

**An introduction to
the benthic ecology of the
Faroe-Shetland Channel (SEA4)**

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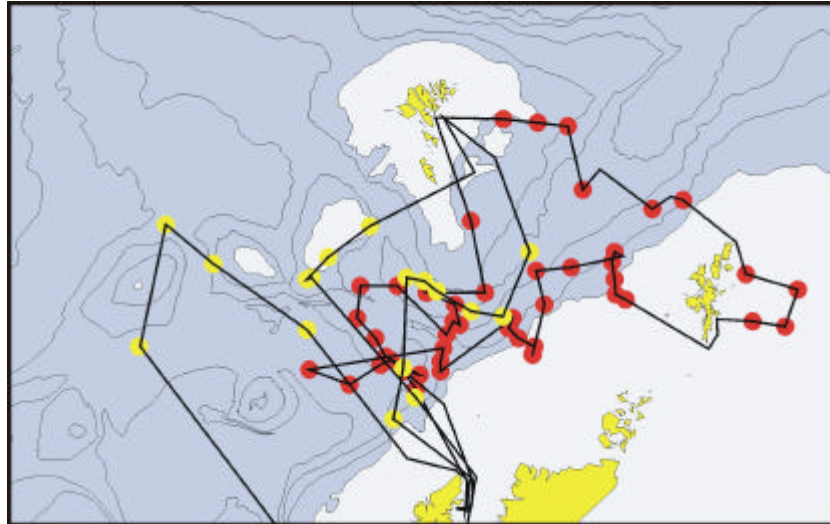
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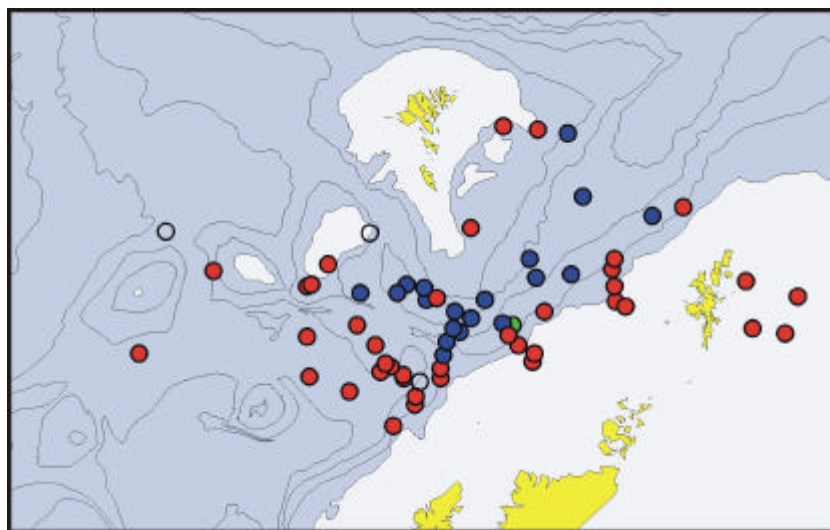
INTRODUCTION

The deep-waters to the north and west of Scotland are the birthplace of deep-sea biology. Under the leadership of Charles Wyville Thomson, the cruises of the HMSS *Lightning* and HMSS *Porcupine* in the late 1860s and early 1870s laid the foundations of this science (Thomson, 1873). These voyages lead directly to the most famous deep-sea expedition of all – the global circumnavigation of HMS *Challenger* (1872-76; Murray & Hjort, 1912).



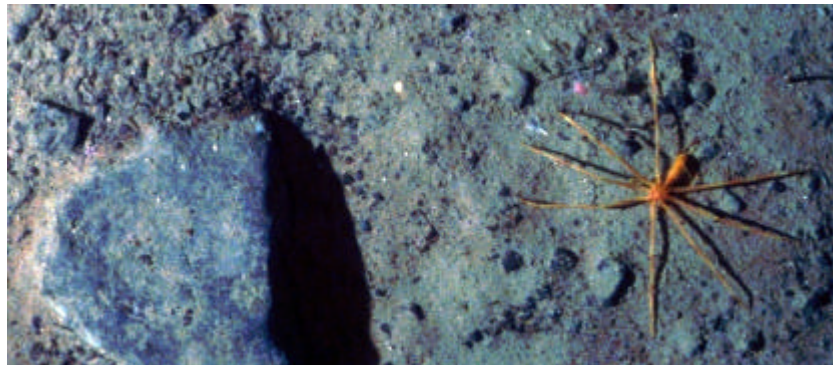
The cruises of the HMSS *Lightning* (yellow) and HMSS *Porcupine* (red) to the north and west of Scotland.

The work carried out from *Lightning* and *Porcupine* was of a truly pioneering nature. Most importantly, it established the existence of extreme temperature ranges in the area and that these are very important in regulating the distribution of animal life.



Bottom water temperature observations from the *Lightning* and *Porcupine* cruises (Red – warm, >4°C; Green – medium; Blue – cold, <2°C).

The results from the *Lightning* and *Porcupine* cruises are still valuable today, and the book recounting these voyages, “The Depths of the Sea” (Thomson, 1873), remains compulsory reading for those interested in the ecology of the region.



Giant sea spiders on the floor of the Faroe-Shetland Channel, one of the characteristic animals of the cold waters identified by the *Lightning* and *Porcupine* cruises.

Despite the significance of the SEA4 area in the early development of deep-sea biology, the area was little studied after these early cruises. It was not until the mid-1990s, and the development of the deep-water oil industry to the West of Shetland that the area was the subject of further major studies.

This report provides an overview of the more recent surveys. The reader is referred to: AFEN (2000), Bett (2000a, b), and Bett (2001) for a more detailed account. The Technical Report on the benthic ecology of the Faroe-Shetland Channel (Hughes, Narayanaswamy and Bett) updates these works, drawing on the data generated by the most recent (1999, 2000 and 2002) DTI surveys.

MODERN SEABED SURVEYS

In 1996 the Atlantic Frontier Environmental Network (AFEN) commissioned a large-scale regional survey of the West of Shetland seabed environment (AFEN, 2000). This survey adopted a new ethos – to make a regional (=strategic) assessment rather than site-by-site specific assessments – and developed a new approach, drawing on the experience of the industry, its regulators, industry contractors and the academic

community. The practical conduct of the survey drew on “modern” technology and techniques for seabed survey (e.g. sidescan sonar), sampling (e.g. Megacorer) and visualisation (e.g. WASP, seabed photography). These seabed survey tools were operated in an integrated fashion, the sidescan sonar mapping guiding the seabed sampling and visualisation which in turn fed back ground-truthing data for the improved interpretation of the sidescan sonar data (see e.g. Masson et al., 2000; Bett, 2000a).

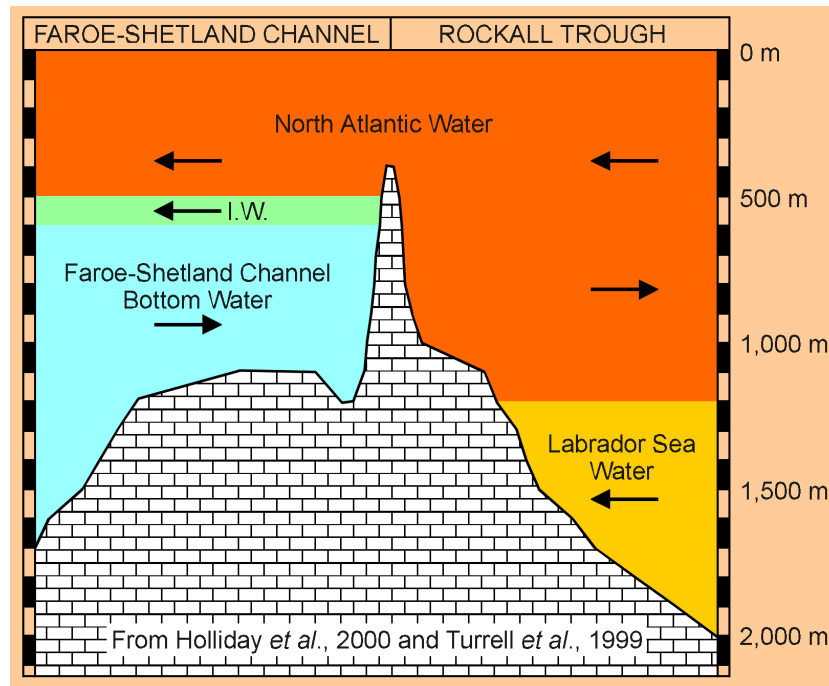


Seabed survey tools: top left – Megacorer; top right – TOBI sidescan sonar vehicle; bottom – WASP seabed photography system.

In 1998 AFEN commissioned a further survey, including areas north and west of Shetland and areas in the Rockall Trough. The general concept and approach of the AFEN surveys was then taken forward by the DTI with a survey of the Wyville Thomson Ridge and central axis of the Faroe-Shetland Channel in 1999. The DTI surveys continued with work during 2000 and the completion of SEA4 field work with the 2002 survey to the north of Shetland.

BENTHIC ECOLOGY OF THE SEA4 AREA

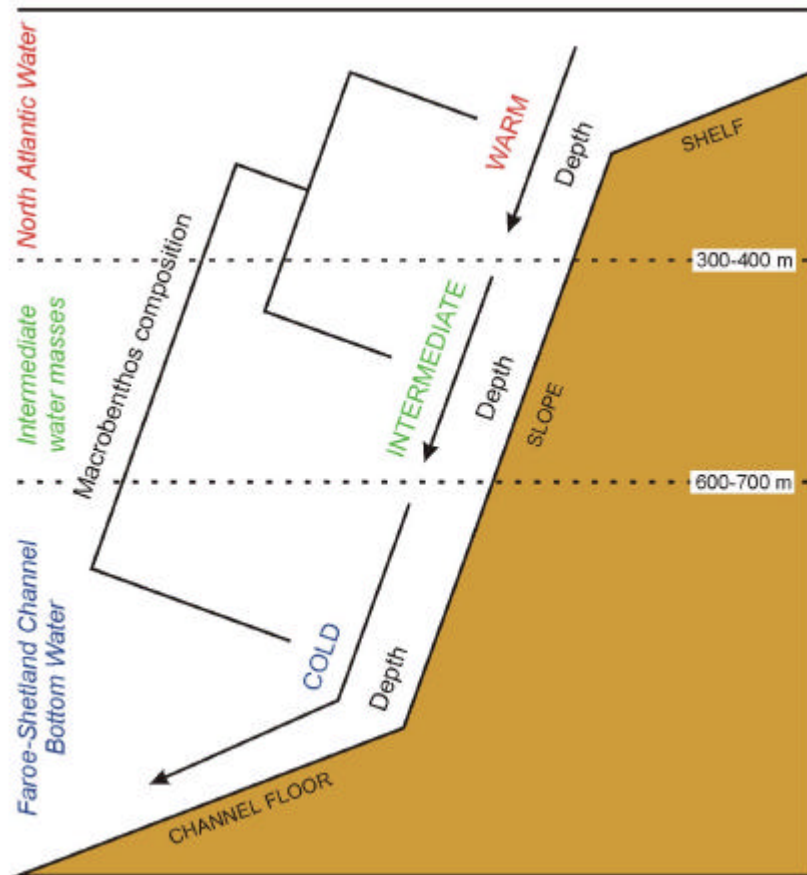
Following the AFEN and DTI surveys, the SEA4 area is undoubtedly the most extensively studied deep-sea area in the world. And perhaps more importantly, all of these studies have been carried out using common approaches and techniques throughout. The resultant dataset of biological and supporting environmental information is a unique resource for the study of deep-sea ecology. And is the more interesting for the complex and varied environmental setting of the SEA4 area.



Hydrography of the SEA4 area (Fareoe-Shetland Channel) and adjacent Rockall Trough.

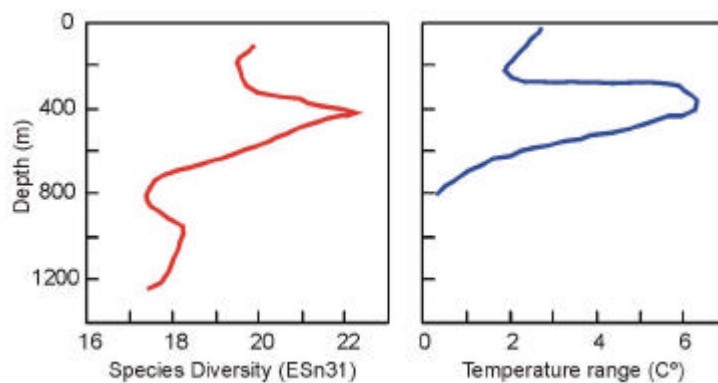
As noted by the early studies from HMSS *Lightning* and HMSS *Porcupine*, the temperature regime in the SEA4 area is critical in determining the benthic ecology of the region. The hydrographic regime in the SEA4 area is rather unique: comparatively warm North Atlantic Water overlies very cold Faroe-Shetland Channel water, producing a region of very rapid temperature change at around 500m water depth. This situation is complicated by waves that travel along the boundary where these warm and cold waters meet. Animals living on the seabed near this boundary may experience large, sudden changes in temperature (up to 8C°) as these waves pass. This is a very unusual condition for deep-sea animals. In most deep-sea areas, temperature changes are minimal (often less than 1C°) and gradual.

Analysis of the distribution of benthic species (macrofauna) in the SEA4 area indicates that the composition of the seabed community tends to vary continuously with depth, as it does in most deep-sea areas, but that there is an enhanced rate of change at depths where major changes in bottom water temperature occur (see Bett, 2001).



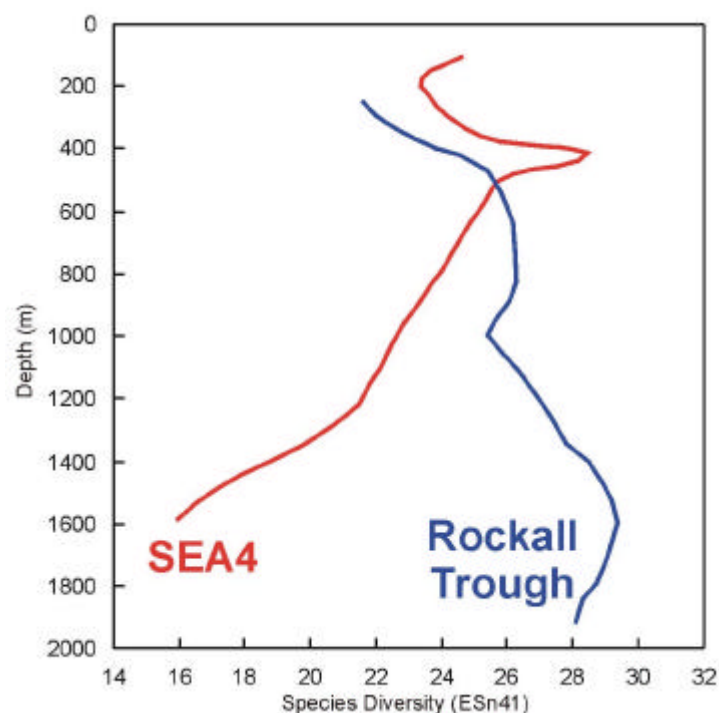
A schematic summary of the benthic ecology of the Faroe-Shetland Channel (Shetland side). Distributions of macrobenthic species appear to be strongly controlled by hydrography (water mass temperature) although there is continuous variation in the composition of the fauna with depth (adapted from Bett, 2001).

The importance of bottom water temperature variations is also apparent in the diversity of the benthos in the SEA4 area, with the diversity of the benthos (macrofauna) appearing to peak in those depths experiencing the greatest of habitat temperature variation (see Bett, 2001).



The apparent relationship between variation in species diversity and habitat temperature range (AFEN 1996 survey data; adapted from Bett, 2001).

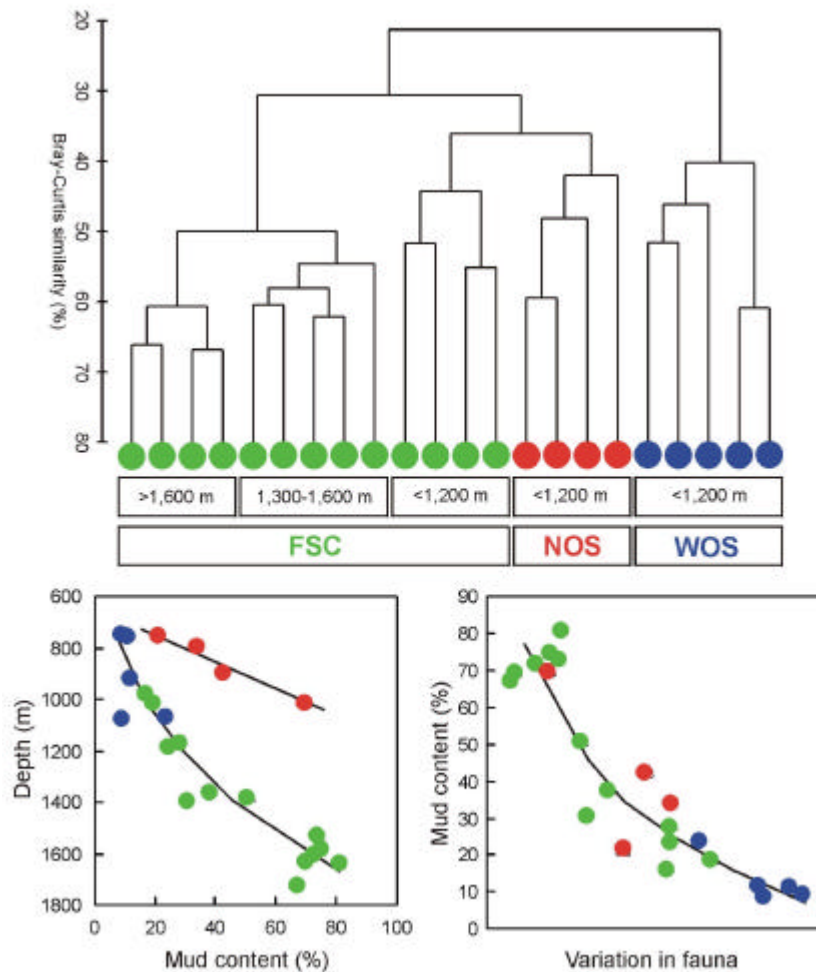
The presence of cold, arctic, waters at depth in the SEA4 area appears to exert a marked influence on the diversity of the deep-sea benthos (macrofauna) of the region most clearly seen when compared with the diversity of the benthos from the adjacent Rockall Trough which does not experience these “arctic” conditions. In the Rockall Trough, in common with many deep-sea areas, diversity tends to increase with depth; however, in the SEA4 area diversity declines with depth. Consequently, at depth, the fauna of the SEA4 area is markedly less diverse than that of the Rockall Trough. This rather dramatic contrast between these adjacent deep-sea areas is thought to result from a mass extinction of the fauna in glacial periods. Being open to the wider Atlantic, the Rockall Trough has been successfully recolonised from areas not subject to impact of glaciation. Whereas the extreme temperature change from the warm Atlantic waters to the “arctic” waters of the deep SEA4 has imposed a physiological barrier to recolonisation (see Bett 2001).



Variation in species diversity with depth in the SEA4 area and the adjacent Rockall Trough (AFEN 1996 and 1998 survey data; adapted from Bett, 2001).

The hydrographic regime of the SEA4 area does exert a dominant control on the large-scale distribution of the fauna in the region, and consequently its diversity. However, other environmental factors, both natural and man-made, do have a significant impact on the benthic ecology of the region.

In the analysis of macrobenthos data, variations in sediment type certainly appear to play a role in influencing the composition of the seabed community, although this effect is often difficult to disassociate from the continuous variation in the community with depth. The effect is best seen when comparing the West of Shetland Slope and the North of Shetland Slope – at a given depth; sediments are muddier North of Shetland.



Variation in macrobenthos community composition with depth and sediment type (as % mud content) in samples from the West Shetland Slope (WOS-blue), the deep Faroe-Shetland Channel (FSC-green) and the North Shetland Slope (NOS-red). Note that although the NOS samples are taken from a comparable depth range to the WOS samples, their fauna has a greater similarity with that of the deeper FSC samples where similarly high sediment mud content is encountered (AFEN 1998 survey data; adapted from Bett, 2000b).

Rather more obvious variations in the benthos in response to seabed type are apparent when the study is based on seabed photographs rather than physical samples (as in the case of the macrobenthos data above). Seabed samplers capable of collecting quantitative samples suitable for the analysis of the macrobenthos, and other environmental parameters, are limited to operation in relatively soft sediments (e.g. muds and fine sands). It is now apparent that the SEA4 region has large areas of coarser sediments (gravel, cobble and boulder) where conventional seabed samplers are either completely ineffective or can only selectively sample local patches of finer sediments. The latter point is important to note when assessing the seabed sample dataset, as it may introduce some bias to the results – for example when operating in the “iceberg ploughmark zone (see below).

The areas of coarser sediment in the SEA4 area have, however, been examined using seabed photography and video techniques that have revealed a wide range of seabed habitats in the region.

DEEP-SEA HABITATS OF THE SEA4 AREA

A conventional view of the deep-sea floor is that it is a large expanse of apparently barren flat mud, a habitat unlikely to excite much interest from outside the academic deep-sea biology community (see Gubbay et al., 2002). The SEA4 area, however, encompasses a much broader range of seabed habitat types – a range of variation likely to rival that of any comparable deep-sea area.



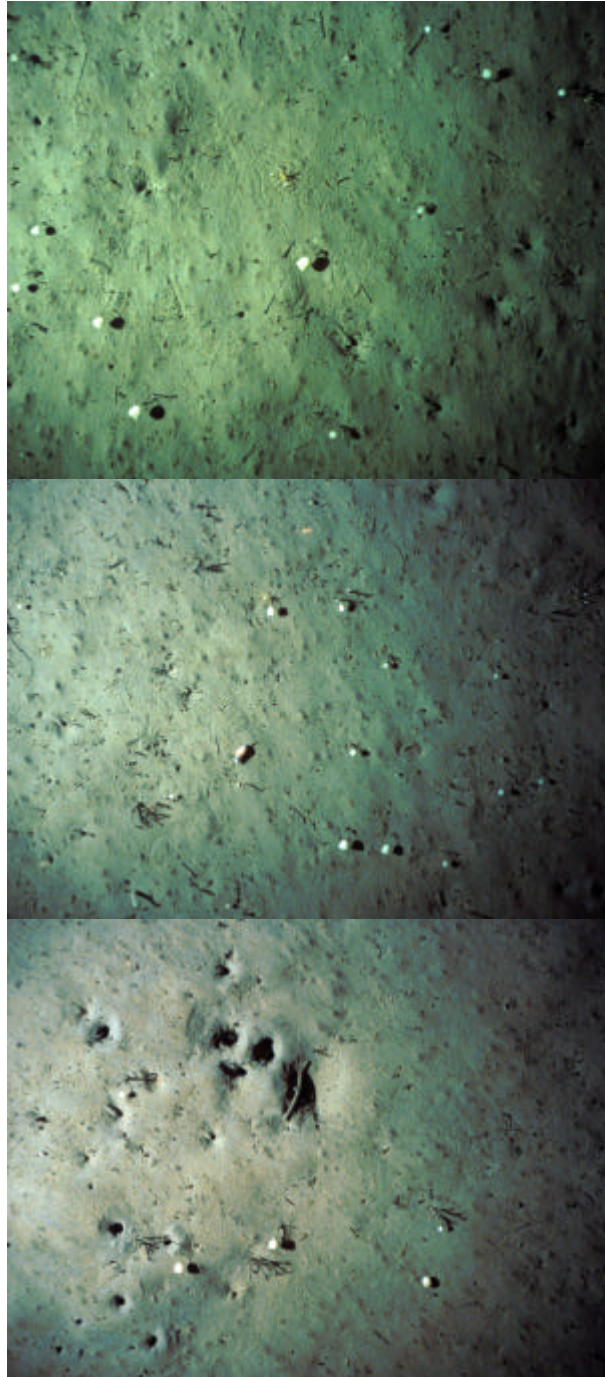
Seabed photographs from the mouth of the Faroe-Shetland Channel, showing level-bottom “typical deep-sea” soft sediment habitat. Larger fauna (megabenthos) is relatively sparse, though their burrows, tracks and feeding marks (star shapes) are abundant.

In the mouth of the Faroe-Shetland Channel and the Norwegian Basin beyond there are certainly large areas of level-bottom “typical deep-sea” soft sediment habitat. Although even here the mud diaper province (see geological technical reports) introduces local seabed habitat heterogeneity. The DTI surveys of the diapirs in 1999 and 2000 did not reveal any evidence of “exotic” seabed communities (e.g. such as associated with active mud volcanoes); however, such communities are known to exist in the Norwegian Basin (Milkov et al., 1999) and may occur in the SEA4 area (Bett, pers. obs.).



Seabed photographs from the mud diaper province at the mouth of the Faroe-Shetland Channel, showing the highly sculptured mud blocks and the gravel and cobble seabed found between the block and on the periphery of the diapirs.

The deep-waters (c. 1000-1200m) of the opposite end of the SEA4 area (Faroe Bank Channel and southern reaches of the Faroe-Shetland Channel) are rather different in character, having sandier sediments that are home to a more abundant population of megabenthos – white stalked sponges being the visually most striking component of the fauna.



Typical deep-water seabed habitat from the Faroe Bank Channel and southern reaches of the Faroe-Shetland Channel, here the sandy sediments support abundant populations of stalked sponges.

Moving towards the southern edge of the Faroe Plateau coarser sediments are encountered with rather different faunas.



Fine gravel habitat from the foot of the Faroe Plateau / Faroe Bank Channel area, there is near uniform gravel cover at the sediment surface that is carpeted by small brittlestars (too small to resolve in the images reproduced here) with occasional larger megabenthic animals (a feather star and solitary hydroid are shown).

Moving on to the lower slope of the Faroe Plateau, sediments are coarser still, with a further change in the associated fauna. The lack of fine sediments in this area is indicative of significant bottom water currents (see geological technical reports).

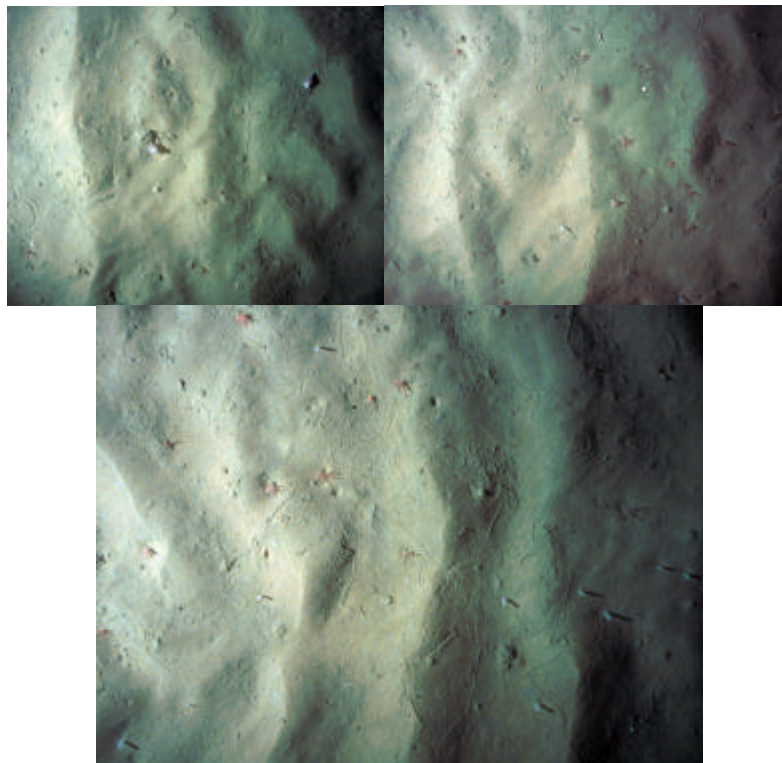


Lower slope of the Faroe Plateau, here there is continuous seabed cover by gravel, cobble and boulders, promoting the development of larger sessile megabenthos (sponges and soft corals shown).

Other seabed habitats in the SEA4 area are also indicative of significant bottom water flows that result in the transport of fine sediments: barchan sand dune fields and sandy contourite deposits (see geological technical reports).

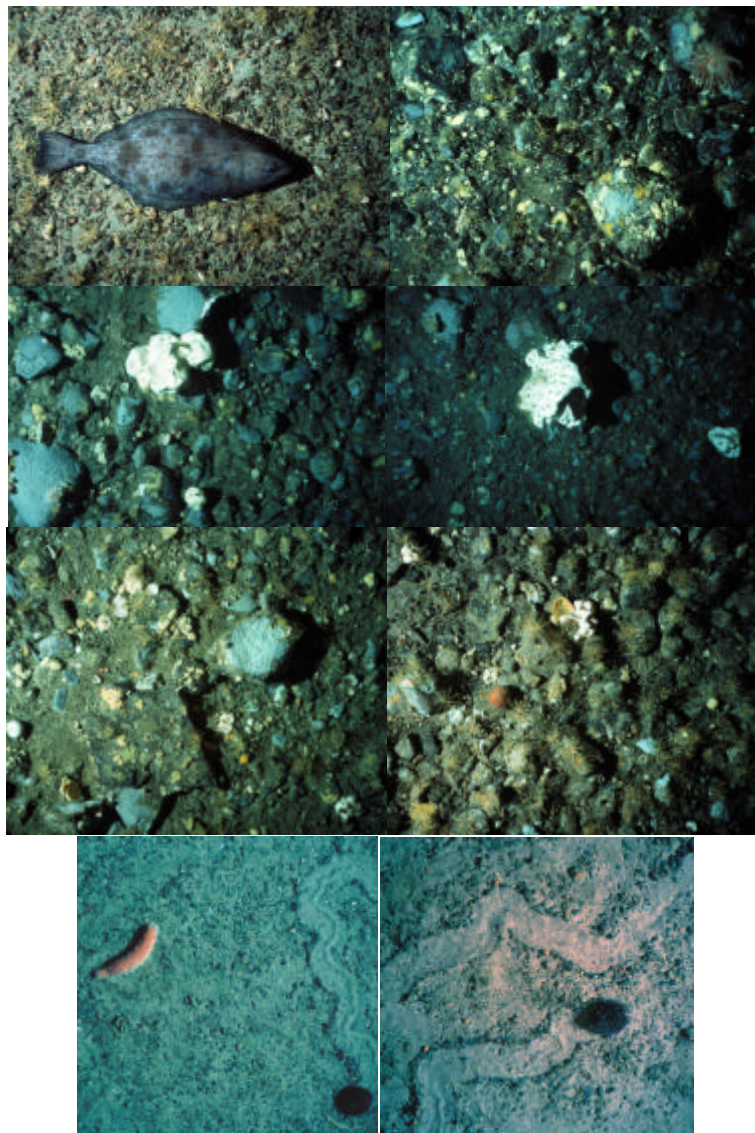


Seabed photographs from the barchan sand dune field in the southern Faroe-Shetland Channel (c. 1200m water depth), small anemones are numerous on these dunes (see Wynn, Masson & Bett, 2002 for further details).



Seabed photographs from the West of Shetland sandy contourite (c. 900m water depth), this habitat supports a unique and novel community of surface dwelling enteropneusts (acorn worms) (see Bett, 2001 for further details).

Coarse sediment habitats are not restricted to the deeper reaches of the SEA4 area, and indeed are particularly widespread on the upper slope (c. 300-500m) in a more-or-less continuous band zone known as the “iceberg ploughmark zone” throughout the region (see geological technical reports). During glacial periods, grounding icebergs gouged furrows in the seabed turning coarser sediments (cobbles and boulders) aside in an action similar to that of a plough harrow (see Belderson, Kenyon & Wilson, 1973). The action of bottom currents has subsequently, at least partially, infilled the furrows with finer sediments. These processes have acted to produce a complex, spatially heterogeneous, mosaic habitat that can repeatedly alternate from “piles of boulders” to open fine sediment areas. The coarse sediment (cobble and boulder) area can support diverse biological communities that exhibit significant local variation in their composition and abundance.



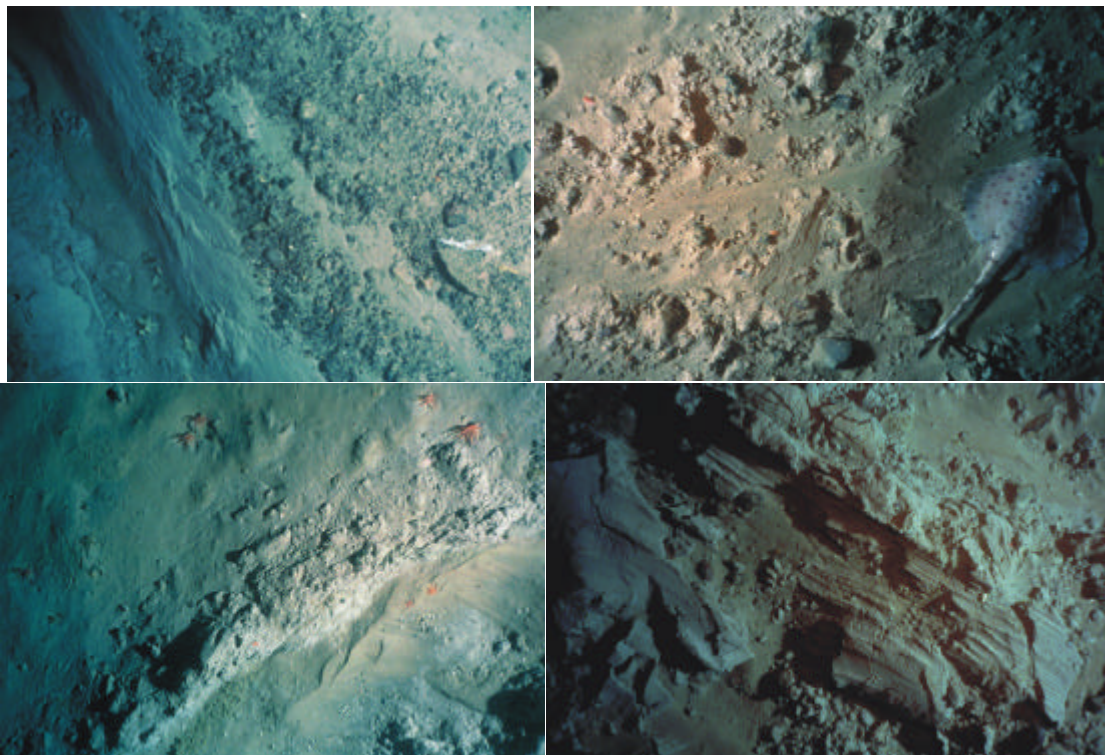
Seabed photographs from the “iceberg ploughmark zone”, this is a mosaic habitat of finer sediments areas (lower two images, showing seacucumber and heart urchins) and coarser sediment gravel / cobble / boulder). The coarse sediment areas often have a well-developed encrusting epifauna and abundant populations of mobile megabenthos and demersal fish.

MAN-MADE IMPACTS ON THE BENTHIC ECOLOGY OF THE SEA4 AREA

Two major industries operate on the deep-sea floor in the SEA4 area – the oil and gas industry and the fishing industry – both of these industries may be expected to exert some adverse impact on the ecology of the deep-sea benthos.

Results from the AFEN 1996 survey (West Shetland Slope) suggested the occurrence of localised contamination of the seabed by heavy metals (Barium) and hydrocarbons as a result of drilling operations (Bett, 2000a). However, the dominant signal in hydrocarbon contamination of deep-water sediments in the SEA4 area was from other sources (shipping and terrestrial; see McDougall, 2000).

The potential impact of the oil industry was specifically investigated during the course of the AFEN 1996 survey; the impact of the fishing industry was not – although it was never the less encountered during most of the large-scale surveys undertaken in the SEA4 area. Bett (2000c) documents the observations of potential fishing impacts recorded during the AFEN 1996 and 1998 and DTI 1999 surveys – in the form of trawl marks and discarded / lost fishing gear observed on the seabed, and a core sample taken in (presumed) trawl disturbed ground. The DTI 2000 survey recorded the presence of trawl marks in the iceberg ploughmark zone to the north of Shetland. The effects of deep-sea trawling on benthic communities is little known, though clearly is likely to be highly destructive to communities of sessile organisms (i.e. sponges) (see Bett, 2000c for further details).



Seabed photographs showing physical disturbance (“trawl marks”) of the seabed presumed to result from the action of demersal trawling in the SEA4 area.

OTHER ISSUES

Deep-water corals

At the outset of the large-scale survey programme in the SEA4 area, deep-water corals were specifically identified as a potential issue in the region. The colonial, bank-forming, stony coral *Lophelia pertusa* was known to occur in the area (see review of Rogers, 1999). Consequently, the first of the surveys (AFEN 1996) specifically investigated areas of suspected coral occurrence. In that survey and subsequent surveys the coral was only infrequently encountered, and then only as isolated colonies. Neither the photographic investigations nor the sidescan sonar surveys (see geological technical reports) provide any evidence for the mass occurrence of *Lophelia* (or other colonial stony corals) in the SEA4 area.

Lophelia pertusa certainly occurs in the SEA4 area, and may be encountered anywhere on the upper slope (“the iceberg ploughmark zone”), though it seems unlikely that it occurs at greater depth, i.e. in areas of permanently cold water. Note that *Lophelia* is often referred to as a cold-water coral to distinguish it from tropical (hermatypic) corals. The lower habitat temperature of *Lophelia* is typically reported as 4°C (e.g. Rogers, 1999), although it can certainly withstand lower temperatures (see Bett, 2000a), there do not appear to be any reliable records of occurrence in “arctic” waters (<2°C).

Taxonomy of the deep-water fauna

Taxonomy, the science of identification and classification of species, of the deep-water fauna in the SEA4 area is significantly incomplete, as is typically the case in any deep-sea area. In the analysis of the benthos (macrofauna) undertaken following the large-scale survey, approximately one half of all species recovered could not be identified to a known species. Accurate identification of species is fundamental to all biological / ecological knowledge. The time-scales of environmental impact assessments and detailed taxonomic investigations are incompatible. Consequently, additional efforts are required to ensure that taxonomy advances and that the specimens and data derived from the large-scale surveys have a long-term value.

All of the specimen material from the AFEN and DTI surveys has been curated by the National Museums of Scotland (Royal Museum, Chambers Street, Edinburgh), where they are now an internationally significant collection. This action alone will promote the taxonomy of the SEA4 fauna and ensure the long-term value of the material and data. Additionally, AFEN established a taxonomic bursary scheme that has funded specific taxonomic studies of the SEA4 (and SEA7) deep-water fauna (see <http://www.ukooa.co.uk/issues/Afen/project5.htm>). Other industry funded taxonomic initiatives have also been instituted (e.g. BP Biodiversity Fellowships, see <http://www.soc.soton.ac.uk/GDD/BP/>).

The photographic investigations undertaken during the large-scale surveys have proved to be extremely valuable in assessing the larger fauna (megabenthos and fish) of the SEA4 area. However, there have been few collections of supporting specimen material with which to confirm the identifications of the fauna made from the photographs. Trawling for specimen material can be practically difficult in rough ground areas and may be rather destructive, both to the seabed environment and the specimens

themselves. However, direct collection of targeted specimens is now a practical possibility.

The exploration and production activities of the industry in the SEA4 area have resulted in the deployment of numerous remotely operated (ROV) vehicles in the region. These vehicles are capable of detailed observation of the fauna and targeted collection of specimen material. There is considerable scope for advancing taxonomy by this means; indeed ROVs offer the possibility to undertake a wide range of detailed biological investigations in the SEA4 area (see e.g. Hudson & Wigham, 2003).



Seabed photographs taken during industry ROV operations West of Shetland (images courtesy of BP and Subsea7).

SUMMARY AND CONCLUSIONS

1. Following the AFEN and DTI large-scale surveys, the deep-water benthos of the SEA4 area are well known; at least as well known as any other deep-water area worldwide.
2. The ecology of the benthos in the SEA4 area is very strongly influenced by the hydrography of the region, particularly the complex temperature regime.
3. Seabed type (i.e. coarser / finer sediment) also exerts a strong influence on the ecology of the region, although it is often difficult to distinguish from the continuous change in the composition of the fauna that occurs with depth.
4. The deep waters of the SEA4 area are rich in seabed habitat types; the distribution of these habitats appears to be well understood / mapped (see geological technical reports).
5. It seems likely that any environmental effects resulting from the activities of the oil and gas industry will be highly localised. However, the environmental impacts of the deep-water trawling industry are already obvious and extensive.
6. As may be expected in any deep-water area, there are significant limitations to the current taxonomic knowledge of the SEA4 fauna. Several initiatives are currently underway to address this problem.

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SEA 4: An overview of the benthic ecology of the Faroe-Shetland Channel.

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SUMMARY

Five large-scale seabed surveys have been undertaken in the SEA4 area over the last seven years. In the course of these surveys, 366 sites were sampled for benthic macrofauna, sediment type, organic content, heavy metals and hydrocarbons. The sampling sites span a large range of water depths (96 to 2315 m) and seabed types. In addition, a transect of 15 stations ranging from 150 m to 1000 m water depth, the West of Shetland Transect, has been time-series sampled (1996, 1998 and 2000). The various data from these surveys is compiled and analysed here to provide a general overview of the benthic ecology of the SEA4 area.

Deep-sea macrofaunal assemblages contain many poorly known and undescribed species, making direct comparisons between datasets difficult. To allow 'safe' comparisons between surveys, the entire data set (excluding the West of Shetland Transect) was summarized to generic level. Multivariate analysis of the resulting data set indicated that two main macrofaunal assemblages occur within the SEA4 area, approximately separated by the 500 m bathymetric contour. This depth corresponds with the boundary between the northward flowing, warm North Atlantic waters and the deeper cold water flows from the Norwegian Sea. The temperature of the overlying water column appears to exert a strong influence on the benthic ecology of the area. Within the macrofauna, there are significant decreases in the number of genera, biomass and diversity with water depth (also correlating with sediment mud content, total organic carbon and, total organic nitrogen, and a decrease in mean sediment grain size). However, there is no significant trend in the abundance of macrofauna with depth. No latitudinal trends could be discerned in the biological data.

The detailed study of macrofaunal assemblages along the West of Shetland Transect indicated an increase in macrofaunal abundance with depth, although biomass reduced with depth. There is also some indication of a parabolic trend in diversity with depth, as has been reported for other deep-sea regions, although in the present case the maximum is rather shallower than reported elsewhere (and like a result of the unique hydrographic conditions of the Faroe-Shetland Channel). Three main faunal assemblages were identified, which appear to be related to the habitat temperature range that they experience, the corresponding depth bands are: 150 to 350 m, 350 to 700m, and 700 to 1000 m.

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1 Introduction

The deep waters to the north and west of Scotland are subject to the environmental pressures of two major commercial operations: deep-water fisheries and the oil and gas industry's expansion into the Atlantic Frontier. In relation to prospective oil and gas operations in the deep-waters around Scotland, both the industry and its regulator (Scottish Office Agriculture, Environment and Fisheries Department, SOAEFD, and the UK Department of Trade and Industry, DTI) resolved to implement a new approach to environmental monitoring. Rather than carry out a number of separate local investigations of particular spots of immediate commercial interest, large-scale regional surveys of the seabed environment were undertaken. The aim of these surveys was not to replace local studies in advance of any planned development, but to provide the regional setting and enable an assessment of larger-scale environmental processes that might not be evident at the local-scale. To this end, five large-scale surveys have now been carried out within the SEA 4 area: AMES 1996, AMES 1998, DTI 1999, DTI 2000 and DTI 2002. The 1996 and 1998 surveys were co-ordinated through the Atlantic Frontier Environmental Network (AFEN), a consortium of all of the operators with interests in the areas to be surveyed and other relevant bodies (Joint Nature Conservation Committee, Scottish Office Agriculture Environment Fisheries Department, Department of Trade and Industry). The 1999, 2000 and 2002 surveys were funded by the Department of Trade and Industry. The details of the individual surveys have been published separately (e.g. Bett, 2001; Shimmield, 2001).

This report synthesizes the results from macrobenthos samples taken during these surveys and correlates the observed distributions with the physical and chemical nature of the sea floor. This provides a description of the current state of the seabed environment that can be used to examine regional processes and serve as a comparator for future studies. As part of these large-scale surveys, a downslope transect, the West of Shetland Transect, was established; this consisted of 15 stations situated along a bathymetric gradient ranging from approximately 150 to 1000 m water depth. Samples were collected from these 15 stations in 1996, 1998 and 2000, allowing an assessment of the temporal variation of macrofaunal assemblages.

The methods used in the surveys involved an amalgamation of standard seabed environmental survey techniques, as routinely employed in shallow-water settings (e.g. the North Sea), with approaches normally employed in the deep sea by the academic community. The survey designs, sampling techniques, parameters to be assessed and analytical methods to be employed were devised and agreed through the joint efforts of the DTI, AFEN, SOAEFD, SOC, SAMS and subcontracted consultancies.

2 The Faroe-Shetland Channel

2.1 Geology

All five surveys included sidescan sonar (or swath bathymetric in 2002) mapping of the seabed areas prior to the benthic sampling (Masson, 1997, Masson and Jacobs, 1998). Masson et al. (2000) and Masson (2001) detail the results of the sidescan sonar mapping of various survey areas. Depth-banded seabed facies were observed in most of the areas surveyed, although a number of other localised fabrics and features were also identified

(Masson, 2001). In the west of Shetland area the following main bands were recognised (Figure 1):

- (i) Outer continental shelf (120 to 200 m), having a variable cover of sand overlying a gravel substrate. In some areas there are indications of iceberg ploughmarks and other glacial features which in some cases are partly buried beneath a sand sheet.
- (ii) Iceberg ploughmark zone (<200 to about 500 m), ploughmarks dominate this zone, though few now have any significant topographic relief.
- (iii) 'Sediment wave' zone (approximately 500 to 850 m), a relatively 'featureless' zone with long wavelength sediment waves.
- (iv) Ultra-low backscatter zone (approximately 850 to 1,000 m), an unusual zone of extremely low backscatter that appears to correspond with a sandy contourite sheet.
- (v) Faroe-Shetland Channel floor (>1,000 m), a relatively featureless zone.

The West of Shetland area is fully covered by seabed sediment charts compiled by the British Geological Survey (BGS 1:250,000 sea bed sediments: Flett, Millar, Foula, Judd). These charts largely confirm the expectation that sediment type varies with depth, grading from coarse sands on the shelf edge to finer sediments on the floor of the Faroe-Shetland Channel.

2.2 Hydrography

The hydrographic regime of the Faroe-Shetland and Faroe Bank Channels is complex, with warm North Atlantic waters overlying cold waters flowing from the Norwegian Sea (Turrell et al., 1999). The boundary between the warm and cold waters is dynamic and may occur variously between 400 and 600 m depth. The boundary is neither sharp nor does it occur at a fixed depth. Intermediate water masses separate the uppermost warm layer (North Atlantic Water) from the sub-zero temperature water of the channel floor (Faroe-Shetland Channel Bottom Water), and internal waves may propagate at the boundaries of the various water masses (Sherwin, 1991). On the eastern flank of the Faroe-Shetland Channel (FSC), the upper warm water masses flow along-slope to the northeast and the deeper cold water masses flow along-slope to the southwest. The hydrography is extremely dynamic, and large variations in temperature have been recorded around 400m water depth. The rate at which temperature changes may occur was illustrated in a dataset recovered from a recording current meter moored near the seabed in the survey area for ten months prior to the 1996 survey. The current meter was located at a depth of 550 m and recorded a temperature of -0.8 to 8.9 °C, i.e. spanning the temperature range of all the water masses recognised in the FSC. The maximum rate of temperature change recorded was 7.0 °C in one hour, with an intrusion of cold water that lasted some 4-5 hours. Such rapid temperature fluctuations might result from internal waves at the warm-cold boundary, generated by the flow of North Atlantic Water over the Wyville-Thomson Ridge (Sherwin, 1991).

2.3 Benthic Ecology

In stark contrast to the relatively well-known hydrographic and geological setting of the Faroe-Shetland Channel (FSC), the benthos of the SEA4 region are rather poorly known. The western flank of the FSC has, however, been the subject of extensive biological investigations in recent years, principally through the Internordic

BIOFAR programme (Nørrevang et al., 1994). Of the numerous BIOFAR publications to date, there are several of particular interest to the general ecology of the region. Four of these publications relate to two significant 'biological habitats': that of the bank-forming coral *Lophelia pertusa*, and that referred to by fisherman variously as "ostur", "duffs", "ostebund" or "cheese bottoms" representing the mass occurrence of large demosponges, particularly *Geodia* spp. The distribution of *Lophelia* and its faunal associates are detailed by Frederiksen et al. (1992) and Jensen and Frederiksen (1992) respectively. Similarly, the distribution of large demosponges and their faunal associates are detailed by Klitgaard (1995) and Klitgaard et al. (1997), respectively. In both the case of *Lophelia* and the mass sponge aggregations, their distributions may be related to areas where seabed slope matches the characteristic slope for the propagation of internal wave energy (see also Rice et al., 1990). Both of these biological habitats were also found to support a large number of associated species, some 250 in each case, although these species were thought to be almost entirely facultative, rather than obligate, associates.

The eastern side of the FSC has received comparative little biological study. Dyer et al. (1982) carried out some trawl sampling of the West Shetland Shelf that also included the use of a trawl headline camera. On the coarse substrates (sands and gravels) of the shelf, the authors found the tubicolous epibenthic polychaetes *Ditrupa* and *Hyalinoecia* to be particularly abundant along with the echinoids *Cidaris* and *Echinus*. Little else has been published on the benthic ecology of the survey area in recent decades, leaving only nineteenth century studies. In 1880, the *Knight Errant* expedition carried out some dredging on the West Shetland Shelf (Tizard and Murray, 1882); similarly the 1882 cruise of HMS *Triton* is also relevant. However, it is the results of the HMS *Lightning* (1868) and HMS *Porcupine* (1869) cruises (Thomson, 1873) that remain the most useful in respect of the deep-waters west of Shetland. These studies indicated the likely strong influence of bottom water temperatures on the distribution of the fauna in the FSC. Results from the 1996 and 1998 surveys compared the benthic assemblages found to the north and south of the Wyville-Thomson Ridge (see Bett, 2001), and demonstrated that the extreme thermal gradient present on the West Shetland Slope has a substantial influence on the distribution and diversity of the macrobenthos. The deep-water faunas north and south of the ridge are highly distinct, and there is a marked difference in the diversity of the two faunas. Bett (2001) also reported the occurrence of sponge dominated communities at mid-slope depths (c. 500 m) north and west of Shetland, and the discovery of a population of sediment surface dwelling enteropneusts associated with a sandy contourite deposit at the base of the West Shetland Slope (c. 900 m).

3 Methods

A full account of the 1996 and 1998 surveys, the data obtained and its analysis and interpretation is available as a CD-ROM (AFEN 2000, see in particular: Bett and Axelsson, 2000; Bett, 2000; Bett and Gage, 2000). The 1996, 1998, 2000 and 2001 surveys were undertaken from the research vessel RRS *Charles Darwin* and the 2002 survey undertaken from the MV *Kommandor Jack*. The bulk of the sampling undertaken during the surveys followed stratified random sampling schemes (Bett, 2001) with additional sampling carried out on bathymetric transects (West and North of Shetland Transects) and to target specific seabed features and fabrics revealed by the preceding acoustic surveys.

3.1 Sampling and ship-board sample processing

The methods for the surveys were an amalgamation of standard seabed environmental survey techniques, as routinely employed in shallow-water settings (e.g. the North Sea), with approaches normally employed in the deep sea by the academic community. The varied seafloor and sediment types within the area necessitated the use of a three seabed sampling devices: Day grab, box corer and Megacorer. The Day grab is a small frame mounted, warp-activated, two scoop sampler, which takes a sample of 0.1 m² (Holme and McIntyre, 1984). The box corer was of the USNEL MkII type (Hessler and Jumars, 1974), which takes a 0.25 m² sample, and closes with a single warp-activated spade. The Megacorer, manufactured by Bowers and Connelly (Oban), is an hydraulically damped multiple corer of a similar concept to that described by Barnett et al. (1984). The Megacorer can collect up to twelve 10 cm diameter cores in a single deployment, though during the surveys it was frequently deployed with fewer core tubes fitted to increase sediment penetration. Typically, differential-GPS was used during the surveys to determine the vessel's position and an ultra-short baseline (USBL) acoustic navigation system was also employed to navigate redeployed gear relative to the vessel.

Details of sample handling protocols for each gear and each type of sample retained (e.g. macrobenthos, total organic carbon, total organic nitrogen, aliphatic and aromatic hydrocarbons, 'heavy metals', and sediment particle size distribution are available on CD-ROM (AFEN 2000).

3.2 Laboratory methods

The analysis of macrofaunal samples was carried out by commercial consultancies: Environment and Resource Technology Ltd (ERT), OPRU Environmental Science and Interpretation (OPRU; Now part of BMT Cordah Ltd.), and Unicmarine Ltd. Sediment characterisation, and chemical analyses were carried out by ERT, OPRU, the British Geological Survey, and NITG-TNO (Baker, 1997; McDougall, 1997; Smith, 1997; Tulloch, 2003). The various methods employed are detailed on CD-ROM (AFEN 2000).

For the purposes of the analyses presented here, the full faunal dataset was first reduced to those taxa typically regarded as macrobenthic. To this end, meiobenthic (foraminiferans, nematodes, acarids, harpacticoids and ostracods), parasitic (copepods and isopods) and planktonic (e.g. ostracods, branchiopods, calanoids, larval forms and euphausiids) taxa were removed prior to analysis. The large number of unknown / undescribed species encountered during these surveys and the number of different taxonomists involved suggests the need for caution in analysis. Consequently, the taxonomic resolution of the full dataset was further reduced to generic level, or higher for the purposes of general analysis. Faunal samples from the West of Shetland transect have all been examined by a single worker (B.E. Narayanaswamy) enabling analysis to be reliably carried out at the species level.

3.3 Statistical Analyses

Data presentation and analysis were carried out with the aid of a number of commercially available software

packages (PRIMER, Plymouth Marine Laboratory; BIODIVERSITY PRO, Natural History Museum and Dunstaffnage Marine Laboratory; Minitab 13; PCORD Version 4; CANOCO V4.5). Unless otherwise stated, the following generally apply to the various analyses performed:

a) Analysis is performed on a site by site (rather than sample by sample basis), i.e. where replicate data were available for any single site they were averaged, or otherwise amalgamated as appropriate, prior to analyses.

b) Data expressed as percentages (e.g. silt/clay content, total organic carbon, etc.) were arcsin transformed (Sokal and Rohlf, 1995) prior to parametric statistical analyses.

c) All correlations were calculated using Spearman's rank (non-parametric) procedure (Siegel and Castellan, 1988).

d) All primary biological data, i.e. abundance and biomass, were $\log(x+1)$ transformed (Sokal and Rohlf, 1995) prior to parametric statistical analyses (Field et al., 1982).

e) Multivariate analyses (cluster analysis and non-metric multi-dimensional scaling) were performed on fourth root transformed data and the Bray-Curtis similarity measure employed.

f) For faunal samples analysed as part of the West of Shetland Transect, the box corer and Day grab data were adjusted by a correction factor to make them more comparable with the megacorer data. This is based on a comparison of the sampling gear undertaken by Bett (2000). No significant differences were detected between the sampling efficiencies of the Day grab and box corer. However, comparison of box corer and Megacorer efficiencies revealed a major (and statistically significant) difference on average, box core abundance was only 39 % (and biomass only 53 %) of that recorded by the megacorer (Bett 2000). A correction factor was therefore applied to the Day grab and box corer data in an attempt to remove the influence of this variation in sampling efficiency.

g) For the West of Shetland Transect, Canonical Correspondence Analysis (CCA) was undertaken using the CANOCO package (ter Braak and Smilauer 2002). CCA was used to analyse the relationship between polychaete community structure and the suite of environmental variables measured. This method has been found to be useful and effective in evaluating the relationship between faunal composition and environmental variables (ter Braak, 1987; Brown et al., 1992). Within CCA, depth was removed from the analysis using the forward selection, as it was a co-variable. The statistical significance of the relationship between polychaetes and environmental variables was tested using a Monte Carlo permutation test within CCA (Manly, 1991; ter Braak, 1992). The results give the significance of the first eigenvalue and the sum of the eigenvalues (ter Braak, 1987). The eigenvalues presented measure the total amount of variance, whilst the canonical eigenvalues measure the variance with respect to the environmental variables used (ter Braak and Smilauer, 2002).

4 Results

4.1 Temporal variation in the macrobenthos of the West of Shetland Transect

Faunal Standing stock

A general linear model (GLM) analysis of variance was undertaken to determine if there were any significant difference in standing stock between the three study years. In all groups, including total macrobenthos, there were no significant differences ($p > 0.05$) in standing stock between years.

Abundance

Total macrofaunal abundance exhibited a similar distribution with depth in all three years, with a maximum occurring around 700 to 800 m depth (Figure 2a). A significant linear correlation between abundance and depth was evident ($t = 2.709$; $p < 0.05$).

Polychaete abundance was similar in all three years and showed a similar distribution to that of the total macrofaunal abundance with a peak at deeper stations (Figure 2b). Polychaete abundance also exhibited a positive correlation with depth ($t = 2.431$; $p < 0.05$). Crustacean abundance peaked at more intermediate depths of 450 to 550 m (Figure 2c) and did not correlate with depth. Mollusc abundance peaked at depths of 600 to 800 m (Figure 2d) and exhibited a significant linear correlation with depth ($t = 2.260$; $p < 0.05$). In contrast the echinoderms were the only phylum whose abundance significantly declined with depth ($t = 2.129$; $p < 0.05$)(Figure 2e).

Total macrofaunal abundance correlated significantly with several environmental variables, notably sediment organic matter content ($r_s = 0.564$; $p < 0.05$) in 1996, sediment mud content in 1998 ($r_s = 0.663$; $p < 0.01$) and sediment particle size in 2000 ($r_s = 0.661$; $p < 0.01$). Abundance of the different phyla correlated significantly with a range of environmental variables, the most significant of these are shown in Table 1.

Biomass

Total macrofaunal biomass generally exhibited the same overall pattern in all three years with a maximum occurring between 350 to 450 m depth. Biomass values at the 150 m, 300 m and 350 m stations in 2000 appeared to be notably higher in comparison to 1996 and 1998. When these samples are included in the analysis biomass exhibits a significant negative correlation with depth ($t = 2.150$; $p < 0.05$), otherwise there is no significant relationship with depth (Figure 3a).

Polychaete biomass showed a significant linear relationship ($t = 2.502$; $p < 0.05$) with depth (Figure 3b), with a maximum occurring between 650 to 800 m in all three years. Crustacean biomass generally peaked in all three years between 400 to 600 m (Figure 3c). However in 1996, the 400 m and 450 m stations had higher values in comparison to 1998 and 2000. Removing these higher biomass values lead to crustacean biomass exhibiting a

significant linear relationship with depth ($t = 2.632$; $p < 0.05$) (not shown on figure). Both mollusc and echinoderm biomass values peaked at the 400 m station, but both the 150 m and 350 m stations appeared to have considerably higher values in 2000 compared to the previous two years (Figures 3d and 3e). Molluscan biomass also exhibited a significant negative linear relationship with depth ($t = 2.164$; $p < 0.05$).

Total macrofaunal biomass correlated most strongly with sediment mud content in 1998 ($r_s = 0.796$; $p < 0.001$). Neither 1996 nor 2000 biomass values correlated with any of the environmental variables measured. Biomass of the different phyla, correlated significantly with a range of environmental variables, the most significant of these are shown in Table 2.

Macrobenthic Polychaete Diversity

Variation in macrofaunal species diversity with depth is illustrated in Figures 4a-d. Four measures have been employed, Margalef's species richness (d), Shannon-Wiener diversity index ($H' \log_e$), Pielou's evenness (J') and Simpson's dominance index ($1/d$), the latter has been plotted so that values increase/decrease in line with the other diversity indices. For all the diversity measures and in all years, the overall trend was for a maximum in diversity at intermediate depths, 400 to 550 m. Several environmental variables correlated significantly with diversity, in particular temperature range correlates most strongly with the suite of diversity indices (Table 3). However, in 2000, only Margalef's species richness correlated significantly with any of the environmental variables. Diversity did not correlate significantly with total hydrocarbons and rarely with total organic carbon.

Rarefaction

Rarefaction plots from all years tended to separate the stations out into three groups. One group generally consisted of deeper stations, the other two a mixture of shallow and intermediate stations (Figures 5a - c). In all years the 350 m stations had the highest estimated number of species. In 1996 and 1998 the 800 m station was estimated to have the lowest number of species, this shifted to the 900m station in 2000.

Faunal composition - Polychaeta

Species occurrence

The bathymetric distribution of species was initially assessed by examining their depths of first and last occurrence. In all years (Figures 6a - c) the number of new species added decreased noticeably below 600 m. In 1998 there is a more noticeable increase in the number of new species added at a depth of 400 to 500 m, whereas in 1996 and 2000 the increase, which occurs at a depth of 300 to 400 m is not so apparent. The number of species lost generally showed a similar pattern to that of new species added with a maximum reached at approximately 500 m.

Figure 11 illustrates the plot of cumulative number of species in 1998 with habitat temperature range superimposed (data from TOBI CTD during 1996 survey; see CD-ROM, AFEN, 2000). The shape of the species accumulation curve appears to be linked to the temperature range curve. The rapid decline in the addition of new species at depth may mark the boundary between the water masses; below about 650 m depth, the fauna will be subjected to permanently cold water. This change in species accumulation with depth was also seen in the 1996 results, it showed a similar pattern where species accumulation increased with depth (see Bett, 2000).

Species dominance

Given the apparent importance of bottom water temperatures to the ecology of the region (see further below) an assessment of species dominance was carried out based on depth-based habitat temperature bands: a shallow, warm layer (c. 10-4°C), an intermediate, temperate layer (c. 7.5-0.5°C), and a deeper, cold layer (c. <0.5°C). The percentage distribution of species in three habitat temperature bands is illustrated in Table 6, these values are highly consistent between the three study years. The most abundant species in each temperature band were also quite consistent in all three years. The 'warm' temperature band was generally dominated by *Spiophanes* cf. *wigleyi* and *Glycera lapidum* complex; the 'intermediate' band by *Paramphinome jeffreysii* and *S.* cf. *wigleyi*, and the 'cold' temperature band dominated by *Spiophanes kroyeri* and *Paramphinome jeffreysii* again (Figures 7a - c). *Spiophanes* cf. *wigleyi* and *P. jeffreysii* are species that were dominant in two temperature bands and as a result they have been termed *transitional species*. Figures 8a - c illustrates the distribution of these species with depth. In 2000, *Galathowenia oculata* dominated the warm temperature band, with over 80 individuals per 0.1 m², whereas for the warm band in 1996 and 1998, the most abundant species were approximately 4 - 8x less numerous. Between 500 to 700 m, *P. jeffreysii* showed a rapid increase in abundance, but this was followed by a sharp decline at the 800 m station. However, coinciding with this decline was a rapid increase in the number of *S. kroyeri*, which then changed at the 900 m station where *S. kroyeri* decreased and was matched by an increase in *P. jeffreysii* (Figures 8a - c).

Polychaete community analysis

Multivariate analysis

In all three years, hierarchical cluster analysis separated the stations into two groups, which showed a similarity of approximately 20 % (Figures 9a - c). In general the 650 to 1000 m stations ('cold') formed one group, the second group ('warmer') was partially sub-divided into two further groups generally comprising shallow stations in one and intermediate stations in the other. The non-metric multi-dimensional scaling plots tended to reflect the patterns shown by the dendrograms, two main groups ('shallower' and 'deeper') with a third ('intermediate') group linking them (Figures 9d - f). Comparable patterns in the cluster analyses and multi-dimensional scaling ordinations are seen in all three years. Bett (2000) has suggested that faunal distribution illustrated by dendrograms and ordination plots in the Faroe-Shetland Channel are influenced predominantly by the hydrography of the Channel.

Canonical correspondence analysis

In all three years, axis one separated the shallow stations from the deeper stations (Figures 10a - c), and axis two further separated the stations into shallow-intermediate and intermediate-deep stations. ter Braak (1986) suggested that eigenvalues >0.5 account for a large percentage of variance in species composition; in all three years the eigenvalue of axis one was >0.5 . The results shown in Table 4 imply that there is a high correlation between environmental variables and the composition of the polychaete fauna, indicating that most of the variance in species composition is accounted for by the environmental variables. Between 60 % and 65 % of the variability in polychaete species composition was explained by the 10 environmental variables that were measured.

On all three plots, the temperature eigenvectors were most strongly associated with species, e.g. *Glycera lapidum* complex, that are most abundant at the shallow stations. This suggests that they are more tolerant of varying water temperatures. Mean sediment grain size, sediment organic matter content and sediment mud content were associated with the fauna at the deeper stations. In both 1996 and 2000, several of the deeper stations and associated species appeared to lie on the inverse of the temperature range (drawn in blue on the ordination plots) possibly implying that they are not able to tolerate a wide range of temperatures.

An unrestricted Monte Carlo permutation test was applied to the forward selection of the environmental variables. Each year had two or three environmental variables accounting for a significant proportion (<0.05) of the variance seen (Table 5). These variables (Table 5) accounted for between 45 % and 56 % of the total variability and of these variables, maximum temperature accounted for the highest proportion of that variability measured between 26 and 31 %.

4.2 Regional Assessment (the full dataset)

Figure 1 indicates the location of the 366 sites where macrofaunal samples were obtained. The deep-water areas to the north and west of Scotland are topographically complex, cover a large range of water depths (96 to 2315 m) and seabed facies.

A total of 65,014 macrofaunal individuals were identified, belonging to 769 Genera. Identification of the macrofauna has been carried out by different taxonomists, which may lead to some inconsistencies within the data set. Most obviously, genera have sometimes been questioned (e.g., ?*Cerebratulus*), and organisms from different surveys identified as this have been grouped together, although they may not actually belong to the same genus. It was beyond the scope of this report to cross-check the identification of individuals. We assume that inconsistencies introduced in this manner are minor, and do not significantly influence the overall results.

Of the 769 taxa identified, 34.1% were polychaetes, 34.8 % were crustaceans, 18.6 % were molluscs, 6.7 % were echinoderms, with minor taxa accounting for the remainder. Of the 65,014 individuals, polychaetes accounted for 63.5 %, crustaceans for 17.8 %, molluscs for 10.0 % and echinoderms for 3.5 %. The most abundant genera

overall were, in decreasing order of abundance: *Myriochele*, *Spiophanes*, *Paramphinome*, *Aricidea*, *Notomastus*, *Chaetozone*, *Thyasira*, *Yoldiella*, *Minuspio*, *Paradoneis*, *Glycera* and *Aonides*. All the aforementioned were found in total numbers of greater than 1000 individuals, and all are polychaetes with the exception of *Thyasira* and *Yoldiella*, which are bivalve molluscs.

Macrobenthos abundance and biomass

A very weak, positive correlation exists between macrofaunal abundance and depth ($r_s = 0.111$, $p < 0.034$) (Figures 13a and 14), with maximum abundances observed around 800-900 m water depth. The stations with the highest abundances (>7000 individuals m^{-2} ; CS2, CS3, CS4, CS7 and NS700) were at mid-slope depths and had elevated abundances of the polychaetes *Paramphinome*, *Minuspio* and *Spiophanes*, together with the bivalve *Thyasira*. Biomass values should be interpreted with care, as it is notoriously difficult to obtain accurate blotted wet-weight biomass values. More accurate methods, such as obtaining ash free dry weight (Rowe, 1983) destroy the specimens. Biomass was not significantly correlated with depth (Figures 13c and 15), although it was significantly correlated with C/N Ratio ($r_s = 0.229$, $p < 0.012$) and TOC ($r_s = 0.13$, $p < 0.05$).

Diversity

There is a significant decrease in the number of genera observed with increasing water depth ($r_s = -0.53$, $p < 0.001$) (Figure 13b; Figure 16). All univariate measures of diversity were also significantly correlated with water depth, i.e., Margalef's Species Richness ($r_s = -0.58$, $p < 0.001$), Pielou's Evenness ($r_s = -0.33$, $p < 0.001$) (Figure 18), Fisher's Index ($r_s = -0.62$, $p < 0.001$), Shannon-Weiner diversity index ($r_s = -0.57$, $p < 0.001$) (Figure 19), Simpson's Index ($r_s = -0.47$, $p < 0.001$), $ES_{(30)}$ ($r_s = -0.57$, $p < 0.001$) (Figure 20). Figure 17 illustrates the variation in macrobenthic species diversity with depth for Margalef's Species Richness, the Shannon-Wiener diversity index ($H' \log_e$), and the expected number of species in a rarefied sample of 30 individuals (ES_{30}). As the ES_{30} is calculated through rarefaction, it is not influenced by sample size, in the same way that other univariate indices may be, and is a more standardised index of diversity. For all indices there is a significant decrease in diversity with depth ($p < 0.001$), with no obvious increase at mid-bathyal depths.

Number of genera also displayed significant correlations with several of the physical and chemical parameters tested: mean sediment grain size (ϕ m) ($r_s = 0.43$, $p < 0.001$), sediment mud content ($r_s = -0.51$, $p < 0.001$), TOC ($r_s = -0.20$, $p < 0.001$), TON ($r_s = -0.155$, $p < 0.005$), total hydrocarbons ($r_s = -0.42$, $p < 0.001$) and Barium concentration ($r_s = -0.24$, $p < 0.001$). The results for Number of Genera are mirrored in those for all the diversity indices measured, all of which significantly correlated with mean sediment grain size (ϕ m), sediment mud content, TOC, TON, total hydrocarbons and Barium concentration.

Sedimentary parameters.

Figure 21 illustrates the distribution of mean sediment grain size at all the sampling stations, and Figure 22 illustrates the variation in sediment grain, (mean particle diameter, μ m), sediment mud content and total organic

carbon (%) with water depth. Mean sediment grain size decreases significantly with water depth ($r_s = -0.72$, $p < 0.001$), as is suggested by Figure 21. Sediment mud content ($r_s = 0.84$, $p < 0.001$) (Figure 22), TOC ($r_s = 0.37$, $p < 0.001$) (Figures 22 and 23), TON ($r_s = 0.29$, $p < 0.001$), total hydrocarbons ($r_s = 0.35$, $p < 0.001$) (Figures 24 and 25) and Barium concentration ($r_s = 0.41$, $p < 0.001$) (Figures 24 and 26) also correlate significantly with water depth.

Multivariate analyses

Figure 27 shows the 2-dimensional Multi-Dimensional Scaling (MDS) ordination of all the sites, based on fourth root transformed abundances and Bray-Curtis similarities. The stress value of this ordination (0.21) is quite high, so that not too much reliance should be placed on the details of the plot in itself (Clarke and Warwick, 1994). The combination of clustering and ordination analyses, however, is an effective way of checking the adequacy and consistency of both representations. When cluster analysis was carried out, 6 groups were formed at around a 15% similarity level; these clusters have been superimposed on the MDS Ordination (Groups A to G, Figure 27) and indicate that there is good agreement between the two techniques. Of the six groups formed Groups A, B, C and F are very small.

Group A contains three sites all located towards the south of the Faroe-Shetland Channel, just to the north of the Wyville-Thomson ridge, between approximately 800 and 1200 m water depth. Group B contains only one Site (NK1), which was located at 432 m water depth. This site contained a low number of Genera (21), together with a relatively high abundance of the echinoderm *Ophiacantha*. Group C contains two sites: FSC1200 and M1; FSC1200 was located at 1158 m water depth and M1 was located at 474 m water depth. Both these sites had a combination of low macrofaunal abundances together with low numbers of Genera; Site M1, in fact, had the lowest abundance of any of the sites (310 individuals m^{-2}), together with the lowest number of taxa (15 Genera). Group F contains only one site (FSC300); the macrofaunal assemblage at this site was unusual in that it was dominated by the polychaete *Aonides*.

The majority of the sites fall into two main groups: Groups D and G. Group G contains mainly stations less than 500m depth (4 stations deeper than this are contained within the group, and the deepest of these is 530m deep). Group D contains sites located in greater than 500 m water depth. There is therefore a clear distinction between the biological assemblages which occur above and below 500m water depth. Group E contains all the stations less than 650 m water depth sampled during the DTI 2002 survey and represent the most northerly shallow water stations sampled.

The relationship between the biotic data and a suite of environmental variables (Water Depth, Mean sediment grain size (i m), sediment mud content, TOC, TON, total hydrocarbons and Barium) was further examined using the "Bio-Env Procedure" in PRIMER. This procedure calculates the correlation (\tilde{n}_w) between the similarity matrix calculated for the biological data used in the MDS and different combinations of the environmental variables. This showed that the single abiotic variable which best groups the sites, in a manner consistent with the faunal patterns, is water depth ($\tilde{n}_w = 0.608$). This is in accordance with what is suggested by the ordination.

The best overall combination of environmental variables is water depth, C/N ratio and Barium concentration ($\bar{n}_w = 0.610$).

Latitudinal trends

Substantial variation in seabed type and associated fauna is apparent with depth, but there also appears to be evidence of along-slope variation within the survey area. The along-slope variation is most marked in respect of the relative development of an encrusting epifauna between 300 and 600 m water depth. The encrusting fauna, principally sponges, is well developed in the north and mid geographic regions but only poorly developed in the south, observations that have been supported by photographic studies. To further examine latitudinal trends in the entire data-set, the data-set was sub-divided into three groups according to the main depth zones identified on the West of Shetland Transect, i.e., 150 to 349 m (81 Stations), 350 to 699m (88 Stations) and 700 to 2315m (197 stations). These stations were correlated against the distance north from the most Southerly site (referred to as Latitude).

Among the stations located between 150 to 349 m, none of the statistical measures used to describe the assemblages, nor any of the physical/chemical parameters were significantly correlated with depth. The Latitude of the sampling stations was significantly correlated with depth, however, which probably reflects the large number of shallower stations (i.e., <200 m) towards the south. The following parameters were significantly correlated with Latitude: Mean sediment grain size (\bar{i} m) ($r_s = -0.81$, $p < 0.001$), sediment mud content ($r_s = 0.71$, $p < 0.001$), TOC ($r_s = -0.54$, $p < 0.001$), TON ($r_s = -0.25$, $p < 0.026$), total hydrocarbons ($r_s = -0.42$, $p < 0.001$), C/N ratio ($r_s = -0.64$, $p < 0.001$) and Barium concentration ($r_s = 0.26$, $p < 0.038$). As none of these were significantly correlated to depth, they can be said to represent latitudinal trends.

Within the 350 to 699m depth zone, Depth is significantly correlated to Latitude ($r_s = 0.23$, $p < 0.034$), Abundance ($r_s = 0.29$, $p < 0.006$), Number of Genera ($r_s = -0.28$, $p < 0.008$), Margalef's Species Richness ($r_s = -0.38$, $p < 0.001$), Pielou's Evenness ($r_s = -0.28$, $p < 0.008$), Fisher's Index ($r_s = -0.50$, $p < 0.001$), Shannon-Weiner diversity index ($r_s = -0.36$, $p < 0.001$), Simpson's Index ($r_s = -0.31$, $p < 0.003$), $ES_{(30)}$ ($r_s = -0.40$, $p < 0.001$), Mean sediment grain size (\bar{i} m) ($r_s = -0.32$, $p < 0.032$), sediment mud content ($r_s = 0.40$, $p < 0.003$), TOC ($r_s = 0.25$, $p < 0.017$), Total Hydrocarbons ($r_s = 0.68$, $p < 0.002$) and Barium concentration ($r_s = 0.64$, $p < 0.001$). The following were also correlated with Latitude: Fisher's Index ($r_s = -0.27$, $p < 0.008$), Simpson's Index ($r_s = -0.21$, $p < 0.046$), $ES_{(30)}$ ($r_s = -0.21$, $p < 0.044$), Mean sediment grain size (\bar{i} m) ($r_s = -0.35$, $p < 0.016$), sediment mud content ($r_s = 0.44$, $p < 0.001$), TOC ($r_s = -0.26$, $p < 0.012$), total hydrocarbons ($r_s = 0.58$, $p < 0.014$) and Barium concentration ($r_s = 0.36$, $p < 0.002$). It is impossible to separate latitudinal and depth trends.

Within the deepest depth zone, 700 to 2315 m, Depth is again significantly correlated to Latitude ($r_s = 0.27$, $p < 0.001$), number of individuals m^{-2} ($r_s = -0.25$, $p < 0.001$), number of genera ($r_s = -0.33$, $p < 0.001$), Margalef's species richness ($r_s = -0.34$, $p < 0.001$), Pielou's evenness ($r_s = -0.15$, $p < 0.030$), Fisher's index ($r_s = -0.31$, $p < 0.001$), Shannon-Weiner diversity index ($r_s = -0.39$, $p < 0.001$), Simpson's index ($r_s = -0.30$, $p < 0.001$), $ES_{(30)}$ ($r_s = -0.34$, $p < 0.001$), biomass ($r_s = -0.20$, $p < 0.012$), mean sediment grain size (\bar{i} m) ($r_s = -0.63$, $p < 0.001$),

sediment mud content ($r_s = 0.62$, $p < 0.001$), TOC ($r_s = 0.46$, $p < 0.001$), TON ($r_s = 0.46$, $p < 0.001$), C/N ratio ($r_s = -0.21$, $p < 0.021$), total hydrocarbons ($r_s = -0.28$, $p < 0.001$) and Barium concentration ($r_s = -0.28$, $p < 0.001$). Latitude is also correlated with Margalef's species richness ($r_s = -0.27$, $p < 0.001$), Pielou's evenness ($r_s = -0.30$, $p < 0.001$), Fisher's index ($r_s = -0.33$, $p < 0.001$), Shannon-Weiner diversity index ($r_s = -0.38$, $p < 0.001$), Simpson's index ($r_s = -0.34$, $p < 0.001$), $ES_{(30)}$ ($r_s = -0.40$, $p < 0.001$), mean sediment grain size (\hat{m}) ($r_s = -0.70$, $p < 0.001$), sediment mud content ($r_s = 0.75$, $p < 0.001$), TON ($r_s = 0.36$, $p < 0.001$), TOC ($r_s = 0.17$, $p < 0.015$), Total Hydrocarbons ($r_s = 0.59$, $p < 0.001$), C/N ratio ($r_s = -0.44$, $p < 0.001$) and Barium concentration ($r_s = 0.57$, $p < 0.001$). Macrofaunal number of species and number of genera are therefore significantly correlated with increasing depth within this zone, but not with Latitude.

5 Discussion

5.1 The SEA4 Surveys

A key element in the surveys was the use of sidescan sonar (and swath bathymetric) mapping of the seabed. There was a two-way relationship between the mapping and the direct investigation (sampling and photography) phases of the survey. The direct investigations provide ground-truth for the sidescan sonar and the sidescan sonar provided both guidance to the sampling programme and additional input to the interpretation of the resultant sample data. Many of the major seabed fabrics identified by sidescan sonar were largely bathymetrically constrained such that they fit quite naturally to a bathymetrically defined sampling programme.

The contribution of the joint use of sidescan sonar and seabed photography is well demonstrated in the zone of iceberg ploughmarks west of Shetland. Sidescan sonar establishes the extent of this zone and seabed photography indicates that the iceberg ploughmarks frequently have expression at the seabed. Seabed photography further indicated that there are biological responses to this local variation in the seabed. This variation does not, however, appear to be detected by the conventional analysis of macrobenthos by remote sampling. The use of macrobenthos as a routine tool in environmental monitoring is based on the preponderance of sedimentary habitats in the marine environment. When assessing outer continental shelf and upper slope areas west of Shetland, and elsewhere on the UK Atlantic Margin influenced by the last glaciation, it is important to note that macrobenthos sampling will self select for areas of open sediment and consequently produce a somewhat biased picture of the seabed in these areas. In these areas, where gravel pavements and major accumulations of glacial erratics may be frequently encountered, the additional use of seabed photography for both general reconnaissance and for biological assessment is recommended.

Throughout the surveys the choice of sampling device and, in relation to the macrobenthos, the choice of sample size and sieve mesh were based on a mixture of best practice and practical necessity. The work of Bett et al. (1994) has shown that hydraulically damped multiple corers are likely to generate better quantitative samples than box corers (or grabs). This difference relates principally to the down wash generated by the bow wave of box corers that may 'blow away' superficial sediments and fauna. The most obvious demonstration of this effect is seen in relation to the recovery of phytodetritus with seabed samples. Phytodetritus, the degraded remains of

surface ocean plankton blooms, may be present on the deep seabed as an easily re-suspended layer on the sediment surface. When present, phytodetritus is regularly recovered in multiple corer samples but almost never in box corer samples, as proved to be the case for example during the 1998 field work (Bett, 1999). Reliable, quantitative, recovery of the surface sediment layer may be particularly significant in determining an accurate baseline for potential environmental contaminants.

Although hydraulically damped multiple corers, such as the Megacorer employed during this survey, offer improved sampling characteristics over box corers they nevertheless have other limitations. In the present survey, the Megacorer was not particularly effective at depths less than 500 m as a result of both the increasing frequency of rocks and stones on the seabed and the limited thickness of surface sediments. The box corer succumbed to similar problems at depths less than 300 m, leaving only the Day grab as an effective sampler for the shelf and shelf edge in the west of Shetland region. One unusual observation on sampler performance was the near-inability of the box corer to sample in the contourite sands where the Megacorer was nevertheless effective. Testing for between gear bias in survey parameters has revealed no differences between Day grab and box corer. However, macrobenthos abundance and biomass appear to vary significantly between box corer and Megacorer samples, the box corer producing lower estimates. These quantitative differences are appreciable, with abundance approximately 40 % higher in Megacorer samples, a value similar to that determined by Bett et al. (1994) in a comparison of meiobenthos abundances from box corer and multiple corer samples. This was taken into account with the samples from the West of Shetland Transect, where a correction factor was added to both abundance and biomass values in order to make the results more comparable (see above).

A second practical difference between box corer and Megacorer samples relates to physical sample size, being maximally 0.250 and 0.094 m² respectively. Deep-sea studies of the macrobenthos most commonly employ box corers and frequently use the full sample size, although the use of the 'vegematic' modification (Jumars, 1975) giving a sample size of 0.09 m², is also common. Shallow water studies have typically employ grab samplers, with a sample size of 0.1 m². The principal motive in using a physically larger sample size in the deep-sea relates to the expectation of reduced faunal density at greater depths. Highly diverse assemblages with low densities may appear to have low diversities if insufficient replication is carried out; this may potentially explain the decrease in diversity with increased water depth observed within the SEA4 region. Twelve individual samples were obtained from one station on the floor of the Faroe-Shetland Channel during the DTI 2000 Survey (FSC 9; 55447#2 to 55447#15). For the purpose of the analyses presented here, the results of these samples were pooled, and this site did not have a higher diversity than others within the area, indicating that the observed decrease in diversity with increased water depth is an accurate observation, and not a result of insufficient sampling.

A further practical difference in the approach of deep-sea and shallow-water macrobenthos studies is the choice of sieve mesh size. Within these two environments workers tend to use a range of sieve meshes. A previous attempt to standardise deep-sea studies failed to reach agreement (Benthos Method Workshop, Copenhagen, 1991) and the more recently published criteria for the description of deep-sea benthic communities (SCOR Working Group 76, 1994), indicating the use of a 0.5 mm mesh for the macrobenthos, is not universally accepted. The principal motive for the suggested use of finer sieve mesh sizes in the deep-sea is the expectation

that deep-sea macrobenthos are smaller than their shallow-water counterparts. Little or no work has been undertaken to formally establish this supposed difference in typical body size. The expectation of smaller body size in the deep sea stems largely from observations that the relationships of density and biomass with depth have different slopes, with biomass declining more rapidly than density (Rowe, 1971; Rowe and Menzel, 1971). This is taken to indicate that body size declines with depth, but may simply indicate the general truism that large animals are rare. Within the SEA4 survey area neither macrofaunal density nor biomass are significantly correlated with depth.

5.2 The hydrographic regime

The hydrography of the Faroe-Shetland Channel (FSC) has been the subject of scientific study for over 100 years, making it one of the most intensively studied oceanic areas in the world (Hansen, 1985). That it is still the subject of detailed studies (e.g. Turrell et al., 1999) is a measure of both its complexity and its importance. It appears that the hydrography, particularly bottom-water temperature, is the key to understanding the large-scale distribution of the fauna in the FSC. While absolute temperature is undoubtedly a very significant environmental variable, the variation in temperature range is perhaps of greatest interest. Westerberg (1990) has mapped temperature variations throughout much of the FSC. Within the west of Shetland survey area, Westerberg (1990) indicates the 0 °C isotherm ranging from 400-800 m and the 7 °C isotherm ranging from 300-500 m, and is in close agreement with the TOBI data. Westerberg (1990) also assessed temperature range in terms of temperature variance (standard deviation), indicating maximal variance at depths between 500 and 600 m west of Shetland. This is well reflected by the extreme temperature range (10 C°) encountered by the current meter deployed at 550 m west of Shetland.

Some of the variation in bottom water temperatures encountered at intermediate depths in the Faroe-Shetland Channel is probably related to the passage of internal waves. Sherwin (1991) suggests that internal waves are generated by tidal flows across the Wyville-Thomson Ridge, and has recorded a 40 m oscillation in the 2 °C isotherm in a 12 hour period. Sherwin further suggests that the internal waves so generated propagate up (to the northeast) the channel expending their energy through mixing along the edges of the channel. Unique observations of a phenomenon known as the *Nolter Maelstrom*, made by US Navy submersible operators working at around 500 m on the West Shetland Slope close to the Wyville-Thomson Ridge are also related in Sherwin (1991). These reports describe a regular (tidal) occurrence of sand/mud swirls at the seabed followed by a rapid increase in current speeds to 2.5 knots (130 cms⁻¹) and a sharp drop in water temperature. Sherwin (1991) further records that the *Maelstrom* effect propagates to the northeast, parallel to the bathymetric contours. Such an effect, influencing bottom water temperatures and near-bottom current speeds, would clearly have a substantial impact on the ecology of the West Shetland Slope.

5.3 The sedimentary environment

The sedimentary environment of the SEA4 Region is described by Masson (2001) based on a joint assessment of the TOBI sidescan sonar coverage and the seabed samples recovered as part of the present survey. This indicates

that the key features of the present day sedimentary environment are i) low sediment input and deposition rates, and ii) reworking of superficial sediments by bottom currents. Upper slope (<500 m) sediments are influenced by the northeast directed flow of the slope current, where flows of in excess of 75 cms⁻¹ may occur. The presence of the rippled contourite sand sheet at the base of the slope suggests peak bottom water flows of around 30-40 cms⁻¹ presumably directed to the southwest (though note that seabed photography in this area shows indications of both northeast and southwest flows, see Masson, 2001). The presence of substantial quantities of gravel at the seabed on the lower slope and floor of the Faroe-Shetland Channel appears to indicate low sedimentation rates rather than erosion by strong bottom currents, i.e. the gravel lies in / on relatively fine grained sediments (sandy muds / muddy sands). Both north and south of the Wyville-Thomson Ridge, silt and clay content tends to increase markedly below *c.* 1,000 m. In the Faroe-Shetland Channel this depth coincides with the transition from the slope setting to the basin floor (Bett, 2001).

5.4 Macrofaunal abundance and biomass

In general, the abundance and biomass of deep-sea macrobenthos may be expected to decline with water depth, reflecting a decline in the availability of food to the benthos (Vinogradova 1962; Rowe and Menzel, 1971; Rowe 1983; Gage and Tyler, 1991). Variations have been previously found in the deep sea (e.g. Jumars and Gallagher, 1982; Rowe, 1983; Schaff et al., 1992; DeMaster et al., 1994) and this pattern has not been observed for the assemblages from the SEA4 area (Figures 2, 3, 13, 14 and 15). Along the West of Shetland Transect and in the entire data set, macrofaunal abundances increase with depth. This is not matched by a decrease in macrofaunal biomass, which may be expected if the deeper communities contained higher abundances of smaller individuals; there was no significant correlation between biomass and depth within the entire data set, while along the Transect biomass achieved maximum values between 350 and 450 m depth. Notably, the highest biomass values within the entire data set were also observed at around these depths, although there was substantial variability in the results.

The use of various sieve mesh sizes in the determination of deep-sea macrobenthos complicates the wider comparison of the abundance and biomass values for the SEA4 Region. Romero-Wetzel and Gerlach (1991) studied the macrobenthos of the Vøring Plateau (1200 to 1500 m, Norwegian Sea) using box core samples sieved on a 0.5 mm mesh. At this deep, cold-water location these authors recorded mean abundance and biomass values of 57 individuals 0.1 m⁻² and 0.4 g 0.1 m⁻², appreciably lower than those observed at corresponding depths in the present survey. Gage (1977; 1979) provides data for the macrobenthos of the Rockall Trough from box core samples sieved on a 0.42 mm mesh that may be considered broadly comparable with results presented here from a 0.5 mm mesh. Despite similarities in abundance, the biomass of the Rockall Trough macrobenthos appears to be appreciably lower than that recorded in the SEA4 region.

Peaks and troughs in abundance and biomass may be related to similar patterns observed in the environmental variables, e.g. along the Transect. Generally low faunal abundance corresponds with the highest temperature range, the exception being crustaceans where it appears they peak at a similar depth to maximum temperature range. Mollusc and echinoderm peaks in 2000 corresponded to peaks in total organic carbon. In the 1996 survey,

Bett (2000) suggests that at intermediate depths, peaks in macrofaunal abundance coincide with organically enriched sediment. Russell et al. (1999) found that sediments collected at intermediate depths along the West of Shetland Transect were enriched with labile organic matter compared to shallower and deeper stations.

Given their intimate contact with sediments it is not surprising that the ecology of the benthic fauna is frequently, strongly controlled by variations in sediment type. In some deep-sea settings, for example abyssal plains, the variation in sediment type may be so minimal as to be of no practical consequence. This, however, is not the case in the SEA4 region where sediment type ranges from coarse sands on the shelf to fine sandy muds on the Faroe-Shetland Channel floor. Despite this wide variation in sediment type, the unique hydrographic conditions of the Faroe-Shetland Channel appear to be the dominant influence on the ecology of the area.

5.5 Diversity

In contrast to abundance and biomass, macrobenthic species diversity may be expected to exhibit a parabolic, rather than monotonic, relationship with depth. Although not a universal finding, several authors have indicated a diversity maximum at intermediate (bathyal) depths (e.g. Rex, 1981; Maciolek et al., 1987). Paterson and Lambshead (1995) studied the diversity of macrobenthic polychaetes on the Hebridean margin (Rockall Trough) and observed a parabolic relationship with depth, where diversity peaked at the base of the slope (1800 m) before declining in the deeper Rockall Basin. The processes potentially governing this parabolic relationship are frequently referred to Huston's (1979) dynamic equilibrium model of species diversity by invoking varying rates of competition and disturbance with depth (e.g. Gage and Tyler, 1991).

For all diversity indices calculated, along the West of Shetland Transect in each year a peak was observed at intermediate depths (c. 400 to 550 m). A similar pattern is seen when using rarefaction, although the peak in diversity using this technique is seen at the 350 m station in all years. In general, diversity values were higher at stations situated at shallow-intermediate depths in comparison to those at greater depths. Similar results have also been found from the 1996 survey on the West Shetland Slope with a peak in diversity at a depth of approximately 400 m (Bett, 2000). However, the depth of the maximum peak is much shallower in comparison to other regions. Macrofaunal diversity in the Northwest and some regions of the Northeast Atlantic has been found to exhibit a parabolic type distribution with depth (e.g. Etter and Grassle, 1992; Paterson and Lambshead, 1995; Rex, 1981; 1983; Rex et al., 1993). These observations contrast with those for the entire dataset, where there was a decrease in diversity with water depth. Similarly, evenness remains relatively constant at all depths along the Transect, the exception being the 800 m station where there is a sharp drop in evenness and a corresponding increase in dominance (Figure 4), whereas within the entire data set there is a significant decrease in evenness with water depth. These differences may be as a result of the different levels of taxonomic resolution in the two studies; i.e., there may be a decrease in higher-level diversity with increasing depth, together with a mid-slope maxima in diversity at the species level.

When Grassle and Maciolek (1992) published the diversity results from an extensive and detailed survey of the macrobenthos from the New Jersey / Delaware slope, numerous authors were stimulated to enter in to a debate

on species richness in the deep sea and the relative diversity of deep- and shallow-water marine environments (e.g. Gage and May, 1993; Gray, 1994; May, 1992; 1994; Poore and Wilson, 1993). Grassle and Maciolek's (1992) data appeared to add weight to a long held expectation that the deep sea, particularly the deeper bathyal areas, was a particularly species rich environment (e.g. Hessler and Sanders, 1967). This view was not held by Poore and Wilson (1993) or Gray (1994.), who pointed to the occurrence of equally high species richness in shallow-water settings. The results from the present study strongly indicate that, at the Generic level, there is a continuous decrease in diversity with water depth in the SEA4 region.

Several environmental variables correlated significantly with the diversity maxima observed at 400 to 550 m along the transect, with habitat temperature range correlating most strongly with the suite of diversity indices. Although there may be a hydrographic control of macrobenthic diversity within the SEA4 region, other factors should also be considered. A biological barrier may be present in the Channel due to the thermocline preventing the dispersion of larvae into other water masses; i.e. larvae may be transported horizontally within a water mass but not vertically into another. As a result, over time the faunas may have evolved in relative isolation into two groups, warm and cold.

Between 300 and 600 m water depth well-developed epifaunal communities exist which may increase habitat complexity (e.g., Barthel, 1992; Bett and Rice, 1992; Klitgaard, 1995). The presence of epifaunal communities may increase the diversity of the macrobenthos through an increase in the availability of microhabitats. It is also worth considering the 300-600 m depth band as an ecotone where two "communities" meet (e.g. Odum, 1971), resulting in an increased diversity through the presence of species from both of the bounding communities and, potentially, the presence of 'specialist' eurythermic species restricted to the ecotone itself. As generally applied to the deep-sea setting, biological zonation is not intended to infer depth bands of homogeneous fauna with major changes only occurring at the boundary between zones. Instead, continuous variation with depth is expected, with regions of increased rates of change marking the position of zone boundaries (Carney et al., 1983). As depth increases, successive replacement of species is generally expected to occur in deep-sea communities. Regions that have a high rate of species replacement are thought to mark zone boundaries (Carney et al. 1983). Changes in environmental variables with depth e.g. temperature as well as the tolerance of species to changes in the environment will influence the distribution of the species.

The result of the present study contrast with those of Gage et al. (2000) who observed higher dominance and lower evenness values at shallower stations along the Hebridean Slope. The high levels of dominance were thought to be as a result of higher hydrodynamic levels, as opposed to along the West of Shetland Transect, where intermediate depths were found to have higher levels of hydrodynamic disturbance. Along the Transect, the unstable physical environment may promote increased species diversity. High species diversity appears to coincide with the greatest change in water temperature and more coarse sediment grain size compared to the deeper stations where there is comparatively finer sediment and little change in water temperature.

The pattern of a decrease in generic diversity with water depth, may be confused by the topographical complexity of the slope region, so that different patterns may be observed when different parts of the slope are

examined. In other areas, depth has been found not to be the main variable influencing species diversity; Etter and Grassle (1992), for example, found that sediment diversity showed a significant correlation with species diversity as opposed to depth.

5.6 Faunal Composition

Within the SEA4 region, polychaetes were the dominant benthic taxon, comprising over 40 % of the total number of individuals collected at each station. As the overall trend in polychaete distribution with depth is similar to that observed in the total macrofaunal assemblage, polychaetes have been used as a proxy for determining macrofaunal community patterns (Glover et al., 2001). Along the West of Shetland Transect, polychaete biomass was more variable than its abundance, accounting for between 1 % and 85 % of the total biomass recorded. Between 350 m and 500 m, polychaete biomass accounted for <20 % of the total biomass, whereas at stations with depths >550 m it generally accounted for more than 40 % of the total biomass. This is similar to the results found on the West Shetland Slope where 20 % - 40 % of the total biomass on the upper slope and shelf was attributed to polychaetes, whereas polychaetes accounted for between 60 % and 80 % of the total biomass on the lower slope and Channel floor (Bett, 2000). In Arctic studies undertaken by Paul and Menzies (1974), polychaetes contributed 42 % of the total number of individuals yet only 5 % of the total biomass.

Analysis of the large-scale distribution of the entire macrobenthic database revealed two major faunal assemblages within the SEA4 region; these were apparent through cluster analyses and ordination. The distribution of the fauna appears to strongly reflect the distribution of water masses in the Faroe-Shetland Channel, with an upper (shallow) warm layer, a lower (deep) cold layer. This was also observed in the distribution of the fauna along the West of Shetland Transect, where an intermediate assemblage was also observed. Within all three of these temperature / water mass zones, there is nevertheless a strong bathymetric gradient in the distribution of the fauna. Depth, as pressure, may be significant in itself, but clearly there are a number of depth-correlated parameters (i.e. sediment grain and organic content) that may well exert a substantial parallel influence on the distribution of the fauna.

Hydrographic control of the distribution of the deep-sea fauna has been suggested by a number of authors and is thought to control some of the major bathymetric zones, e.g. the bathyal to abyssal transition (Menzies et al., 1973; Gage and Tyler, 1991). For example, in studying the bathymetric distribution of the megabenthos in the Rockall Trough, Gage (1986) suggests that major changes in the fauna at around 1,000 m depth correspond with the position of the permanent thermocline. The hydrographic regime of the Faroe-Shetland Channel is very different to that observed in the Rockall Trough. In the CCA plots produced from the West of Shetland Transect, the temperature eigenvectors were most closely associated with the shallower stations and the species that occur at these depths e.g. *Spiophanes* cf. *wigleyi* and *Glycera lapidum* complex. This indicates that they are more tolerant of varying water temperatures. The majority of the species at the deeper stations appear to lie on the possible inverse of temperature range, implying that they are unable to tolerate a wide range of temperatures. Deeper stations that have a low temperature range also appear to lie along this possible gradient, corroborating

the species results. A comparable hydrographic regime to that of the SEA4 area was encountered by Weissshappel and Svavarsson (1998) in a study of the diversity of benthic amphipods to the north of Iceland. In their study area, comparatively warm North Atlantic Water (c. 0 to 300 m) overlies subzero temperature Norwegian Sea Deep Water (c. >500 m) with an intervening layer of Arctic / Polar Water of intermediate temperature. Using CCA, the authors showed that water temperature appeared to be the main variable controlling the distribution of amphipods.

Species dominance

Numerically dominant species along the West of Shetland Transect 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. The differences in dominant species were most apparent in the warm water band between the three years. *Spiophanes* cf. *wigleyi* was dominant in both the warm and intermediate temperature bands whereas *Paramphinome jeffreysii* was dominated both the intermediate and cold temperature band. An interesting point occurs between the 700 to 900 m depth band where *P. jeffreysii* is the dominant species at both the 700 and 900 m stations, however, at 800 m the number of individuals decreased sharply in all three years and coincided with a sharp increase in the number of *Spiophanes kroyeri*. One reason why two, as opposed to three, temperature bands were recognised within the entire data set may be that key species which belong to the same genus, such as *Spiophanes* cf. *wigleyi* and *Spiophanes kroyeri*, have been grouped together, resulting in a loss of the more subtle distribution patterns.

There has been some discussion as to what type of feeding mode *P. jeffreysii* employs. In some studies it has been classified as a predator (Fauchald and Jumars, 1979), whereas Rosenberg (1995) suggests that *P. jeffreysii* is a sub-surface deposit feeder. *Paramphinome jeffreysii* has been recorded inhabiting the sediment to a depth of 10 cm (Josefson, 1981; Romero-Wetzel and Gerlach, 1991). This, in conjunction with studies undertaken by Rosenberg (1995) implies that this species of amphinomid is actually a sub-surface deposit feeder. It is possible that *P. jeffreysii* and *S. kroyeri* are then possibly competing for similar food sources. 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. Why *S. kroyeri* should be numerically dominant at the 800 m station remains unresolved. The results from 1996 corroborate this latter result (Bett, 2000).

5.7 Potential environmental impacts

Although essentially intended as a 'baseline' survey, the west of Shetland region has already been subject to a number of potential environmental impacts, most notably from the oil and fishing industries. The oil industry has been active in the west of Shetland area for some time. Of the extensive suite of metals analysed during the course of these studies, barium is potentially of the greatest interest as it may serve as a tracer of drilling discharges (Hartley, 1996). Both Barium and total hydrocarbon concentrations increase significantly with water depth (note that this is likely a response to increasing silt/clay content rather than an indication any form of contamination). Detailed analysis of the hydrocarbon constituents in these samples indicated the presence of

weathered low-toxicity oil-based drill mud (McDougall, 2000). The latter author reports that the hydrocarbons in sediments west of Shetland have a predominantly biogenic (background) signal, with a few instances of specific drilling related inputs and a widespread low level petroleum hydrocarbon contamination attributed mainly to shipping operations, predominantly (88 %) from fishing and merchant vessels. Although hydrocarbon contamination attributable to the oil industry appears to be the minority source in the west of Shetland area (McDougall, 2000), such contamination may well have an environmental impact on the benthic fauna, albeit localised.

Impacts of deep-sea trawling have been encountered at various locations within the SEA4 region (Bett, 2000). The majority of trawl marks have been observed on the upper slope (300 to 600 m) in the north and mid regions of the survey area, coincident with the area of best-developed epifaunal communities (Bett, 2001). The impact of trawling on deep-sea benthic communities on the Atlantic Margin is undoubtedly widespread, but its effects remain a matter of speculation. Trawling is likely to have a direct and largely lethal effect on the epifaunal megabenthos in a trawl's path. There are also likely to be direct and indirect effects on the infaunal macrobenthos in the trawl path. By reducing the epifauna, the macrobenthos may be indirectly affected through removal of habitat (e.g. sponges), the reduction of other biological interactions and the reduction of habitat heterogeneity generally. Direct impacts on the macrobenthos are also possible via the ploughing action of the trawl gear on the seafloor; observations of this type of seabed disturbance were made during the 1998 Survey. Roberts et al. (2000) found similar results in a survey on the continental slope off NW Scotland. Their results indicate that the physical impacts of deep-sea trawling to the seabed have been found at depths >1000 m. The effects of trawling on the deep-water benthos are still poorly understood, particularly in an area where the benthos may have a reduced rate of recovery. The description of the benthic environment presented here may, in part, already be influenced by the actions of deep-sea trawling.

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Table 6	Comparison of the percentage of polychaete species that are restricted to one of the three main temperature bands in 1996, 1998 and 2000.

Phylum		Environmental variable	r_s	p-value
<u>Polychaeta</u>	1996	Ba/Al	0.611	<0.02
	1998	Ba/Al	0.759	<0.002
	2000	Mean sediment grain size	0.754	<0.002
<u>Crustacea</u>	1996	Organic content	0.694	<0.01
	1998	Silt/clay	0.685	<0.01
	2000	Temperature range	0.636	<0.02
<u>Mollusca</u>	1996	Total organic carbon	0.674	<0.01
	1998	n/s	-	-
	2000	Mean sediment grain size	0.883	<0.001
<u>Echinodermata</u>	1996	Mean sediment grain size	0.819	<0.001
	1998	n/s	-	-
	2000	n/s	-	-

Table 1. Significant Spearman's rank correlation coefficient for phylum abundance versus environmental variables for 1996, 1998 and 2000; $n = 15$, $r_s = 0.521$.

Phylum		Environmental variable	r_s	p-value
<u>Polychaeta</u>	1996	Silt/clay	0.815	<0.001
	1998	Maximum temperature	0.760	<0.002
	2000	Total organic carbon	0.739	<0.005
<u>Crustacea</u>	1996	n/s	-	-
	1998	Temperature range	0.857	<0.001
	2000	Total hydrocarbons	0.657	<0.01
<u>Mollusca</u>	1996	Minimum temperature	0.537	<0.05
	1998	Ba/Al	-0.627	<0.02
	2000	n/s	-	-
<u>Echinodermata</u>	1996	Mean sediment grain size	-0.638	<0.01
	1998	Minimum temperature	0.552	<0.05
	2000	n/s	-	-

Table 2. Significant Spearman's rank correlation coefficient for individual phylum biomass versus environmental variables for 1996, 1998 and 2000; $n = 15$, $r_s = 0.521$.

	<i>Margalef – species richness</i>		<i>Shannon – species diversity</i>		<i>Pielou – species evenness</i>		<i>Simpson – species dominance</i>	
	Environmental variable	r_s	Environmental variable	r_s	Environmental variable	r_s	Environmental variable	r_s
1996	Temperature range	0.729	Temperature range	0.701	Organic content	-0.568	Temperature range Sed. grain size	0.589 -
1998	Maximum temperature	0.733	Temperature range	0.767	Temperature range	0.752	Sed. grain size	-0.707
2000	Temperature range	0.652	-	-	-	-	-	-

Table 3. Spearman's rank correlation of the different diversity indices versus environmental variables. Only the most significant correlation has been illustrated here; $n = 15$, $r_s = 0.521$

		<i>Axes</i>			
		1	2	3	4
CCA	<u>1996 – species</u>				
	Eigenvalues	0.82	0.51	0.45	0.34
	Species – env correl.	0.99	0.99	0.99	0.99
CCA	<u>1998 – species</u>				
	Eigenvalues	0.78	0.43	0.39	0.35
	Species – env correl.	0.99	0.97	0.97	0.96
CCA	<u>2000 – species</u>				
	Eigenvalues	0.78	0.41	0.36	0.26
	Species – env correl.	0.99	0.97	0.98	0.96

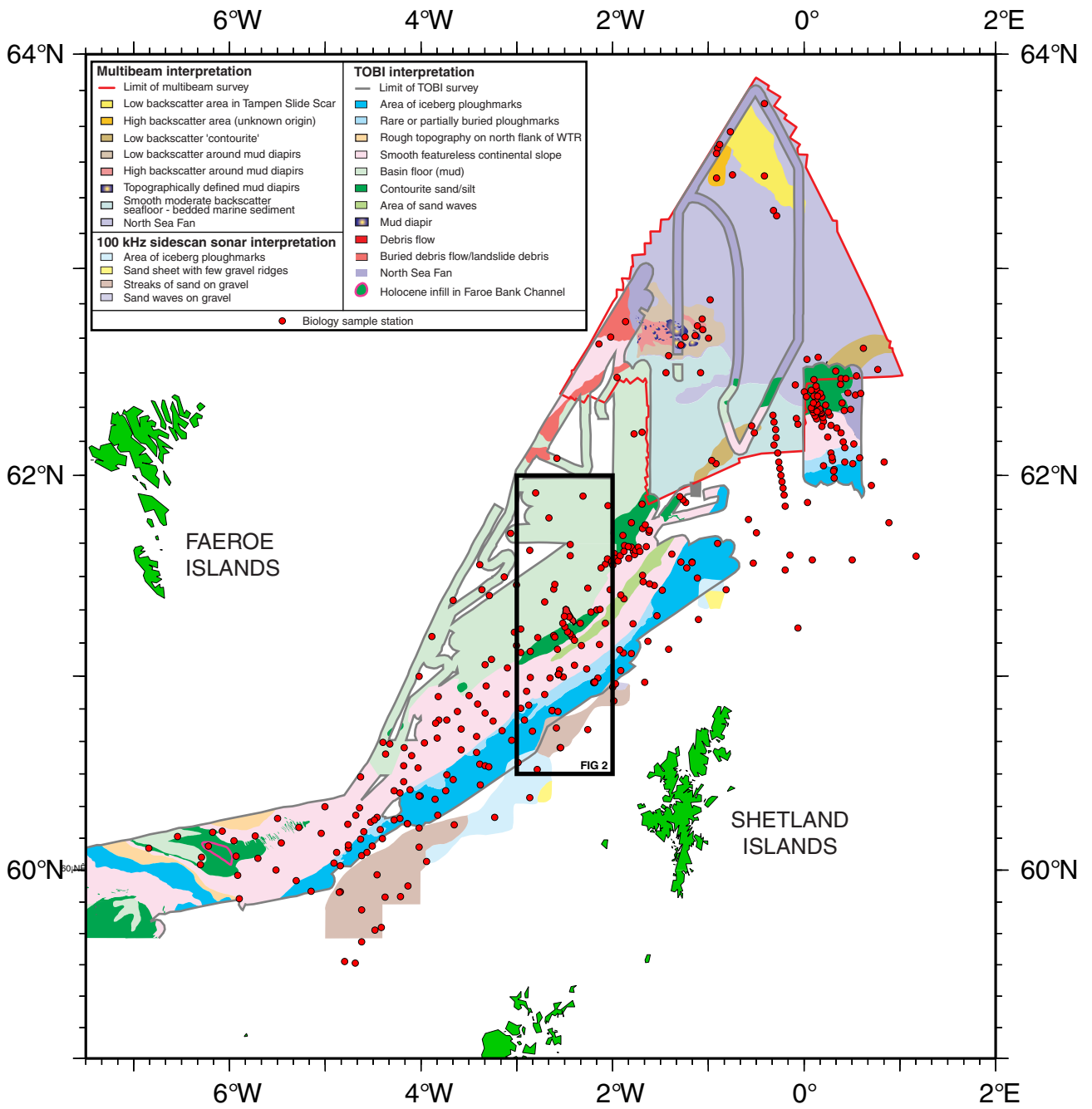
Table 4. Results of canonical correspondence analysis (CCA) for polychaete species and environmental variables in 1996, 1998 and 2000.

<i>Year</i>	<i>Unconstrained eigenvalue</i>	<i>Canonical eigenvalue</i>	<i>Variance of variable</i>	<i>Variable</i>
1996	4.35	2.85	0.80	Max
			0.43	Sed
			0.38	Min
1998	4.48	2.77	0.73	Max
			0.41	Range
			0.4	Org con.
2000	4.07	2.43	0.76	Max
			0.36	Min

Table 5. Results of the Monte Carlo permutation test based on forward selection with 999 unrestricted permutations analysing the influence of the environmental variables on polychaete species abundance. Variance of environmental variable accepted at the ≤ 0.05 level. (Min = minimum temperature, Max = maximum temperature, Range = temperature range, Sed = mean sediment grain size, Org = Organic content).

<i>Temperature band</i>	<i>1996 transect</i>	<i>1998 transect</i>	<i>2000 transect</i>
Warm	20.7 %	21.8 %	20.1 %
Intermediate	33.1 %	36.1 %	33.8 %
Cold	8.2 %	8.1 %	7.1 %

Table 6. Comparison of the percentage of species that are restricted to one of the three main temperature bands in 1996, 1998 and 2000.



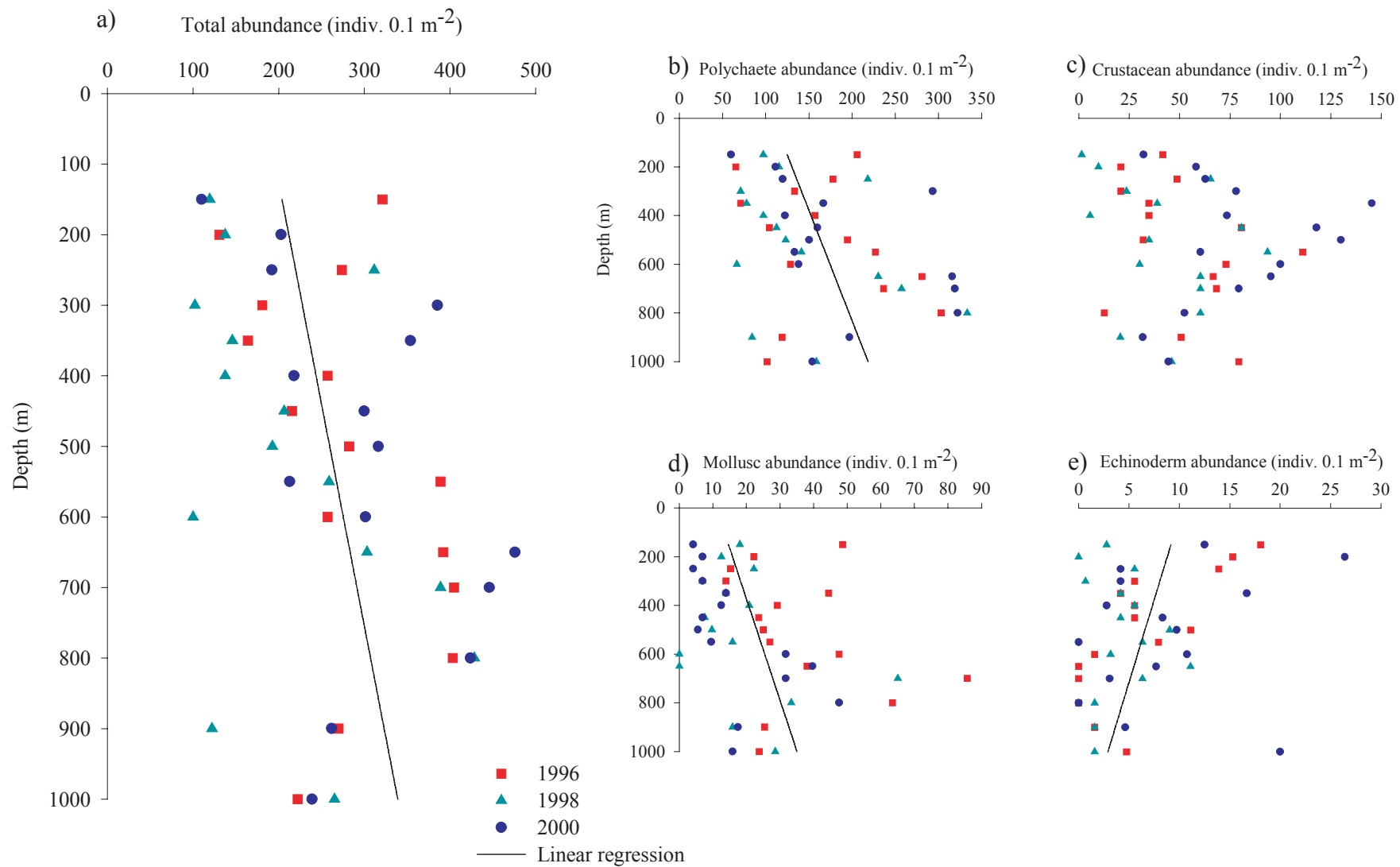


Figure 2. Macrobenthic abundance from the 15 stations situated along the transect in 1996, 1998 and 2000.

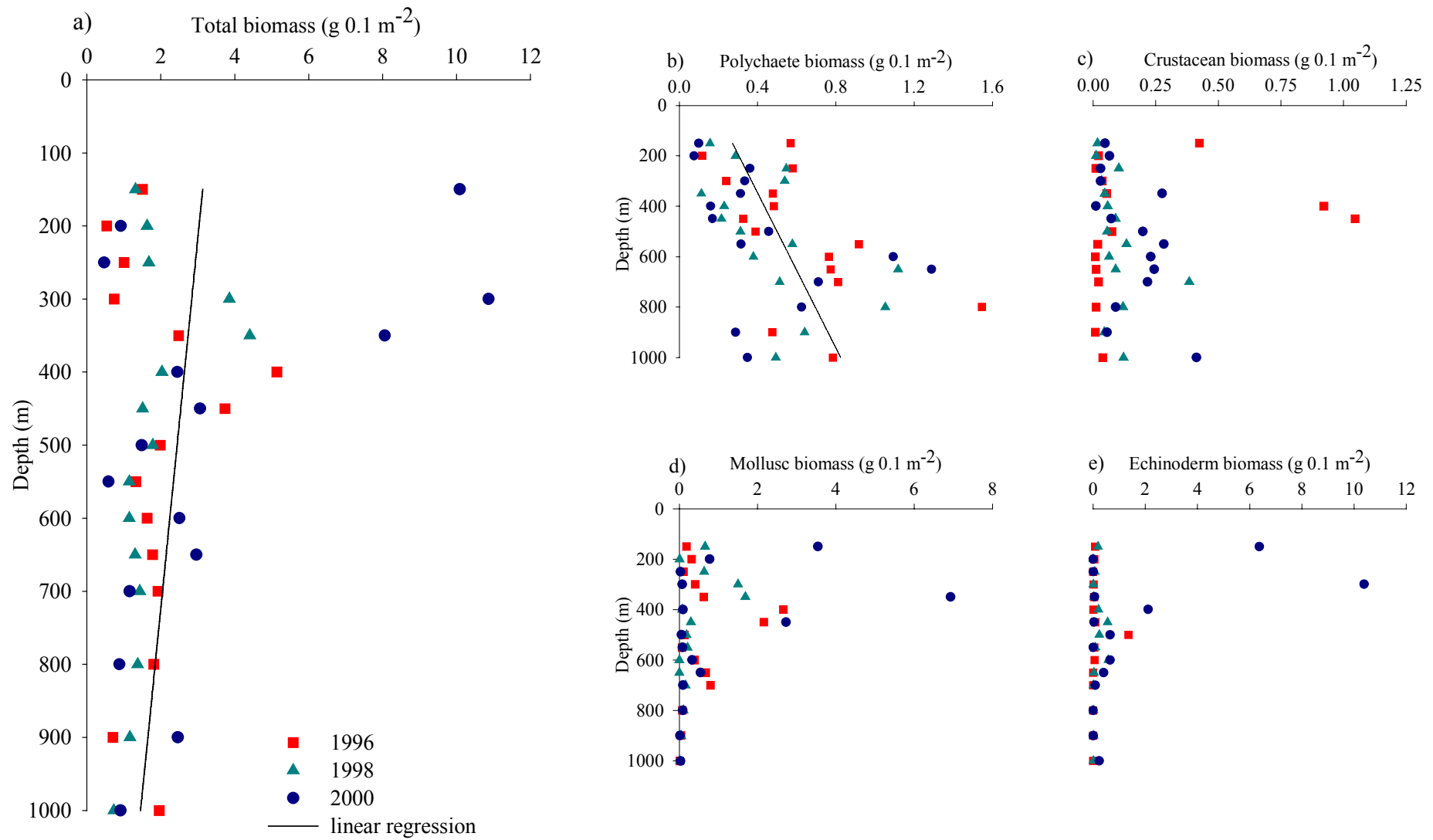


Figure 3. Macrobenthic biomass from the 15 stations situated along the transect in 1996, 1998 and 2000.

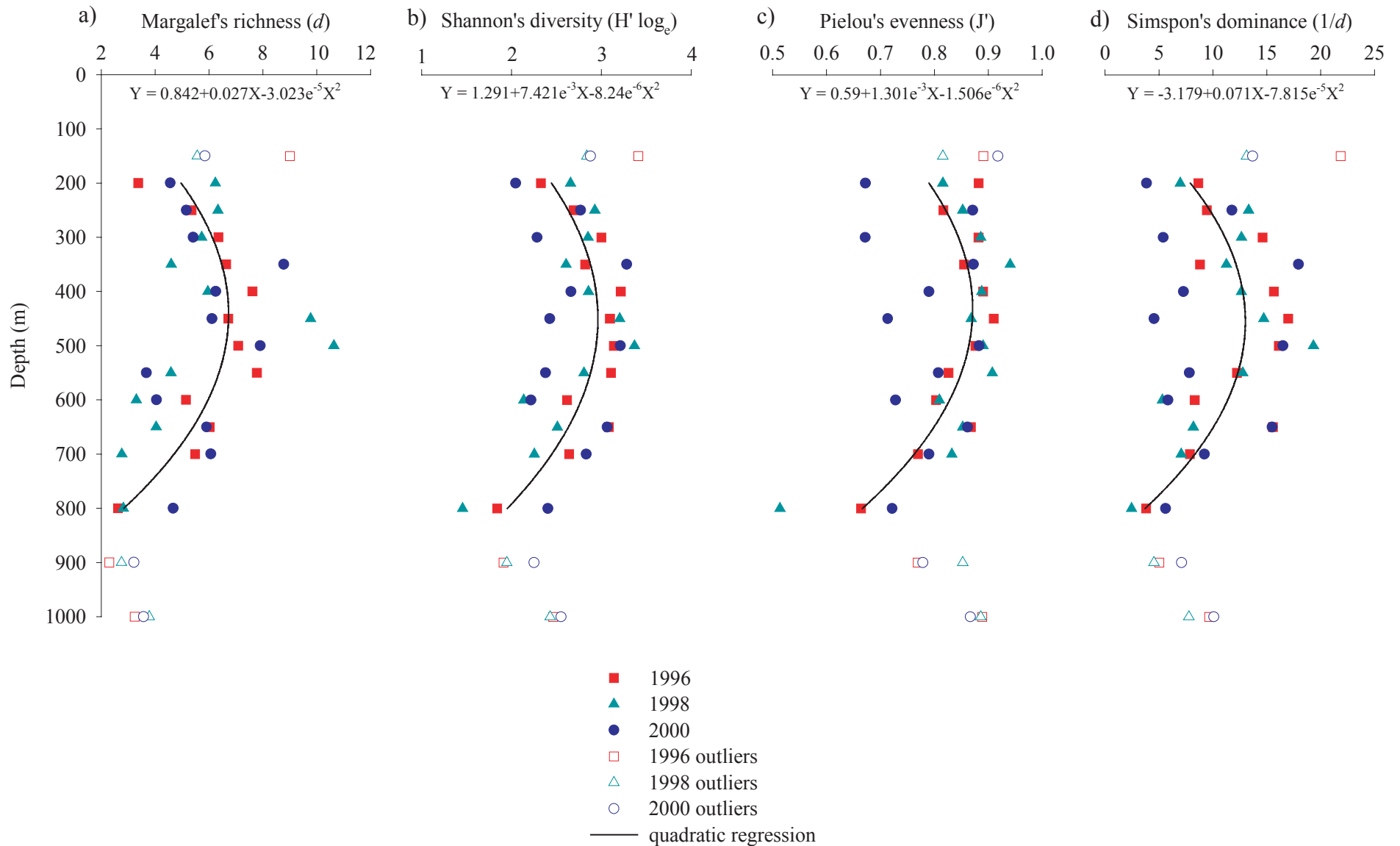


Figure 4. Comparison of changes in the suite of diversity indices used in 1996, 1998 and 2000. The open symbols represent stations that have been excluded from the regression analysis, shaded symbols have been used in the analyses.

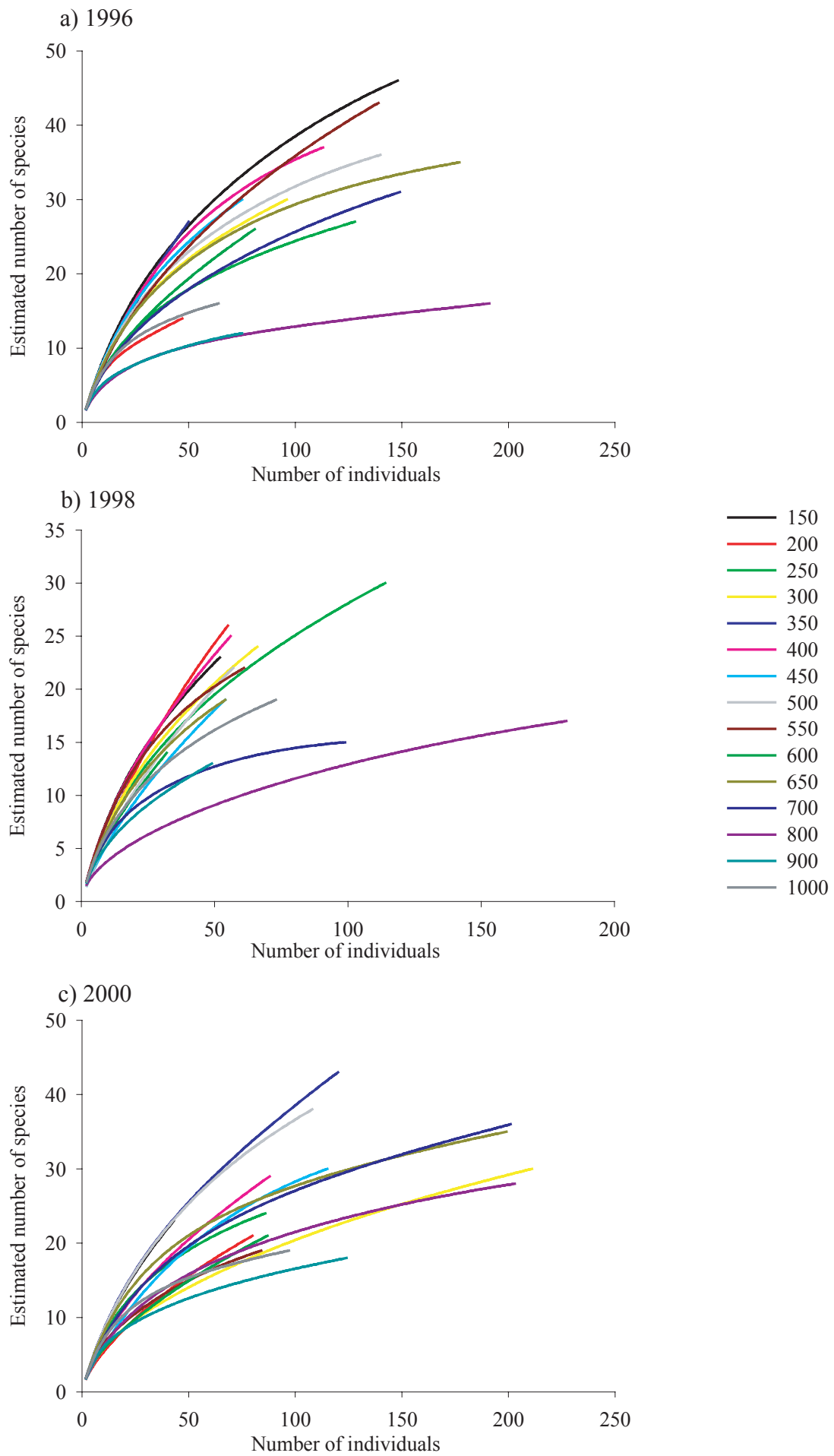


Figure 5. Rarefaction curves of the 15 sampling stations in 1996, 1998 and 2000.

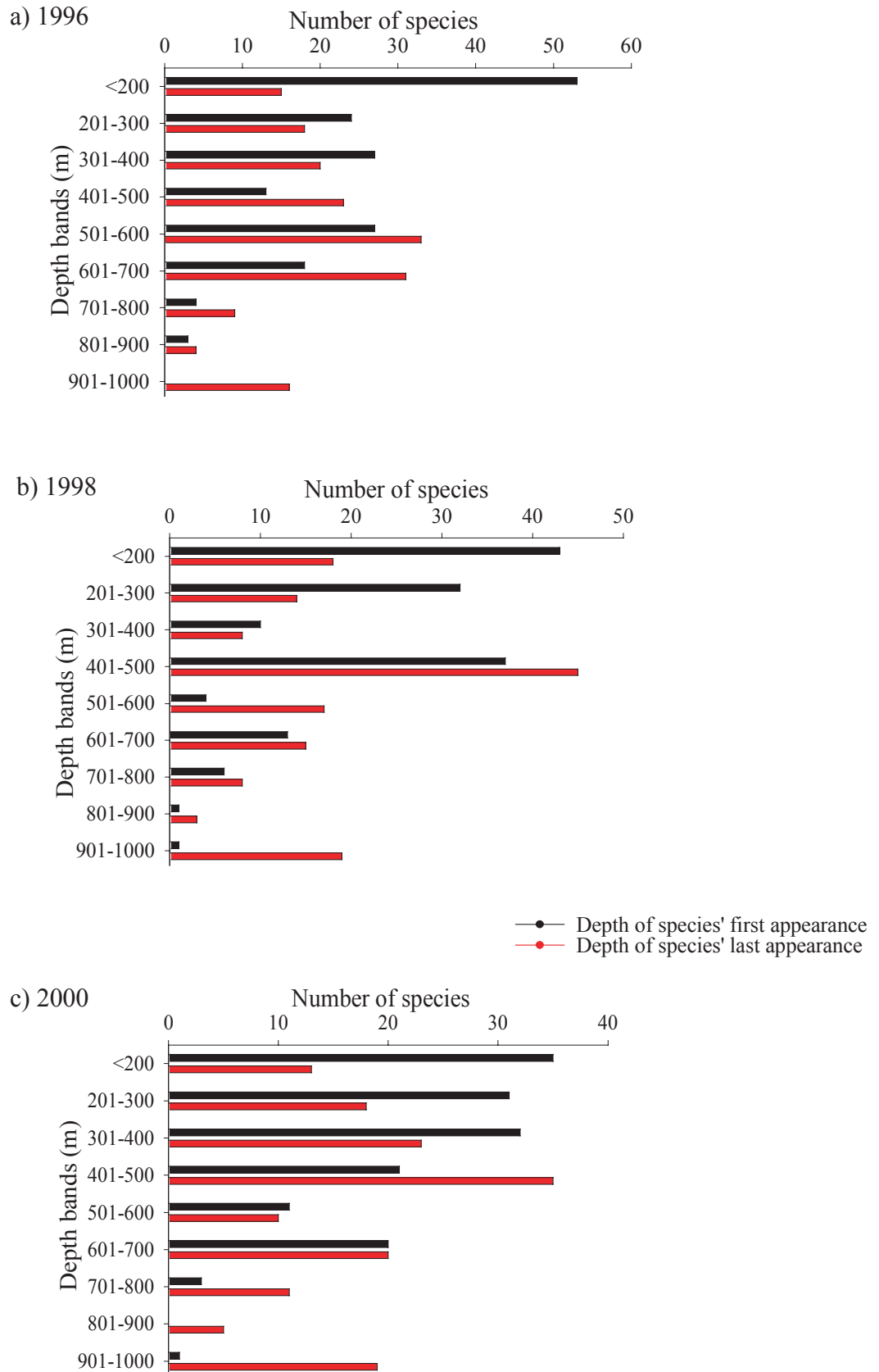


Figure 6. Polychaete species accumulation and loss, based upon the first and last appearance of the species with depth along the transect in 1996, 1998 and 2000.

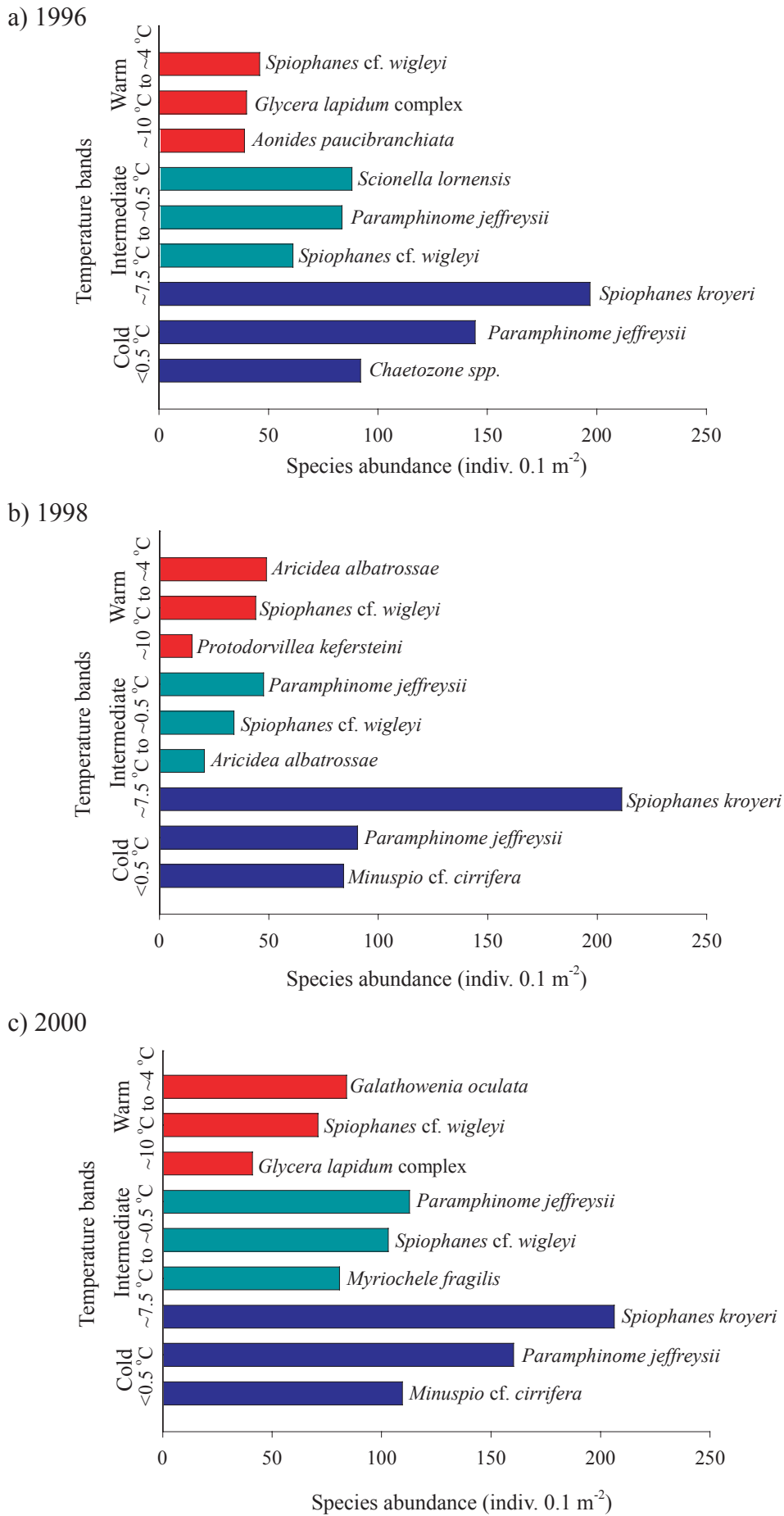


Figure 7. The three most abundant species found in each temperature band in 1996, 1998 and 2000. Warm = red; Intermediate = green; Cold = blue

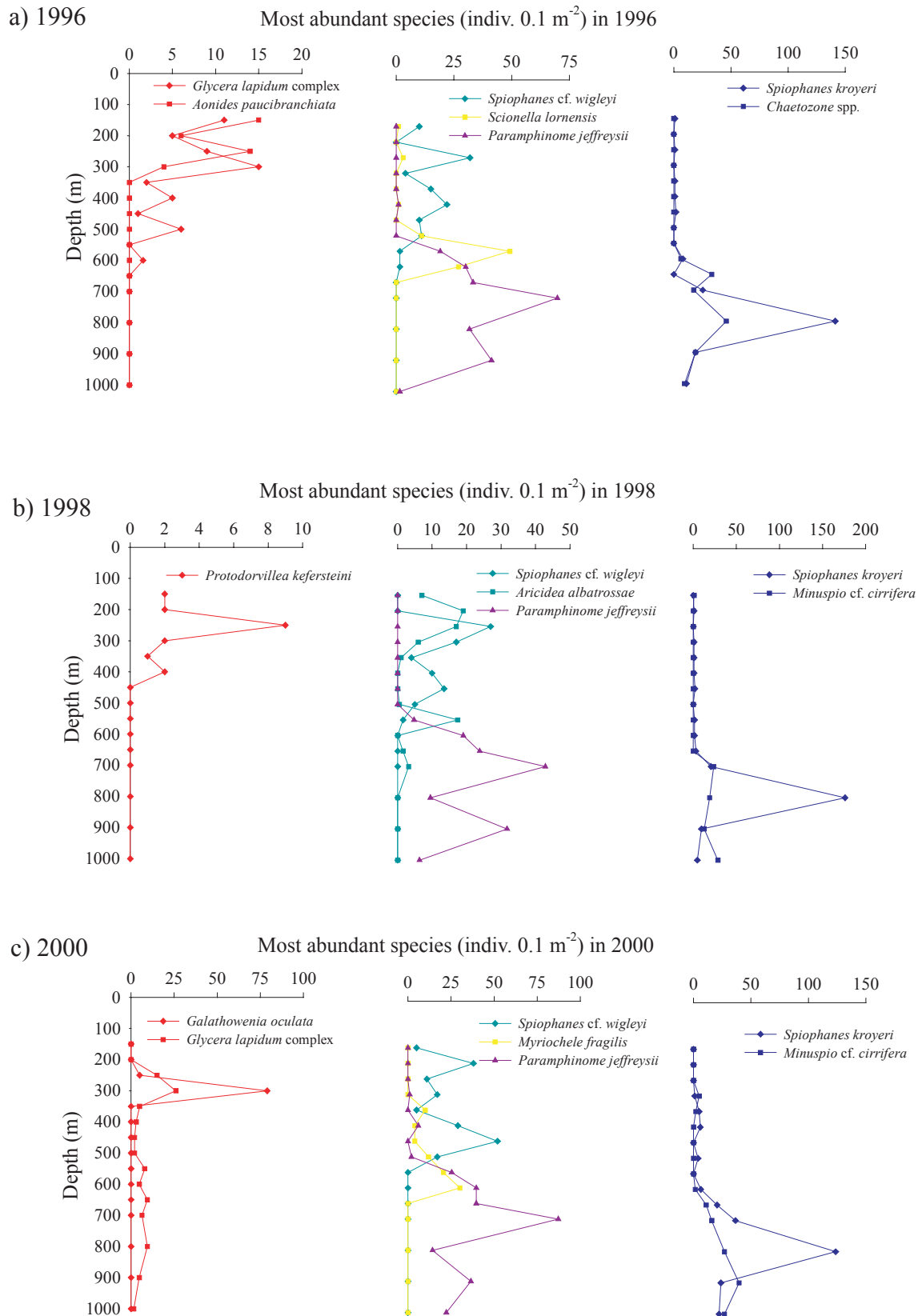


Figure 8 a-c. Distribution of the most abundant polychaete species found in each temperature band. Species that are considered transitional species have been plotted on the intermediate temperature graph.

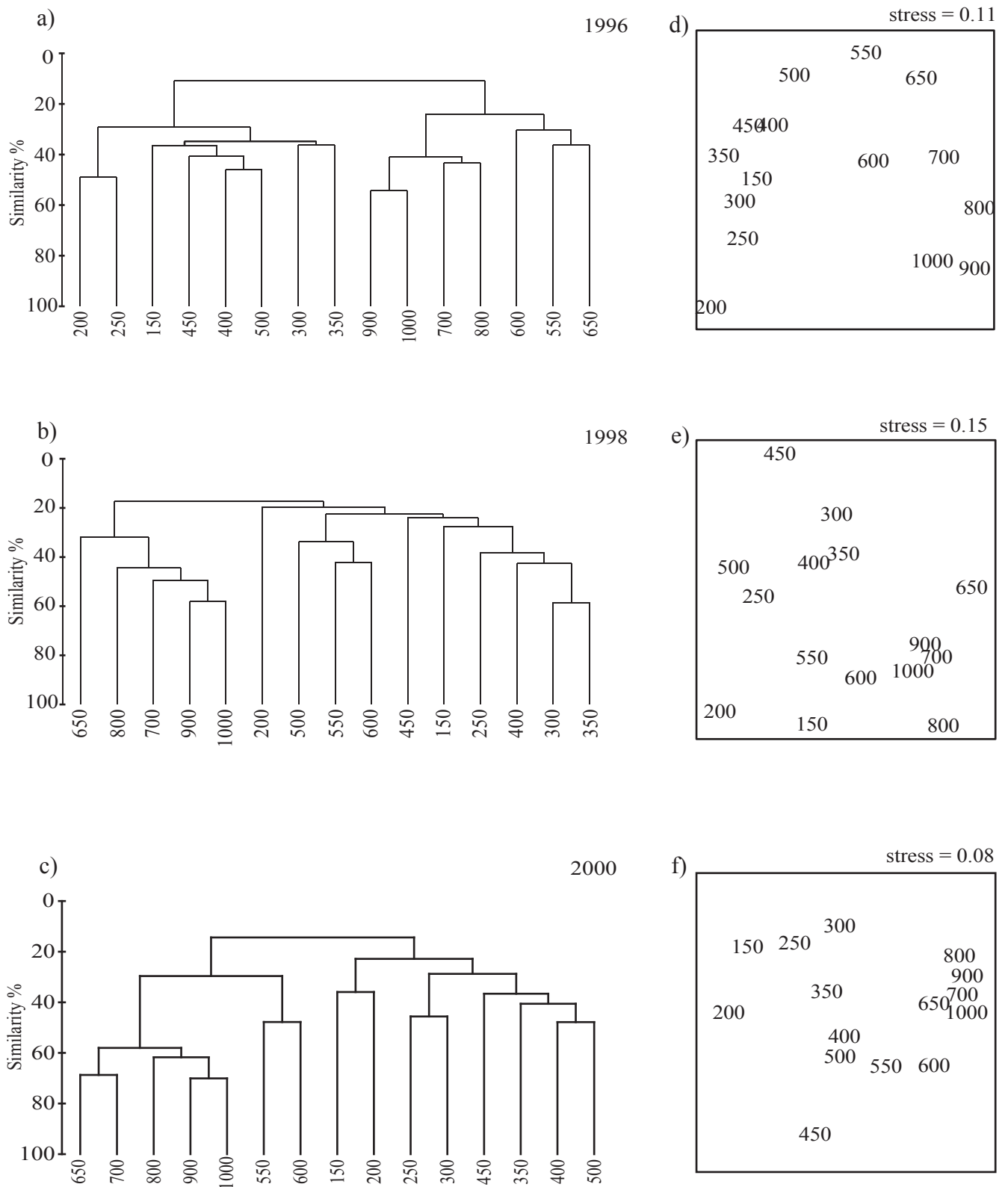


Figure 9 a-f. Comparison of hierarchical dendrograms (9 a-c) and non-metric multi-dimensional scaling ordinations (9 d-f) of 1996, 1998 and 2000

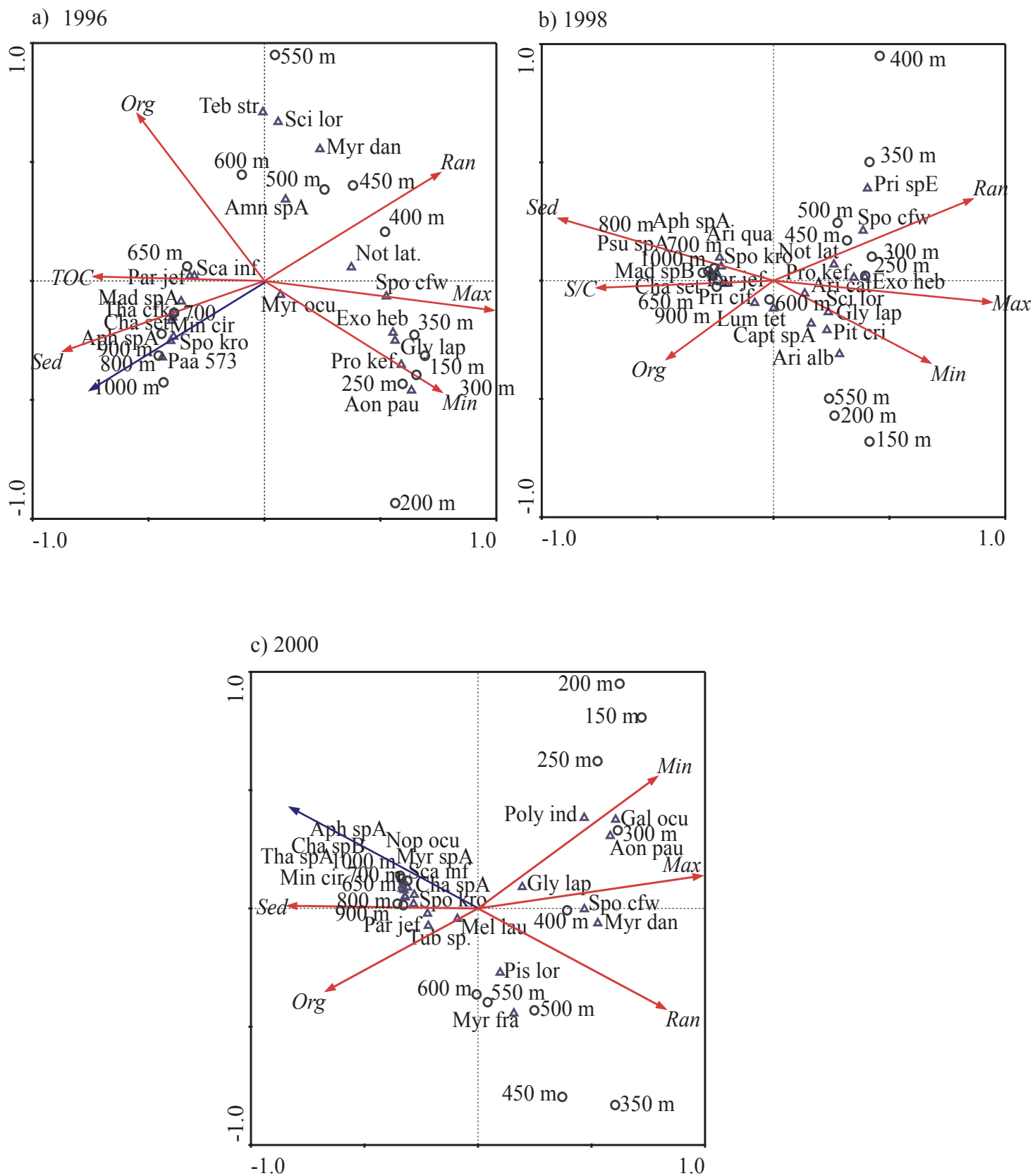


Figure 10a-c. Canonical correspondence analysis (CCA) ordination plots of the 20 most abundant polychaete species, station and environmental variables in 1996, 1998 and 2000. Max = maximum temperature, Min = Minimum temperature, Ran = temperature range, Sed = mean sediment grain size, Org = organic content, TOC = total organic carbon, S/C = silt:clay fraction. Δ = polychaete species \circ = station, \rightarrow = environmental variable, \rightarrow (blue) = possible inverse of an environmental variable.

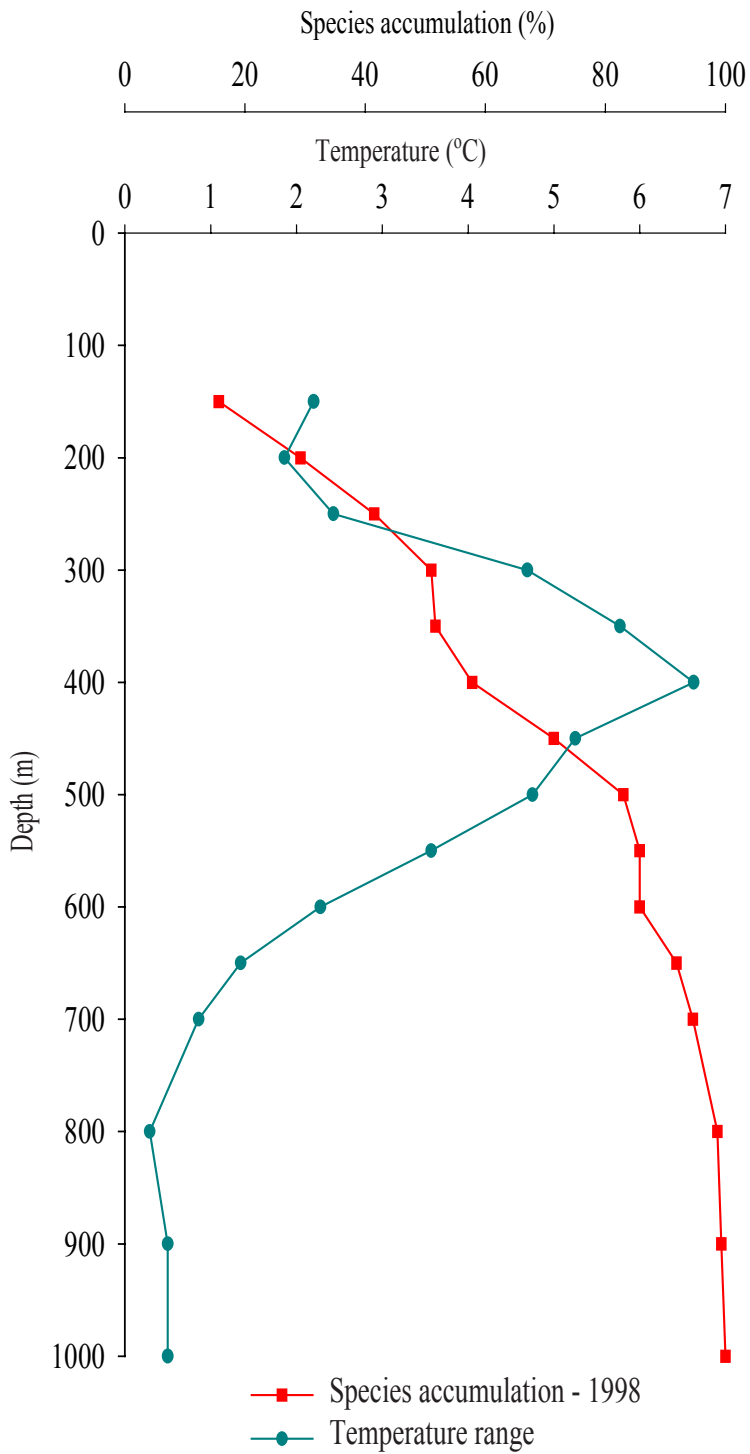
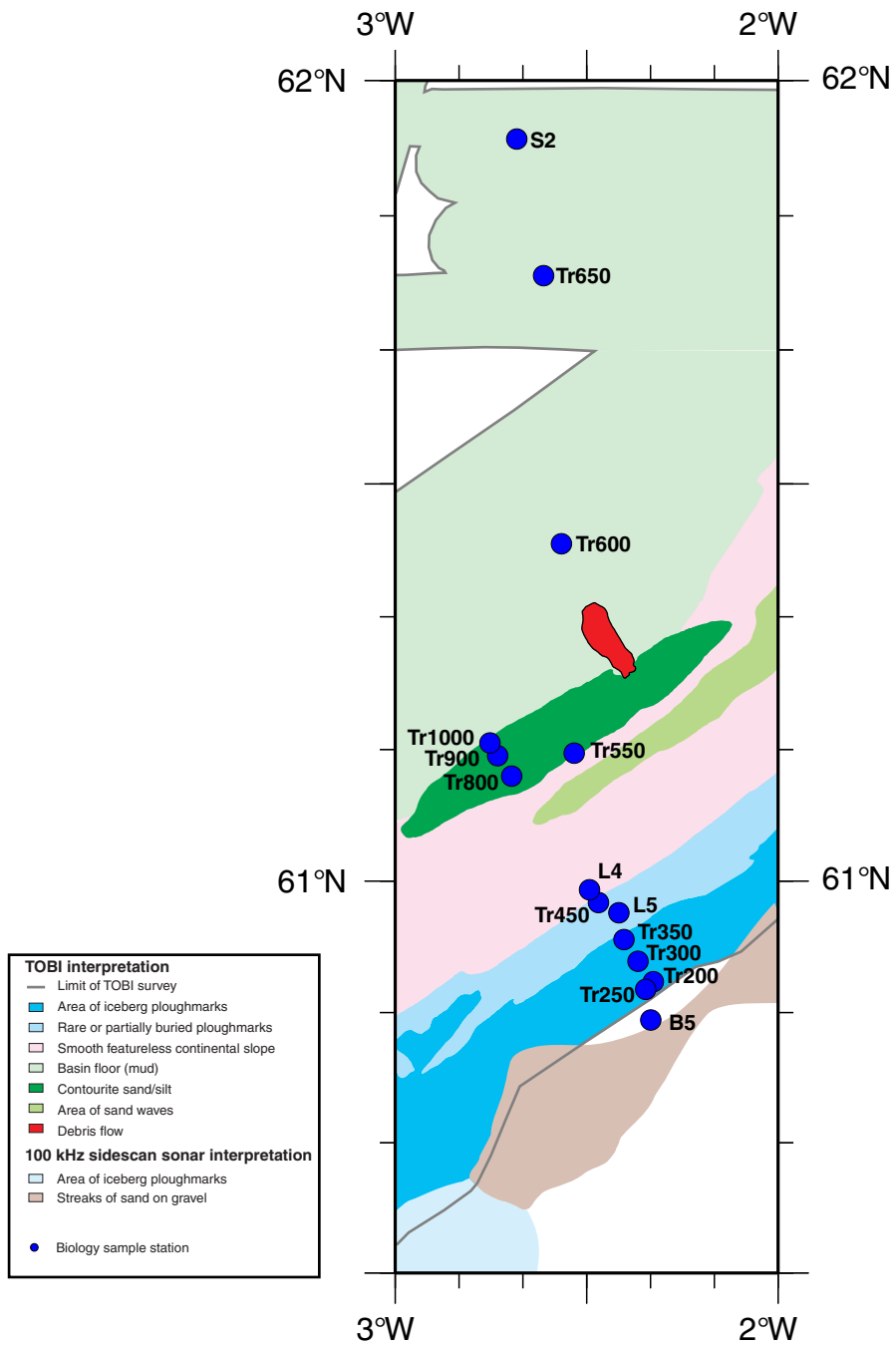


Figure 11. Polychaete species accumulation plot from 1998 with the temperature range superimposed.



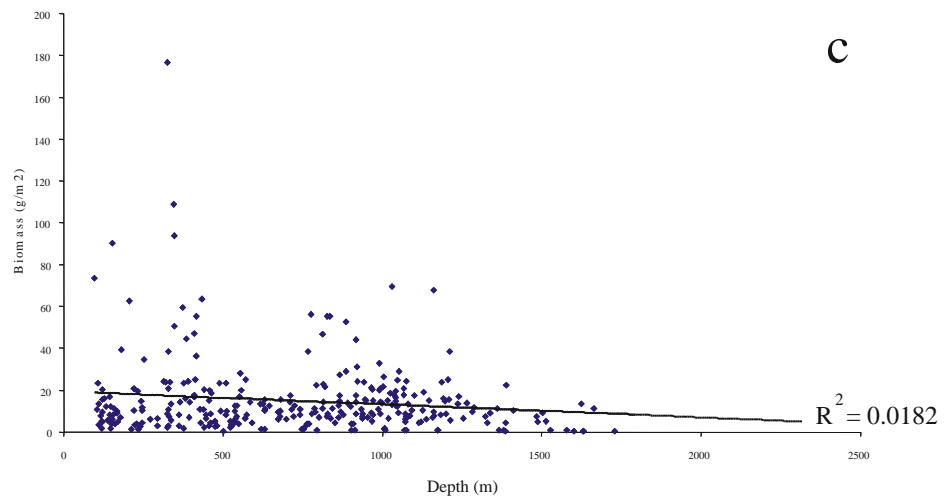
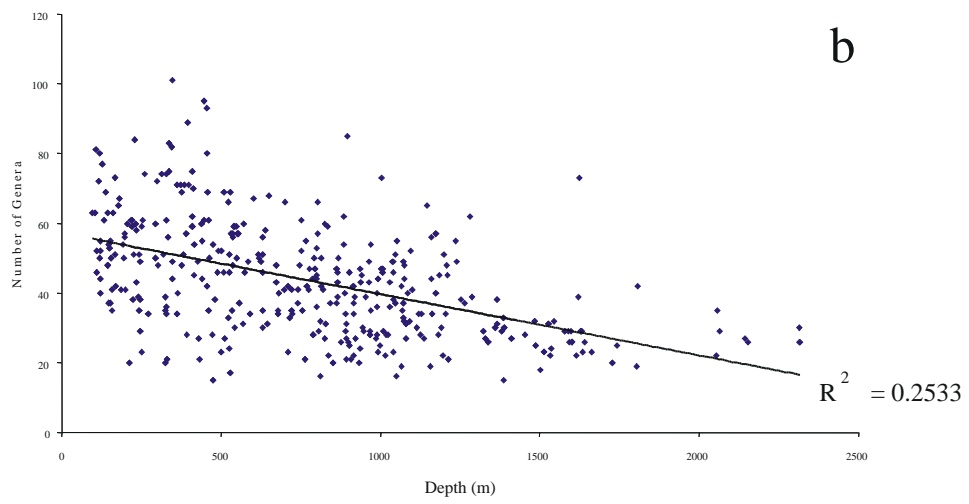
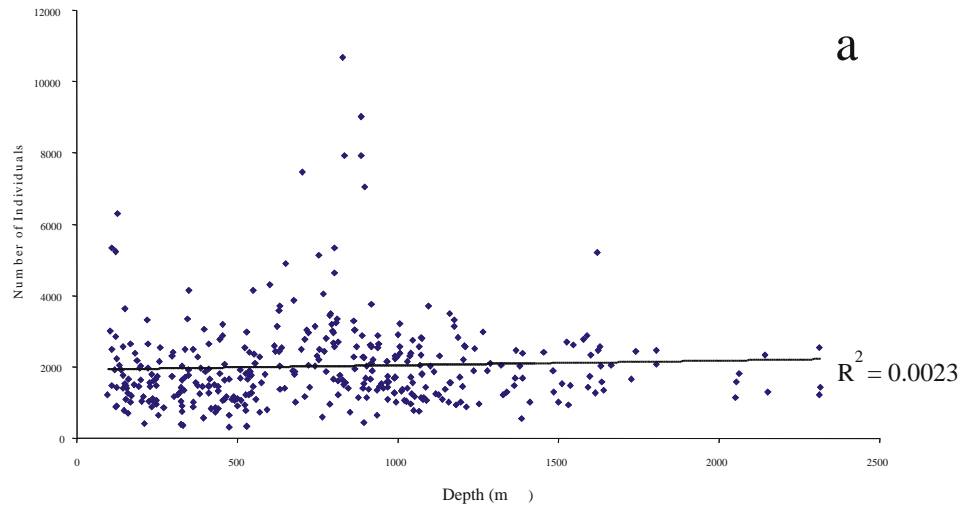
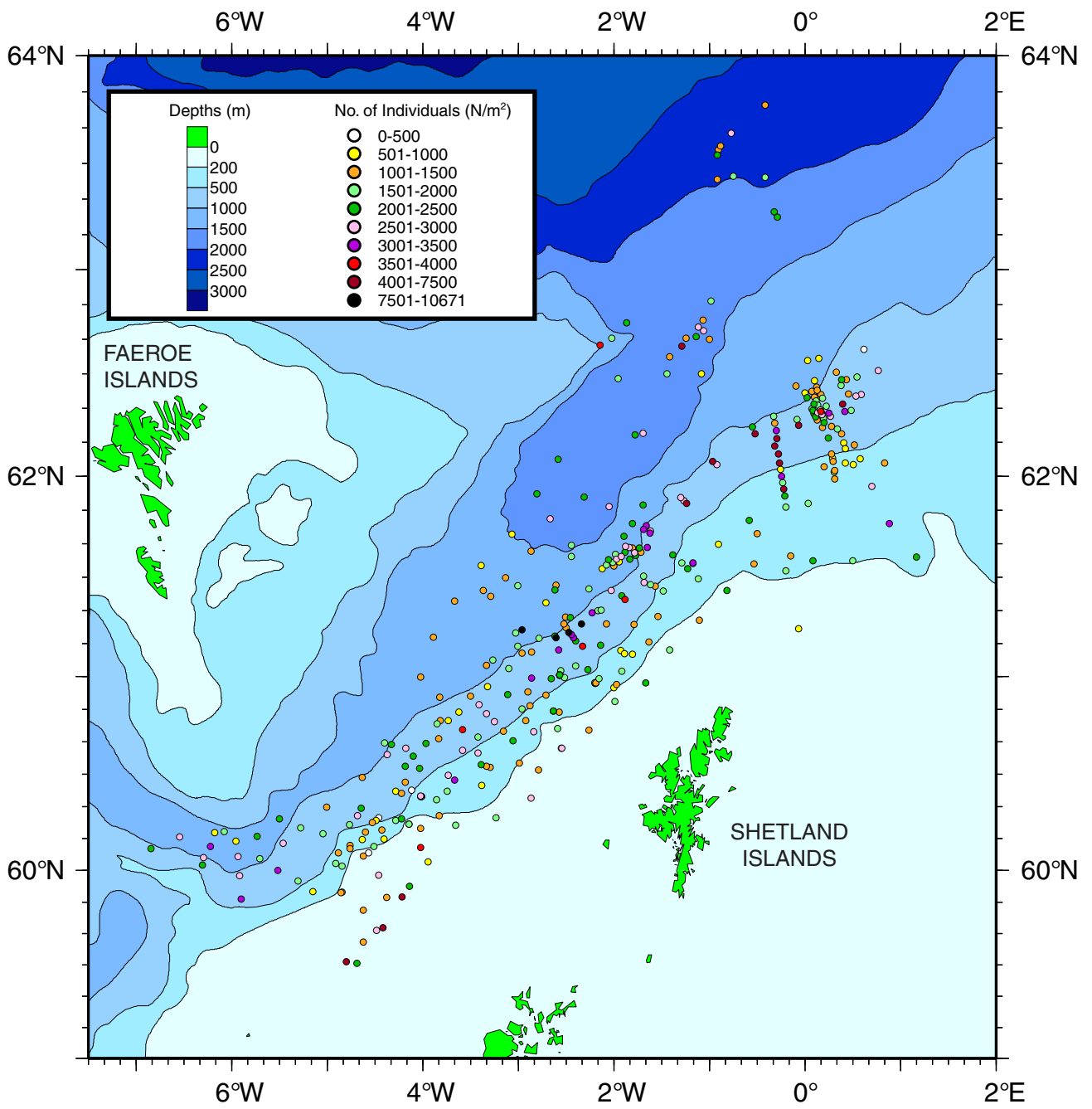
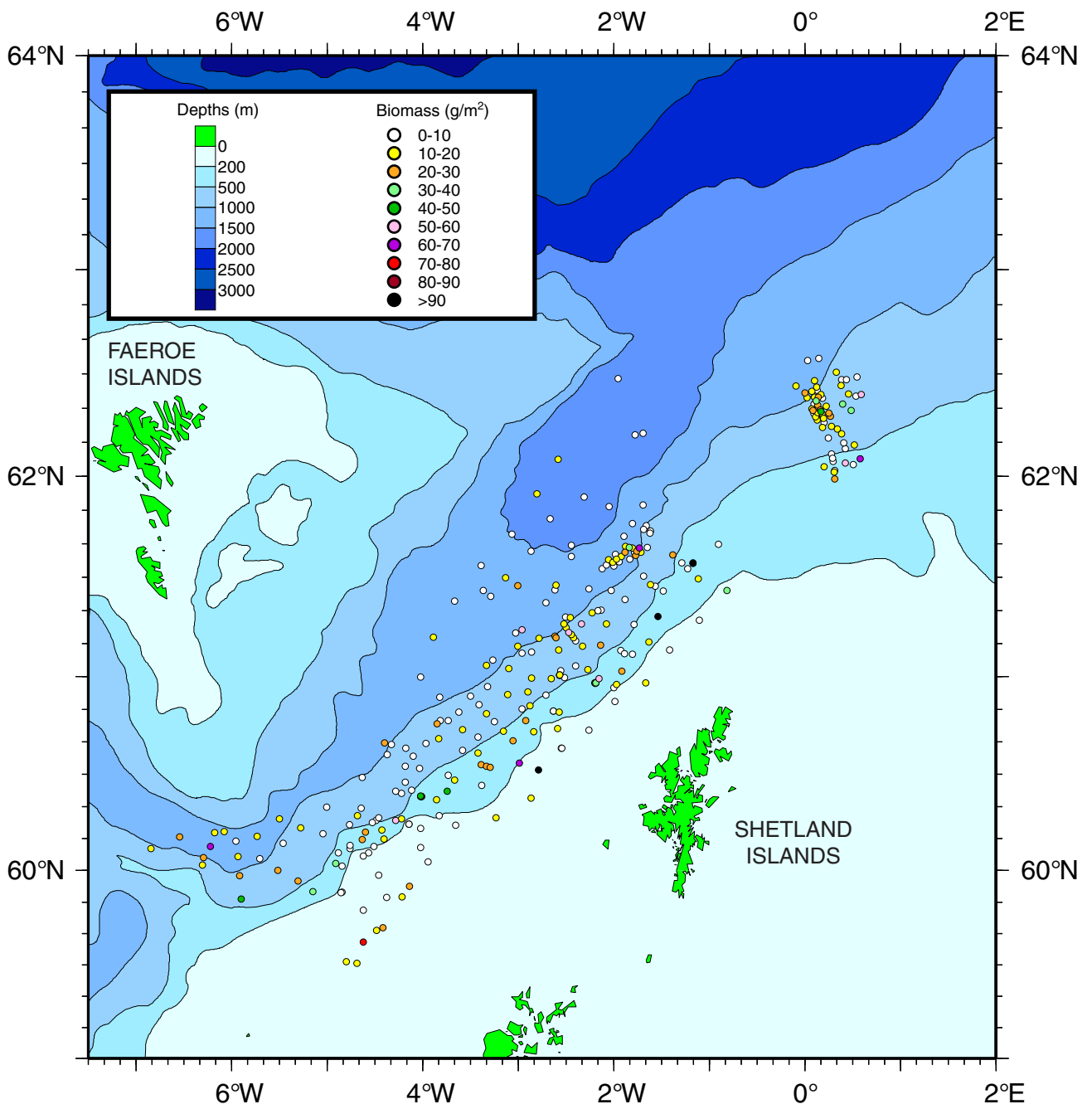
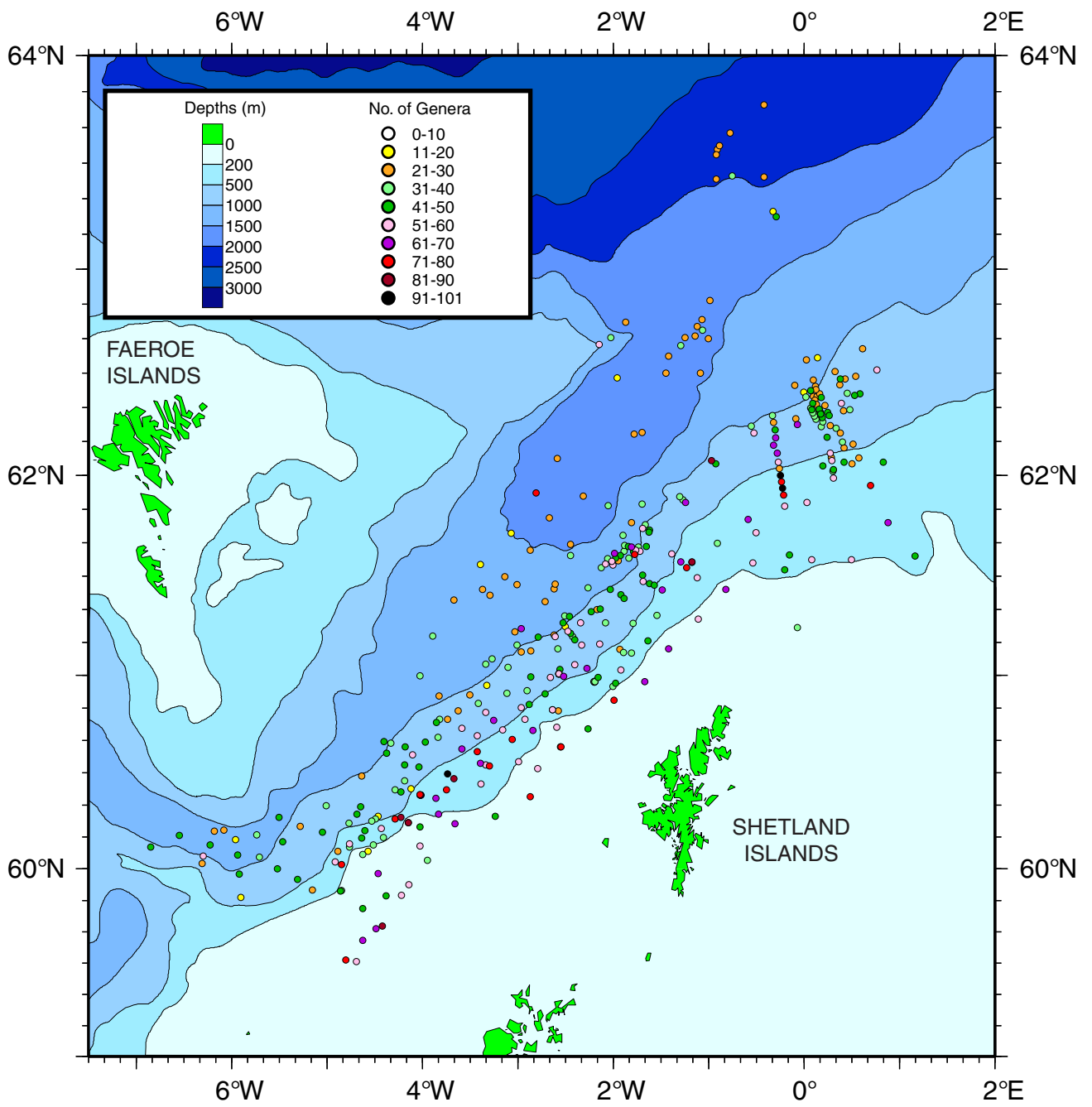


Figure 13: a) Number of Individuals (Number m^{-2}), b) Number of Genera, and c) Biomass (gm^{-2}) of the macrofaunal plotted against depth. Correlation coefficients (R^2) are indicated.







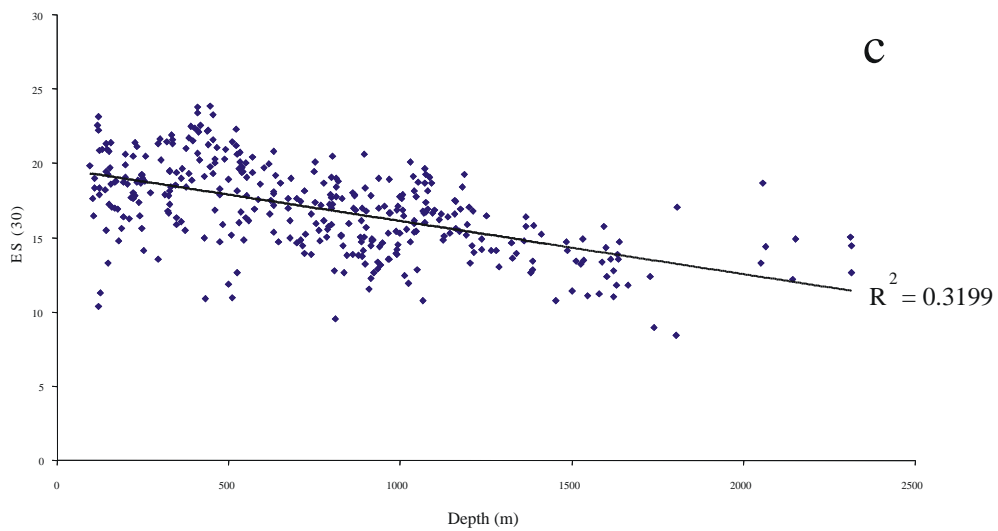
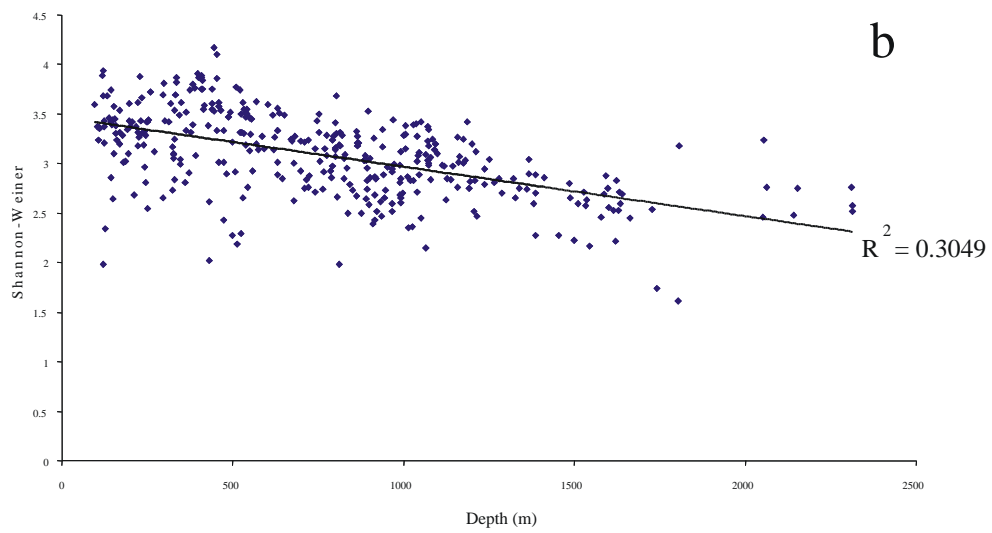
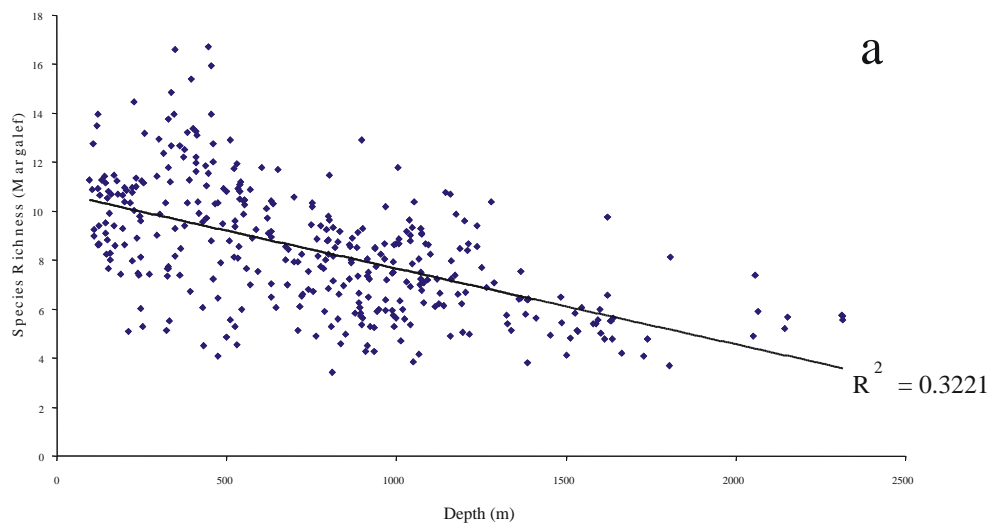
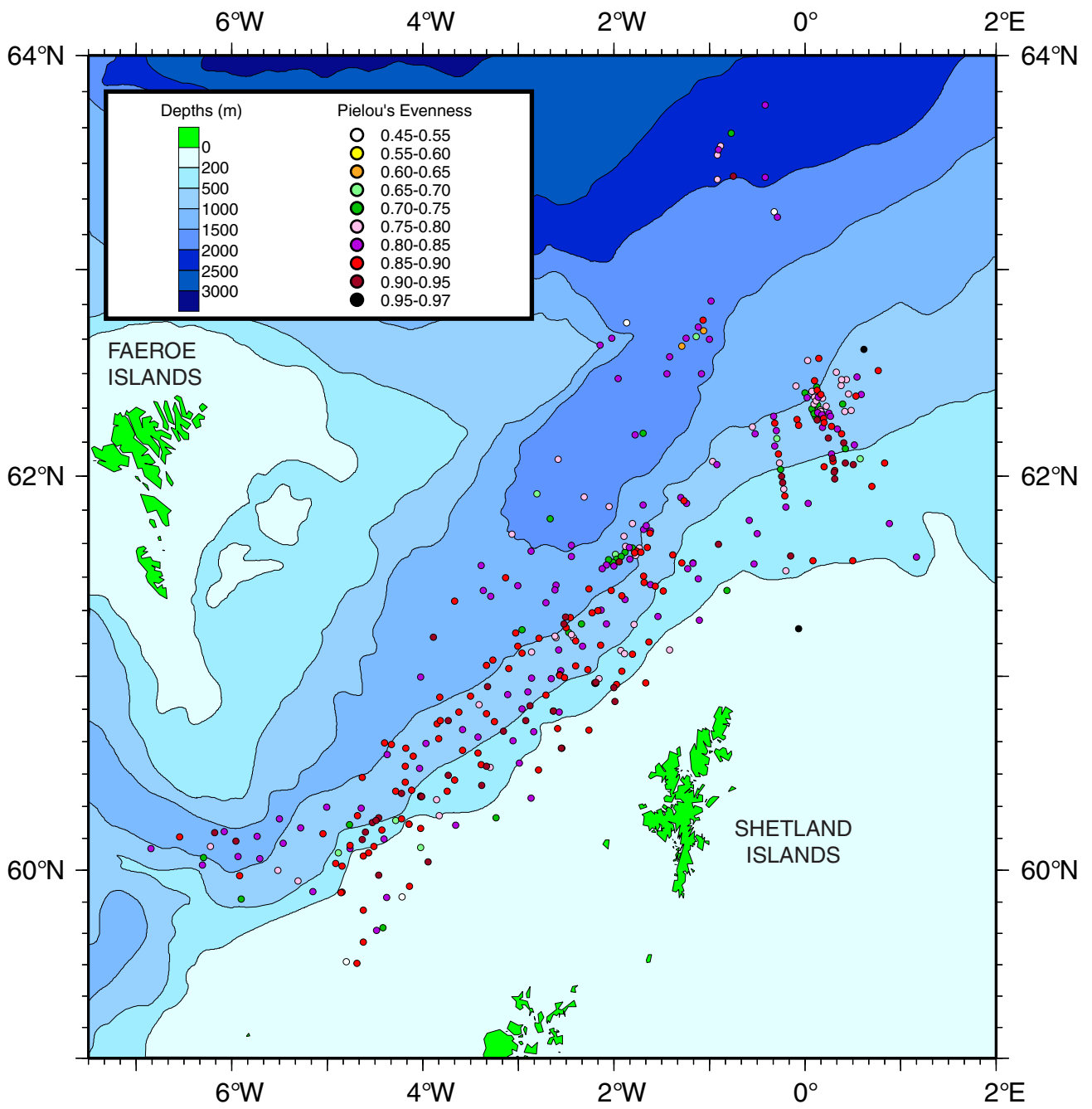
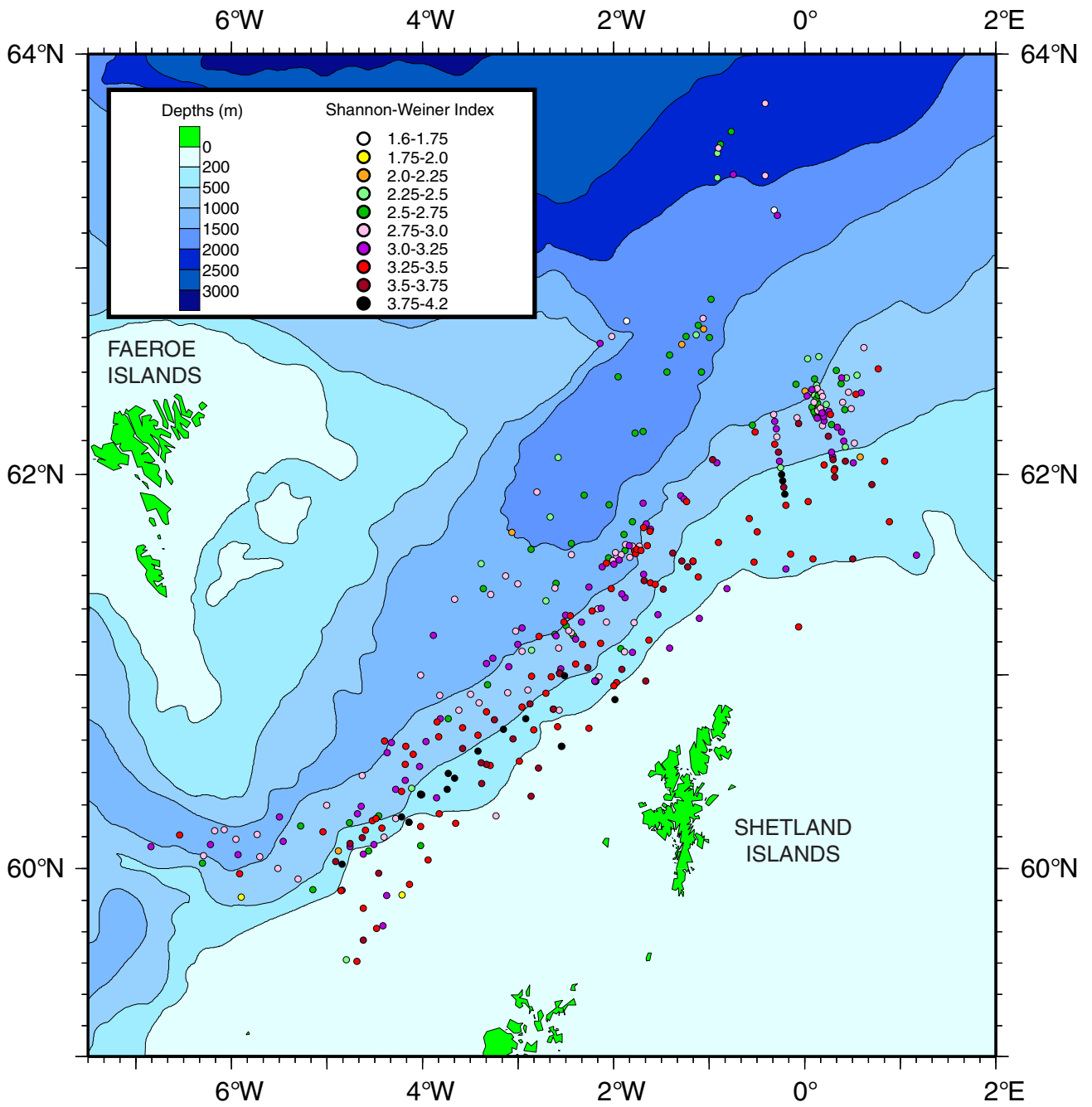
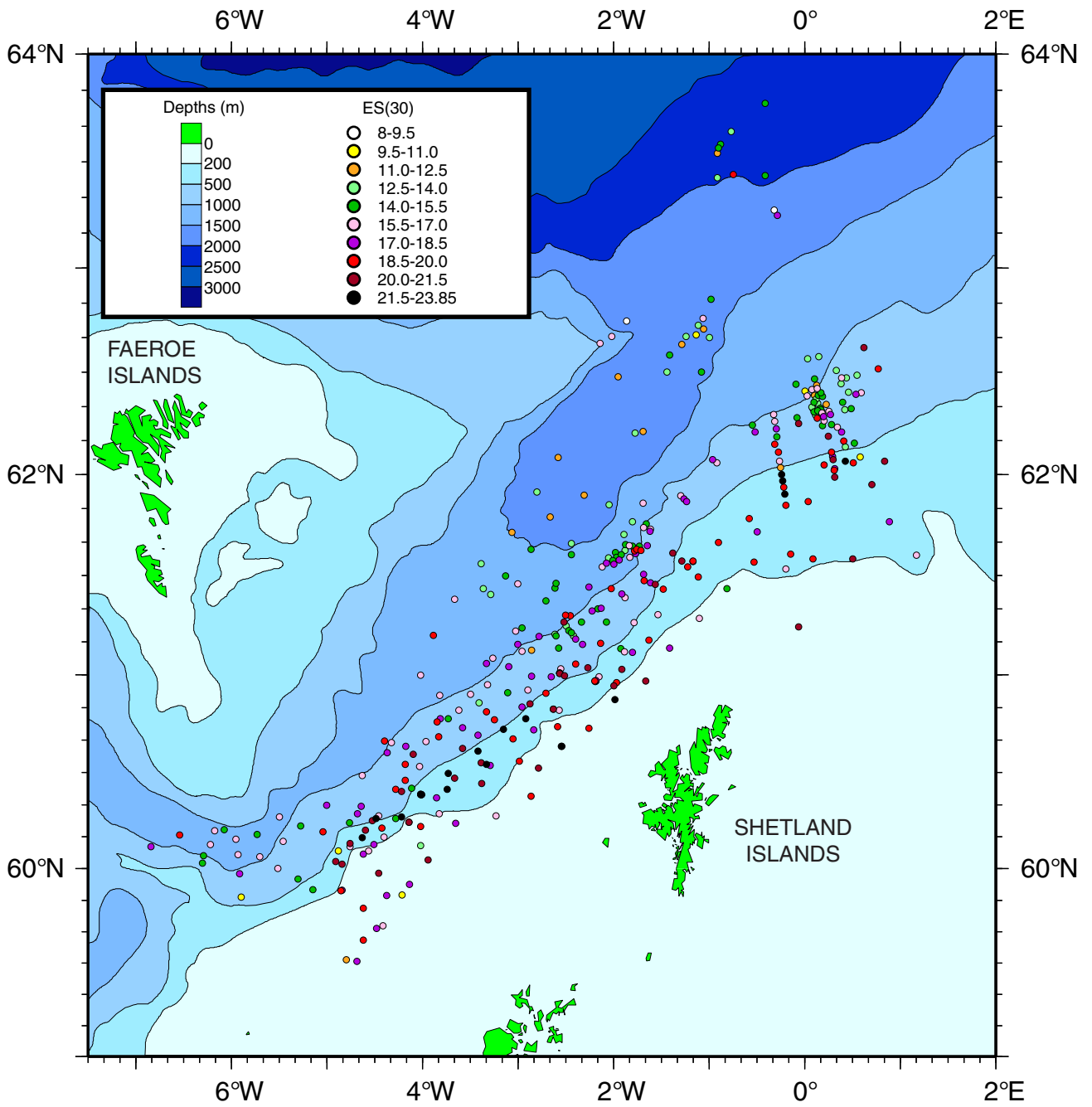
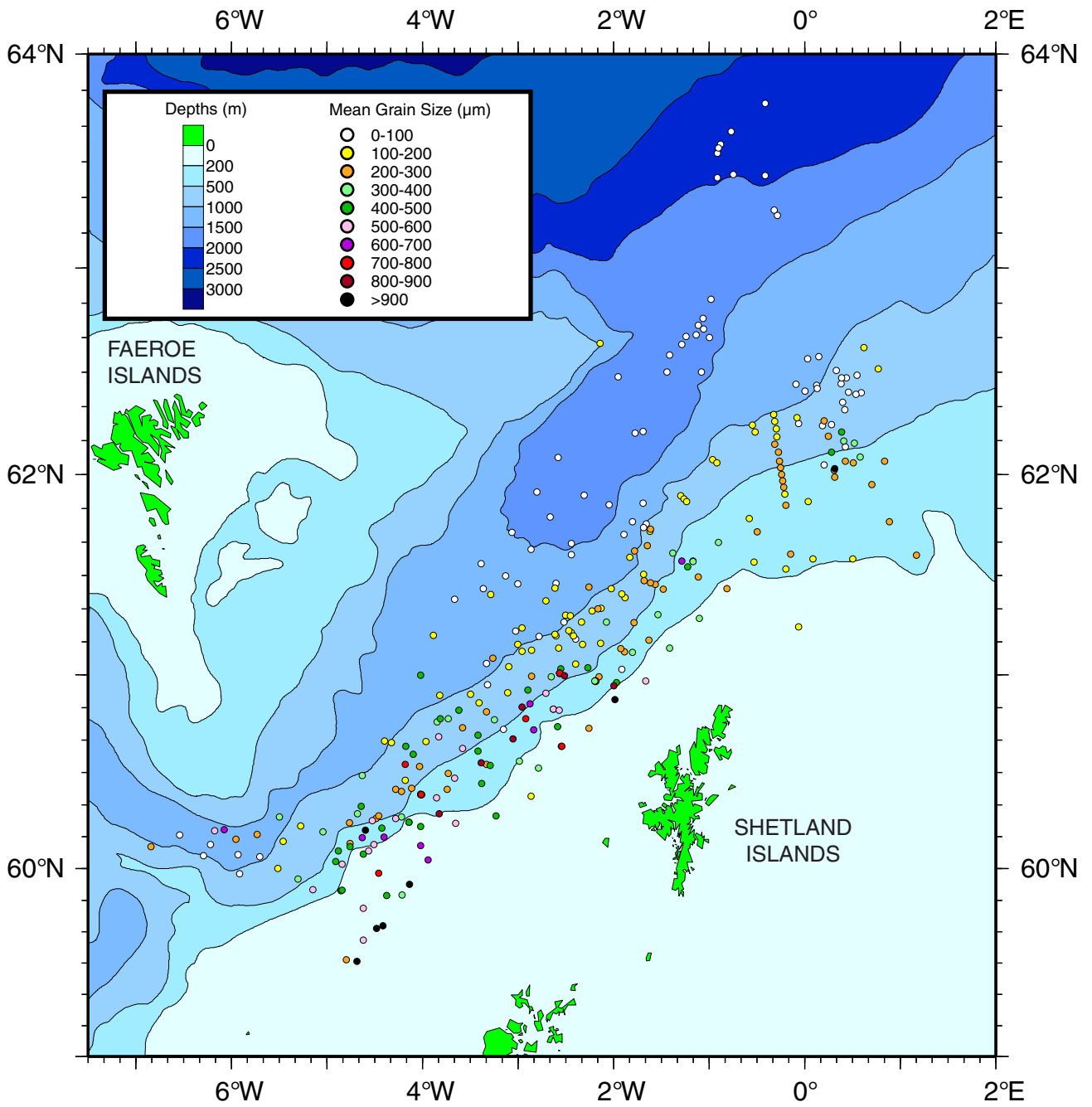


Figure 17: a) Margalef's Species Richness, b) Pielou's Evenness and c) Shannon-Weiner diversity index against water depth (m). Correlation coefficients (R^2) are indicated









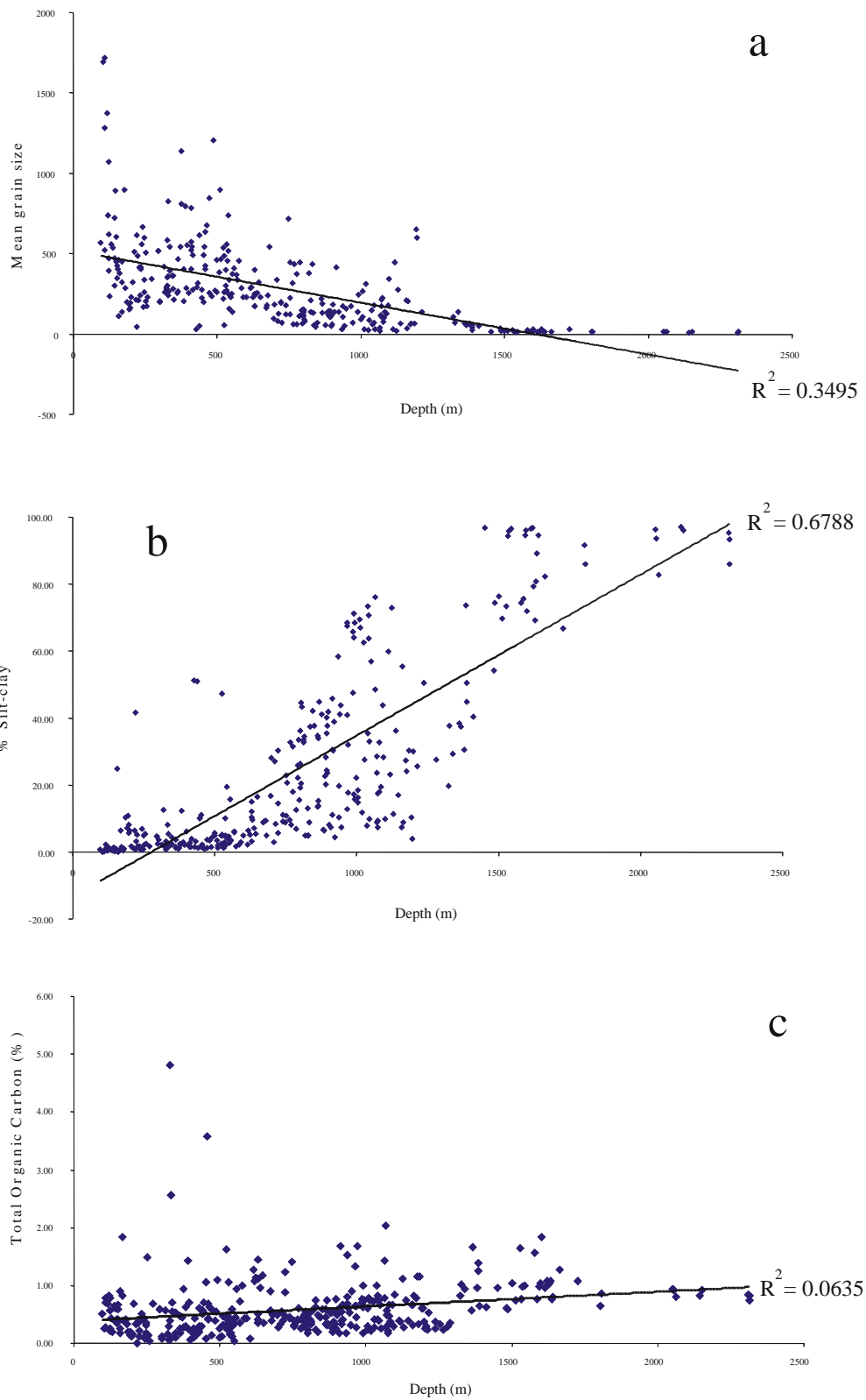
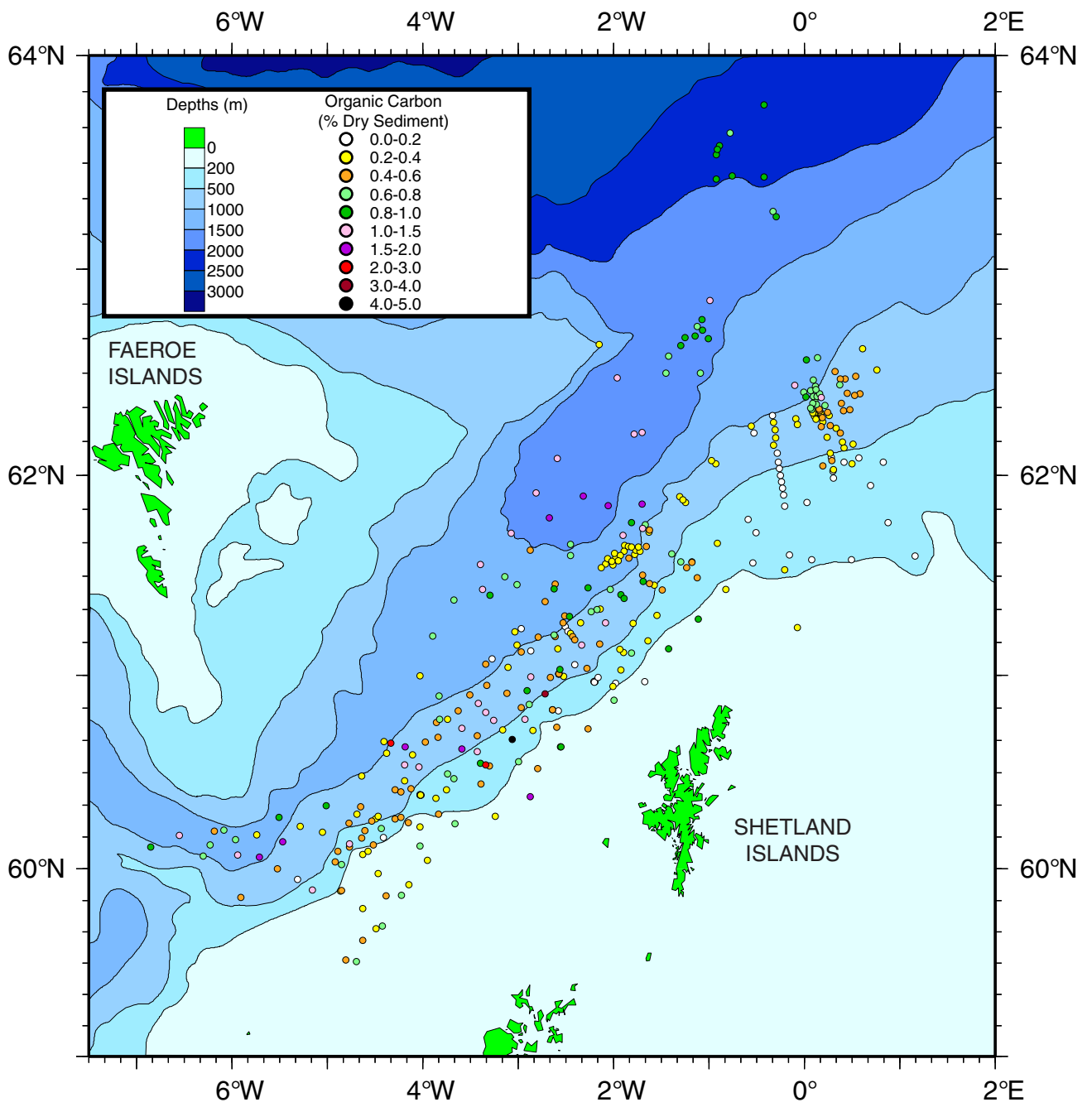


Figure 22: a) sediment grain size (mean particle diameter (μm)) b) Silt/Clay Ratio, and c) Total Organic Carbon (%) against water depth. Correlation coefficients (R^2) are indicated.



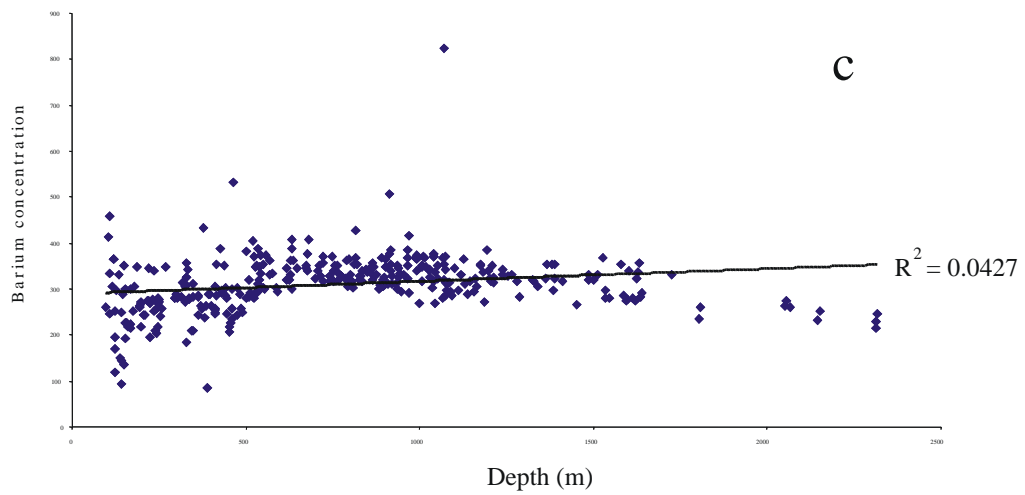
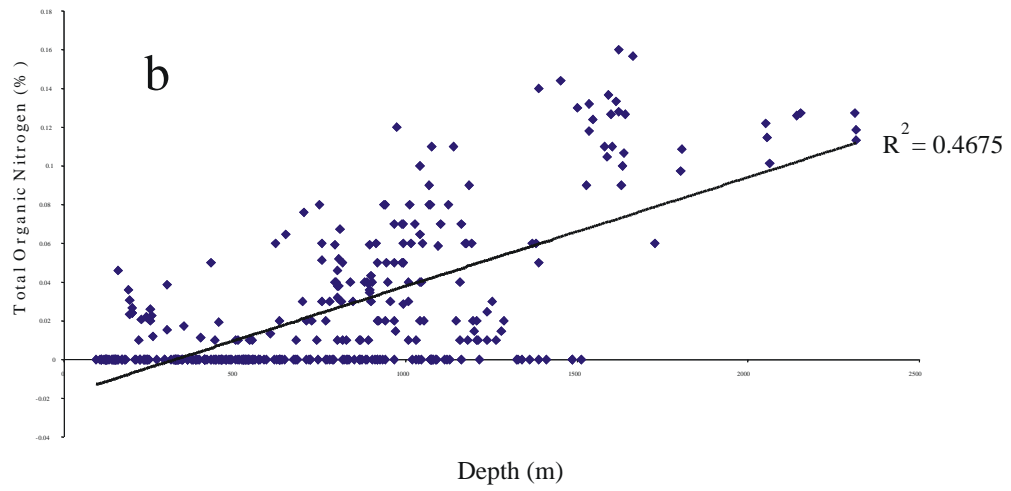
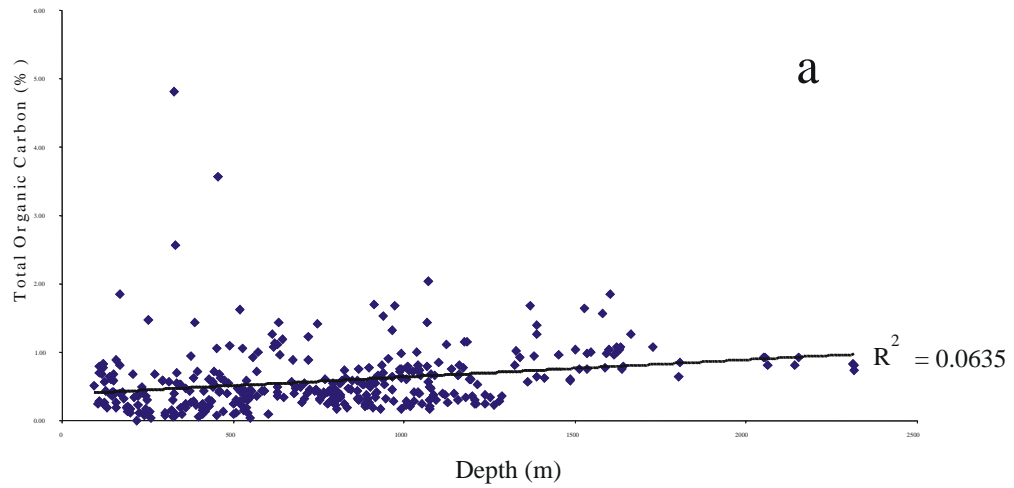


Figure 24: a) Total Organic Carbon (%), b) Total Organic Nitrogen (%), and c) Barium concentration (mgkg^{-1}) against water depth. Correlation coefficients (R^2) are indicated.

