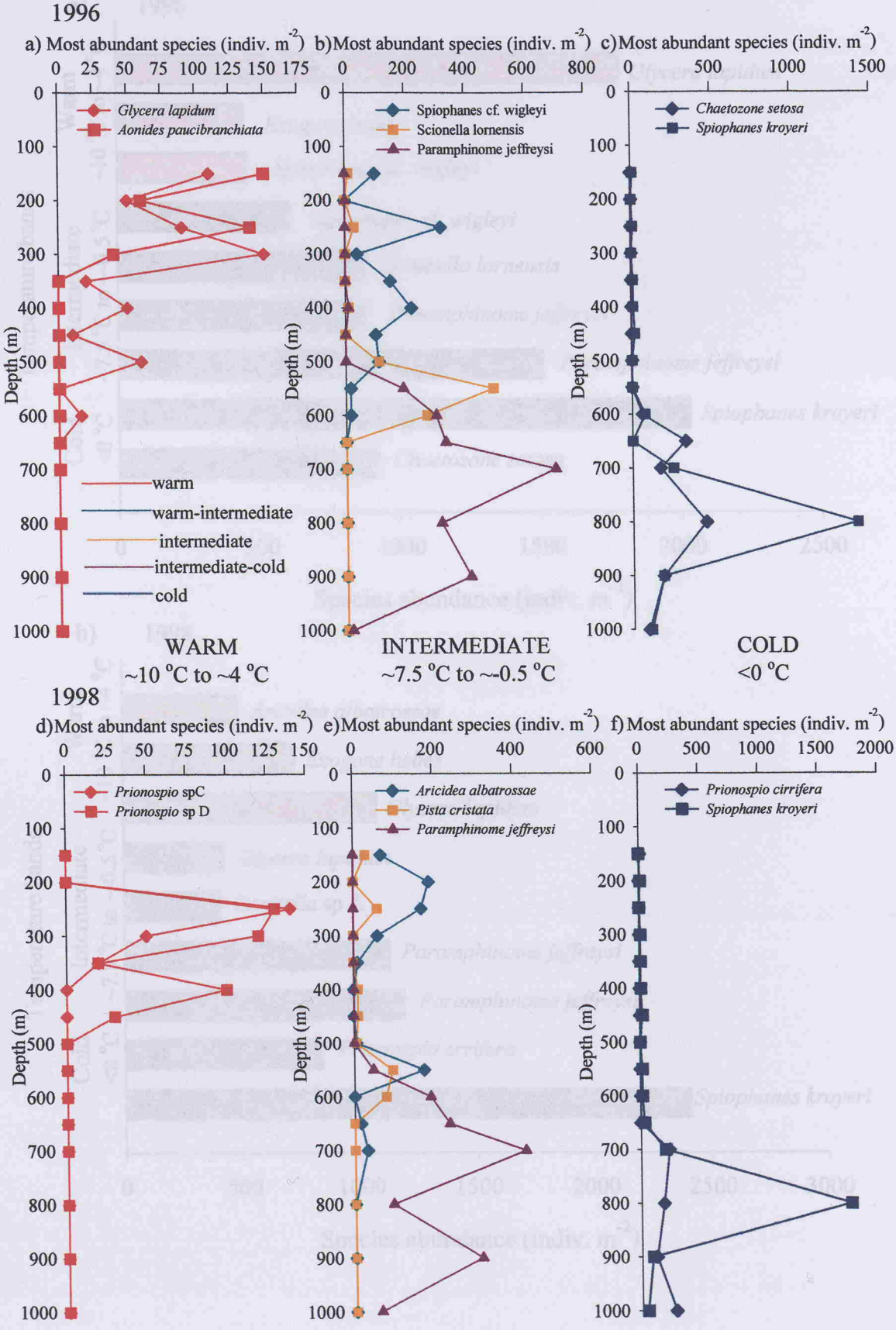
6.3.1.3. Total - >250 µm size fraction

In the total - >250 µm size fraction, four out of the 10 dominant species were found in both years (Figure 6.5a,b). *Paramphinome jeffreysi* was the only transitional species to occur in both years, whilst *Spiophanes kroyeri* dominated the cold-water band in both years. Each of the four species showed similar distributions in 1996 compared to 1998 (Figures 6.6a-f).

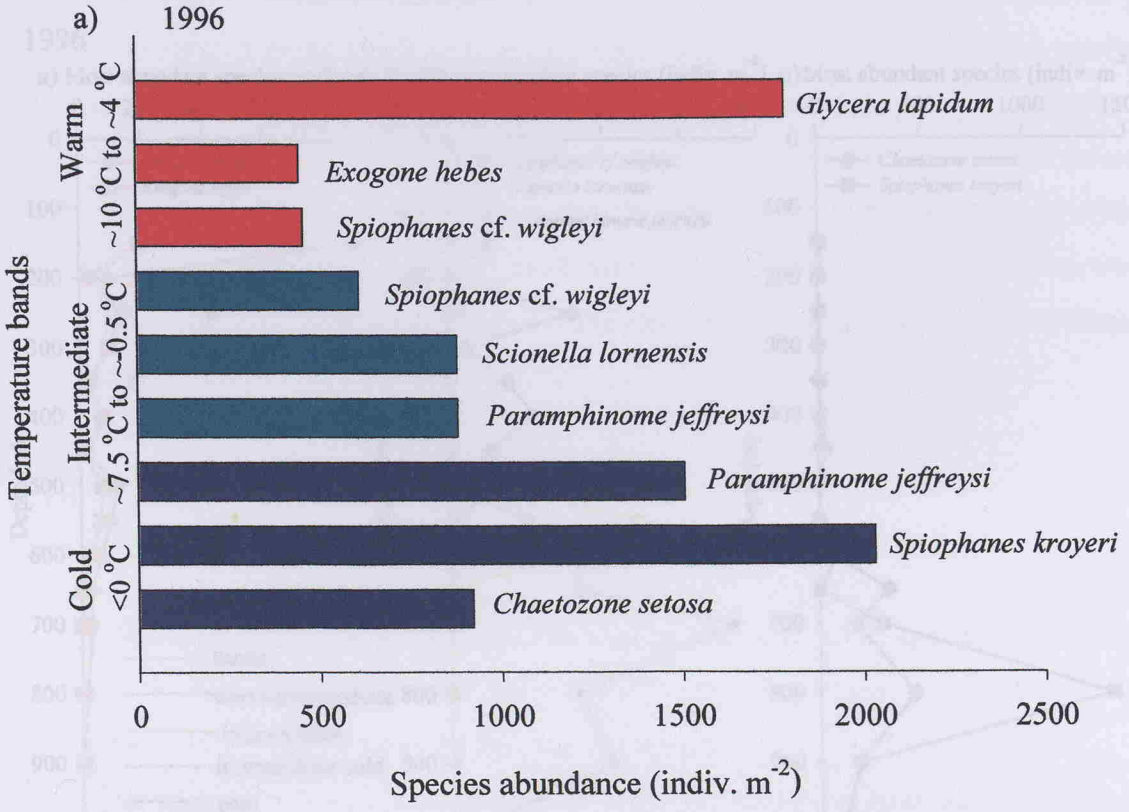
Figures 6.3a,b. Vertical distribution of the three most abundant polychaete species in each temperature band in the >500 µm size fraction. Warm = red, Intermediate = green, Cold = blue.

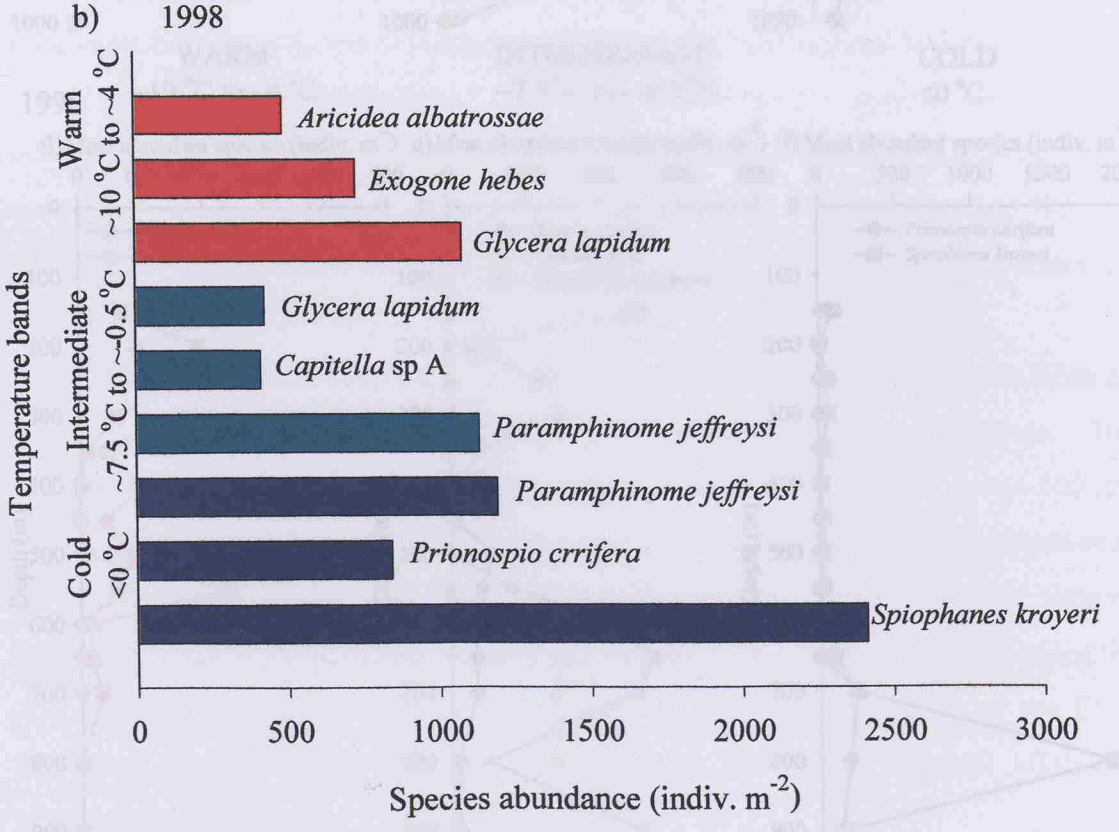


Figures 6.4a-f. Distribution of the most abundant polychaete species in each temperature band with depth in the >500 µm size fraction. Species that are considered transitional species i.e. inhabit the boundary of two temperature bands have been plotted on the intermediate temperature graph.

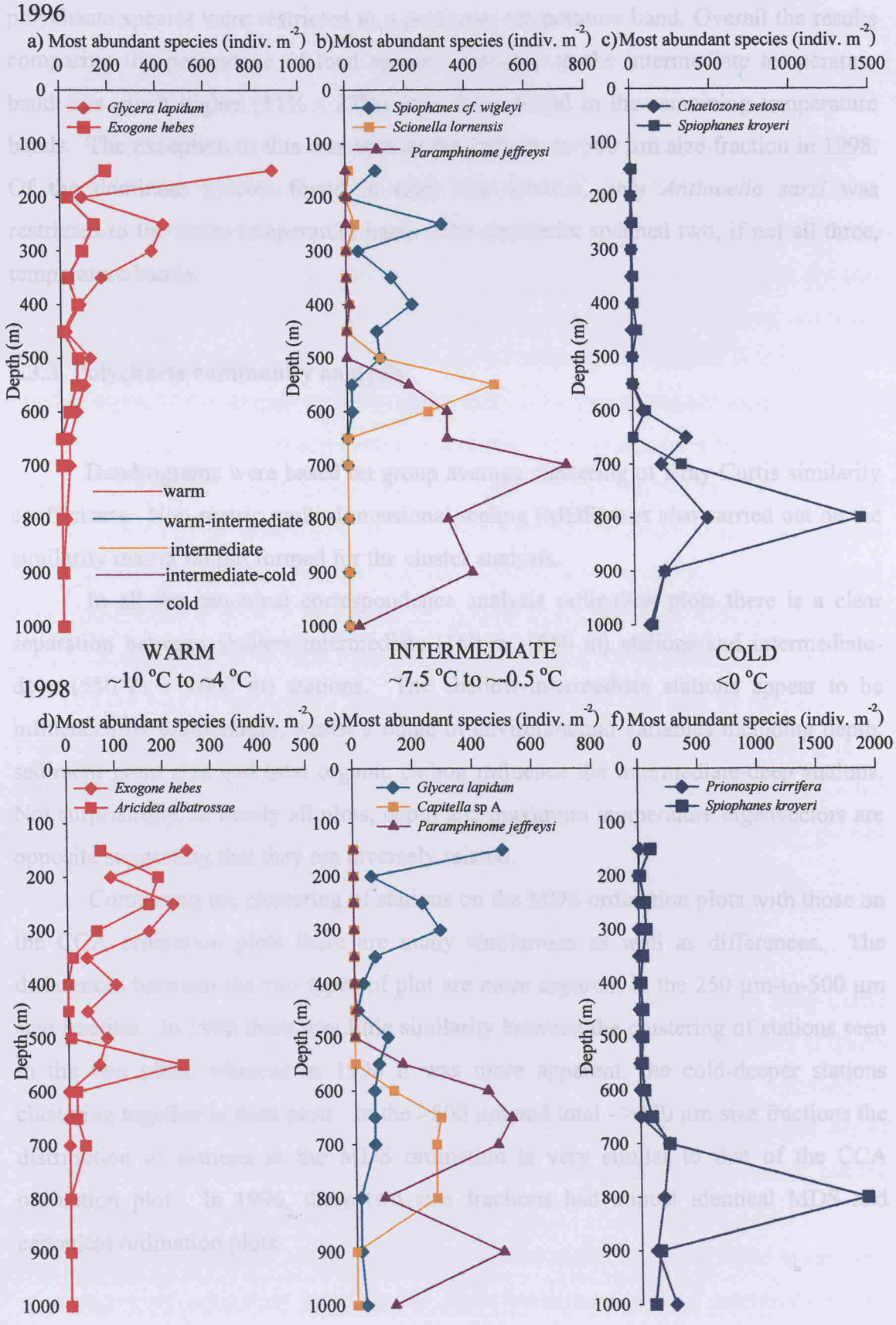


Figures 6.5a,b. Vertical distribution of the three most abundant polychaete species in each temperature band in the Total - >250 µm size fraction. Warm = red, Intermediate = green, Cold = blue.





Figures 6.6a-f. Distribution of the most abundant polychaete species in each temperature band with depth in the Total - >250 µm size fraction. Species that are considered transitional species i.e. inhabit the boundary of two temperature bands have been plotted on the intermediate temperature graph.



6.3.2. Restriction of species to particular temperature bands

A simple analysis based on presence/absence was used to determine whether polychaete species were restricted to a particular temperature band. Overall the results comparing the percentage of total species restricted to the intermediate temperature band was much higher (11% - 27%) than those found in the remaining temperature bands. The exception to this was seen in the 250 μm-to-500 μm size fraction in 1998. Of the dominant species found in each size fraction, only *Antinoella sarsi* was restricted to the warm temperature band. The remainder spanned two, if not all three, temperature bands.

6.3.3. Polychaete community analysis

Dendrograms were based on group average clustering of Bray Curtis similarity coefficients. Non-metric multi-dimensional scaling (MDS) was also carried out on the similarity matrix output formed for the cluster analysis.

In all the canonical correspondence analysis ordination plots there is a clear separation between shallow-intermediate (150 m - 550 m) stations and intermediate-deep (550 m – 1000 m) stations. The shallow-intermediate stations appear to be influenced by temperature, whilst a range of environmental variables including depth, sediment grain size and total organic carbon influence the intermediate-deep stations. Not surprisingly, in nearly all plots, depth and maximum temperature eigenvectors are opposite suggesting that they are inversely related.

Comparing the clustering of stations on the MDS ordination plots with those on the CCA ordination plots there are many similarities as well as differences. The differences between the two types of plot are more apparent in the 250 μm-to-500 μm size fraction. In 1996 there was little similarity between the clustering of stations seen in the two plots, whereas in 1998 it was more apparent, the cold-deeper stations clustering together in both plots. In the >500 μm and total - >250 μm size fractions the distribution of stations in the MDS ordination is very similar to that of the CCA ordination plot. In 1996, these two size fractions had almost identical MDS and canonical ordination plots.

6.3.3.1. 250 µm-to-500 µm size fraction

The dendrograms produced by the Bray Curtis coefficient are shown in figures 6.7a,b. These show very similar results to the non-metric two-dimensional scaling ordination plots (Figures 6.7c,d). A clear separation between the deep (600 m - 1000 m) and shallow (150 m - 550/600 m) stations is apparent with the 550 m/600 m stations generally separating out from the rest of the stations.

Using canonical correspondence analysis, temperature is the strongest environmental variable associated with the distribution of the stations on the ordination plot in both 1996 and 1998. The species, which appear to be influenced by these eigenvectors, tend mainly to be found in high numbers at the stations, which are also associated with these eigenvectors (Figures 6.8a,b) (NB only the 20 most abundant polychaete species appear on the plot for ease of reading). The same is also true for species found at the deeper stations, which tend to be more strongly associated with eigenvectors such as total hydrocarbon and depth. The results from the Monte Carlo test imply that maximum temperature accounts for the largest proportion of the variability seen in the distribution of the polychaete species (Table 6.1). Four species in 1996 seemed to lie very close to specific eigenvectors. As can be seen from figure 6.8a, *Spiophanes kroyeri*, *Chaetozone* sp. A. and *Apistobranchus tulbergii* appear to have a strong link with the total hydrocarbon eigenvector, whilst *Aricidea quadrilobata* lies near the depth eigenvector. This suggests that these species may be influenced by these variables. However, using Spearman's rank correlation, there appeared to be no significant correlation between the species abundance and the relevant variable. Of the three species in 1998 that were found near eigenvectors, two, *Capitella* sp. A. and *Chaetozone* sp. B. were found to correlate significantly with total hydrocarbon.

6.3.3.2. >500 µm size fraction

The MDS ordination plots tend to reflect that shown by the Bray-Curtis dendrogram, but differences between the two years are much more apparent (Figures 6.9a-d). In 1996 there appears to be a shallow and deep group with intermediate stations bridging the two, forming a 'U' shaped curve. In 1998, the deeper set of stations group together strongly as do a group of shallow/intermediate stations, but the distinction is not as clear as for 1996.

On examining the canonical correspondence ordination plots, once again there is a degree of separation between the shallow-intermediate and intermediate-deep

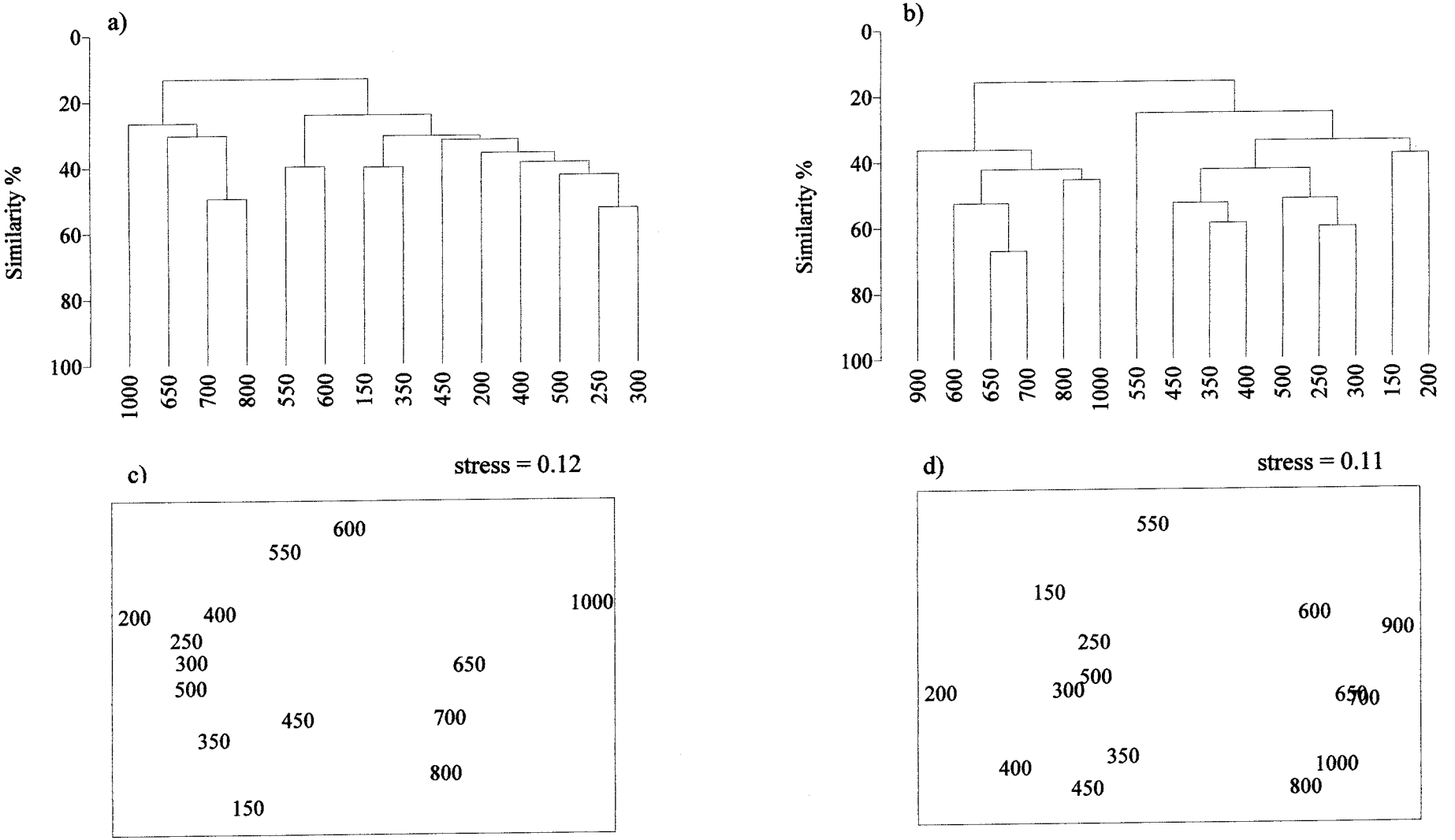
stations. As with the smaller size fraction, temperature eigenvectors appear to be closely associated with the shallower stations (Figure 6.10a,b) (NB only the 20 most abundant polychaete species appear on the plot for ease of reading). The ordination plot for 1996 suggests that there may be another environmental variable influencing the fauna, which has not been taken into consideration (this line has been drawn in red on the plot). This line is the inverse of the temperature range eigenvector, suggesting that species situated in this area cannot tolerate a wide range of temperatures. However, in 1998 this does not appear to be the case. Using the Monte Carlo test, maximum temperature once again is the environmental variable found to be most influencing the species community (Table 6.1).

In 1996 *Exogone hebes* was seen to lie close to the maximum temperature eigenvector. This particular species was also strongly correlated with maximum temperature ($r_s = 0.872$, $\alpha = 0.05$). In 1998 three species appeared to be influenced by specific environmental variables, *Prionospio* sp. C., *Prionospio* sp. E. and Maldanid sp. B. (Figure 6.10b). Of these, *Prionospio* sp. E. correlated significantly with the temperature range ($r_s = 0.629$, $\alpha = 0.05$), while Maldanid sp. B. showed a significant correlation with total hydrocarbon ($r_s = 0.541$, $\alpha = 0.05$).

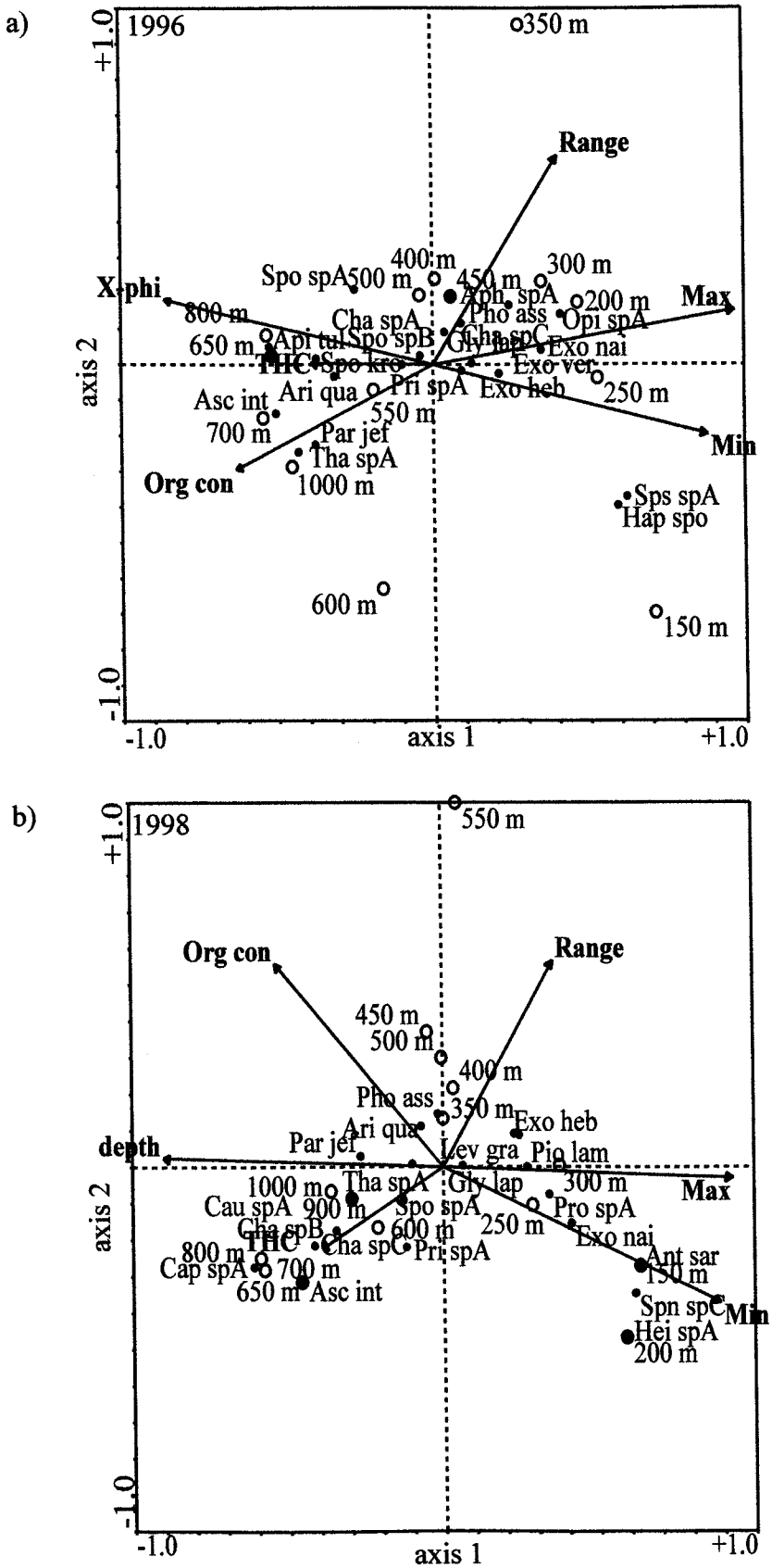
6.3.3.3. Total - >250 µm size fraction

The distribution of stations between the two years is slightly different and becomes more apparent when using MDS ordination (Figures 6.11a-d) rather than cluster analysis dendrograms. In 1996 as with the >500 µm size fraction, there is a separation of shallow and deep stations by a group of intermediate stations. By comparison in 1998 this is not so clear. The 200 m and 450 m stations fall out as individual entities i.e. not clustering with any other station.

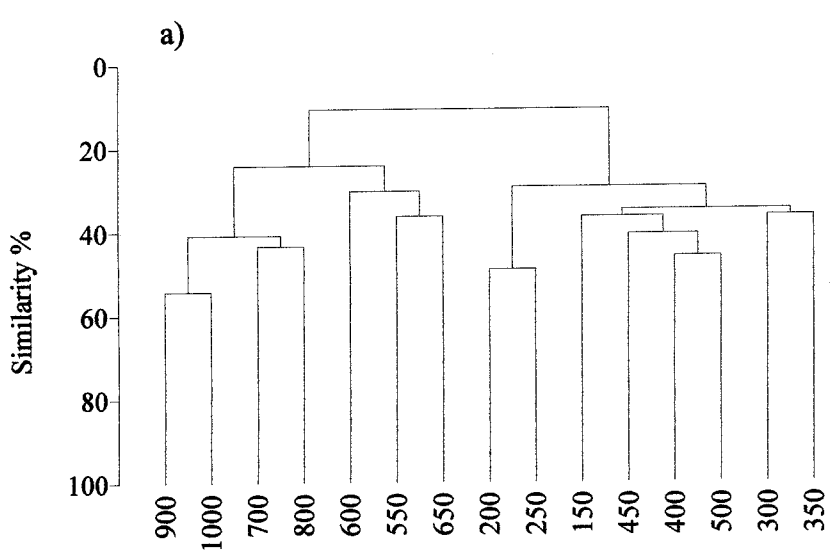
Figures 6.7a-d. Cluster analysis and non-metric multi-dimensional scaling ordination of polychaete species in the 250 µm-to-500 µm size fraction in 1996 (a and c) and 1998 (b and d).

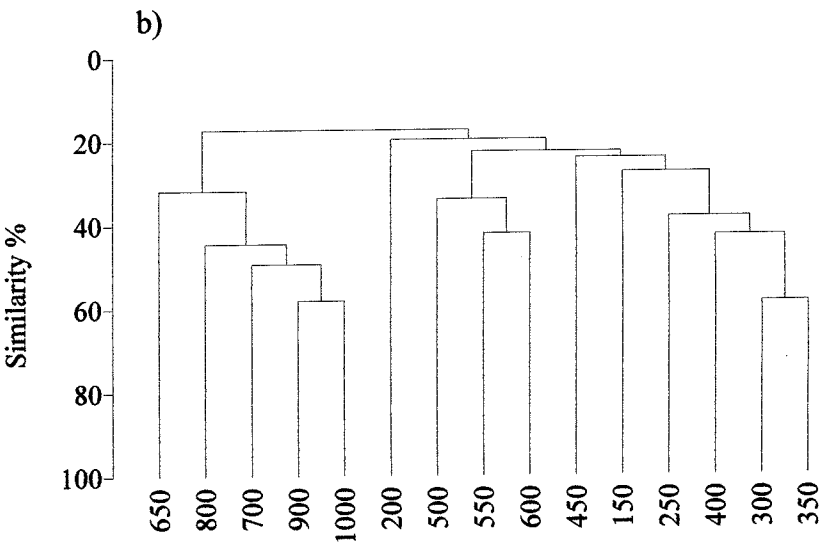


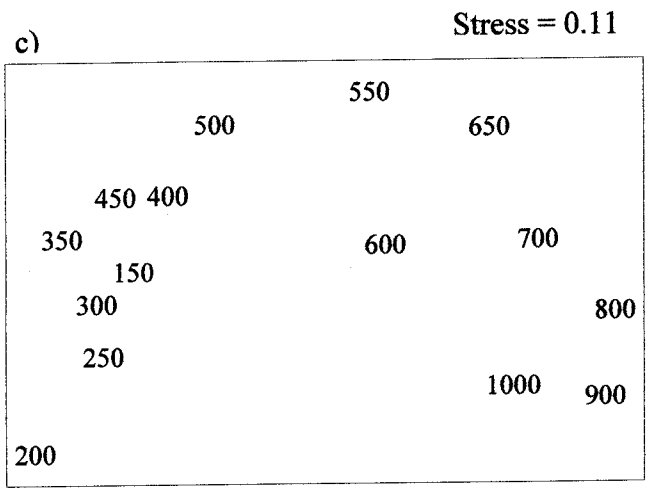
Figures 6.8a,b. CCA ordination plots of the 20 most abundant polychaete species (see appendix II for list of abbreviations), stations and environmental variables for the 250 µm-to- 500 µm size fraction in 1996 and 1998. Max = maximum temperature, range = temperature range, X-phi = mean sediment grain size, S.C = silt:clay, THC = total hydrocarbons. o= station, • = fauna, ⟶ = environmental variable

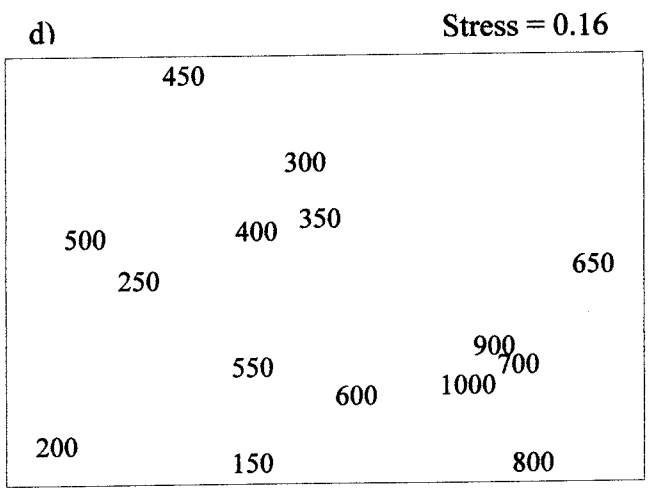


Figures 6.9a-d. Cluster analysis and non-metric multi-dimensional scaling ordination of polychaete species in the >500 µm size fraction in 1996 (a and c) and 1998 (b and d).

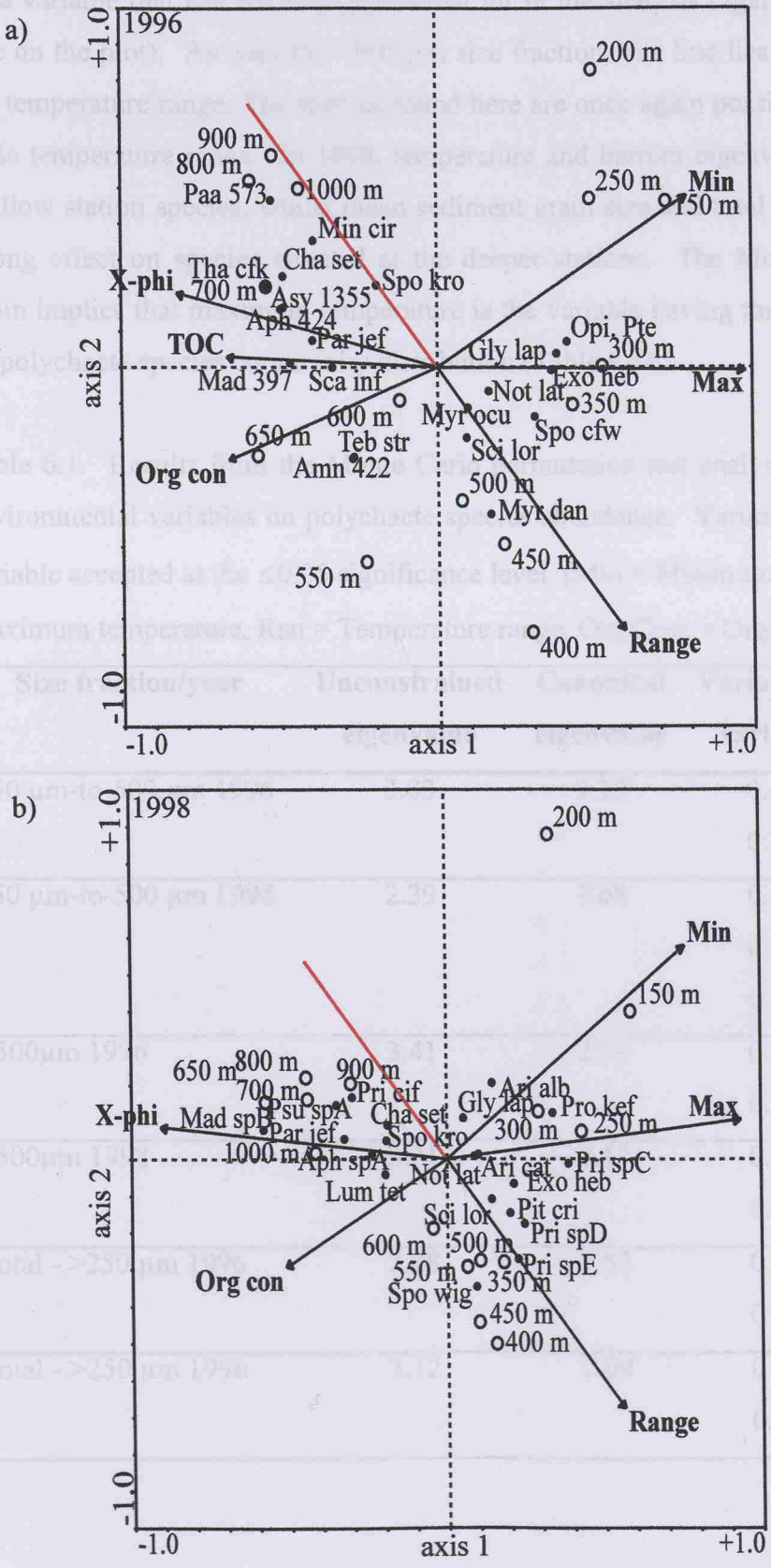








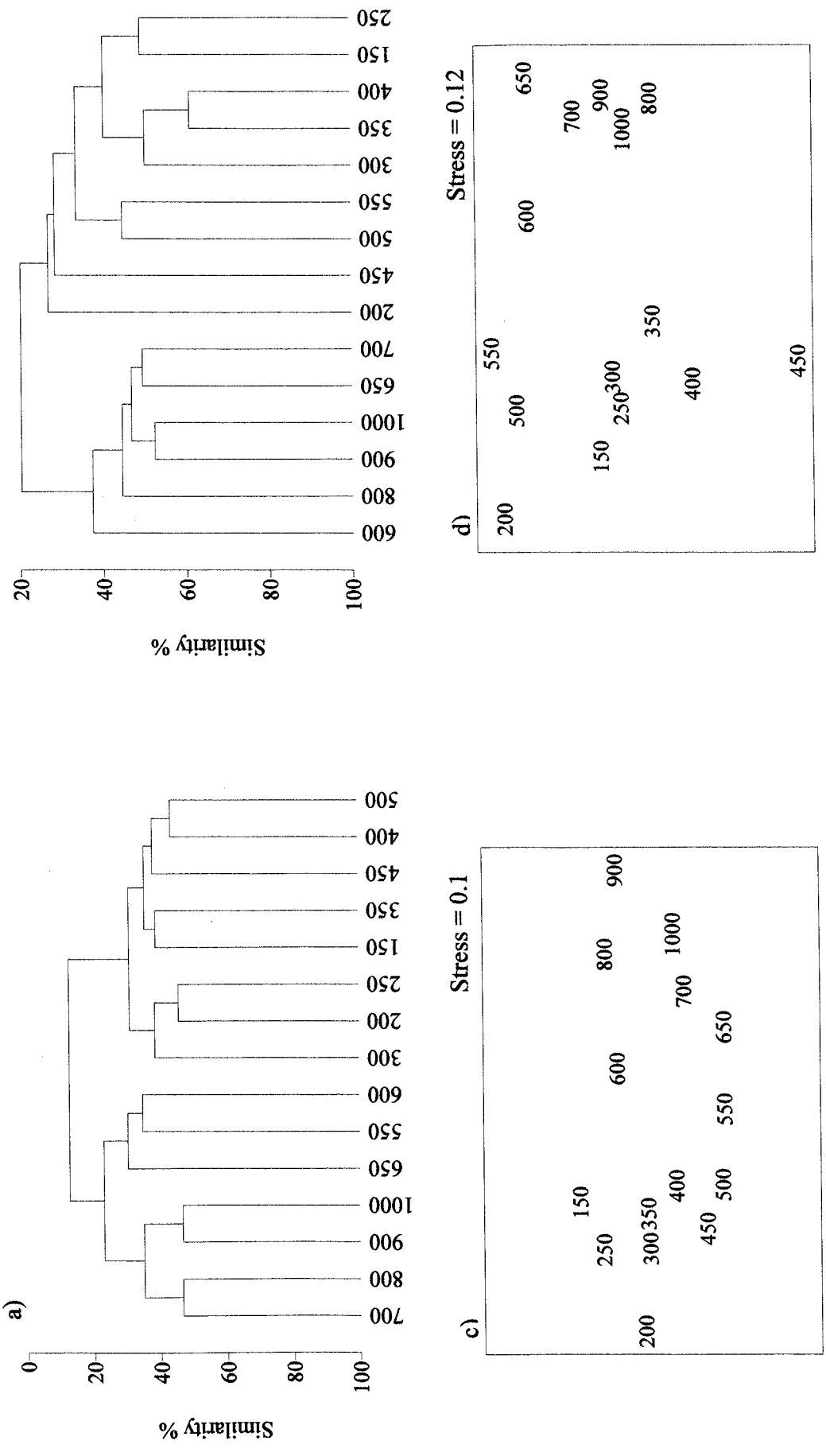
Figures 6.10a,b. CCA ordination plots of the 20 most abundant polychaete species (see appendix II for list of abbreviations), stations and environmental variables for the >500 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content. o = station, • = fauna, ⟶ = environmental variable. The red lines indicates species and stations lying along the inverse of an environmental variable.



In the total - >250 μm size fraction, the CCA ordination plots tend to reflect patterns seen in the individual size fractions (Figures 6.12a,b) (NB only the 20 most abundant polychaete species appear on the plot for ease of reading). In 1996 there is still a group of stations and species, which appear as though they should be influenced by a variable that has not been accounted for in the analysis (again indicated by a red line on the plot). As with the >500 μm size fraction, this line lies diagonally opposite the temperature range. The species found here are once again possibly not tolerant of a wide temperature range. In 1998, temperature and barium eigenvectors influence the shallow station species, whilst mean sediment grain size and total hydrocarbon have a strong effect on species situated at the deeper stations. The Monte Carlo test once again implies that maximum temperature is the variable having the strongest influence on polychaete species community distribution (Table 6.1).

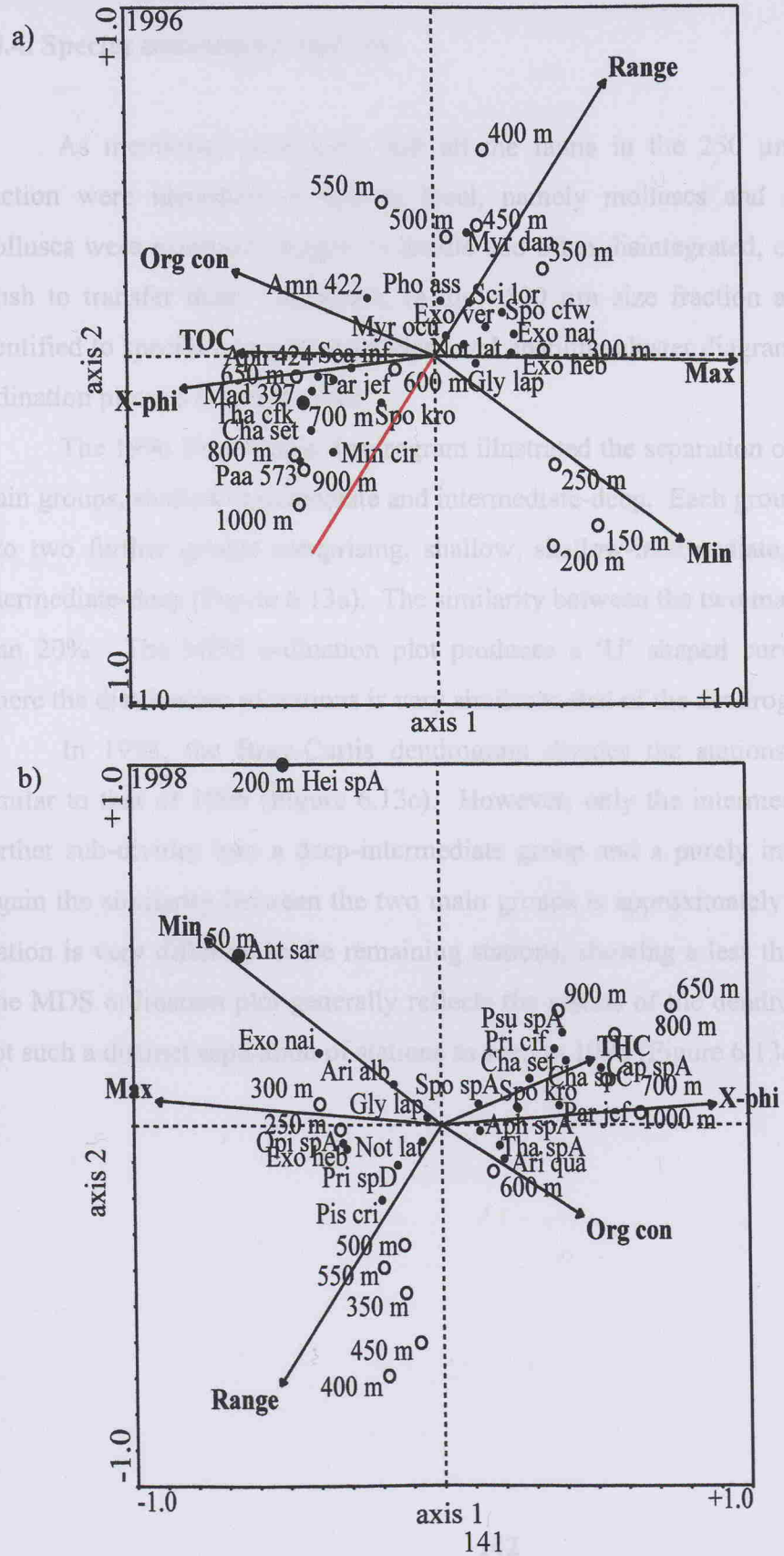
Table 6.1. Results from the Monte Carlo permutation test analysing the influence of environmental variables on polychaete species abundance. Variance of environmental variable accepted at the ≤0.05 significance level. (Min = Minimum temperature, Max = Maximum temperature, Ran = Temperature range, Org Cont = Organic Content).

Size fraction/year	Unconstrained eigenvalue	Canonical eigenvalue	Variance of variable	Variable
250 μm-to-500 μm 1996	3.03	2.12	0.40	Max
			0.26	Min
250 μm-to-500 μm 1998	2.39	1.68	0.41	Max
			0.26	Org Cont
			0.23	Min
>500μm 1996	3.41	2.35	0.52	Max
			0.32	Min
>500μm 1998	3.31	2.17	0.39	Max
			0.33	Ran
Total - >250 μm 1996	3.78	2.57	0.53	Max
			0.34	Min
Total - >250 μm 1998	3.12	2.09	0.42	Max
			0.32	Min



Figures 6.11a-d. Cluster analysis and non-metric multi-dimensional scaling ordination of polychaete species in the Total - >250 µm size fraction in 1996 (a and c) and 1998 (b and d).

Figures 6.12a,b. CCA ordination plots of the 20 most abundant polychaete species (see appendix II for list of abbreviations), stations and environmental variables for the Total - >250 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content, TOC = total organic carbon. o = station, • = fauna, ⟶ = environmental variable. The red line indicates species and stations lying along the inverse of an environmental variable.



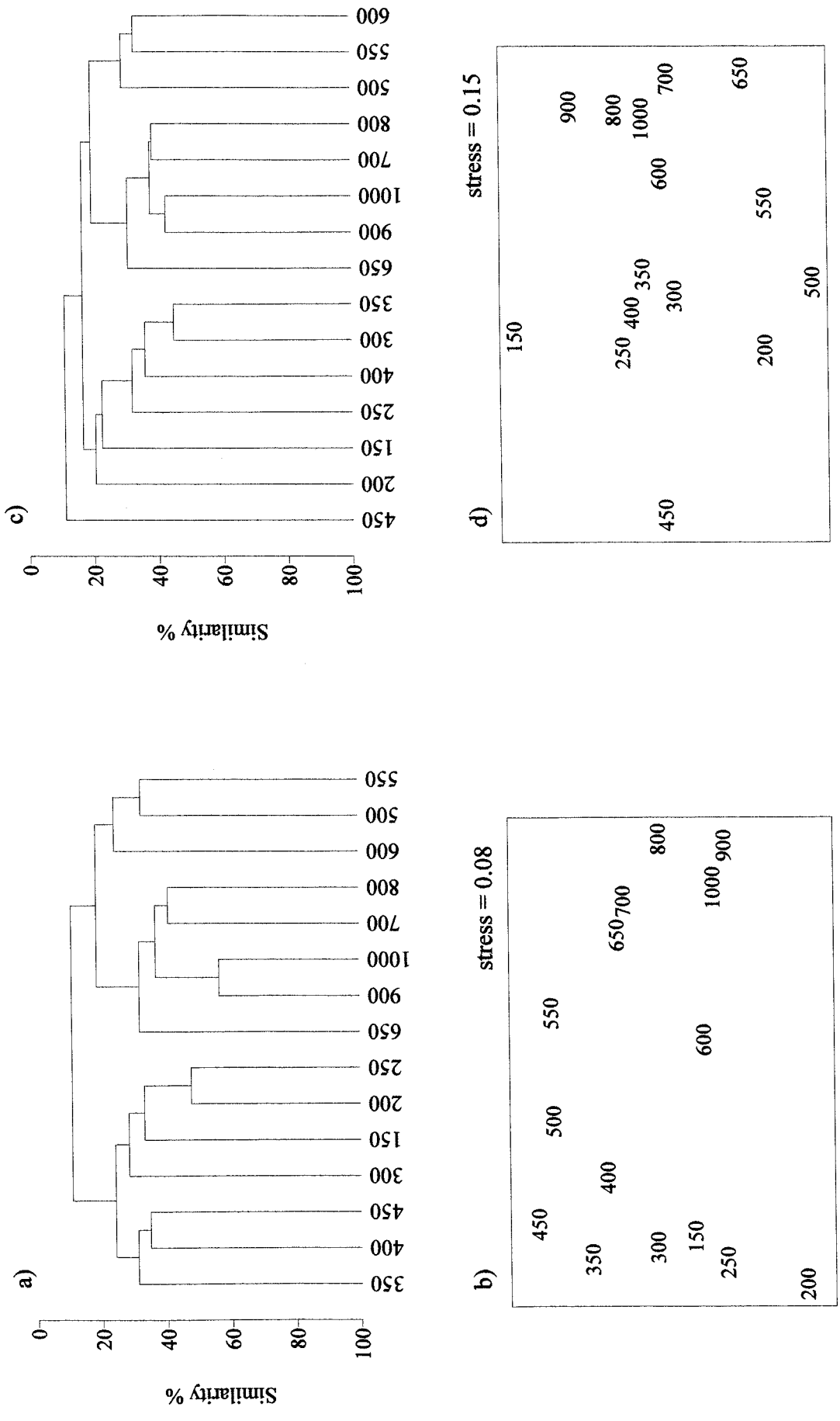
In 1996 no particular species appeared to be linked to a specific eigenvector. By comparison, in 1998 several species appeared as though they would be influenced by specific environmental variables. However, only *Capitella* sp. A. correlated significantly with total hydrocarbon ($r_s = 0.665$, $\alpha = 0.05$).

6.3.4. Species community analysis

As mentioned previously, not all the fauna in the 250 μm-to-500 μm size fraction were identified to species level, namely molluscs and amphipods. The molluscs were extremely fragile to handle and often disintegrated, even when using a brush to transfer them. However, in the >500 μm size fraction all the fauna were identified to species or putative species level enabling cluster diagrams and MDS/CCA ordination plots to be constructed.

The 1996 Bray-Curtis dendrogram illustrated the separation of stations into two main groups, shallow-intermediate and intermediate-deep. Each group was sub-divided into two further groups comprising, shallow, shallow-intermediate, intermediate and intermediate-deep (Figure 6.13a). The similarity between the two main groups was less than 20%. The MDS ordination plot produces a 'U' shaped curve (Figure 6.13b), where the distribution of stations is very similar to that of the dendrogram.

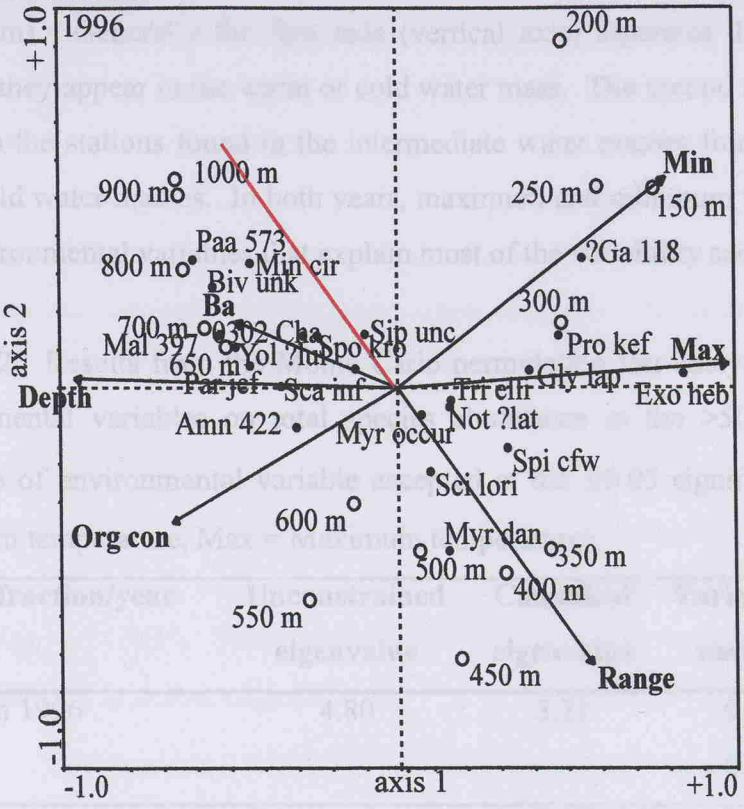
In 1998, the Bray-Curtis dendrogram divides the stations into two groups similar to that of 1996 (Figure 6.13c). However, only the intermediate-deep stations further sub-divides into a deep-intermediate group and a purely intermediate cluster. Again the similarity between the two main groups is approximately 20%. The 450 m station is very different to the remaining stations, showing a less than 20% similarity. The MDS ordination plot generally reflects the results of the dendrogram, but there is not such a distinct separation of stations as seen in 1996 (Figure 6.13d).



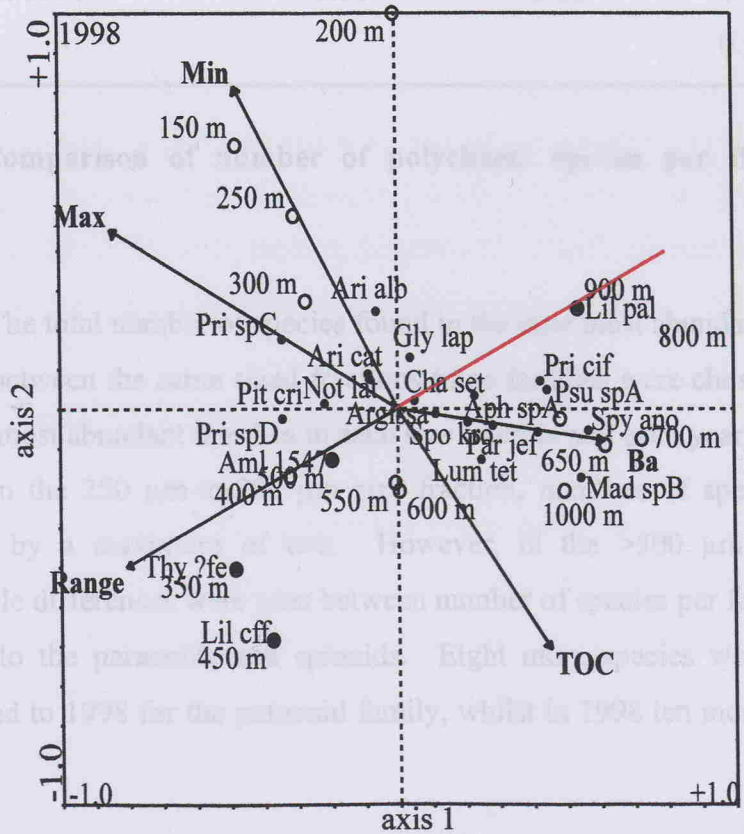
Figures 6.13a-d. Cluster analysis and non-metric multi-dimensional scaling ordination of all the species in the >500 µm size fraction in 1996 (a and c) and 1998 (b and d).

Figures 6.14a,b. CCA ordination plots of the 20 most abundant species (see appendix II for list of abbreviations), stations and environmental variables for the >500 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content, TOC = total organic carbon, Ba = barium. o = station, • = fauna, ⟶ = environmental variable. The red lines indicate species and stations lying along the inverse of an environmental variable.

a)



b)



In both 1996 and 1998, the CCA ordination plots appear to separate the species into three main groups (Figures 6.14a,b) (NB only the 20 most abundant species appear on the plot for ease of reading). Group I was based upon the minimum /maximum temperature eigenvectors; Group II were associated with the temperature range eigenvector; Group III were associated with depth and barium (normalised to aluminium). Generally the first axis (vertical axis) separates the stations based on whether they appear in the warm or cold water mass. The second axis (horizontal axis) separates the stations found in the intermediate water masses from those found in the warm/cold water masses. In both years, maximum and minimum temperature were the two environmental variables that explain most of the variability seen (Table 6.2).

Table 6.2. Results from the Monte Carlo permutation test analysing the influence of environmental variables on total species abundance in the >500 μm size fraction. Variance of environmental variable accepted at the ≤0.05 significance level. (Min = Minimum temperature, Max = Maximum temperature).

Size fraction/year	Unconstrained eigenvalue	Canonical eigenvalue	Variance of variable	Variable
>500μm 1996	4.80	3.21	0.62	Max
			0.45	Min
>500 μm 1998	5.58	3.60	0.56	Max
			0.50	Min

6.3.5. Comparison of number of polychaete species per five most abundant families

The total number of species found in the nine most abundant families were very similar between the same sized fractions (nine families were chosen as they constitute the five most abundant families in each size fraction and each year).

In the 250 μm-to-500 μm size fraction, numbers of species per family only differed by a maximum of two. However, in the >500 μm size fraction, more noticeable differences were seen between number of species per family, especially with respect to the paraonids and spionids. Eight more species were collected in 1996 compared to 1998 for the paraonid family, whilst in 1998 ten more species of spionids

were collected in comparison to 1996. Adding the two size fractions together provided some interesting results. Overall, numbers of species per family were fairly similar between the two years, although not as similar as comparison of the individual fractions. The greatest difference in number of species collected for a particular family was with the spionids with 11 more in 1998. However, addition of the 250 μm-to-500 μm size fraction added a similar number of species to this family in the two years.

6.3.6. Polychaete feeding modes

The different feeding modes of polychaetes were plotted against depth. Several differences and similarities were seen when comparing the 250 μm-to-500 μm size fraction from 1996 with that of 1998 as well as with the >500 μm size fractions.

6.3.6.1. 250 μm-to-500μm size fraction

The 250 μm-to-500 μm size fraction shows a decrease of predatory polychaetes with increasing depth, whilst the deposit feeding polychaetes increase with increasing depth (Figure 6.15a,b). This is the general pattern seen in both years. The abundance of filter feeders is almost negligible.

6.3.6.2. >500 μm size fraction

The >500 μm size fraction in 1996 is very similar to that of 1998. Deposit feeding polychaetes tend to dominate the community (Figure 6.16a,b). The predatory polychaetes show a similar pattern to that of the deposit feeders, peaks and troughs occurring at the same depths. However, at 800 m in both years there is a large increase in the number of deposit feeding polychaetes, which appears to correspond with a marked decrease in the number of predatory polychaetes.

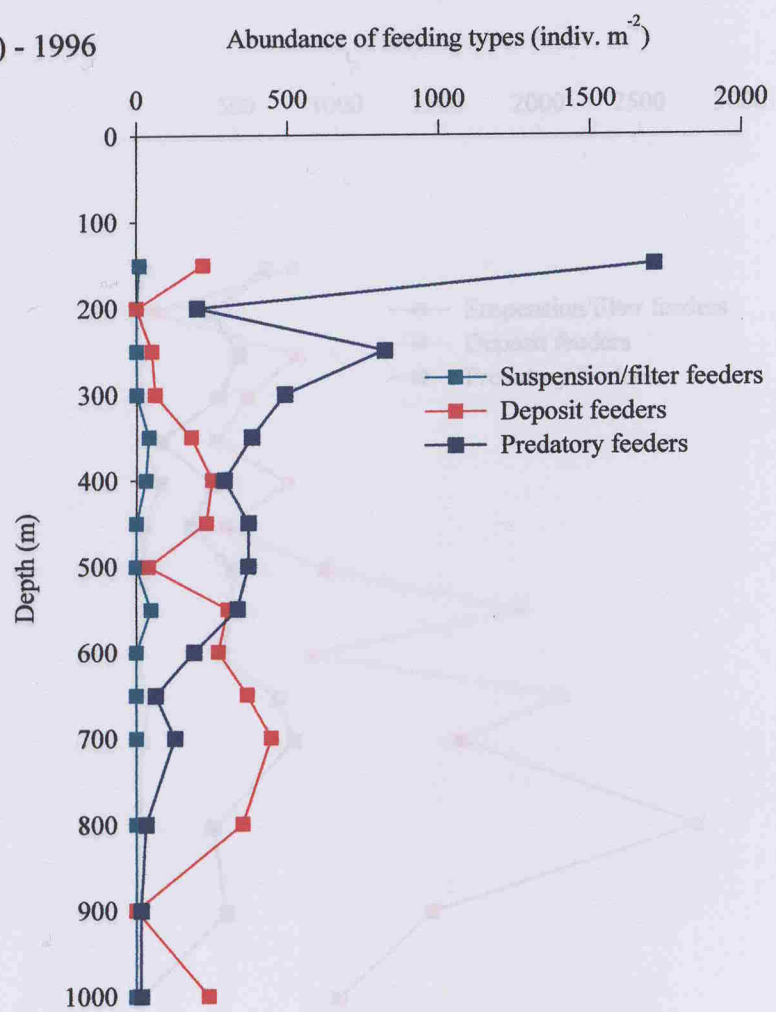
6.3.6.3. Total - >250 μm size fraction

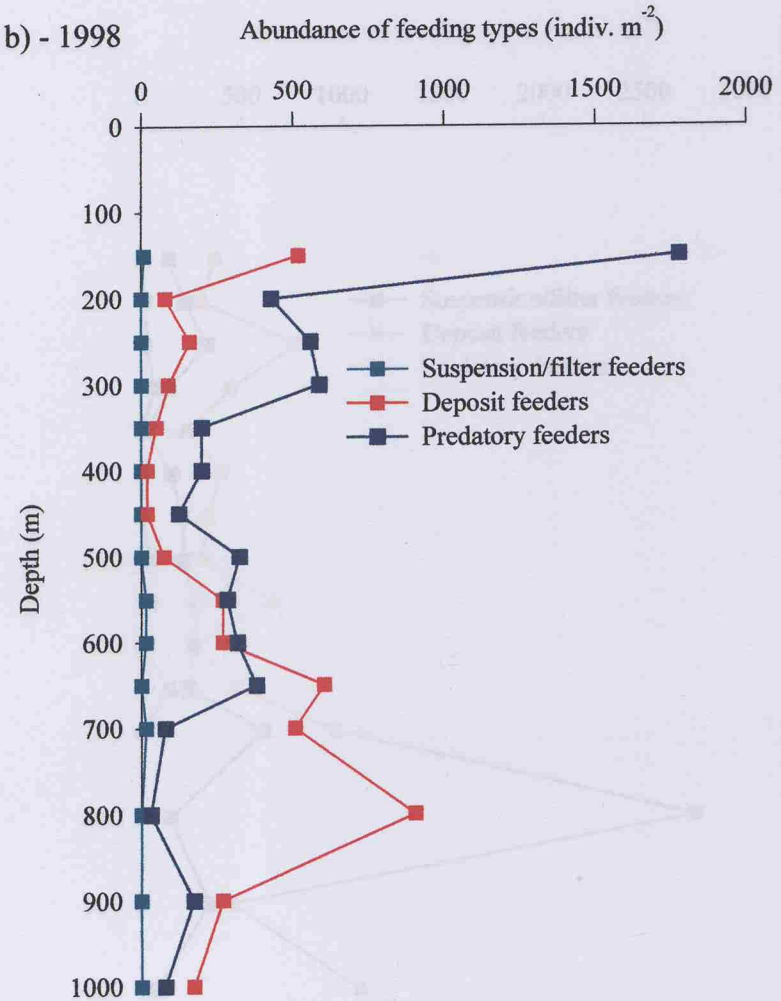
The results for the total - >250 μm size fraction appear to show greater differences between the two years when compared to the other two fractions. In 1996 the greater number of deposit feeding than predatory polychaetes is noticeable when compared to 1998 (Figure 6.17a,b). The plots are generally similar to the >500 μm fraction however, the 250 μm-to-500 μm size fraction appears to have an impact at the

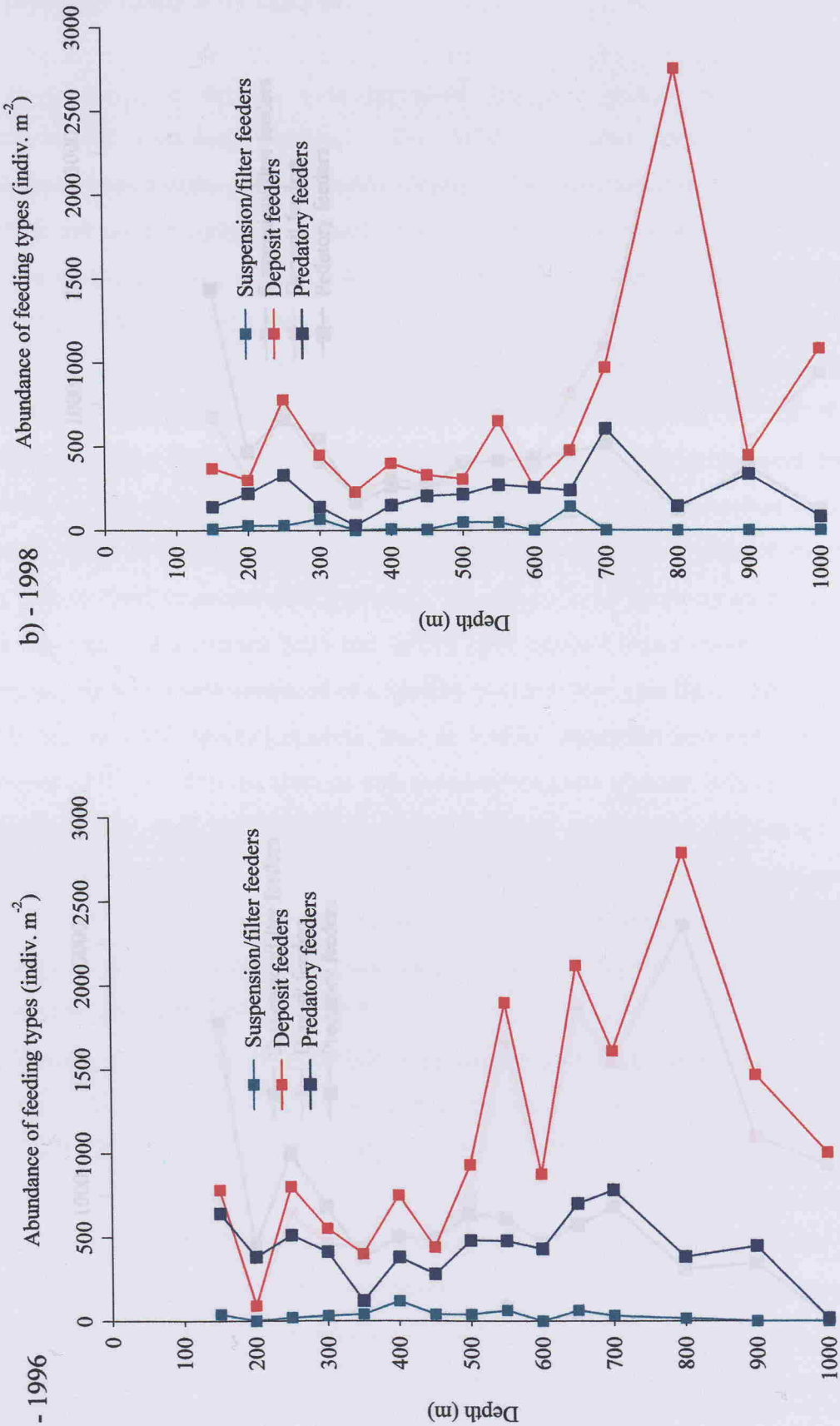
shallowest station, whereby the number of predatory polychaetes is much greater than the deposit feeders.

Using Spearman rank correlation, a variety of results are produced when correlating the three different feeding modes with the suite of environmental variables ($n = 15$, $\alpha = 0.05$, $r_s = 0.521$). Generally the deposit feeding polychaetes in all size fractions show significant correlations with organic matter and temperature range. Predatory polychaetes appear to be influenced by mean sediment grain size, maximum temperature and depth. Finally, suspension-feeding polychaetes have a significant correlation with the temperature range. Results from the Monte Carlo test and CCA ordination appear to support the results obtained using Spearman's rank correlation coefficient. The Monte Carlo test results suggest that temperature is the main environmental variable most influencing mode of feeding at different depths.

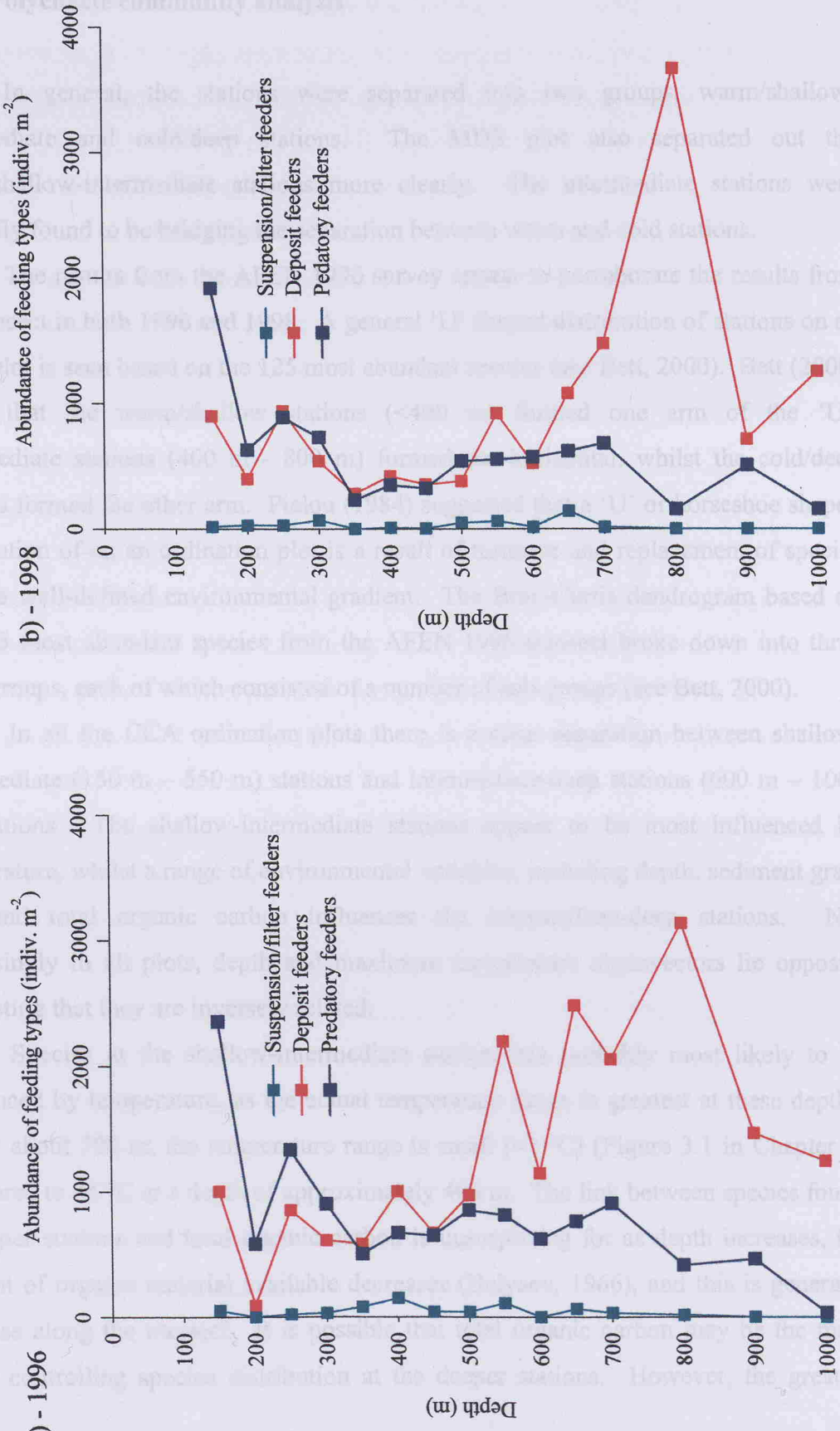
Figures 6.15a,b. Distribution of three different polychaete feeding modes with depth in the 250 µm-to-500 µm size fraction.







Figures 6.16a,b. Distribution of three different polychaete feeding modes with depth in the >500 µm size fraction.



Figures 6.17a,b. Distribution of three different polychaete feeding modes with depth in the Total - >250 µm size fraction.

6.4. DISCUSSION

6.4.1. Polychaete community analysis

In general, the stations were separated into two groups, warm/shallow-intermediate and cold/deep stations. The MDS plot also separated out the warm/shallow-intermediate stations more clearly. The intermediate stations were generally found to be bridging the separation between warm and cold stations.

The results from the AFEN 1996 survey appear to corroborate the results from the transect in both 1996 and 1998. A general 'U' shaped distribution of stations on an MDS plot is seen based on the 125 most abundant species (see Bett, 2000). Bett (2000) found that the warm/shallow stations (<400 m) formed one arm of the 'U'. Intermediate stations (400 m - 800 m) formed the horizontal, whilst the cold/deep stations formed the other arm. Pielou (1984) suggested that a 'U' or horseshoe shaped distribution of on an ordination plot is a result of turnover and replacement of species along a well-defined environmental gradient. The Bray-Curtis dendrogram based on the 125 most abundant species from the AFEN 1996 transect broke down into three main groups, each of which consisted of a number of sub-groups (see Bett, 2000).

In all the CCA ordination plots there is a clear separation between shallow-intermediate (150 m – 550 m) stations and intermediate-deep stations (600 m – 1000 m) stations. The shallow-intermediate stations appear to be most influenced by temperature, whilst a range of environmental variables, including depth, sediment grain size and total organic carbon influences the intermediate-deep stations. Not surprisingly in all plots, depth and maximum temperature eigenvectors lie opposite suggesting that they are inversely related.

Species at the shallow-intermediate stations are probably most likely to be influenced by temperature, as the actual temperature range is greatest at these depths. Below about 700 m, the temperature range is small (<1 °C) (Figure 3.1 in Chapter 3) compared to >6 °C at a depth of approximately 400 m. The link between species found at deeper stations and total organic carbon is unsurprising for as depth increases, the amount of organic material available decreases (Belyaev, 1966), and this is generally the case along the transect. It is possible that total organic carbon may be the main factor controlling species distribution at the deeper stations. However, the greatest

amount of TOC was recorded at a depth of 700 m. Below a depth of 500 m, organic content is higher than stations situated above 500 m.

Of the species associated with a specific eigenvector, both *Capitella* sp A and *Chaetozone* sp B (family Capitellidae) were associated with total hydrocarbons and also showed a significant correlation with this variable. Capitellids are known to contain opportunistic species (Horng and Taghon, 1999) and are also characteristic of organically enriched and disturbed sediments (Grassle and Grassle, 1976). It is possible that the higher concentration of total hydrocarbons at some stations provides an opportunity for capitellids to inhabit a niche that is unsuitable for other species. Capitellid species were only found in relatively high numbers at the 650 m station in the 250 μm-to-500 μm size fraction in 1998, although, these numbers considerably influenced the total number of individuals.

6.4.2. Species community analysis

Using all the species in the cluster analysis and ordination plots, some differences were seen when comparing these results with those based purely on polychaete species. Greater differences were seen in the 1996 Bray-Curtis dendrograms compared to 1998. However, the 1996 MDS ordination plots were quite similar in 1996 whilst less so in 1998. The dendrograms from the transect share some similarities with that produced using all the species from the 1996 AFEN survey, the stations grouping into shallow, intermediate and deep (see Bett, 2000). However, the sub-divisions are different even though there is general evidence of depth related groupings. The 1996 MDS ordination plot is very similar to that of the AFEN 1996 survey, whereby a 'U' shaped curve is formed (see Bett, 2000). The shallower stations form one arm of the 'U', the deep stations forming the other arm, whilst the intermediate stations appear to bridge the two. Bett (2000) suggested that the distribution of the fauna from the dendrograms and ordination plots were based primarily upon Channel hydrography. The sub-divisions were possibly based upon more local factors such as depth-related environmental variables.

It is more difficult to directly compare the CCA ordination plots of all species with that of just polychaete species as the actual individuals are shown. In 1996, several species lie close to the temperature range eigenvector as do the stations that have a relatively high temperature range. In both the polychaete species and total

species plots, several species lie along a possible inverse temperature range eigenvector (drawn in red on the Figures 6.8a, 6.10a, 6.14a). This is also confirmed by stations that have a low temperature range lying along this possible gradient. In 1998, few species appear to be associated with the temperature range eigenvector, different to that seen in the polychaete species ordination plot. More species in 1998 appear to be associated with minimum and maximum temperature whilst species found in greater numbers at the deep stations appear to be associated with depth and barium eigenvectors.

Weishappel and Svavarsson (1998) studied benthic amphipods in an area to the North of Iceland, which has a comparable hydrography to the Faeroe-Shetland Channel i.e. relatively warm North Atlantic Water (~0 m – 300 m) overlies cold Norwegian Sea Deep Water (>500 m). Arctic/Polar water forms an intermediate later between the two. Using Canonical correspondence analysis, Weishappel and Svavarsson (1998) found that water temperature appeared to be the main variable controlling amphipod distribution. The CCA ordination plots also showed a separation of stations along the primary axis depending on whether stations were found in the warm or cold water mass. The secondary axis also further separated them depending on whether stations were found in the intermediate or warm/cold water masses (see Weishappel and Svavarsson, 1998).

6.4.3. Species dominance

The numerically dominant species in each temperature band, warm, intermediate and cold, were identified as well as those that were found to extend from the warm temperature band into the intermediate and also from the cold temperature band into the intermediate. Differences in dominant species were seen between the two years and also between size fractions.

Paramphinome jeffreysi was found to be a species that dominated the intermediate band, but could inhabit the cold temperature band as well. The results from the 1996 AFEN survey corroborating this (Bett, 2000). However, species of *Spiophanes* were numerically more dominant in the cold temperature band, extending into other temperature bands, but actual numbers were low by comparison. However, Bett (2000) found that *Spiophanes* was most abundant in the warm temperature band but extended into the intermediate temperature band.

Table 6.3 illustrates the similarity of the percentage distribution of species in the three main temperature bands. The cold band shows most similarity but the warm and intermediate temperature bands from the transect have a higher proportion of species restricted to this band compared to the AFEN 1996 survey. However, the AFEN 1998 survey is based on 391 species as opposed to 169 in 1996 and 147 in 1998 along the transect. Results from 1996 and 1998 (>500 μm size fraction) are comparable, more so than with the AFEN 1996 survey. A possible reason for the large difference may be as a result of a larger number of samples in the survey (approximately 180 stations) and thus increased number of species (Bett, 2000).

Table 6.3. Comparison of the percentage of all species analysed that are restricted to a particular temperature band in the >500 μm size fraction.

Temperature band	>500 μm 1996 – transect	>500 μm 1998 – transect	>500 μm 1996 – AFEN survey
Warm	20.7%	21.8%	9.7%
Intermediate	33.1%	36.1%	15.3%
Cold	8.2%	8.1%	4.0%

6.4.4. Feeding modes

In the small size fraction, predatory polychaetes dominate at the shallower stations whilst the deposit feeders were dominant at the deeper stations. This differed from the >500 μm fraction where deposit feeding polychaetes dominated the community at all depths. In all size fractions and in both years, deposit-feeding polychaetes were the most abundant at the 800 m station, as a result of high numbers of *Spiophanes kroyeri*. Flach *et al.* (1998) found high numbers of active suspension and interface feeders at the shallowest OMEX station (~200 m). They also found that the high numbers of interface feeders were mainly spionids, although no mention was made of the species. The abundance of deposit feeders also increased linearly with increasing water depth along the OMEX transect (Flach *et al.*, 1998), whilst Rosenberg (1995) also found a similar result in the Skaggerak. As mentioned in Chapter 4, *S. kroyeri* appeared to increase in abundance to the possible detriment of *Paramphinome jeffreysi*.

Paramphinome jeffreysi has been classified as a predator (Fauchald and Jumars, 1979) and the ITI (Wrc plc, 1992). However, Rosenberg (1995) suggests that, unlike most other amphinomids, *Paramphinome jeffreysi* is actually a sub-surface deposit feeder. Josefson (1981) and Romero-Wetzel and Gerlach (1991) have found that *P. jeffreysi* can inhabit the sediment down to a depth of 10 cm. Rosenberg (1995) suggested that high densities of *P. jeffreysi*, and the fact that they were found buried deep in the sediment, implies that this species of amphinomid is actually a sub-surface deposit feeder. If this is the case, then *P. jeffreysi* and *Spiophanes kroyeri* are possibly competing for a similar food source. The alternating temporal dominance of these taxa may thereby reflect some kind of perturbation, poor recruitment or a range of factors that have not been measured in this study. Jones and Thompson (1987) also noted some association between *Chloeia* (an amphinomid), *Prionospio cirrifera* and a burrowing urchin. The spionid family are known to be opportunistic polychaetes as well as characteristic of disturbed sediments (see Grassle and Grassle, 1974; Fauchald and Jumars, 1979). Why *S. kroyeri* should be numerically dominant at the 800 m station remains unresolved.

The greatest number of suspension feeding polychaetes was found at the 400 m, 550 m and 650 m stations. A study undertaken by Gray (1974) showed that suspension-feeding polychaetes were mainly restricted to sandy habitats. However, the 400 m and 550 m stations have a relatively high silt/clay fraction (Figure 3.4). Increased numbers of suspension feeders in a high silt/clay environment has also been found by Rosenberg (1995) in an area known as the Deep Trench in the Skaggerak. The western part of the Deep Trench experiences strong near bottom currents (up to 50 cm s^{-1}), which can suspend and transport material towards the Deep Trench (Rosenberg, 1995).

In the Faeroe-Shetland Channel the current speed was measured two metres above the seabed at a water depth of 550 m. The current velocity varied between 0 and 50 cm s^{-1}, with the most frequent between 7.5 cm s^{-1} and 22.5 cm s^{-1} (see Bett, 2000). Lampitt (1985) found that fresh detrital material in the Porcupine Seabight could become re-suspended if currents 1 m above the seafloor exceeded 7 cm s^{-1}. Therefore at the 550 m station, the average velocity was greater than 7.5 cm s^{-1} possibly allowing re-suspension of detrital material to take place, thus leading to an increase in the number of suspension feeders observed.

The increased number of suspension feeders at the 650 m station may be as a result of internal waves breaking on the slope at a depth shallower than 650 m. Sherwin (1991) proposed that internal waves in the Faeroe-Shetland Channel were generated by tidal flows across the Wyville-Thomson Ridge. These internal waves were propagated up the Channel in a north-easterly direction. Wunsch (1968) and Cacchione and Wunsch (1973) suggested that increased local mixing would lead to particle re-suspension and lateral tongue-like extrusions containing the particles would form from the sides of the Channel (Dickson and McCave, 1986; Thorpe *et al.*, 1990). The particles come out of suspension as turbulence decreases and thus increases the flux of material to suspension feeders below. Paterson and Lambshead (1995) concluded, that occasional strong currents (>15 cm s^{-1}) would influence and structure the macrobenthos in the Rockall Trough. Flach *et al.* (1998) also found an increase in suspension and interface feeders in mid-slope regions along the OMEX transect as this mid-slope region has higher deposition, re-suspension and also lateral advection of material. On the slopes of a trench in the Skagerrak, Rosenberg (1995) found high numbers of suspension and interface feeders, which happened to coincide with strong bottom currents that transport suspended material.

6.4.5. Do environmental variables influence the feeding modes seen?

Suspension feeding polychaetes appeared to be most strongly influenced by the Channel hydrodynamics and in particular are closely associated with temperature range and mean sediment grain size. Deposit feeders were strongly influenced by the temperature range and organic content of sediment. Predatory polychaetes were most strongly influenced by mean sediment grain size whilst peaks in predatory polychaetes tended to coincide with stations that had coarse sediment. Peaks in deposit feeding polychaetes tie in with increased amounts of organic content, the exception being the 800 m station. Suspension feeders have higher numbers at the possible boundaries between water masses or slightly below, tying in with the theory that particles fall out of suspension and the increased flux of food to the fauna below.

The data presented here neither lead to the acceptance nor rejection of the hypothesis, that water mass structure does not influence distribution of individual species down the transect and that species will remain within a definite temperature

band. As illustrated in this study, some species are able to inhabit the entire temperature range, whilst others are restricted to a specific temperature band. However, results also presented from this study shows that the dominant feeding mode does change with depth and that environmental variables concomitant with depth do influence the feeding modes of polychaetes leading to this second hypothesis being rejected.

STUDIES IN BENTHIC MACROFAUNAL ECOLOGY IV: SPECIES VS FAMILY – WHAT TAXONOMIC LEVEL SHOULD BE USED?

7.1. INTRODUCTION

7.1.1. Identification: species-level vs family-level

There has been considerable debate over the past few years regarding the level of taxonomy that should be used for detecting changes in the environment, particularly disturbances arising from pollution. Traditionally, organisms were identified to species level in environmental monitoring and pollution assessment studies as the purpose has been to identify major patterns in community structure and to relate them to the measured environmental variables (Olsgard *et al.*, 1998). It is generally felt that the same level of discrimination would not be seen if the fauna were identified to a level higher than species.

Results from the Group of Experts on the Effect of Pollution (GEEP) workshop held in 1986 suggested that identification of fauna to species level was not always required (Bayne *et al.*, 1988). The community ecology group at this workshop analysed macrofauna and meiofauna data collected from putative pollution gradients in Frierfjord and Langesundfjord in Norway (Bayne *et al.*, 1988). Heip *et al.* (1988), Herman and Heip (1988) and Warwick (1988a,b) all found that data analysis using multivariate techniques was robust to the aggregation of species data into higher taxonomic groupings. Warwick (1988c) analysed five data sets (3 macrofaunal, 2 meiofaunal) and described the benthic assemblages in relation to pollution gradients. The results were then subjected to aggregation at various hierarchical taxonomic levels. Warwick (1988c) concluded that little information regarding the effects of anthropogenic variables was lost at higher taxonomic level, even at phylum. This only holds true for the macrofauna. For the meiofauna information is lost above family level (Somerfield and Clarke, 1995). Similar conclusions were reached by Ferraro and Cole (1990) in assessing pollution impacts on macrobenthos in the Southern California Bight region as well as by Gray *et al.* (1990) in studies undertaken in the Ekofisk and Eldfisk oil fields in the North Sea. Warwick (1988c) even went so far as to suggest that compared to environmental variables anthropogenic effects alter community composition at a taxonomic level higher than species. Olsgard *et al.* (1998) suggested that as disturbance increased in an area, faunal gradients would become stronger and thus identification of organisms to a higher taxonomic level would enable clearer taxonomic identification of community structural changes.

To identify the fauna to species level is labour intensive, requires great expertise and is expensive. In the macrofauna, problems are often encountered with a number of polychaete families, e.g. Cirratulidae, Capitellidae and Spionidae (Warwick, 1988c). Few studies have used macrofaunal results where the level of identification has been higher than species, such as genera or family. Recently, however, comparison of species-level results with family-level results has been undertaken by a few workers such as Warwick,*et al.* (1988), Gray *et al.* (1990) and Olsgard *et al.* (1997, 1998). In Warwick's studies of macrofauna in Loch Linnhe, the Clyde Sea and Bay of Morlaix, samples analysed to species level gave no extra information compared to family level results (Warwick, 1988c). However, for areas where little prior investigation has taken place, or baseline studies/ecologically orientated surveys are being undertaken, identification to species level is not only desirable but necessary (Olsgard *et al.*, 1998). In regions of regular monitoring, the argument put forward is that identification to family level may suffice (Olsgard *et al.*, 1998).

If groupings of family data were similar to species data groupings when employing multivariate techniques, then this would be a strong indication that identification to family level only would be sufficient. However, by identifying the fauna to a level higher than species, the question raised is whether the higher-level taxa will meet adequately the purpose of the study (Olsgard *et al.*, 1998).

Warwick *et al.* (1988) suggested possible advantages of identifying fauna to a level higher than species when using multivariate analyses. Depth and sediment granulometry have been identified as two of the most important natural variables that affect the structure of the benthic community. Species, by having finer adaptational tuning to depth and sediment may obscure a response to a contaminant over an area covering a range of depth and sediment types. These variables generally influence the fauna more by species replacement than by actual changes in the proportion of the major taxa present (Warwick *et al.*, 1988). Warwick found that ordination plots of abundance and biomass were more strongly correlated with a contamination gradient than were species ordinations. Heip *et al.* (1988) found that it was viable to identify copepods and nematodes to a level higher than species for pollution monitoring. This also reduced the amount of time spent in identifying by as much as 90% (Heip *et al.*, 1988). However, several authors (Warwick *et al.*, 1988; Gray *et al.*, 1990; Vanderklift *et al.*, 1996; Olsgard *et al.*, 1997) have stated that additional investigations comparing species level results with those of family level results should be undertaken.

7.1.2. Hypothesis

- Higher level taxa, e.g. family, allow the same level of discrimination between stations as is possible with species level data.

7.2. ANALYTICAL METHODS

7.2.1. Multivariate analyses

7.2.1.1. Cluster analysis

See Analytical Methods section in Chapter 4, page 52.

7.2.1.2. Non-metric multidimensional scaling and ordination

See Analytical Methods section in Chapter 4, page 52.

7.2.1.3. Canonical Correspondence Analysis

See Analytical Methods section in Chapter 4, page 52.

7.3. RESULTS

To test the hypothesis given on page 160, polychaetes were identified to both family and species level. This allows for a comparison to establish which level of identification was necessary.

7.3.1. Polychaete family community analysis

The clustering of stations in the Bray-Curtis dendrograms and MDS-ordination plots is usually into two groups, occasionally three. The groups consist of shallow-intermediate stations and intermediate-deep stations. As seen with polychaete species Canonical Correspondence Analysis (CCA) ordination plots, there is a definite separation of stations based on depth. The shallow-intermediate (150 m – 550 m) stations are mainly influenced by the three temperature eigenvectors (see Figures 7.2a,b). The remaining variables e.g. depth, mean sediment grain size, total organic content, appear to influence the intermediate-deep stations (550 m - 1000 m). Once again an inverse relationship is often seen between depth and maximum temperature.

7.3.1.1. 250 µm-to-500 µm size fraction

The Bray-Curtis dendrograms illustrating the family data for 1996 and 1998 are similar in that there is a clear separation between the warm-shallow stations and the cold-deep stations, approximately 40% similarity between the groups (Figures 7.1a,b). The intermediate stations generally cluster between the two groups. This pattern is reflected in the grouping and spacing of points in the two-dimensional scaling plots (Figures 7.1c,d). However, it is difficult to separate out the shallow and intermediate stations.

Using CCA, temperature and mean sediment grain size are the two main environmental parameters influencing the distribution of the families (Table 7.1). The results from the Monte Carlo tests imply that temperature and mean sediment grain size account for between a third and a half of all the variability seen. Families associated with the temperature eigenvectors generally dominate at the shallower stations. At the cold-deep stations, family distribution appears to be more influenced by organic content and depth (Figures 7.2a,b). Some families, such as syllids, dorvilleids and

ampharetids, were all closely associated with the temperature range eigenvector, whilst spionids, cirratulids and capitellids were found to lie near the organic content (removed in 1998) and total hydrocarbon (removed in 1996) eigenvectors. However, no significant correlation was found between these families and organic content and total hydrocarbons, the exception being cirratulids. In 1998 the cirratulid family correlated significantly ($\alpha = 0.521$, $r_s = 0.593$) with total hydrocarbons.

7.3.1.2. >500 μm size fraction

The MDS ordination plots reflect the results of the Bray-Curtis dendrograms. In 1996 there is not such a clear separation of cold-deep stations and warm-shallow stations as seen in 1998 (Figures 7.3a-d). The cold-deep stations and warm-shallow stations have a similarity of 40% in 1996 and 50% in 1998.

In the >500 μm size fraction, temperature and mean sediment grain size are the variables that have the greatest influence over the distribution of the families (Table 7.1). Temperature accounts for the greatest proportion of the variability in both years. The ordination plots illustrate the distribution of the species and stations in relation to the environmental variables. In both years, glycerids and syllids lie close to a temperature eigenvector. The families generally found at the deepest stations appear to be closely associated with silt/clay and total organic carbon as opposed to the other variables (Figures 7.4a,b).

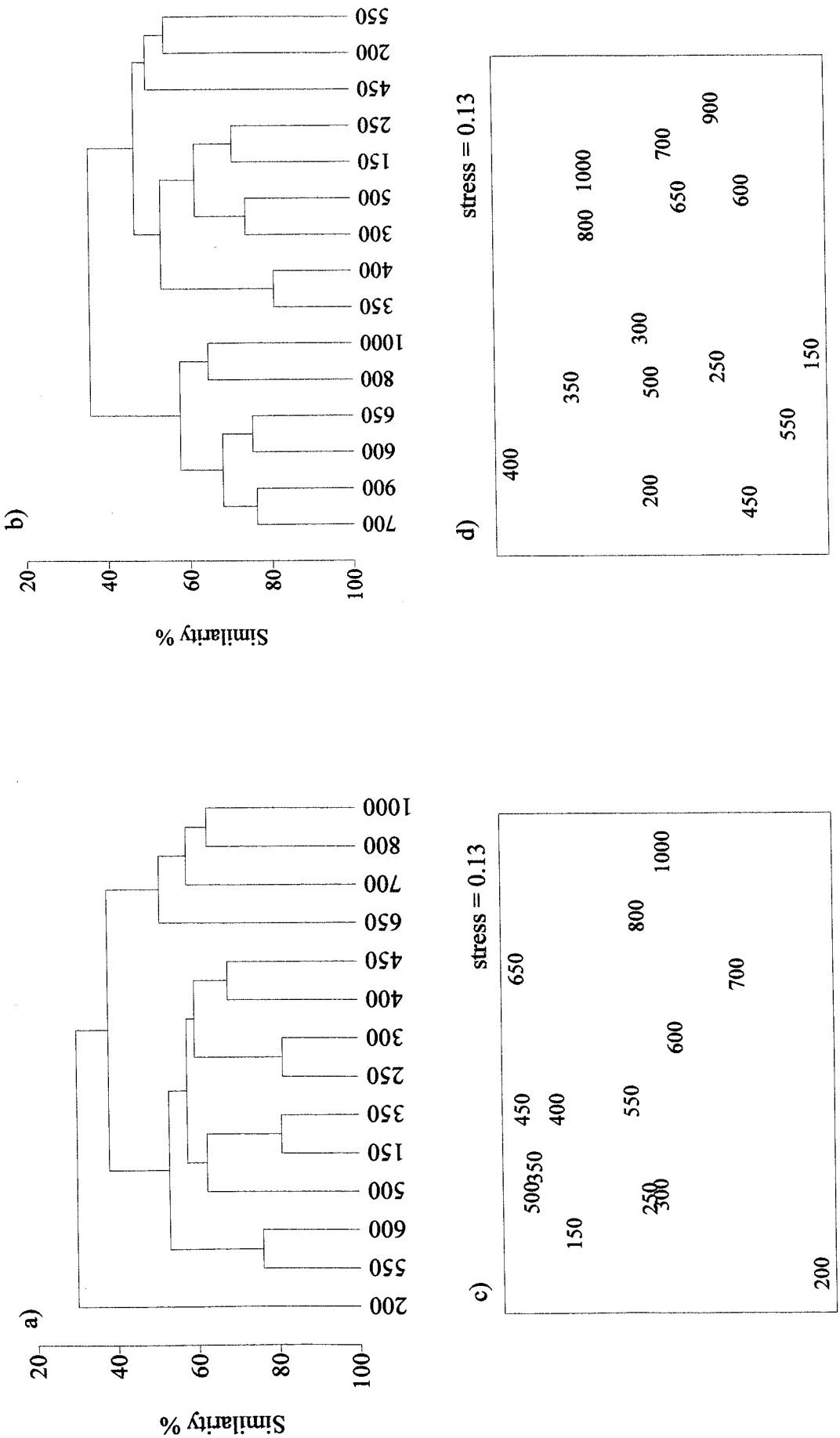
7.3.1.3. Total - >250 μm size fraction

Figures 7.5a,b illustrate the Bray-Curtis dendrograms of the total - >250 μm size fraction. The dendrogram for 1996 appears to be quite different from that of 1998, in that there are three distinct clusters as opposed to two in 1998 (Figures 7.5a,b). The three groups in 1996 comprise shallow, intermediate and deep stations with a similarity of nearly 40%, whereas in 1998 the two groups are shallow-intermediate stations and intermediate-deep stations with a similarity of nearly 50%. The MDS ordination plots generally reflect the same pattern seen in the dendrograms (Figures 7.5c,d). In 1996 the stations fall into the three groups that are seen in the dendrograms. In 1998 however, the stations are distributed in a 'U' shaped pattern suggesting that the stations forming the two uprights are composed of quite different families.

The total - >250 μm size fraction CCA ordination plots reflect a combination of the 250 μm-to-500 μm and >500 μm size fraction plots. Families that group near the temperature range eigenvector e.g. sabellids are seen in all three size fractions (Figures 7.6a,b). Again temperature and mean sediment grain size are the variables most strongly influencing the distribution of the families (Table 7.1). However, temperature accounts for most of the variability. The majority of the families are associated with the temperature eigenvectors as seen in all size fractions and in both years. No particular family appears to be strongly associated with a specific environmental variable.

Table 7.1. Results from the Monte Carlo permutation test analysing the influence of environmental variables on polychaete family abundance. Variance of environmental variable accepted at the ≤0.05 significance level. (Min = Minimum temperature, Max = Maximum temperature, Ran = Temperature range, X-phi = mean sediment grain size).

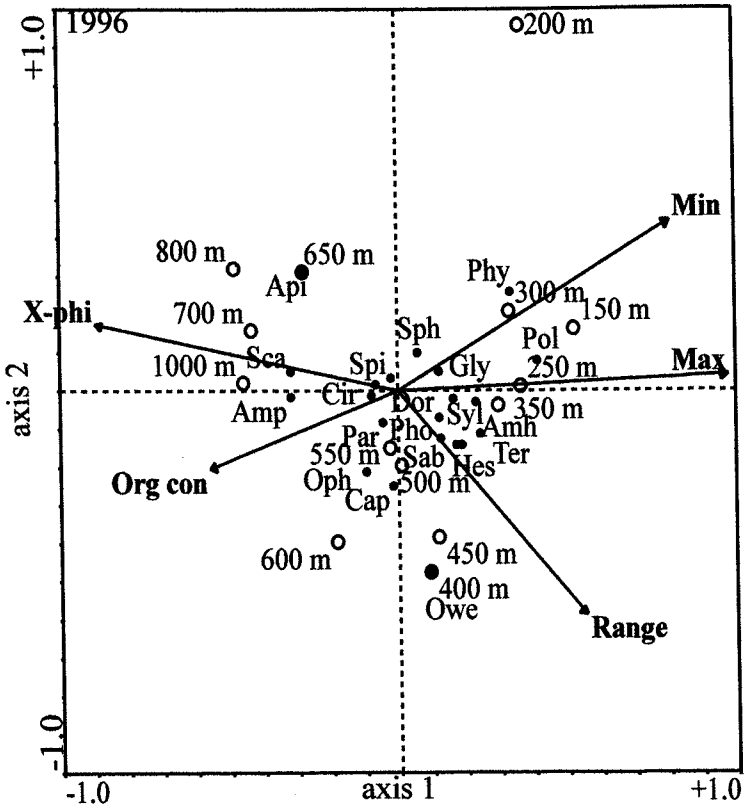
Size fraction/year	**Unconstrained eigenvalue**	**Canonical eigenvalue**	**Variance of variable**	**Variable**
250 μm-to-500μm 1996	0.89	0.66	0.19	Max
250 μm-to-500μm 1998	0.91	0.66	0.19	X-phi
			0.11	Ran
>500μm 1996	0.87	0.60	0.17	Max
			0.09	X-phi
>500μm 1998	0.758	0.53	0.16	Max
			0.10	X-phi
			0.07	Min
Total - >250 μm 1996	0.81	0.57	0.17	Max
Total - >250 μm 1998	0.73	0.51	0.15	Max
			0.08	Min
			0.07	X-phi



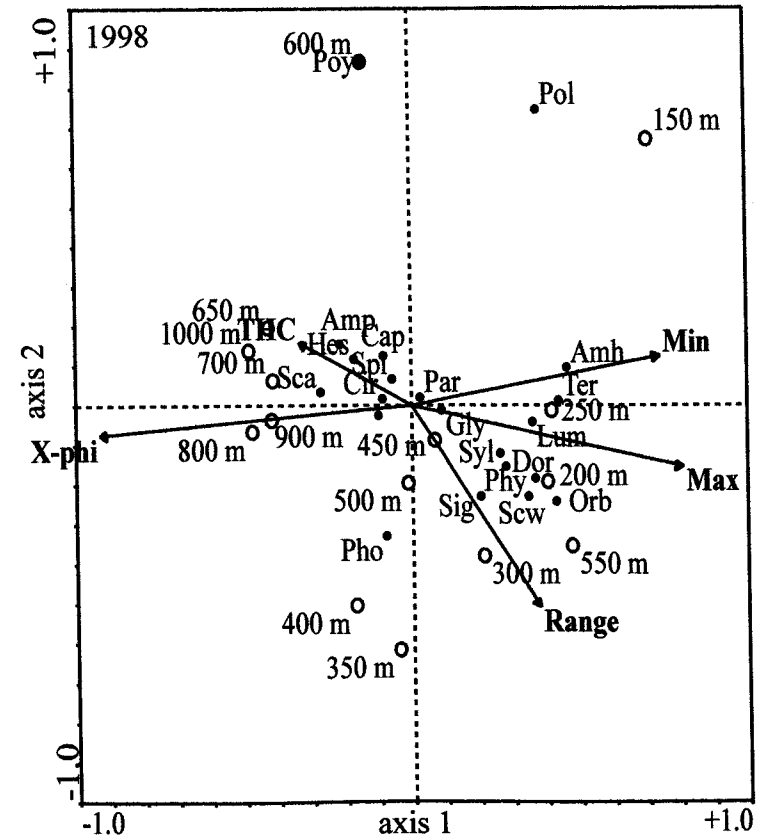
Figures 7.1a-d. Cluster analysis and non-metric multi-dimensional scaling ordination of polychaete species in the 250 µm-to-500 µm size fraction in 1996 (a and c) and 1998 (b and d).

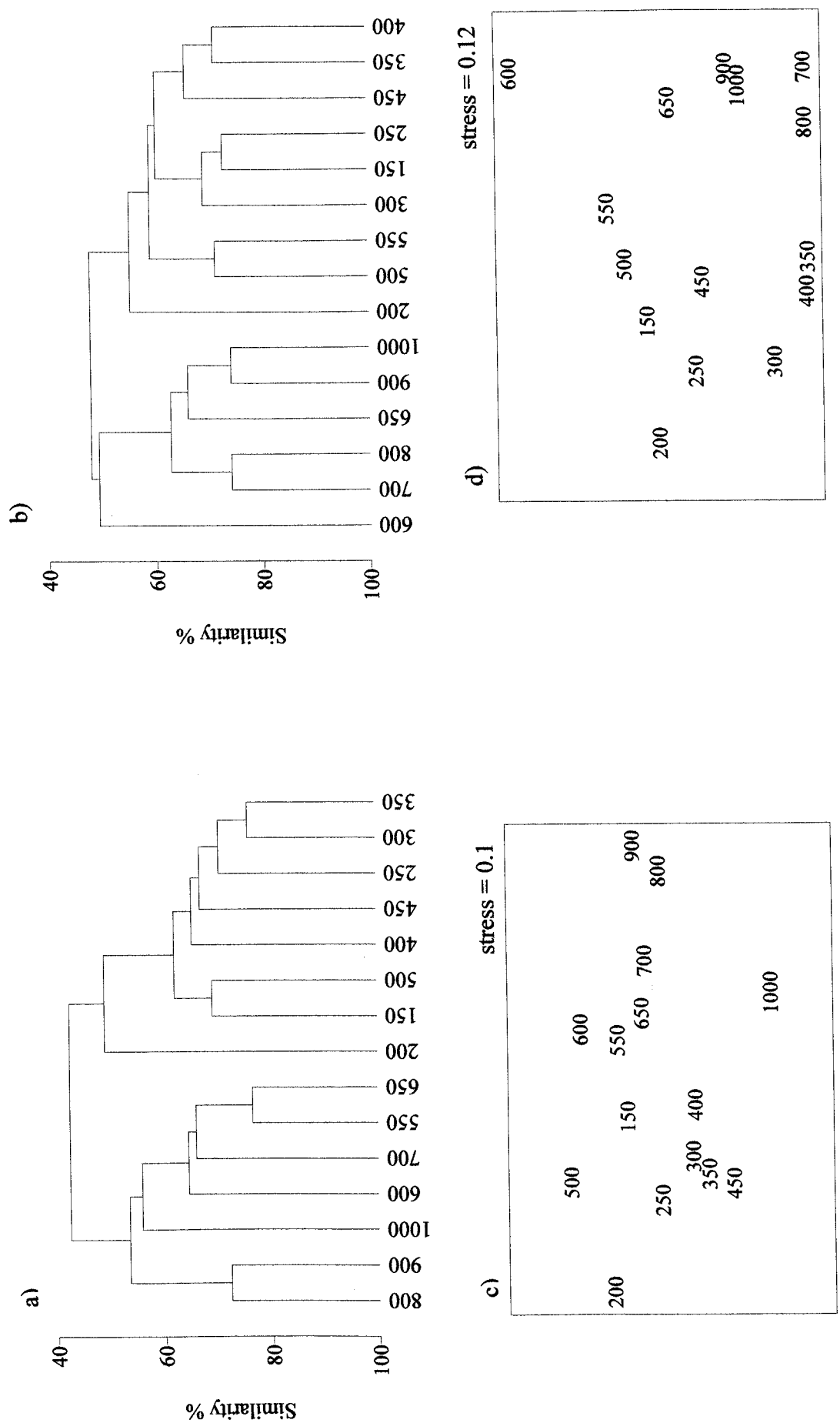
Figures 7.2a,b. CCA ordination plots of the 20 most abundant polychaete families,(see appendix III for list of abbreviations) stations and environmental variables for the 250 µm-to-500 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content, THC = total hydrocarbons. o = station, • = fauna, ⟶ = environmental variable

a)



b)

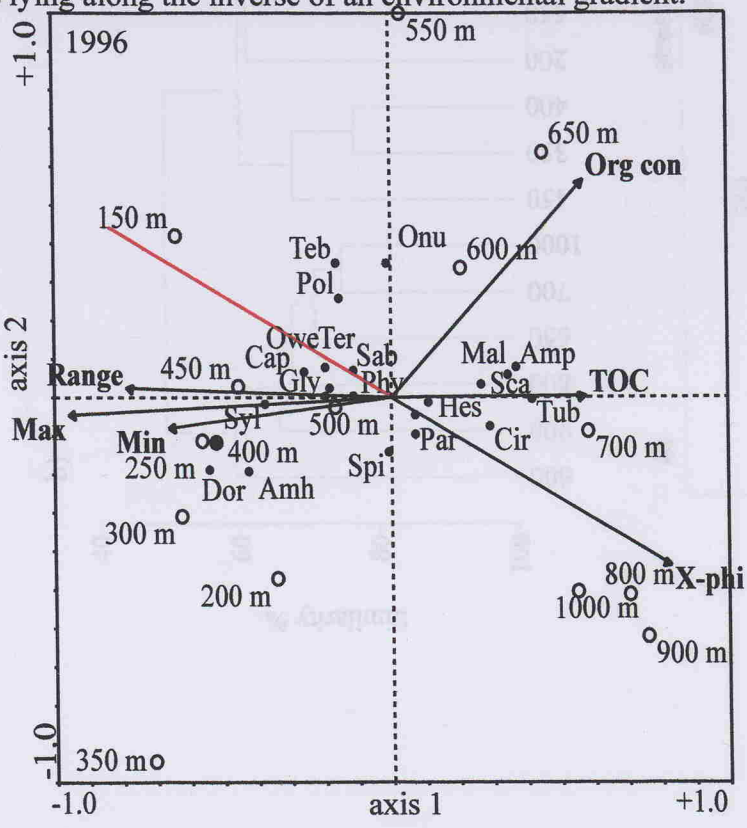




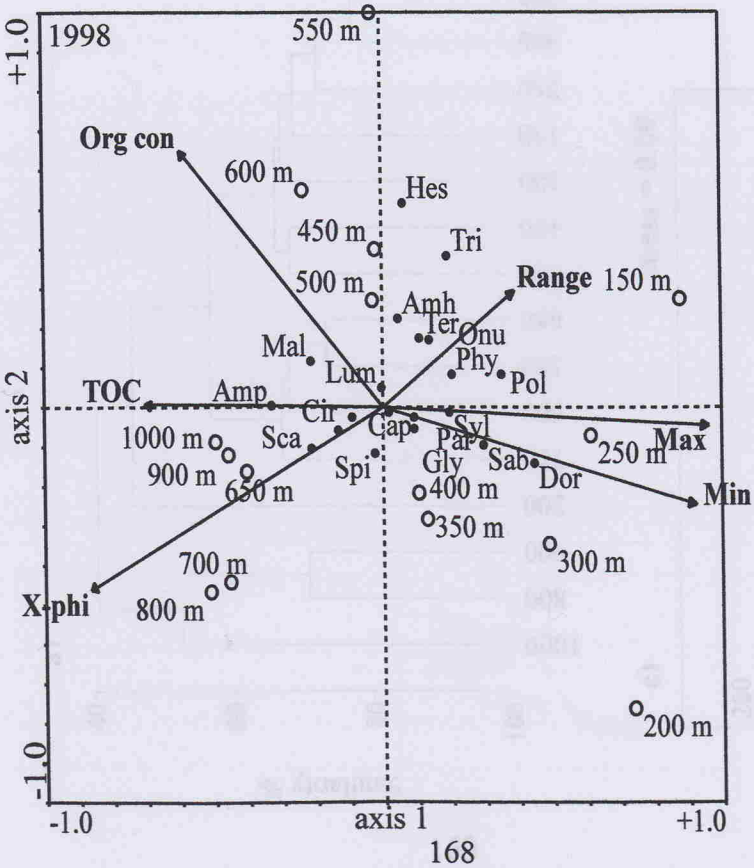
Figures 7.3a-d. Cluster analysis and non-metric multi-dimensional scaling ordination of polychaete families in the >500 µm size fraction in 1996 (a and c) and 1998 (b and d).

Figures 7.4a,b. CCA ordination plots of the 20 most abundant polychaete families, (see appendix III for list of abbreviations) stations and environmental variables for the >500 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content, TOC = total organic carbon, S.C = sil/:clay, THC = total hydrocarbons. o = station, • = fauna, ⟶ = environmental variable. The red line indicates families and stations lying along the inverse of an environmental gradient.

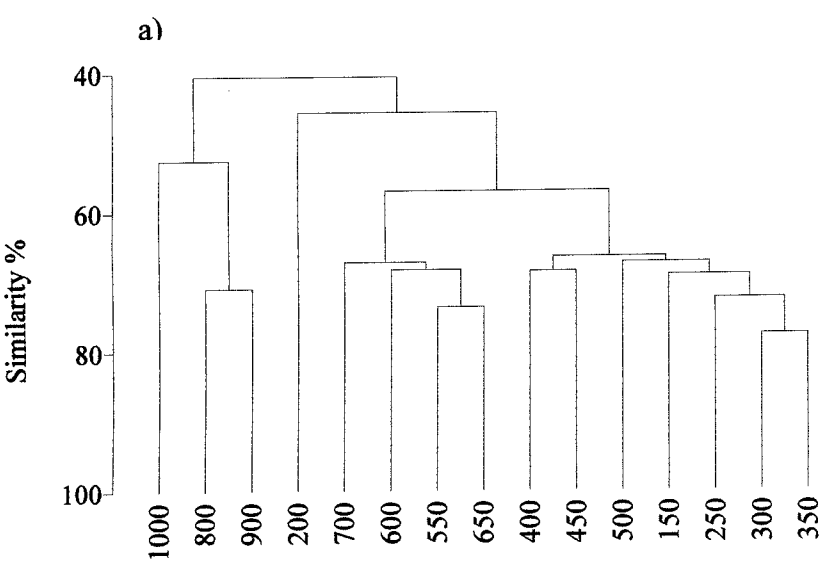
a)

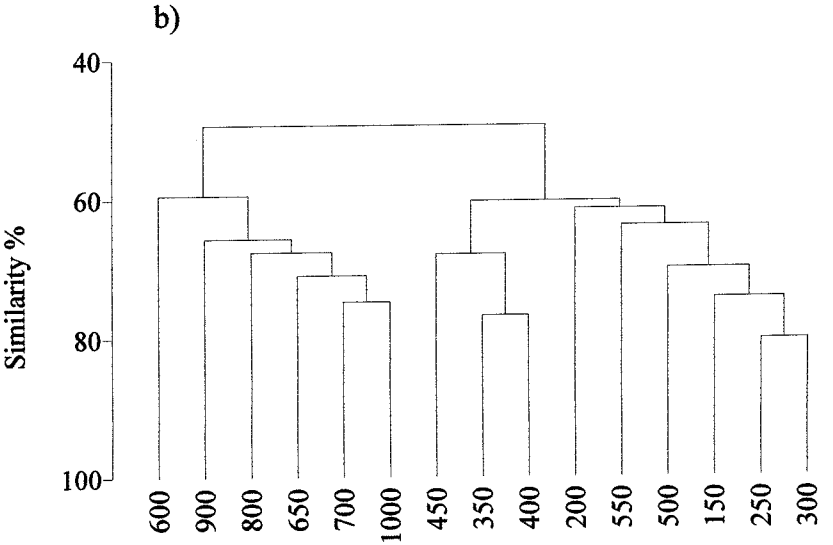


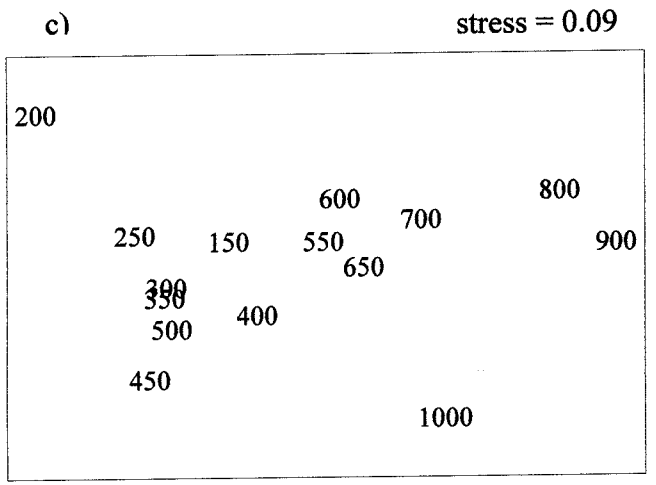
b)

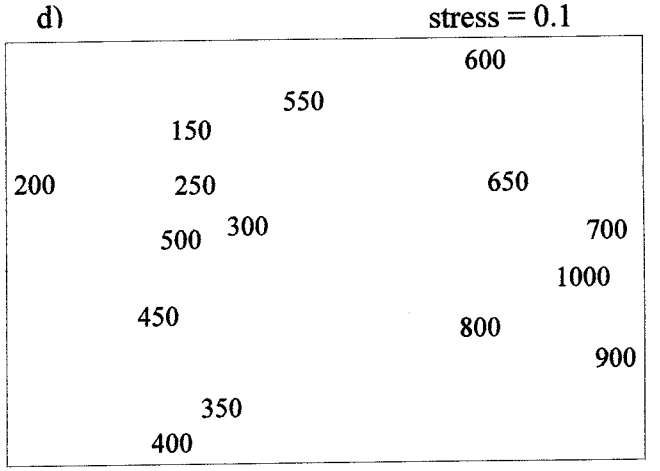


Figures 7.5a-d. Cluster analysis and non-metric multi-dimensional scaling ordination of polychaete families in the Total - >250 µm size fraction in 1996 (a and c) and 1998 (b and d).

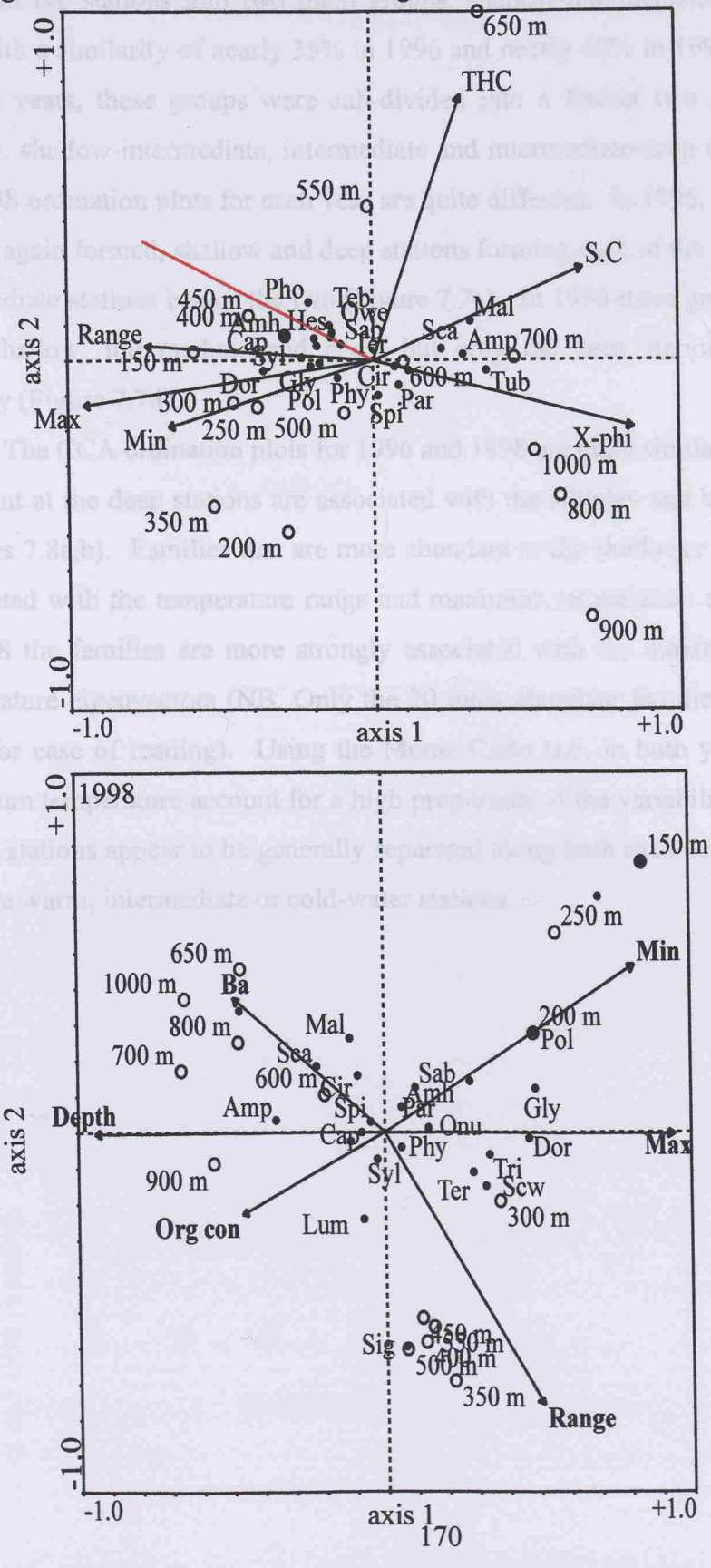








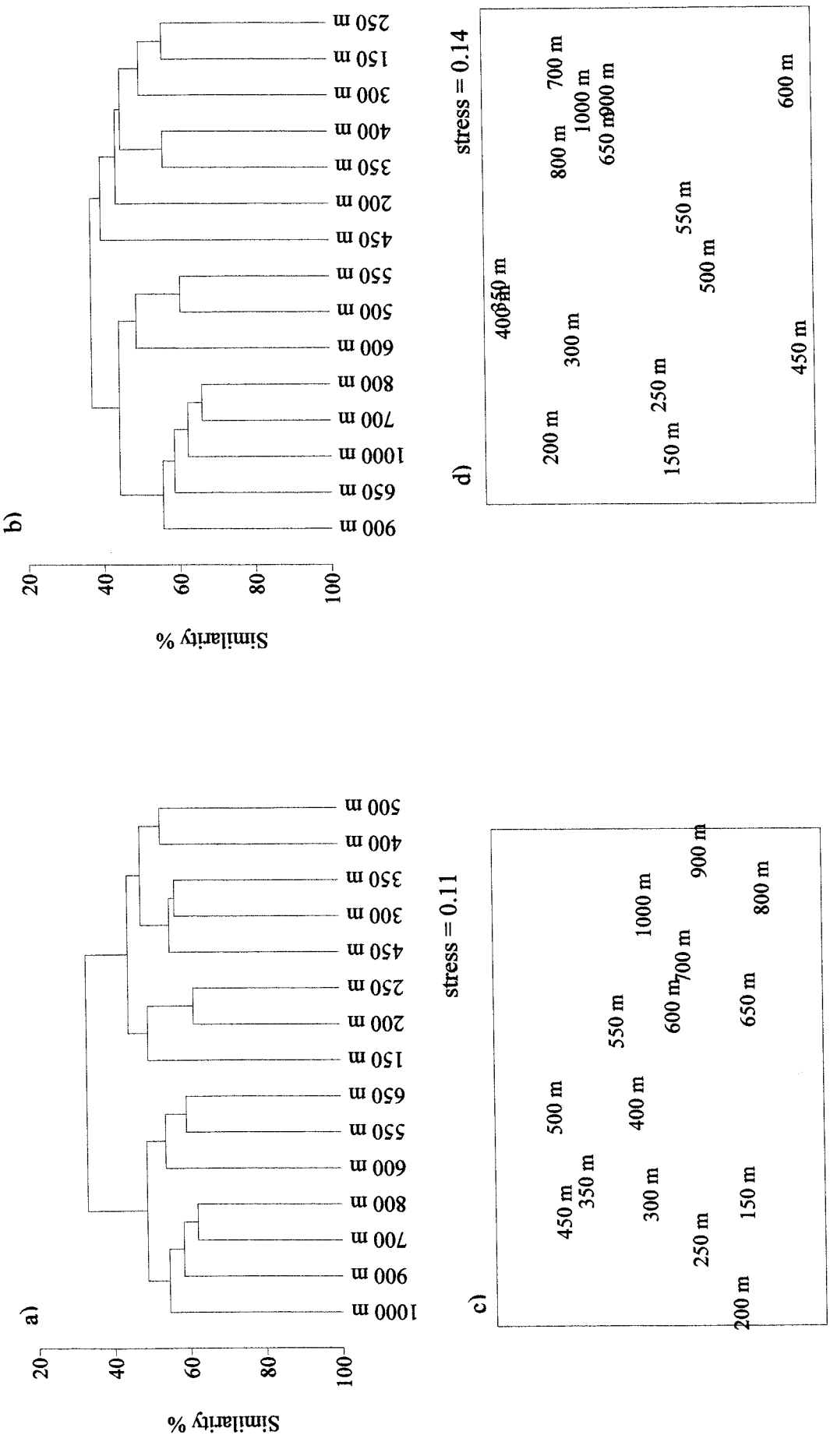
Figures 7.6a,b. CCA ordination plots of the 20 most abundant polychaete families, (see appendix III for list of abbreviations) stations and environmental variables for the Total - >250 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, S.C = silt/clay, Org con = organic content, THC = total hydrocarbons, Ba = barium. o = station, • = fauna, ⟶ = environmental variable. The red line indicates families and stations lying along the inverse of an environmental gradient.



7.3.2. Family community analysis

Using all the families in the >500 μm size fraction, Bray-Curtis dendrogram and MDS/CCA ordination plots were produced. In both 1996 and 1998, the dendrograms separated the stations into two main groups, shallow-intermediate and intermediate-deep with a similarity of nearly 35% in 1996 and nearly 40% in 1998 (Figures 7.7a,b). In both years, these groups were sub-divided into a further two groups comprising shallow, shallow-intermediate, intermediate and intermediate-deep stations. However, the MDS ordination plots for each year are quite different. In 1996, a 'U' shaped curve is once again formed, shallow and deep stations forming each of the uprights, whilst the intermediate stations bridge the two (Figure 7.7c). In 1998 three groups of stations are seen, shallow, intermediate and deep, but only the deep stations cluster together strongly (Figure 7.7d).

The CCA ordination plots for 1996 and 1998 are quite similar. Families that are abundant at the deep stations are associated with the silt/clay and barium eigenvectors (Figures 7.8a,b). Families that are more abundant at the shallower stations are closely associated with the temperature range and maximum temperature eigenvectors, whilst in 1998 the families are more strongly associated with the maximum and minimum temperature eigenvectors (NB. Only the 20 most abundant families are shown on the plots for ease of reading). Using the Monte Carlo test, in both years maximum and minimum temperature account for a high proportion of the variability seen (Table 7.2). Again, stations appear to be generally separated along both axes depending on whether they are warm, intermediate or cold-water stations.



Figures 7.7a-d. Cluster analysis and non-metric multi-dimensional scaling ordination of all families in the >500 µm size fraction in 1996 (a and c) and 1998 (b and d).

Figures 7.8a,b. CCA ordination plots of the 20 most abundant families (see appendix III for list of abbreviations), stations and environmental variables for the >500 µm size fraction in 1996 and 1998. Max = maximum temperature, Min = minimum temperature, range = temperature range, X-phi = mean sediment grain size, Org con = organic content, TOC = total organic carbon, S.C = silt/clay, Ba = barium. o = station, • = fauna, ⟶ = environmental variable

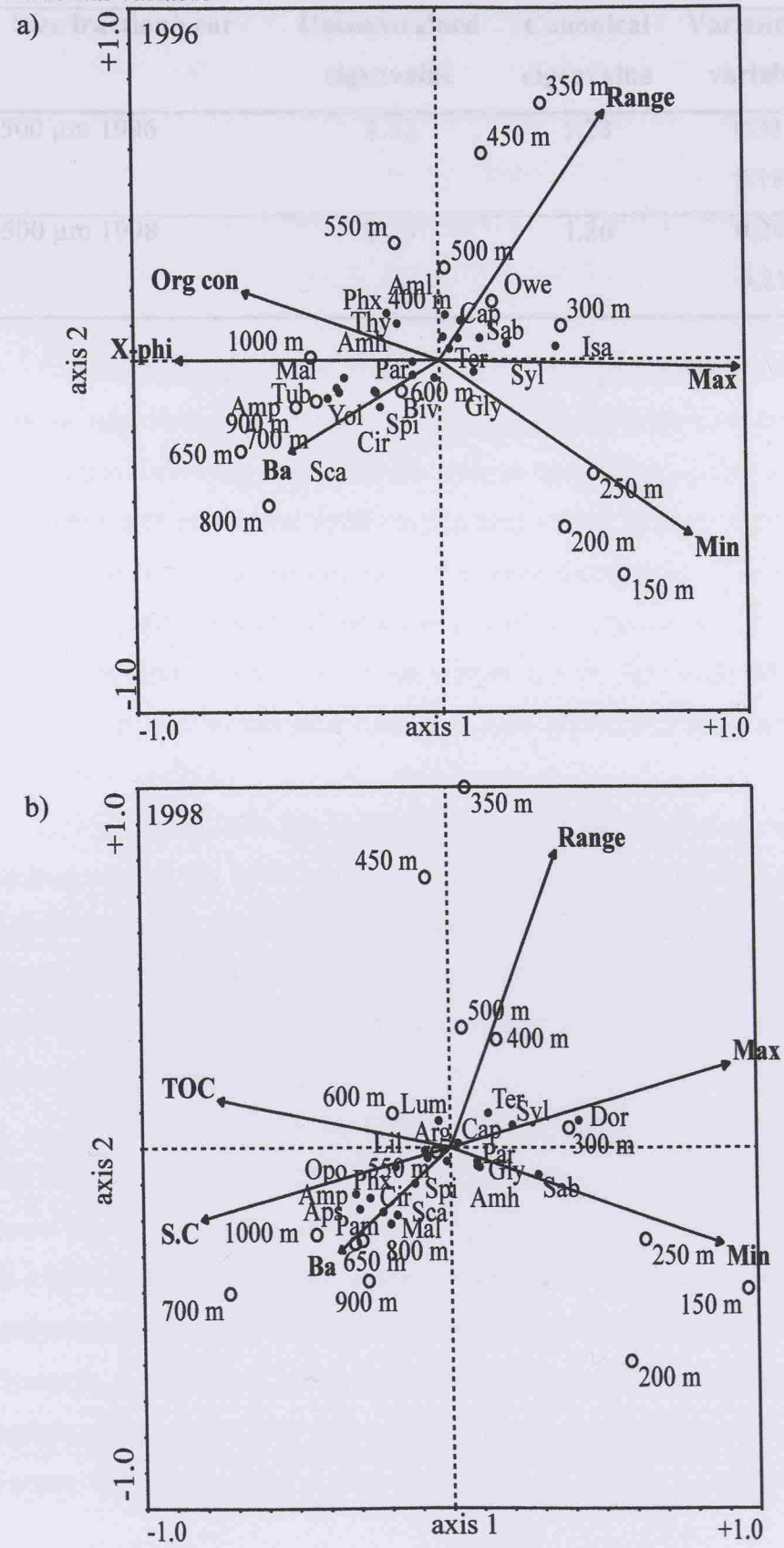


Table 7.2. Results from the Monte Carlo permutation test analysing the influence of environmental variables on abundance of all families present in the >500 µm size fraction. Variance of environmental variable accepted at the ≤0.05 significance level. (Min = Minimum temperature, Max = Maximum temperature).

Size fraction/year	**Unconstrained eigenvalue**	**Canonical eigenvalue**	**Variance of variable**	**Variable**
>500 µm 1996	1.82	1.23	0.31	Max
			0.18	Min
>500 µm 1998	2.19	1.36	0.28	Max
			0.21	Min

7.4. DISCUSSION

7.4.1. Family community analysis

Studies undertaken by Gray *et al.* (1988), Warwick (1988a,b,c), Somerfield and Clarke (1995) and Olsgard *et al.* (1997; 1998) have all shown that the level of discrimination between species and family is so similar that it is possible to use results from a higher taxonomic resolution e.g. family, to determine environmental/pollution gradients, as opposed to spending long periods of time identifying the fauna to species level. The results presented in this chapter will be discussed in relation to species results.

At both species and family level, the Bray-Curtis dendrograms separated stations into two main groups, shallow-intermediate and intermediate-deep. The stations that form each cluster are the same in the 250 μm-to-500 μm size fraction, but are slightly different in the >500 μm and total - >250 μm size fractions. However, the MDS ordination plots do not show the same distribution of stations. The species ordination plots generally show some sort of 'U' shaped curve, whilst this is not so apparent at family level. The exceptions to this are the family MDS ordination plots for the total - >250 μm size fractions, 1998 showing a more pronounced curve in comparison to 1996.

The results from the Monte Carlo test are quite different. Although maximum temperature is the main variable influencing both polychaete species and family distributions, the second and third variables often differ between the two groups. Minimum temperature is usually also accountable for some of the polychaete species variability, but at family level, mean sediment grain size is as, if not more important than minimum temperature.

Somerfield and Clarke (1995) collected benthic samples from Liverpool Bay and the Fal estuary. Comparing species and genus abundances, Somerfield and Clarke found there were no striking differences between the two in their study. Aggregations to a level higher than genus produced changes in the structure of the community and analysis of similarity (ANOSIM) was less able to discriminate between stations. However, aggregation to family level appeared to have less effect overall on the community analyses than aggregating to phyla level (Somerfield and Clarke, 1995). Ferraro and Cole's study of macrobenthos in the Southern California Bight found that

identification to a level as high as order gave a similar result to that species level (Ferraro and Cole, 1990). Their results also support the results of Heip *et al.* (1988), Warwick (1988a,b) and Kingston and Riddle (1989).

Olsgard *et al.* (1997) sampled several stations around the Valhall oil and gas field. They found that multivariate analyses of species at these stations showed similar patterns at all levels from species to order. However, gross pollution effects were also detectable at phylum level. Olsgard *et al.* (1998) also correlated a variety of environmental variables with the following taxonomic levels: species, genus, family, order, class and phylum at three different oil and gas sites, Valhall, Gyda and Veselefrikk in the North Sea, and over a number of years. These sites are known to have strong pollution gradients (Olsgard *et al.*, 1998). They found that there was no simple relationship between the time for which a stress was applied, or the degree of pollution and the correlation values. Olsgard *et al.* (1998) found that areas that had a longer pollution history generally showed stronger correlations at a higher taxonomic level. The decrease in correlation values between environmental variables and species, genus and family was slight from species to family.

Species that dominate in a particular depth band and are associated with particular variables appear to belong to families that show a similar concomitance e.g. *Glycera lapidum* is strongly affiliated with minimum and maximum temperature and this association is also seen in the family Glyceridae. However, some species from the same families show very different affiliations with the environmental variables, an example of which is the family Spionidae. *Spiophanes kroyeri* is generally associated with the barium eigenvector, whilst *Spiophanes* cf. *wigleyi* is affiliated with the temperature range. Overall the family is found near the centre of the ordination plot, but has a slightly stronger association with barium. This may be as a result of *S. kroyeri* having a greater number of individuals per species than *Spiophanes* cf. *wigleyi*.

Warwick (1988c) suggested that each major taxonomic group would have a set of species that had evolved to a range of natural environmental variables. Pollution into the environment has been relatively recent and so fewer species would be adapted to cope with increased stress. Thus abundance and biomass values of major taxa would be more likely to show a correlation with a pollution gradient in comparison to species.

Ellis and Cross (1981) suggested that identification to a taxonomic level other than species was sometimes preferable, as species identification tends to be more error prone. Statistically, and possibly biologically, it is desirable to correctly identify fauna

to a higher taxonomic level than incorrectly to species level (Green, 1979). Aggregation to a level higher than species appears to be useful/apparent if there is a major pollution gradient in the area, and one that will definitely be picked up by a higher taxonomic level.

As at species level, cluster analysis and MDS/CCA ordination were carried out on all the families in the >500 μm size fraction. Generally the ordination of families is very similar to the ordination plots of species as mentioned previously with the glycerid family. Variability at species level is higher than at family level, even though in both cases the environmental variables explain the majority of the variability. The total and explained variability at family level were half of those seen at species level and thus the variation values of the environmental variables was accordingly reduced (generally half of the species level values). The stress levels when conducting the MDS ordinations were very similar for both family and species plots (Table 7.3), the greatest variation between taxonomic levels occurring in 1996. The slight difference in stress levels between MDS ordinations would suggest that neither taxonomic level is to be preferred over the other.

Table 7.3. Comparison of species and family stress level results of the multi-dimensional scaling ordination plots.

Size fraction/year	Species stress level	Family stress level
>500 μm 1996	0.08	0.11
>500 μm 1998	0.15	0.14

In baseline studies that were conducted at Gyda 1987, Heidrun 1988, Snorre 1989 and Togi 1989 (all in the Norwegian sector of the North Sea) Olsgard *et al.* (1998) found that there was a decrease in correlation values when abundance values at higher taxonomic levels were used compared to species abundances. It was suggested that in areas with weak gradients in faunal composition, analyses at the class or phylum level should be avoided.

The data presented in the current study must lead to the rejection of the hypothesis that using higher level taxa, such as polychaete families, allows the same level of discrimination between stations as is possible with polychaete species data.

However, using the entire species dataset as for the >500 μm size fraction and comparing with the entire family dataset would allow this hypothesis to be accepted as the same level of discrimination between stations could be seen.

GENERAL DISCUSSION AND CONCLUSIONS

8.1. THE FAEROE-SHETLAND CHANNEL

The Faeroe-Shetland Channel is one of the principal pathways for water flowing to and from the Norwegian Sea. The upper surface water flows from the North Atlantic northeastwards into the Norwegian Sea as a surface current and after cooling and sinking, eventually flows out in a southwesterly direction as a cold deep current at a depth of 600 m and deeper (Hansen and Østerhus, 2000) below a pycnocline at a depth of 400 m (Saunders, 1990). Initially the pycnocline was thought to be horizontal (Tait, 1957). However, more recent evidence suggests that the pycnocline is inclined against the West Shetland Slope (Schlichtholz and Jankowski, 1993) and may even move up and down the slope (Schlichtholz and Jankowski, 1993), although this is not always a constant feature. As a result the distribution of the macrobenthos over the intermediate (350 m – 650 m) depth range may therefore be alternately subject to both upper and deeper waters.

At water depths <600 m, bottom currents are particularly active and peaks in current velocities have been recorded at >75 cm s^{-1} (Bett, 2000; Masson, 2000, in press). Comet-like marks are formed on the seabed as a result in peaks in current velocity (Kenyon, 1986) and this links in with oceanographic data that have been collected by Turrell *et al.* (1999). On lower slopes, rippled sand sheets imply that current velocities are lower, between 30 cm s^{-1} and 40 cm s^{-1}. Between 61° 05' N and 61° 20' N, in water depths of 750 m to 950 m, a sandy contourite sheet is present, determined by the thin sheet-like nature of the sand, surface ripples and high levels of sorting (Masson, 2000).

At the 650 m station along the transect, the sediment was found to contain high concentrations of weathered, low-toxicity oil-based drill cuttings (McDougall, 2000). However, McDougall (2000) also states that hydrocarbon contamination as result of activity by the oil industry is a minority source in the West Shetland area.

8.1.1. Why is the classic exponential decline in standing stock not seen?

As has been shown, the Faeroe-Shetland Channel is not typical of a North Atlantic environment. Fauna inhabiting the Faeroe-Shetland Channel do not conform to the expectation of an exponential decline in standing stock with increasing depth as

commonly seen in the deep North Atlantic (see Gage and Tyler, 1991; Bett, 2000). In the analysis on standing stock, depth appeared to be the overall controlling environmental variable. In view of the unusual hydrography of the Channel, it may seem surprising that the hydrography did not appear to have an effect. However, depth and the suite of environmental variables e.g. mean sediment grain size, maximum water temperature, were all found to correlate significantly, suggesting that depth was masking any influence the other environmental variables may have on the fauna. With depth removed, water temperature, mean sediment grain size and total organic carbon were all found to be important controls on the standing stock of the community.

8.1.2. The 250 µm-to-500 µm size fraction does not influence species diversity

Generally values of species diversity indices are lower in the 250 µm-to-500 µm size fraction compared to the >500 µm size fraction. However, by combining the two size fractions, the diversity index values change dramatically, especially with regards to species richness and diversity (Figures 5.7a, 5.8c). Both richness and diversity increase with the addition of the 250 µm-to-500 µm size fraction compared to the >500 µm size fraction. The actual number of species also increases, although differently from station to station. Generally there is an increase of between 3 and 28 species per station, and on average there are approximately 12 new species per station with the addition of the 250 µm-to-500 µm size fraction. Combining the two fractions results in a combination of some stations showing an increase in evenness (350 m, 550 m, 1000 m) (corresponding decrease in dominance) whilst others show an increase in dominance (600 m and 800 m) (decline in evenness). Although in general few stations show an increase in species dominance with the addition of the 250 µm-to-500 µm size fraction to the >500 µm size fraction. In both years, the 450 m, 700 m and 1000 m, stations show an increase in species. The stations showing an increase have a higher evenness value in the smaller size fraction compared to the larger size fraction. These results suggest the importance of collecting the 250 µm-to-500 µm size fraction, but also collecting the fractions separately.

8.1.3. Can the polychaete community be used as a proxy for the entire macrofaunal community?

Maximum and minimum temperature, and not depth and organic matter, are the main variables that influence the structure of the polychaete community. The same is also true when all species in the >500 μm size fraction were analysed. Maximum temperature generally accounts for more of the variability than minimum temperature. The polychaete community was also generally separated into two main groups, which appear to be dependent upon temperature. Further division of the stations was also possibly temperature-based, but with greater influence being exerted by depth and the remaining environmental variables. This same pattern was also seen when using the entire faunal community in the >500 μm size fraction suggesting that polychaetes may be used as a proxy for the rest of the macrofauna in the Faeroe-Shetland Channel. Crustacean species in 1996 were found to show a similar division of species, probably based on temperature, whereas in 1998 there appeared to be no environmental variable that could explain the separation of the crustacean species. Care must be taken when using polychaetes as a proxy. Although the total macrofaunal species data set may show almost identical patterns there may be inherent differences between species of different taxonomic groups. However, in this study it was found that polychaetes could be used as a useful proxy for the rest of the macrofaunal data set.

8.1.4. Control of species distribution

What controls species distribution in the Faeroe-Shetland Channel? It is known that temperature fundamentally controls the distribution of species in the present study area (Chapter 5). However, other factors need to be taken into account.

The Faeroe-Shetland Channel has a strong temperature gradient, decreasing from ~9.68 °C at a depth of 150 m to ~1 °C at 900 m/1000 m and this works effectively as a biological barrier. Thus over time the fauna have evolved in relative isolation into two groups, warm and cold. It is possible that the thermocline acts as a barrier to larval dispersion; the larvae can be transported horizontally within their own water mass, but not vertically. Within each temperature regime other environmental variables become increasingly important, e.g. depth and mean sediment grain size. At various depths it is possible for a number of different types of species to inhabit that

particular region. However, only a sub-set of those species may occur, the identity of which will depend on random recruitment as well as competitive ability. Biological aspects such as competitive ability and feeding mode will also influence the species found in specific regions. As previously mentioned (Chapter 6), polychaete-feeding modes in the Channel are influenced by different environmental variables: suspension feeders are possibly influenced indirectly by the temperature range. The depth of the large temperature range coincides with the depth where internal waves impinge against the slope thus increasing turbulence. The internal waves can cause particles to come into suspension thus increasing the availability of food to this feeding mode. Deposit feeders are associated with organic content and maximum temperature, organic content being highly important to deposit feeders. Predatory feeders are influenced by mean sediment grain size, maximum temperature and depth. At shallower-warmer stations the abundance of fauna is quite high, thus increasing the availability of food to predatory feeders. The sediment grain size is also relatively coarse in comparison to the deeper stations possibly making movement easier for the epifaunal polychaetes. All these factors will also limit the species that may be found in particular temperature bands as well as in subsets of these temperature bands. Therefore, species distribution is primarily controlled by variables based on an evolutionary timescale but at a higher taxonomic level is controlled by present day ecology.

8.1.5. Species vs Family

Research undertaken since the later 1980s has examined the results produced by species level data with that of family level data (e.g. see Gray *et al.*, 1988; Warwick 1988 a,b,c). Generally studies have found that identification of taxa to family level is adequate for some analyses and that a similar level of discrimination is seen compared to species level data. Identification to family level appears to be used where a pollution gradient is already evident. Family level data have been found not to be as useful if the pollution gradient is weak or at an early stage. For this finer discrimination is required.

Using multivariate statistics, Warwick (1988a,b,c) Somerfield and Clarke (1995) and Olsgard *et al.* (1997; 1998) have found that the distribution of stations is similar at family level in comparison to species level. However, in the present study, the Bray-Curtis cluster diagrams showed similar groupings at species and family level, but the MDS ordination plots did not back this up. The distribution of stations on the

plots was quite different and the separation of stations based on water temperature was not as apparent. Results from the Monte Carlo test also suggest otherwise. Although maximum temperature was the main controlling environmental variable, mean sediment grain size was found to be more important in separating the stations further at family level. On the CCA ordination plots, this becomes more apparent as several families lie on the inverse of the mean sediment grain size eigenvector suggesting that they prefer finer sediment.

However, when analysing all the families present in the >500 μm size fraction, only maximum and minimum temperature were found to significantly influence the distribution of the families. On the actual CCA plots, barium and the inverse of barium eigenvectors appear to have the greatest influence on the distribution of the families. Those lying on/near the barium eigenvector are obviously tolerant of high concentrations of this element, whilst the reverse is true for those associated with the inverse of the temperature eigenvector. In both years the families associated with barium were the same, although the 20 most abundant families are not the same in each year.

Using all species and comparing all the families in the >500 μm size fraction similar results are seen again when using only polychaete species and families. The MDS ordinations are not as clear at family level as at species level. At family level, there is greater association of families with the inverse of the barium eigenvectors, whilst at species level this is not so apparent. The separation of stations along the axes is also less clear at family level: at species level, the primary separation is based upon temperature; subsequent separation on the secondary axis is related to the other environmental variables. At family level, the separation along the primary axis is not so well defined. At family level, the most abundant species will affect the overall distribution of the family in relation to the environmental variables e.g. *Spiophanes kroyeri* and *Spiophanes* cf. *wigleyi.*

8.1.6.What size fraction should be used?

In the deep-sea, macrobenthic samples are routinely screened though mesh sizes smaller than those used in shallow water work. For the latter initially 1000 μm mesh sieves were used, thus only the adult macrobenthic individuals were retained on the sieve (Thorson, 1966). However, Reish (1959) collected fauna on differing mesh sizes

and found that whilst for biomass, sieves with larger apertures were adequate (1400 μm), abundance was greatly enhanced with smaller sized screens (500 μm). He also found that only a slightly smaller screen (850 μm) than the one used for biomass was required to record all the species occurring in that particular sample (Reish, 1959).

The move by shallow water biologists to smaller screens prompted deep-sea biologists to employ even finer meshed sieves in order to obtain sufficient macrobenthic fauna for statistical estimates. The deep-sea is known to have lower faunal density and is also thought to have smaller-sized species of macrobenthos (Rowe and Menzel, 1971; Thiel, 1975; Gage, 1978; Gage and Tyler, 1991; Rex and Etter, 1998). However the sieve size used by deep-sea biologists has varied. In the Northwest Atlantic Sanders *et al.* (1965) used a 420 μm sieve whilst Hessler and Jumars (1974) used a 297 μm sieve in the Central North Pacific. In the French deep-water studies starting in the 1970s a 250 μm sieve was employed (Dinet *et al*, 1985) and this is now becoming accepted as the standard size used to determine the lower macrofaunal size limit (Bett and Gage, 2000). However, some recent deep-water studies have applied a 500 μm sieve, for example in the Ocean Margin Exchanges study (*OMEX*) (Flach and Heip, 1996a,b; Flach *et al.*, 1998, 1999) as well as the AFEN 1996 and 1998 surveys (Bett, 2000).

In the present study, between 17% and 80% of the faunal abundance was accounted for by the addition of the 250 μm-to-500 μm size fraction to the >500 μm size fraction. On average there was an increase of 40% per station. The exception to this was the 900 m station in 1996 that only saw an increase of 5%. This was a result of no anterior sections of polychaetes being found and the remaining fragments being badly damaged. However, a large increase of between 13% and 53% was also seen in the number of species collected with the addition of the 250 μm-to-500 μm size fraction to the >500 μm size fraction (Figures 8.1a,b). Although species diversity indices are lower in the 250 μm-to-500 μm size fraction, combining the two fractions leads to an overall increase in species richness (10% to 38%) and Shannon diversity (-4% to 31 %), although at some stations a decrease in Shannon diversity is seen.

Bett and Gage (2000) compared results from two stations in the Northeast Atlantic where both the 250 μm-to-500 μm and >500 μm size fractions were collected. They found that 25% and 40% more specimens were collected, 37% and 154% additional species and a 2% to 4% increase in species diversity (using the Shannon index) was seen with the addition of the 250 μm-to-500 μm size fraction. It is difficult

to make a comparison between the two studies as one has 30 sets of data whilst the other has only two. However from these results it is possible to say that the collection and identification of the 250 μm-to-500 μm size fraction is not only important but vital. However, one main problem still occurs, the use of different fine and coarse mesh sizes in the deep-sea range from 250 μm to 320 μm for fine sieves through to 420 μm and 500 μm sieves for the coarse mesh. This is despite a Deep-Sea Benthos Methods Workshop being held in an attempt to standardise the sieve sizes used (SCOR, 1994).

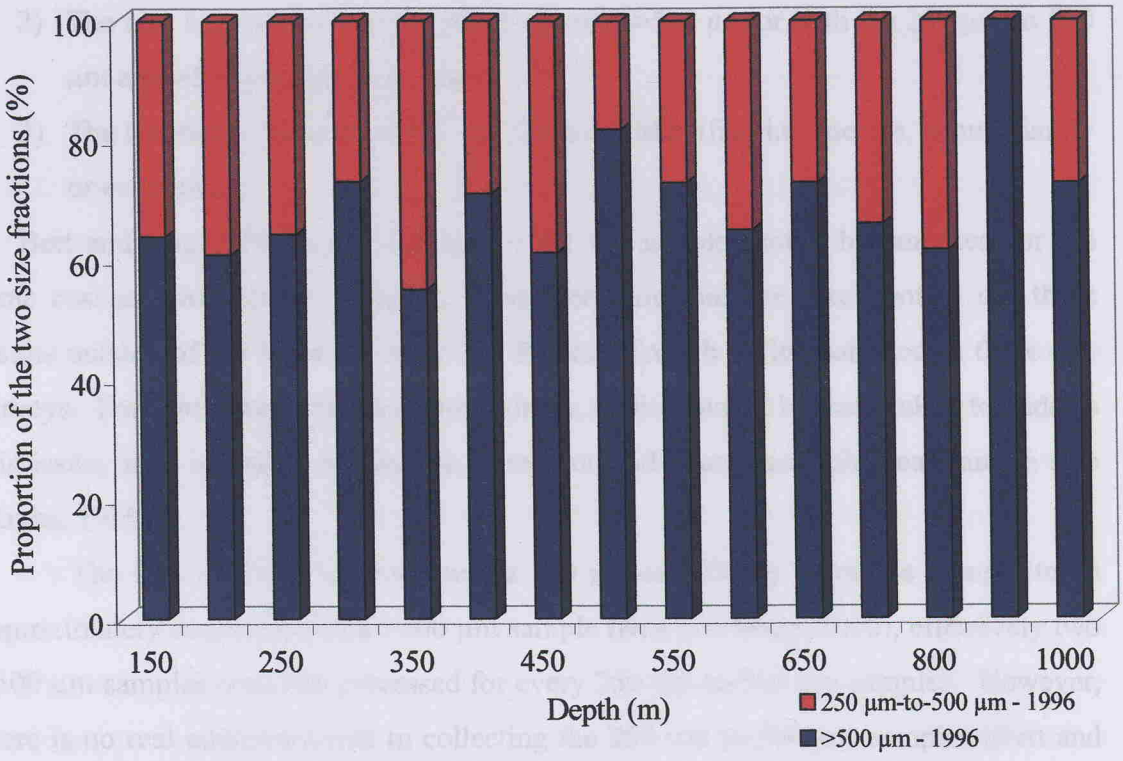
8.1.7. Sample size

Another potential problem is the actual area sampled by the equipment. In the AFEN 1996 and 1998 surveys, three pieces of equipment, a Megacorer, Box corer and Day grab were all utilised in the collection of samples. The nature of the area resulted in the three having to be used. The Day grab samples an area of 0.1 m^2 (Warwick and Davies, 1977; Tyler and Shackley, 1978), whilst the Megacorer used for this study had only 8 core tubes attached, out of a possible 12, samples an area of 0.063 m^2. The USNEL Box corer however, is capable of sampling a total area of 0.25 m^2, although in the AFEN survey (and this transect) a sub-sample of 0.1 m^2 was taken (see Bett, 2000).

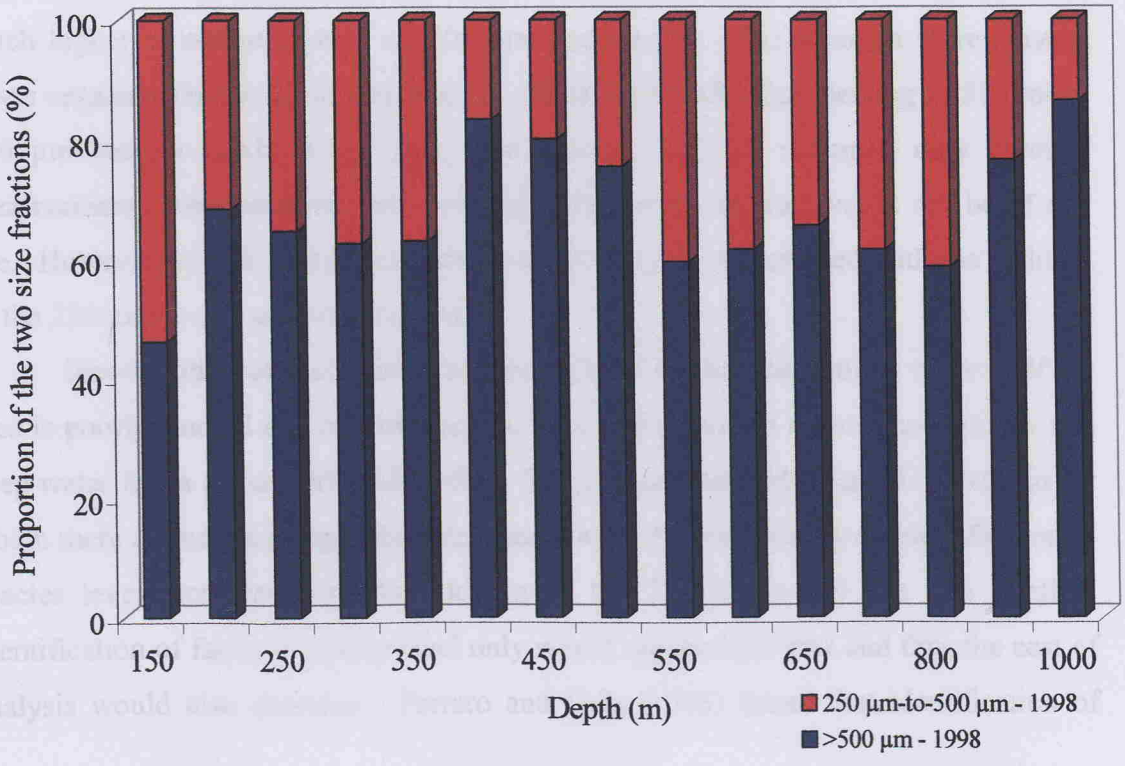
The majority of studies using a box corer have utilised the entire core e.g. work undertaken by J. D. Gage in the Rockall Trough (Gage, 1977: 1979) used the entire 0.25 m^2 by 30 cm deep core . In the AFEN surveys, samples were only collected from the top 10 cm and separated into two fractions 0 cm – 5 cm and 5 cm – 10 cm. Grassle and Maciolek's extensive study was based on 0.09 m^2 samples (Grassle and Maciolek, 1992) collected using the 'vegematic' modification of the USNEL box corer (Jumars, 1975). Bett and Gage (2000) suggested that the use of a 0.1 m^2 samples area was unlikely to introduce any bias towards biological estimates of abundance, species diversity and richness as well as dominance, and neither to have increased parameter variance relative to a larger sample size.

Figures 8.1a,b. Proportional abundances of the number of new polychaete species in each size fraction in 1996 and 1998.

8.1a



8.1b



8.1.8. Time and Costs

The time and money involved to sort and identify the fauna once the collection of samples has taken place depends on a number of factors:

1) The size of sample collected, e.g. 0.1 m^2 opposed to 0.25 m.
2) The size fractions being identified e.g. only >500 μm or both the 250 μm to 500 μm and >500 μm size fractions.
3) The taxonomic level to which the fauna are identified i.e. species, genus, family or even order.

Bett and Gage (2000) stated that five 0.1 m^2 samples could be analysed for the same cost as two 0.25 m^2 samples. However, care must be taken not to use these results outside of the West Shetland and Rockall Trough region sampled in these two surveys. For other deep-sea areas, preliminary studies should be undertaken to address this issue, as it is nearly impossible to recommend a universal physical sample size (Krebs, 1999).

The cost involved in processing a 250 μm-to-500 μm sample is thought to be approximately double that of a >500 μm sample (Bett and Gage, 2000), effectively two >500 μm samples could be processed for every 250 μm-to-500 μm samples. However, there is no real additional cost in collecting the 250 μm-to-500 μm samples (Bett and Gage, 2000) and the small size fraction should be routinely collected (T.D. Nickell, pers. comm.). The actual time involved in sorting and identification of the fauna is much higher in comparison to a >500 μm size sample, even although there may be fewer organisms in the small size fraction. Thus the benefit of processing a 250 μm-to-500 μm sample needs to be taken into account. If, for example, only biomass measurements were required then processing the small fraction would not be of any use. However, in this study abundance and diversity have increased with the addition of the 250 μm-to-500 μm size fraction.

Identification of macrofauna to species level is time consuming; more so if the area is poorly studied and requires several keys and papers to ensure that shallow and deep water fauna are correctly identified. The Faeroe-Shetland Channel is a region for which there are no recent specific taxonomic keys. The complexity of identification to species level increases with the addition of the 250 μm-to-500 μm size fraction. Identification of fauna to family level only would require less time and thus the cost of analysis would also decrease. Ferraro and Cole (1995) found that identification of

fauna to family level cost 55% less than identification to species level, although this result was dependent on several criteria: whether the dominant species belonged to taxonomically complex families or to a few uncomplicated families; and most importantly whether the taxonomic expertise was available (Ferraro and Cole, 1995).

8.1.9. Problems and limitations, suggestions for change

The main difficulty has been the identification to species level of the 250 μm-to-500 μm size fraction, especially the molluscs and the amphipods. The majority of the taxonomic work carried out has been in the North Sea, North Atlantic and some in the Norwegian Sea. The identification of most of the crustaceans relied heavily on the work undertaken by Sars (1895). The molluscs in the small fraction were so fragile that sometimes even a paintbrush could damage the animals. To ensure that this does not happen the molluscs should not be stored in formalin as without adequate buffering, the acidity dissolves the shells and destroys the colour (Huber, 1998). However, if formalin is not used then this does not aid the preservation of the remaining fauna. If formalin is to be used, then fixation should only be for a very short time. Although fixation need only take place over a day or two, it is not always possible to transfer the samples into a preservative such as alcohol whilst on board ship. Other problems incurred included the specimens often not being intact caused by poor sieving, resulting in increasing difficulty of identification of the specimens (many keys require more than the first few anterior segments to aid identification). Problematic families encountered included the bamboo worms – maldanids, ampharetids and terebellids had often lost their tentacles, whilst spionids had generally lost their palps - one of the key features required for identification.

Another limitation was the lack of sample replication, only one sample per station being collected. This did not allow the determination of within-sample variability at each station. Plotted standing stock values are the actual values; therefore the error could not be calculated.

8.2. CONCLUSIONS

The present study has illustrated that the hydrographic conditions of the West Shetland Slope alter and influence the benthic macrofauna in ways not expected, even although it is classed as being a deep-sea environment (water depth is >200 m).

- Standing stock does not show an exponential decline with depth.
- Species diversity peaks at an intermediate depth range, 450 m – 550 m, this constituting the intermediate depth band in this region.
- Certain species are able to inhabit the entire depth range sampled in this present study and so are able to tolerate an environment with widely fluctuating physical conditions.

The hypothesis tested by this current study regarding the use of higher-level taxa should be accepted with some caution. The area of this current study has not been adequately sampled, e.g. in comparison to the Northeast Atlantic, to enable results from family level and higher to be used in place of species level results.

Depth is not the main variable influencing the benthic macrofauna of the West Shetland Slope. Rather, water temperature appears to control the fauna overall, with other environmental variables, such as sediment grain size, influencing the fauna on a more local scale. Temperature effectively replaces depth as the "master" variable controlling the benthic macrofauna on the West Shetland Slope.

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APPENDICES

APPENDIX I

Comparison of depth bands used in the Analysis of Variance test in1996 and 1998.

Depth (m) 1996	Depth (m) 1998
200	200
296	300
396	398
440	440
494	500
617	605
630	630
709	705
741	748
792	800
831	844.4
899	899
967	962
981	996
1069	1070
1080	1094
1168	1174
1213	1209
1362	1364
1487	1488

APPENDIX II

Definition of species abbreviations used in Canonical Correspondence Analysis ordination plots.

Species code	Species name
Aml 1547	*Ampelisca* WOS98#1547
Amn 422	Amphitritinae WOS96#422
Ant sar	*Antinoella sarsi*
Aph 424	*Aphelochaeta* WOS96#424
Aph sp A	*Aphelochaeta* sp A
Api tul	*Apistobranchus tullbergi*
Arg hab	*Argissa hamatipes*
Ari alb	*Aricidea albatrossae*
Ari cat	*Aricidea catherinae*
Ari qua	*Aricidea quadrolibata*
Asc int	*Ascleirocheilus intermedius*
Asy 1355	*Asychis* WOS96#1355
Biv unk	Bivalvia unknown
Cap sp A	*Capitella* sp A
Cau sp A	*Caulleriella* sp A
Cha set	*Chaetozone setosa*
Cha sp A	*Chaetozone* sp A
Cha sp B	*Chaetozone* sp B
Cha sp C	*Chaetozone* sp C
Exo heb	*Exogone hebes*
Exo nai	*Exogone naidina*
Exo ver	*Exogone verugera*
?Ga 118	*Gammaropsis* WOS96#118
Gly lap	*Glycera lapidum*
Hap spo	*Haplosyllis spongiloca*
Hei sp A	*Hesionura* sp A
Lev gra	*Levinsenia gracilis*
Lil cfc	*Lilljeborgia* cf. *fillicornis*
Lil pal	*Lilljeborgia pallida*
Lum tet	*Lumbrineris tetraura*
Mad 397	Maldaninae WOS96#397
Mad sp B	Maldanid sp B
Min cir	*Minuspio cirrifera*
Myr dan	*Myriochele danielsseni*
Myr ocu	*Myriochele oculata*
Not lat	*Notomatsus latericeus*
Opi pte	*Opisthodonta pterochaeta*
Opi sp A	*Opisthodonta* sp A
Paa 573	Paraonidae WOS96#573

Par jef	*Paramphinome jeffreysi*
Pho ass	*Pholoe assimilis*
Pio lam	*Pionosyllis lamelligera*
Pit cri	*Pista cristata*
Pri cif	*Prionspio cirrifera*
Pri sp A	*Prionospio* sp A
Pri sp C	*Prionospio* sp C
Pri sp D	*Prionospio* sp D
Pri sp E	*Prionospio* sp E
Pro kef	*Protodorvillea kefersteini*
Pro sp A	*Protodorvillea* sp A
Psu sp A	*Pseudoscalibregma* sp A
Sca inf	*Scalibregma inflatum*
Sci lor	*Scionella lornensis*
Sip unc	Sipuncula
Spn sp C	Spionidae sp C
Spo cfw	*Spiophanes cf. wigleyi*
Spo kro	*Spiophanes kroyeri*
Spo sp A	*Spiophanes* sp A
Spo sp B	*Spiophanes* sp B
Spo wig	*Spiophanes wigleyi*
Sps sp A	*Sphaerosyllis* sp A
Spy ano	*Sphyrapus anomalus*
Teb str	*Terebellides stroemi*
Tha cfk	*Tharyx cf. kirkegardi*
Tha sp A	*Tharyx* sp A
Thy ?te	*Thyasira ?ferruginea*
Tri ell	*Tridonta elliptica*
Yol ?lul	*Yoldiella ?lucida*

APPENDIX III

Definition of family abbreviations used in Canonical Correspondence Analysis ordination plots.

Family code	Family name
Aml	Ampeliscidae
Amh	Ampharetidae
Amp	Amphinomidae
Api	Apistobranchidae
Aps	Apseudidae
Arg	Argissidae
Biv	Bivalvia unknown
Cap	Capitellidae
Cir	Cirratulidae
Dor	Dorvilleidae
Gly	Glyceridae
Hes	Hesinoidae
Isa	Isaeidae
Lil	Lilljeborgidae
Lum	Lumbrineridae
Mal	Maldanidae
Onu	Onuphidae
Oph	Opheliidae
Opo	Ophiolepidae
Orb	Orbiniidae
Owe	Oweniidae
Pam	Paramphithoidae
Par	Paraonidae
Pho	Pholoidae
Phx	Phoxocephalidae
Phy	Phyllodocidae
Pol	Polynoidae
Poy	Polyodontidae
Sab	Sabellidae
Scw	Scale worm
Sca	Scalibregmidae
Sig	Sigalionidae
Sph	Sphaerodoridae
Spi	Spionidae
Syl	Syllidae
Ter	Terebllidae
Teb	Terebllinae
Thy	Thyasiridae
Tri	Trichobranchidae

Tub	Tubificidae
Yol	Yoldiellidae

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