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Seafloor biotope analysis of the deep waters of the SEA4 region of Scotland's seas

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I would like to thank Drs Bhavani Narayanaswamy and Thom Nickell of the Scottish Association for Marine Science (SAMS) for making an initial compilation of genus-level data from the AFEN and DTI surveys.

The results detailed here represent the fruits of over six months spent at sea. I would like to thank all those who sailed with me, ship-, science-, and technical-sides, for all their help in producing this exceptionally valuable dataset.

Summary

Scotland's northern deep seas, Strategic Environmental Assessment area 4 (SEA4), are very rich and complex in their environmental conditions and their biological communities. The area is also of considerable historic interest in connection with the development of the modern sciences of deep-sea biology and oceanography. From 1996 to 2002 the area was extensively surveyed through the AFEN and DTI SEA projects that encompassed broad-scale seabed mapping and physical sampling of the seafloor. This report collates the environmental and biological data from these seafloor samples and analyses them with the objective of identifying representative biotopes for the SEA4 area.

Biotopes are here considered to be spatially coherent areas of relatively homogeneous environmental characteristics with relatively homogeneous biological communities. Such areas are identified by the use of a series of complimentary multivariate statistical techniques that attempt to classify the region into major biological community types and understand how these communities are distributed with respect to prevailing environmental conditions. These analyses reveal that water depth, water mass characteristics (particularly variations in temperature) and seabed sediment type are the dominant controls on the distribution of biological communities in the SEA4 area.

Considering these environmental controls and the distribution of major biological community types, the SEA4 area is partitioned into eight proposed primary biotopes. They represent three major hydrographic regimes (a) <300m water depth, warm NE Atlantic waters with relative thermal stability; (b) 300-600m, highly dynamic, varied water masses with extreme thermal variability; and (c) >600m, Arctic water with highly stable thermal regime. Superimposed on these hydrographic / depth boundaries is an additional geographic boundary that represents a SW-NE trend in sediment type (less to more muddy), and a further depth boundary (1200m) reflecting the continuous change in biological communities with increasing water depth. The report includes a detailed characterisation of each of the eight biotopes in terms of their environmental characteristics and biological communities.

These biotopes are named, described, and referenced to the EUNIS habitat classification system. The proposed classification is set in the wider UK and European deep seas context.

The study concludes:

1. That the proposed biotopes are a good reflection of both environmental and biological conditions within the SEA4 area (e.g. they retain 84-100% fidelity to the original biological classification of the region).

2. The SEA4 area, and the 300-600m depth band in particular, is a highly atypical deep-sea environment. It is a boundary region between temperate NE Atlantic and Arctic conditions. In global terms it is rare, occurring only on the north side of the Greenland-Iceland-Faroe-Scotland ridge system. It is important that text book generalisations about the deep sea are not applied to the SEA4 area.

3. The 300-600m depth band has conservation value in terms of (i) "rocky reef habitat"; (ii) the occurrence of 'cold-water corals' (*Lophelia*); and (iii) the occurrence of demosponge aggregations. It also supports the highest biological diversity in the SEA4 area – a diversity maximum that occurs at a much shallower depth (e.g. 400m) than text book generalisations would predict (e.g. 2,500m).

4. A water mass-based classification of European deep-sea areas, closely paralleling existing 'Marine Ecoregions of the World' Provinces, has considerable potential for the further development of UK and European deep-sea habitat classification.

This report also includes an account of sub-biotopes, -habitats and seabed features known to occur in SEA4 that introduce additional variation to local faunas and environmental characteristics, including:

(a) stony reefs / iceberg plough mark zone;
(b) cold-water corals / *Lophelia pertusa*;
(c) demosponge aggregations / ostebund;
(d) deep gravel and cobble pavements;
(e) contourites and other deep sand features;
(f) Pilot Whale Diapirs and similar terrain; and
(g) a putative cold seep.

Contents

1 Introduction

This project aims to identify, map and describe deep-water seafloor biotopes in the SEA4 area of Scotland's seas. The area comprises parts of the Faroe Bank and Faroe-Shetland Channels and the Norwegian Basin located to the west and to the north of Shetland (see Fig. 1). By simple definition, a biotope is a uniform environment supporting a uniform biological community. A more practical definition would be: *a spatially coherent area of relatively homogeneous environmental characteristics with a relatively homogeneous fauna*. For the present study, the fauna assessed was the macrobenthos - *the invertebrate fauna of marine sediments retained when passed through a sieve of 0.5mm mesh*. The primary environmental characteristics assessed were (i) water depth, thought to be among the top three environmental gradients on the planet; (ii) seabed sediment type, a key control on the distribution of the macrobenthos; and (iii) hydrography, the oceanography of the SEA4 area is unusual, dynamic and extreme, and thought to be a major control on the distribution of biological communities in the region. The purpose of the biotope analysis is to contribute evidence-based information to the environmental management of Scotland's deep-water areas.

This work draws very heavily on a series of five dedicated environmental surveys carried out in the SEA4 area between 1996 and 2002. The first two (1996 and 1998) were undertaken on behalf of AFEN (Atlantic Frontier Environmental Network[1]), a consortium of oil companies, UK government environmental advisers (JNCC, FRS) and the UK Department for Trade and Industry (now the Department of Energy & Climate Change, DECC). A further three surveys (1999, 2000, 2002) were carried out as part of DECC's Strategic Environmental Assessment (SEA) process, specifically areas SEA1 and SEA4. Note that the SEA1 area is generally no longer referred to, it was a fringe area along the UK-Faroe boundary that is effectively now part of the SEA4 area.

At the time, these surveys were rather unusual in that they incorporated extensive seafloor mapping, particularly sidescan sonar. These geophysical mapping efforts are not reviewed here, but were crucial to the design of the field sampling programmes on which the present work depends.

[1] Agip (UK) Ltd., Amerada Hess Ltd., Amoco (UK) Exploration Company Ltd., ARCO British Ltd., BG E&P Ltd., BP Exploration Operating Company Ltd., Chevron UK Ltd., Conoco (UK) Ltd., Deminex UK Oil and Gas Ltd., Elf Exploration UK plc., Enterprise Oil plc., Esso Exploration and Production UK Ltd., Fina Exploration Ltd., Marathon Oil UK Ltd., Mobil North Sea Ltd., Phillips Petroleum Company UK Ltd., Saga Petroleum Ltd., Shell UK Exploration and Production, Statoil Ltd., Texaco Britain Ltd., Total Oil Marine plc., Joint Nature Conservation Committee, Fisheries Research Services, and the Department of Trade and Industry.

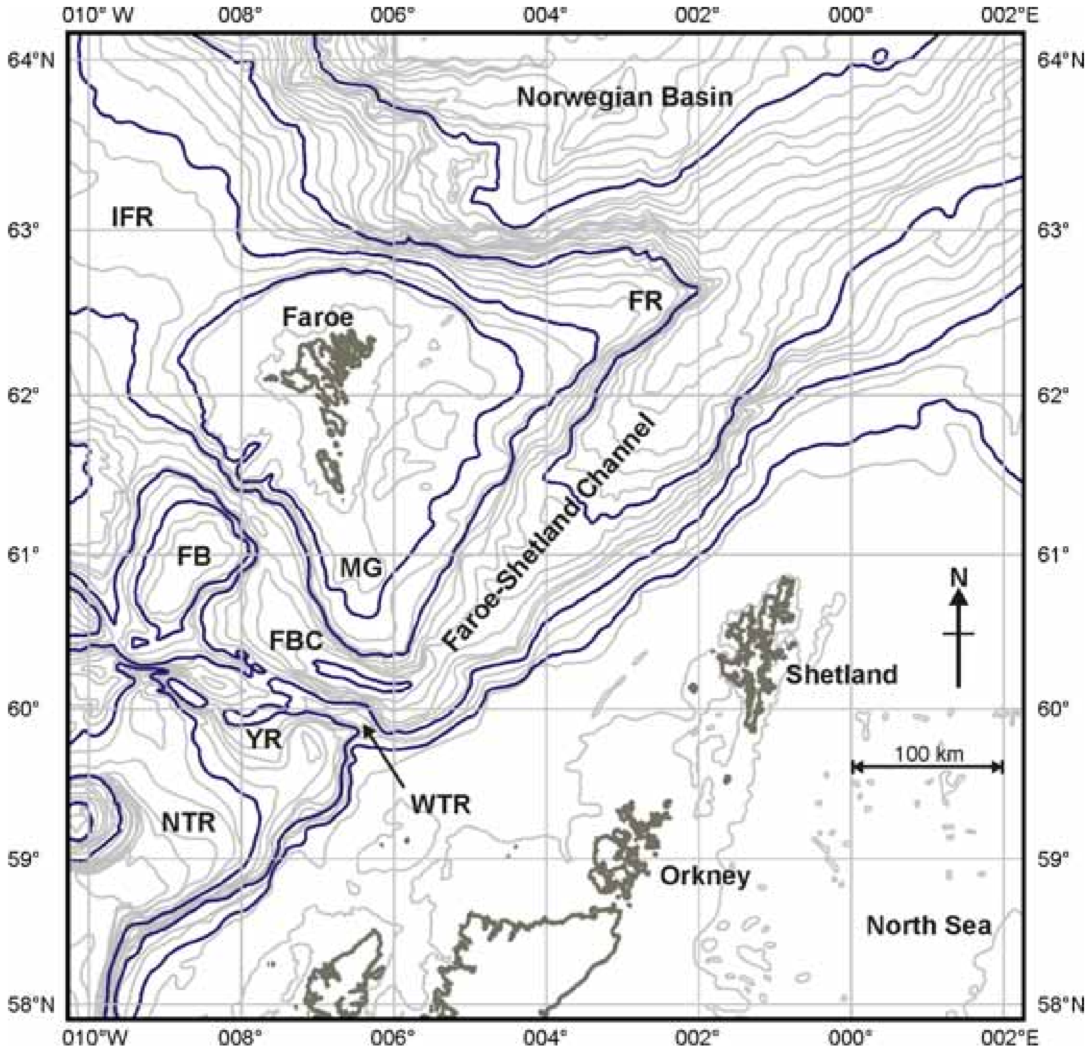

Figure 1. General location map of the Faroe Bank and Faroe-Shetland Channels and Norwegian Basin areas assessed in the biotoping study. (100m bathymetric contours; 300, 600, 1200 and 2400m contours highlighted; IFR, Iceland-Faroe Rise; FR, Fugloy Ridge; FB, Faroe Bank; MG, Munkagrunnurin; FBC, Faroe Bank Channel; YR, Ymir Ridge; WTR, Wyville Thomson Ridge; NTR, northern Rockall Trough).

1.1 Historical perspective

The deep waters to the west and north of Scotland played a key role in the development of deep-sea biology and global oceanography more generally. The 'grandfather' of these sciences was Sir Charles Wyville Thomson, born Wyville Thomas Charles Thomson at Bonsyde, West Lothian, on March 5, 1830. He is most famous as the Chief Scientist of the *Challenger Expedition* (1872-76), generally regarded as the birth of oceanography (Fig. 2). The *Challenger Expedition* was an extraordinary undertaking that would hardly have been credible as a venture without Wyville Thomson's experience leading five earlier cruises aboard HMS *Lightning* (1868) and HMS *Porcupine* (1869-70). The *Lightning* cruise (1868) and the third *Porcupine* cruise (1869) carried out surveys in the SEA4 area. From these cruises Wyville Thomson detected and mapped "Warm and Cold Areas" and noted corresponding changes in the deep-sea fauna (Thomson, 1873) – perhaps representing the first ever described deep-sea biotopes. This was a primary objective of the third *Porcupine* cruise *"to map out as accurately as we could the paths of the warm and cold currents, and to determine the influences of these currents upon the character and distribution of animal life"*. His mapping of the warm and cold deep-water areas enabled him to predict the existence of the barrier between them, the submerged ridge that now bears his name. In the cold area, to the north of the Wyville Thomson Ridge, he noted the very abundant occurrence of the sponge *Hyalonema boreale* (now known as the demosponge *Stylocordyla borealis*), still abundant today on the deep-water sandy contourites of the Faroe Bank Channel (see sub-biotopes section below). In the warm area, to the south of the Ridge, both the *Lightning* and *Porcupine* cruises encountered the "*Holtenia* Ground", a favourite collecting area of Wyville Thomson and his colleagues as a result of the rich diversity of animal life associated with the mass occurrence of the glass sponge *Holtenia carpenteri* (now known as *Pheronema carpenteri*) originally described by Wyville Thomson (Thomson, 1869). Despite lying adjacent to the "*Darwin Mounds*" Marine Protected Area the "*Holtenia* Ground", if it still exists, has not been relocated in the modern era.

Figure 2. Wyville Thomson commemoration, St. Michael's Parish Church, Linlithgow, "*In memory of Sir Charles Wyville Thomson of Bonsyde, Professor of Natural History University of Edinburgh, Director of the Challenger Expedition, erected by his friends and colleagues 1885*".

1.2 Oceanography

As evident in the early work of Wyville Thomson and colleagues (see above) the hydrography, particularly water temperatures, of the SEA4 area is of considerable significance to the ecology of the region. This is not surprising given the rather unique, highly dynamic and rather extreme nature of the oceanography of the Faroe-Shetland Channel. The cold dense waters of the Arctic Ocean are imperfectly held back from spilling into the Atlantic by the topographic barrier of the 'Greenland-Scotland Ridge' (Greenland-Iceland-Faroe-Scotland Ridge). About one quarter of the outflow that does pass the barrier travels through the narrowing Faroe-Shetland Channel and exits into the Atlantic via the Faroe Bank Channel (Tomczak & Godfrey, 1994). This coldwater stream flowing past Scotland is of global significance to ocean climate and circulation. The southwest flowing cold water (<0.5 ºC) is overlain by warmer waters (>2 ºC) travelling in the opposite direction along the West Shetland Slope (see Fig. 3). This produces a rather extreme thermal gradient on the upper continental slope, where warm North Atlantic Water (>8 ºC) is in close proximity to very cold (<-0.5 ºC) Faroe-Shetland Channel Bottom Water (Turrell *et al* 1999).

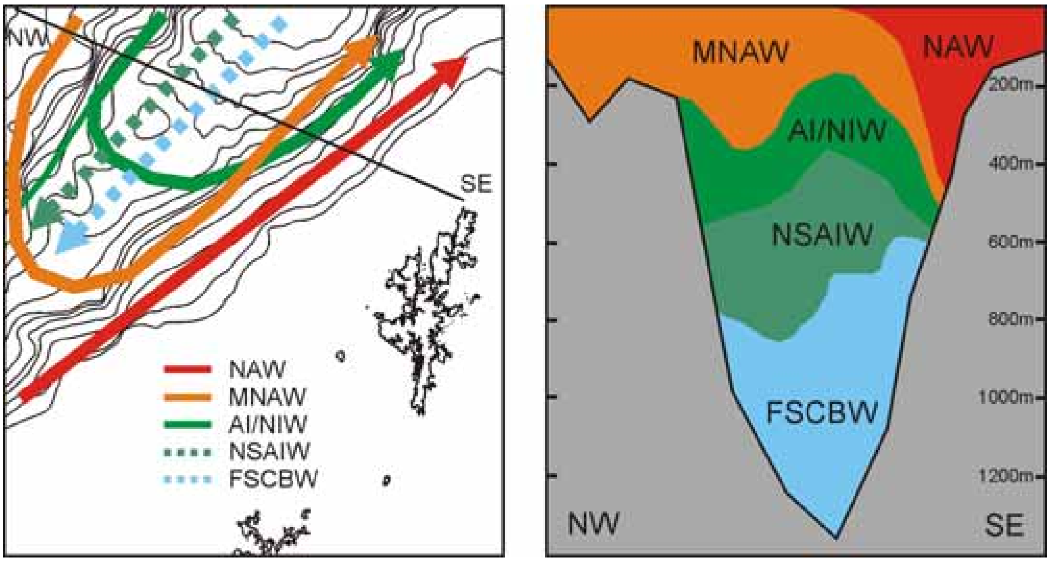

Figure 3. Hydrography of the Faroe-Shetland Channel (adapted from Turrell *et al* 1999; Bett 2000). Left panel shows the general flows of the five main water masses and the location of the channel cross-section illustrated in the right panel. General water mass characteristics on the West Shetland Slope:

Water mass	Temperature (°C)	Depth (m)	Flow
North Atlantic Water (NAW)	>8	<500	NE
Modified North Atlantic Water (MNAW)	8 to 6.5	500-600	NE
Arctic Intermediate/North Icelandic Water (AI/NIW)	5.5 to 2	500-600	NE
Norwegian Sea Arctic Intermediate Water (NSAIW)	0.5 to -0.5	500-600	SW
Faroe-Shetland Channel Bottom Water (FSCBW)	<-0.5	>600	SW

This meeting or boundary between Arctic and temperate North Atlantic waters is of key significance to the biogeography and biotoping of Scotland's deep waters (see further below). Consider that in the case of coastal and shelf seas, the boundary between Arctic and Temperate North Atlantic biogeographic realms in the eastern North Atlantic is located to the north of Norway, c. 74ºN (Spalding *et al* 2007). However, the Arctic-Temperate North Atlantic boundary should be relocated to the southern tip of Shetland (c. 60ºN) in terms of conditions at the seabed in the Faroe-Shetland Channel. In essence the SEA4 area should be regarded as a two-layer system, the upper part (<300m water depth) belonging to the Temperate North Atlantic Realm in common with adjacent shelf and coastal waters, the lower part (>700m) belonging to the Arctic Realm. This situation does not arise in the remainder of Scotland's deep seas, the SEA7 area to the south of the Wyville Thomson Ridge. At around 600m water depth on the northern flank of the Ridge there is a major biogeographic boundary.

It is not possible to exactly map the Arctic-Temperate North Atlantic boundary through the SEA4 area as a result of the complex and highly dynamic nature of the interaction between the water masses in the region. In effect, the boundary is mobile in the water column / on the upper continental slope as a result of long-term changes in the water masses (Turrell *et al* 1999) and shorter-term oscillations (e.g. internal wave-like features) at their boundaries (Hosegood & van Haren, 2004). Temporal variations in the bottom water temperature regime on the West Shetland Slope are illustrated in Fig. 4, note that at the location studied (550m water depth) all five main water masses were encountered during the 10-month period of observation, and that major temperature changes can occur rapidly, indeed Hosegood & van Haren (loc. cit.) illustrate even more rapid temperature oscillations.

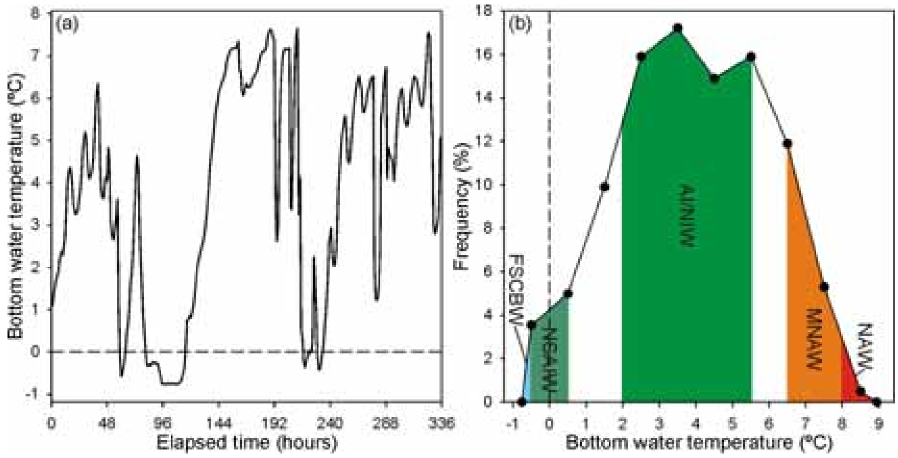

Figure 4. Temporal variability in West Shetland Slope bottom water temperatures. Data from a recording current meter moored 1.5m above the seabed in water depth of 550m, with temperature recorded at one-hour intervals for a period of 10-months. (a) Example data for a two-week period (3-16 February 1996). (b) Temperature frequency distribution for the 10-month period (15 September 1995-11 July 1996); water mass abbreviations, temperature bands, and colour coding follow those of Fig. 3.

1.3 Surficial geology

Following the AFEN surveys of 1996 and 1998, Masson (2001) was able to provide a comprehensive account of the seafloor sedimentary environment to the west of Shetland. With the DTI SEA surveys of 1999, 2000 and 2002, Masson *et al* (2003) updated and extended the account of SEA4 area surficial geology, later providing a more detailed account of conditions in the Faroe Bank Channel area (Masson *et al* 2004). In summary, these authors conclude that large-scale seabed morphology was shaped during the last glaciation, with high sediment input resulting in glacigenic debris fan formation. At the present day the deeper (>200m) waters of the SEA4 area are characterised by low sediment input and deposition rates, and by the reworking of superficial sediments by bottom currents. Sediments generally decrease in grain size with water depth, from sands and gravels on the outer shelf to high silt and clay content muds in the deeper Norwegian Basin. This simple pattern is modified by bottom currents, with stronger currents and so coarser sediments occurring at greater depth in the narrowing southern Faroe-Shetland Channel and Faroe Bank Channel than in the more open Channel and Basin to the north (see Fig. 5).

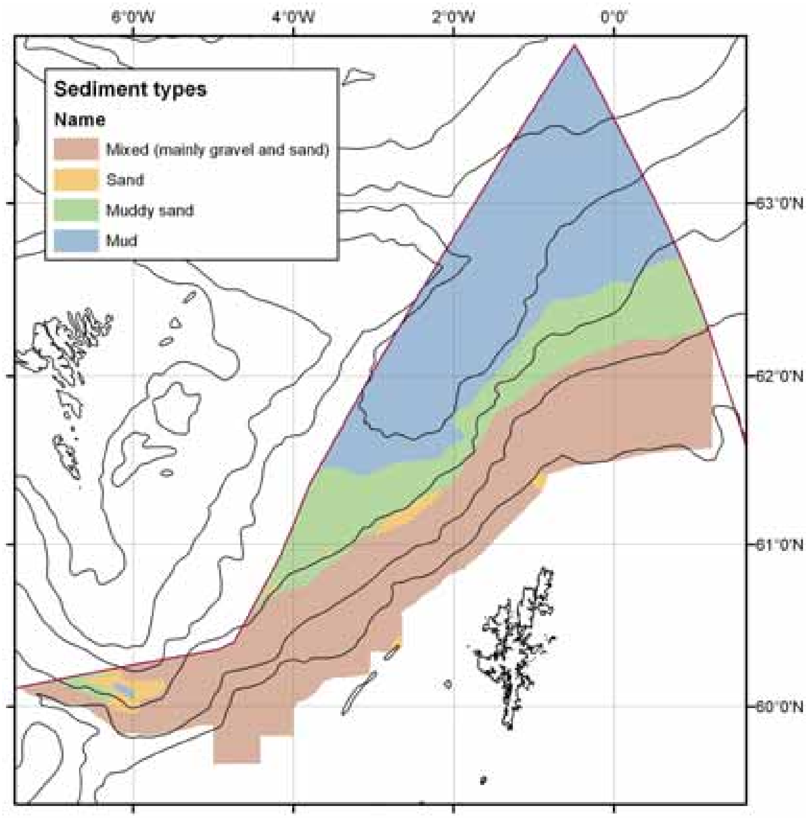

Figure 5. Generalised distribution of seafloor sediment types in the SEA4 area (adapted from Masson *et al* 2003). (The 200m contour and 500m-interval contours are shown, from GEBCO CE; IOC, IHO, BODC, 2003).

1.4 Benthic ecology

Although based on the very first extensive investigations of deep-sea ecology, Wyville Thomson's "*Depths of the Sea*" (Thomson, 1873) remains an extremely valuable account of the benthic ecology of the SEA4 area, with his descriptions and mapping of the "Warm and Cold Areas" and their faunas remaining highly relevant to the present task of biotoping the region. The AFEN surveys of 1996 and 1998 allowed Bett (2001) to provide a comprehensive account of the benthic ecology of much of the SEA4 area. Bett (loc. cit) notes the key role of hydrography in controlling the distribution and diversity of the fauna and in making it highly distinct from the adjacent area of Scotland's deep seas (the SEA7 area) to the south. The latter author also recorded the rather limited occurrence of the coral *Lophelia pertusa*, the more significant occurrence of sponge-dominated communities ('*ostebund*'), and the occurrence of a novel population of sediment surface-dwelling enteropneusts.

The later SEA surveys (1999, 2000, 2002) included a greater use of seabed photography in the description of the regional environment. Bett (2003) provides a descriptive account of the range of seafloor habitats encountered during these photographic surveys, noting that the SEA4 area encompasses a quite exceptional range of seabed types for a deep-sea region. In particular, Bett (loc. cit.) remarks on the occurrence of coarse grained sediments at depth in the SEA4 area, from sand features (contourites and barchan dune fields) to cobble and boulder pavements. Jones *et al* (2007) also comment on the south to north variation in seabed type and associated changes in the benthic fauna along the axis of the Faroe-Shetland Channel based on a subset of the SEA survey phototransects.

Unusually, the AFEN-DTI surveys of the SEA4 area incorporated an element of time-series study, focused on two bathymetric transects, one to the west and one to the north of Shetland. The results of this work were published by Narayanaswamy *et al* (2005, 2010) and Narayanaswamy & Bett (2011). Major temporal change is known to occur in deep-ocean biological communities – and therefore in any corresponding biotope – in both the Atlantic (Hartman *et al* 2012) and Pacific (Smith *et al* 2009). The latter authors suggest that such change is driven by climatic influences on the upper-ocean system that can be rapidly translated to the deep-seafloor. Similar mechanisms could certainly operate in the SEA4 area, and do suggest the need for long-term biological monitoring in deep-sea areas. Decadal-scale change in the hydrography of the Faroe-Shetland Channel has been detected (Turrell *et al* 1999). Given the close link between the distribution of the fauna and hydrographic conditions in the SEA4 area (see e.g. Bett 2001), this may be a key environmental factor in the temporal variation of benthic ecology in the region.

1.5 Biogeography

Large-scale environmental features / factors such as temperature and hydrography more generally are key controls on the large-scale distribution of biological species and communities and consequently biotopes. The SEA4 area lies wholly within the Atlantic Subarctic biogeochemical province (see Fig. 6) as established by Longhurst (2006). These provinces are based on general upper ocean characteristics (environmental and biological). They do not necessarily reflect conditions at the seabed, but do for example suggest that the SEA4 area, and indeed the bulk of Scottish deep-sea areas (i.e. much of SEA7 too), is subject to a relatively uniform seasonality and level of primary food supply.

Large-scale biological classification of the seafloor in the region is provided by Spalding *et al* (2007) in the form of Marine Ecoregions of the World (see Fig. 6). These ecoregions are based on a global assessment of the biogeographic patterns of benthic (seafloor) and neritic (water column) biotas of coastal and shelf waters. In their system, the SEA4 area would be associated with the 'North Sea' ecoregion, while the adjacent SEA7 area would be associated with the 'Celtic Seas' ecoregion, with the adjoining Faroese waters classed as the 'Faroe Plateau'.

The Longhurst (2006) and Spalding *et al* (2007) schemes only deal with upper ocean and shallow seas environments and so should not be expected to reflect conditions at the deep-sea floor. Dinter (2001) provides a biogeographic classification of the OSPAR area that attempts to incorporate the important variations in environmental conditions (e.g. temperature) that occur with depth within this region (see Fig. 7). This scheme classifies the SEA4 area as 'Boreal' for the upper slope (<1000m) and 'Arctic Subregion' for deep waters (>1000m), in contrast to the SEA7 area that is classified as 'Boreal-Lusitanean' (<1000m) and 'Atlantic Subregion' (>1000m).

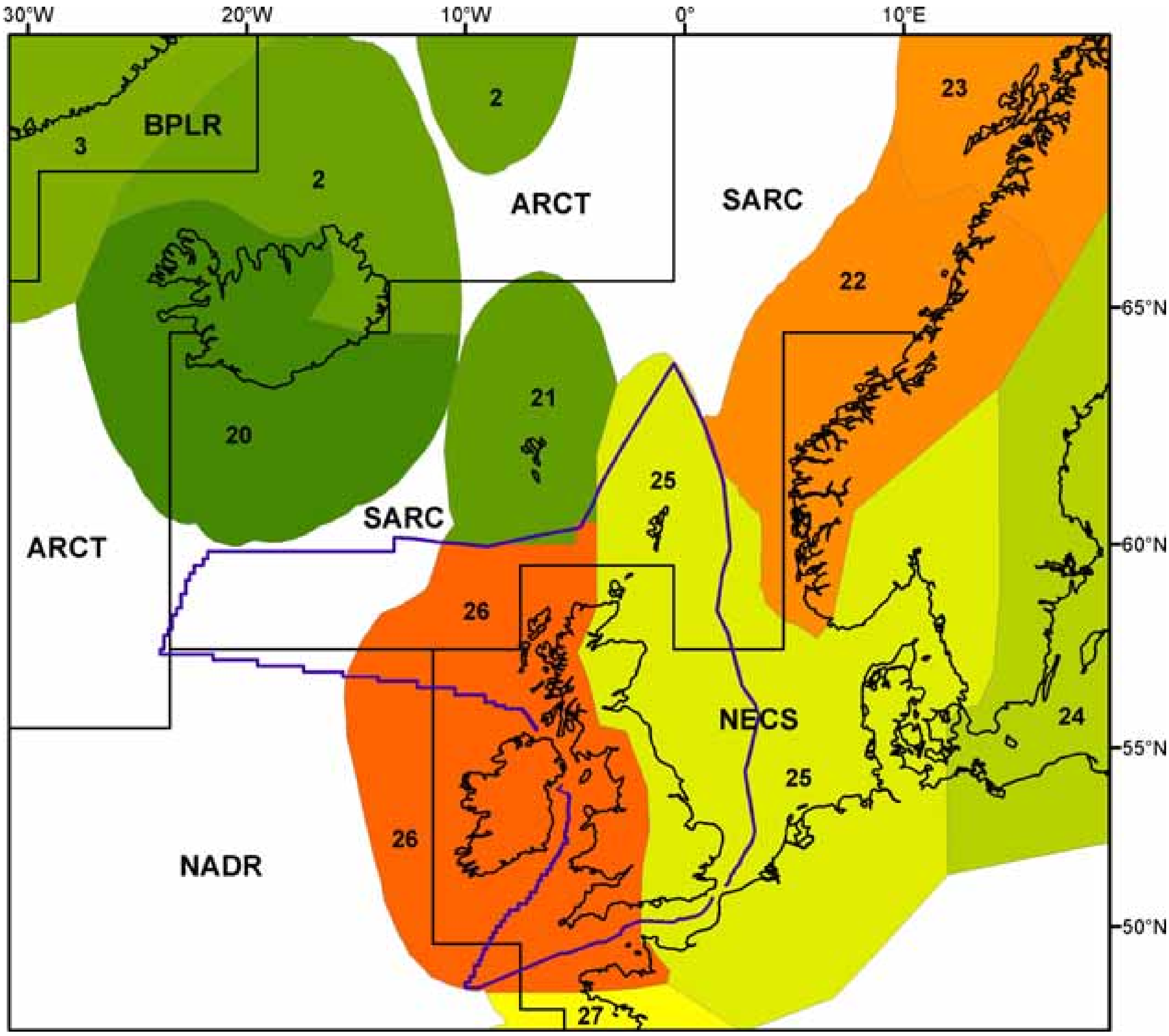

Figure 6. Longhurst (2006) biogeochemical provinces and Marine Ecoregions of the World (MEOW, Spalding *et al* 2007):

Longhurst provinces	**Marine Ecoregions (realm, province)**
BPLR – Boreal Polar	2 – N & E Greenland (Arctic)
ARCT – Atlantic Arctic	3 – E Greenland Shelf (Arctic)
SARC – Atlantic Subarctic	20 – S & W Iceland (Temperate Northern Atlantic, Northern European Seas)
NADR – North Atlantic Drift	21 – Faroe Plateau (Temperate Northern Atlantic, Northern European Seas)
NECS – NE Atlantic Shelves	22 – Southern Norway (Temperate Northern Atlantic, Northern European Seas)
	23 – N Norway & Finnmark (Temperate Northern Atlantic, Northern European Seas)
	24 – Baltic Sea (Temperate Northern Atlantic, Northern European Seas)
	25 – North Sea (Temperate Northern Atlantic, Northern European Seas)
	26 – Celtic Seas (Temperate Northern Atlantic, Northern European Seas)
	27 – S European Atlantic Shelf ((Temperate Northern Atlantic, Lusitanian)

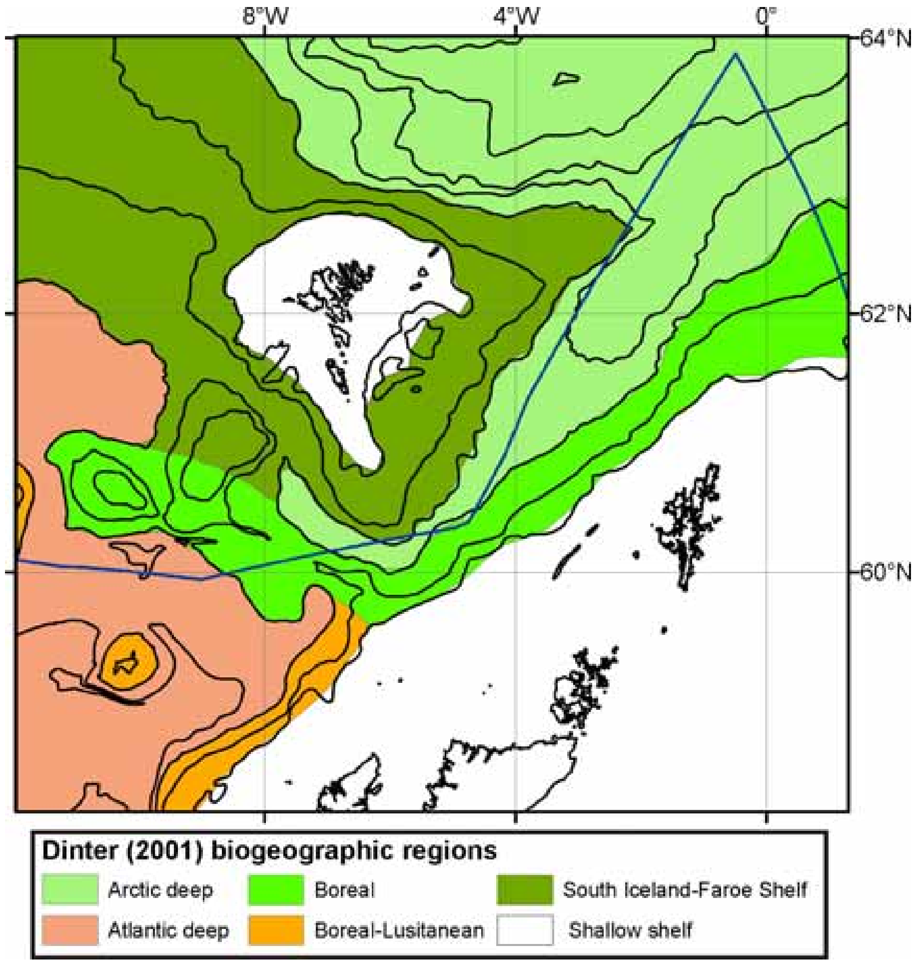

Figure 7. Approximate representation of Dinter's (2001) deep-sea (>1000m) and shelf & upper continental slope (<1000m) biogeographic regions for the OSPAR area.

2 Material

This work is based on the physical seabed samples collected during a series of five cruises carried out in the SEA4 area between 1996 and 2002:

Vessel (cruise no.)	Dates	Cruise report
S/V *Kommandor Jack*	25 Jul-22 Aug 2002	(see Bett, 2007c)
RRS *Charles Darwin* (123)	19 Jul-15 Sep 2000	(see Bett, 2007b)
RRS *Charles Darwin* (119)	13 Aug-14 Sep 1999	(see Bett & Jacobs, 2007)
RRS *Charles Darwin* (112)	19 May-24 Jun 1998	(see Bett, 1999)
RRS *Charles Darwin* (101)	14 Jul-20 Aug 1996	(see Bett, 1997)

The cruise reports referenced above provide full details of each cruise, including survey design, sampling equipment and methods, and metadata for each sample retained. Subsequent laboratory-based processing of the resultant environmental and biological samples is detailed by Bett (2000) and Bett (2001).

For the purposes of the present study all biological analyses are based on macrobenthos, seabed dwelling invertebrates recovered from sediment samples using 500µm mesh sieves. These samples were collected using a Megacore, box core or Day grab as appropriate to local seabed conditions. The use of multiple samplers was a practical necessity given the highly varied nature of the sediments within the SEA4 area, but will have introduced some bias to the apparent density and composition of the macrobenthos (Bett & Gage, 2000; Gage & Bett, 2005). This bias may be highly significant locally (e.g. 50% drop in apparent faunal density between box core and Megacore samples) but is unlikely to influence the regional-scale characterisations undertaken here. Samplers were generally employed in a depth ordered sequence, with the Day grab employed on the outer shelf / shelf edge, the box core on the upper slope ('iceberg plough mark zone'), and the Megacore in deeper waters. Consequently, depth-related trends in the macrobenthos may include some element of sampler bias; however, given the strong environmental trends with water depth (i.e. in bottom water temperature), sampler bias is likely a minimal component.

2.1 Biological data

Initial compilation of the appropriate AFEN and DTI macrobenthos (>500µm) data was undertaken by Drs Bhavani Narayanaswamy and Thom Nickell of the Scottish Association for Marine Science (SAMS). This involved the amalgamation of the datasets from relevant surveys and the removal of those data relating to locations outside the SEA4 area. The resultant dataset was further reduced by combining species within genera.

This genus-level dataset formed the starting point of the analyses carried out at the National Oceanography Centre, Southampton (NOC). Several runs of initial analyses were undertaken that revealed significant problems within these data. In some cases these were obvious nomenclatural errors, but more importantly the primary cause was highly variable taxonomic precision between surveys (e.g. most likely between laboratories / taxonomists). A second important flaw that became evident during the initial analyses was taxon-specific missing data within a particular set of North of Shetland study sites ('N' stations) sampled in 2000. These sites were consequently excluded from further study (as detailed below).

Several attempts at editing the genus-level dataset were undertaken to reduce the taxonomic precision problems, but none could sufficiently alleviate these issues. As a consequence the dataset was reconstructed at the family-level prior to the analysis reported below. This undoubtedly reduced the resolution (inter-location discriminating power) of the analyses but represented a necessary compromise towards coherence (ability to identify common faunas / biotopes).

Further reductions to the dataset were also necessary:

(a) Site NSDS13 was deleted, being only a very small sample ($0.02m^2$) which contained only 10 individual macrofaunal specimens.

(b) Sites NG2, NG3, NG4, NK1, NK2, NK3, NK4, NN1, NN2, NN4, NR1, NR2, NR3, NR4, NR5, NR6, NU1, NU2, NU3, NU4, NU5, NW1, NW2, NW3, NW4 and NW5 were deleted as important polychaete taxa appeared to be missing (this was assessed by reference to immediately surrounding stations and the dataset as a whole).

(c) Taxa originally recorded in the surveys as Sipuncula, Polychaeta, AMPHIPODA, Gammaridea, Isopoda, Tanaidacea, Cumacea, Caridea, Gastropoda, Mesogastropod, Neogastropoda, Opistobranchia, ?Opistobranchia, Nudibranchia, Scaphopoda, Pelecypoda, Asteroidea, Ophiuroidea, OPHIURIDA, Echinoidea, Holothuriodea and Unknown phylum were deleted as having inappropriate taxonomic resolution i.e. lower taxonomic level (family, genus, species) data were available.

2.2 Environmental data – samples

An extensive suite of environmental parameters was included in the original AFEN and DTI sampling programmes (Bett, 2000). However, many of these concerned potential hydrocarbon and 'heavy metal' contamination and have been discounted here. Sedimentology is, however, likely to be of broad-scale biological significance and has been included in the analyses below. Sediment particle size data, particularly mud content (i.e. by weight percentage of particles <63 μm), were collated from the five cruises and matched by site to the macrobenthos data.

2.3 Environmental data – derived

2.3.1 Bathymetry

Sample depth, as used in the analyses below, employed is that recorded during the sampling process, averaged where multiple sampler deployments were made at any one site. For mapping and other presentation purposes, general bathymetry and depth contours from GEBCO CE (IOC, IHO, BODC, 2003) have been used throughout.

2.3.2 Hydrographic data

The importance of bottom water temperatures to the distribution of deep-sea benthos in the waters to the west of Scotland has long been recognised (Thomson, 1873; Bett, 2001). Consequently, bottom water temperature data have been incorporated in the analyses that follow. These data were obtained from the online archive of the British Oceanographic Data Centre[2]. Data relating to the SEA4 area (Faroe Bank Channel / Faroe-Shetland Channel / Norwegian Basin) where drawn from 99 CTD (conductivity-temperature-depth instrument) casts originally collected within the 1996-2002 period (i.e. complimentary to the AFEN and DTI field sampling programmes), as previously employed and published by Narayanaswamy *et al* (2010). Comparative data for the SEA7 area (Northern Rockall Trough) were drawn from 43 CTD casts similarly collected in the 1996-2002 period.

These CTD data were compiled, binned into 10-meter depth bands and descriptive statistics derived (minimum, mean, maximum, range and standard deviation), these values were then smoothed (4253H-twice procedure) in depth order. All statistical operations were carried out in Minitab 16 software. Sample depth was used to match biological data to these temperature statistics.

World Ocean Atlas temperature data were also consulted, in particular the ¼º-grid 2001 dataset (Boyer *et al* 2005). These data provide a good visual summary of bottom water conditions in the regions (Fig. 8). However, this dataset has limited depth resolution, predominantly 100m, in the depth range of interest.

[2] https://www.bodc.ac.uk/data/online_delivery/nodb/

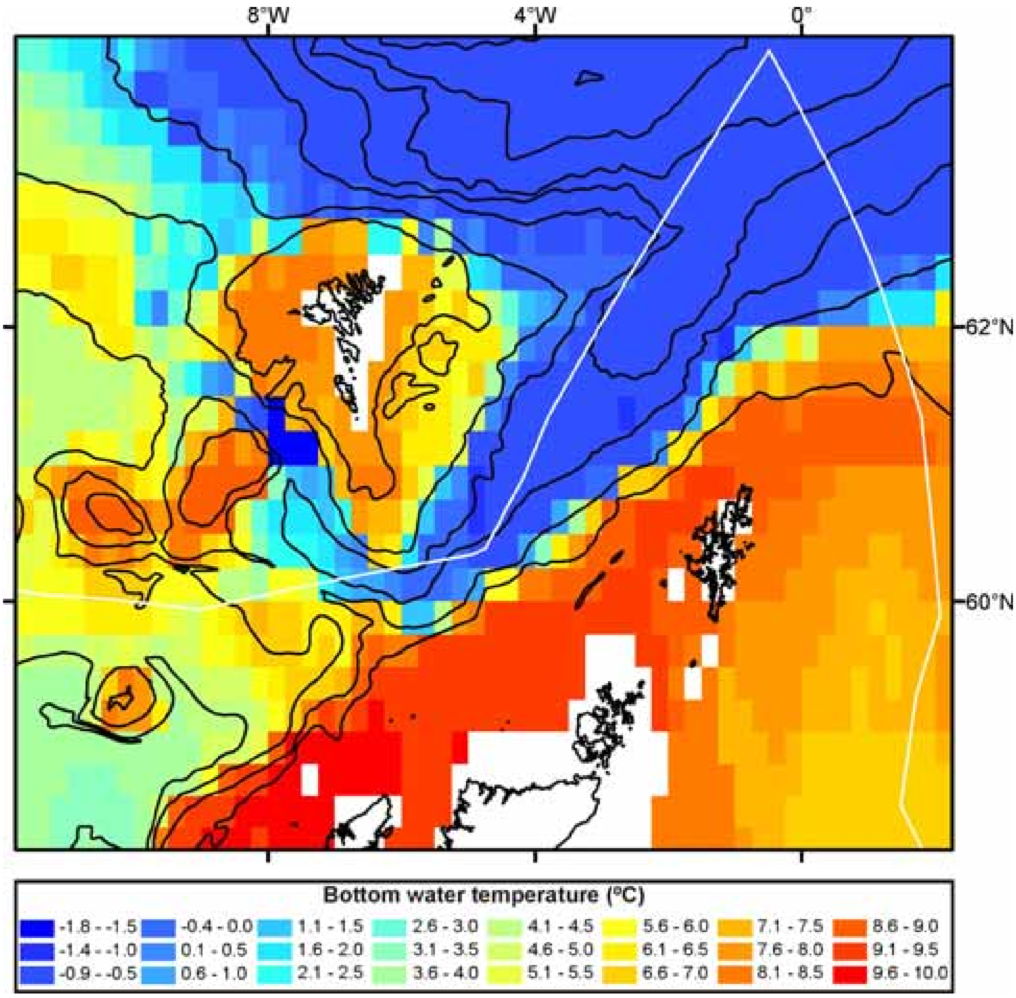

Figure 8. Bottom water temperatures in deep-water areas to the north and west of Scotland, derived from the World Ocean Atlas ¼°-grid 2001 dataset (Boyer *et al* 2005).

3 Analyses

3.1 Environmental data

3.1.1 Hydrography

The hydrography of the Faroe-Shetland Channel, and adjacent Faroe Bank Channel and Norwegian Basin, is complex and highly dynamic (Turrell *et al* 1999). Figure 9 summarises the hydrographic data assessed for the SEA4 area and contrasts it with comparable data from the adjacent SEA7 area. Note the exceptional variability in temperature in the c. 200-700m depth band of the SEA4 area, the uniform 'Arctic' conditions below c. 700m water depth, and the strikingly different conditions in the SEA7 area.

3.1.2 Sedimentology

Sediment mud content (by weight percentage of particles <63µm) was summarised by depth band, with sites grouped in depth order to give n=15 (n=18 in deepest band) and presented as median and interquartile ranges (see Fig. 10). Mud content generally increases with depth in a somewhat exponential fashion. Mud content remains at very low values on the outer shelf and upper slope, to c. 600m water depth, before increasing rapidly thereafter. It is highly variable around 900-1100m water depth, becoming uniformly higher with greater depth.

The general trend in mud content with water depth is apparent when assessed spatially (see Fig. 11); however, local variations are also apparent. As noted by Masson *et al* (2003) there is a trend of increasing mud content from southwest to northeast with the SEA4 area. This is most obvious in a comparison of the shelf edge and upper slope (200-1000m) north of Shetland with the corresponding depth interval to the west of Shetland.

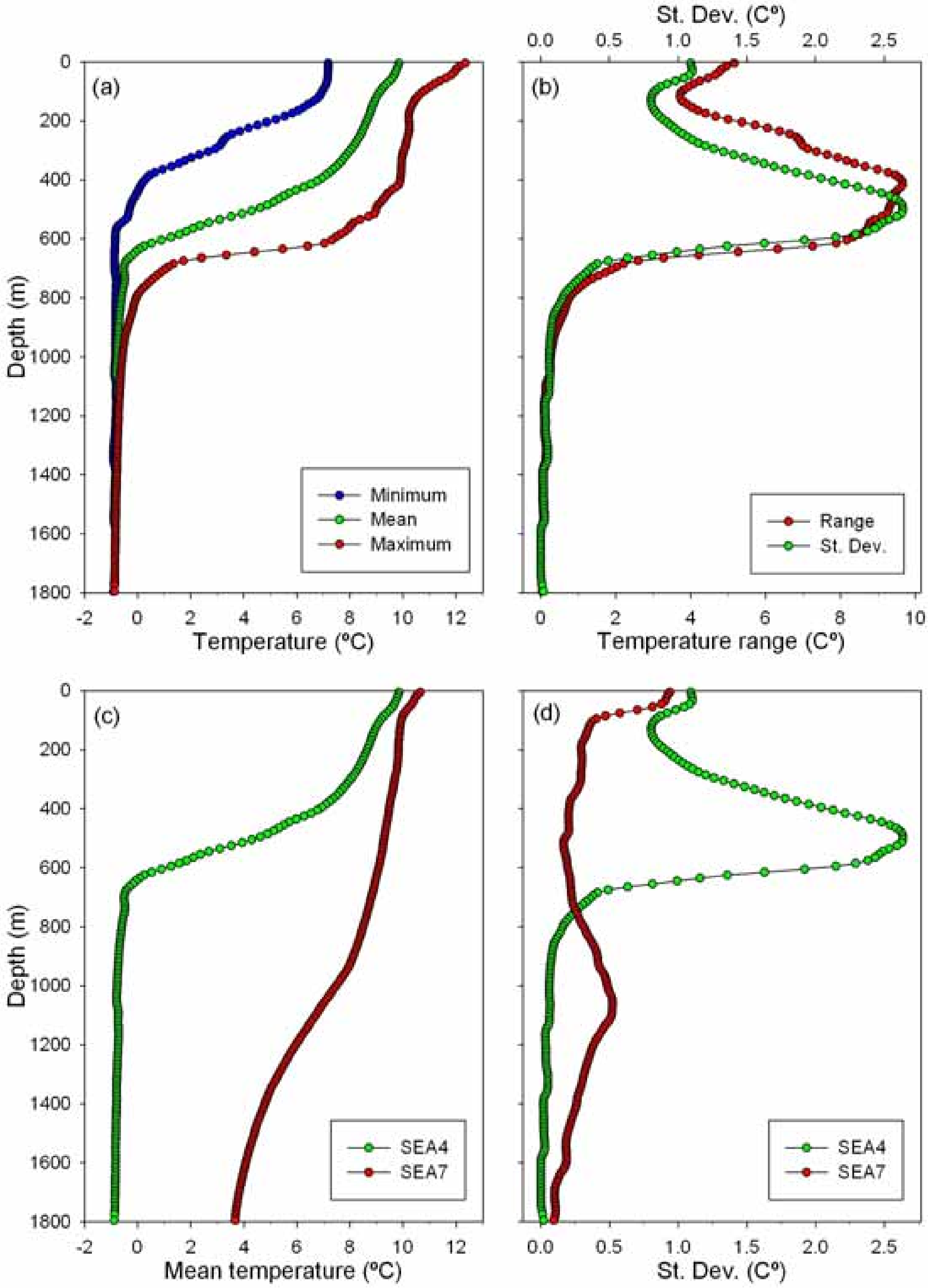

Figure 9. Water column temperature statistics for the Faroe Bank Channel / Faroe-Shetland Channel / Norwegian Basin (SEA 4 area) and Northern Rockall Trough (SEA 7 area). Panels (a) and (b) illustrate temperature range and variability in the SEA 4 area. Panels (c) and (d) compare mean temperature and standard deviation (St. Dev.) between SEA4 and 7 areas.

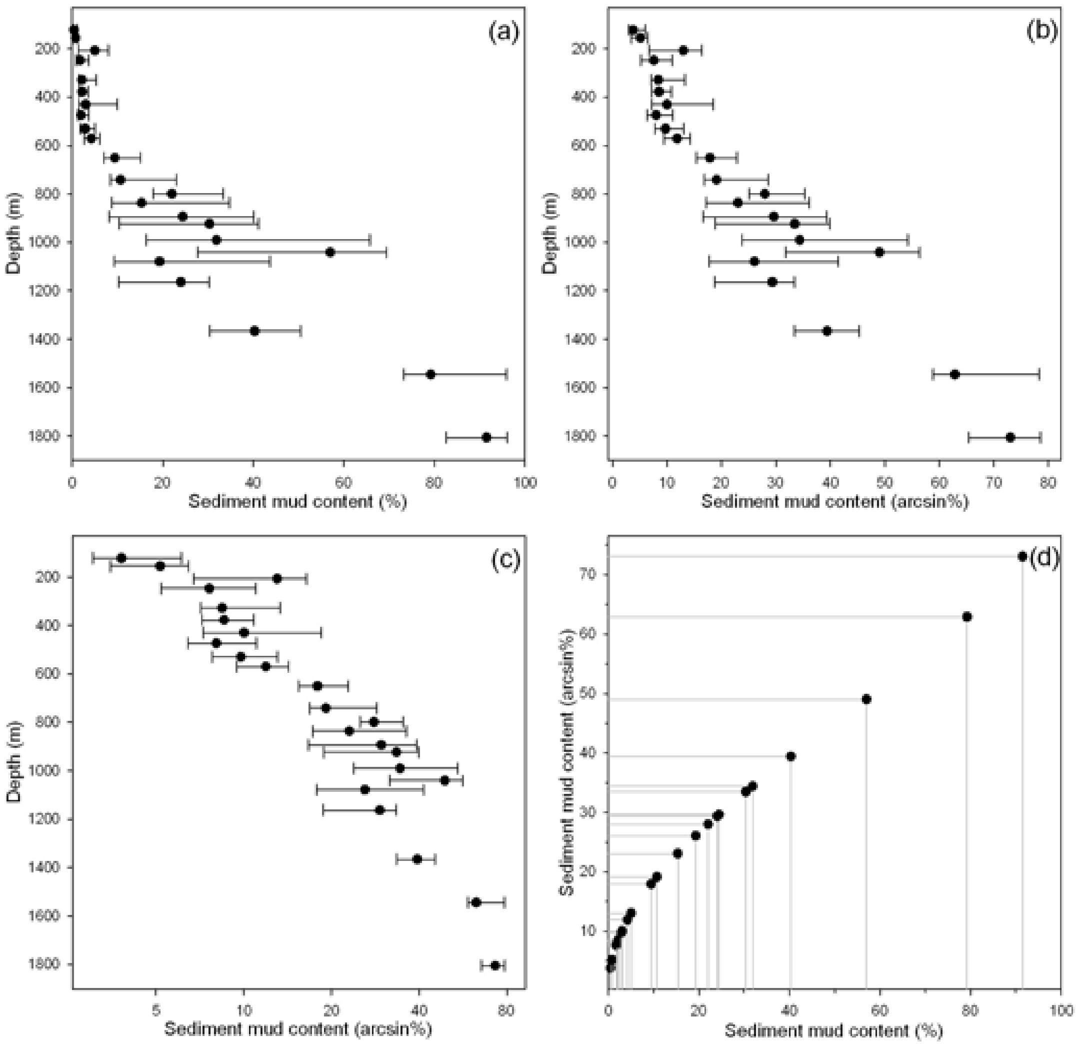

Figure 10. Sediment mud content assessed by depth in the SEA4 area. (a) mud-percentage. (b) arcsin transformation of mud-percentage. (c) arcsin transformation of mud-percentage on log scale. (d) comparison on mud-percent and its arcsin transformation.

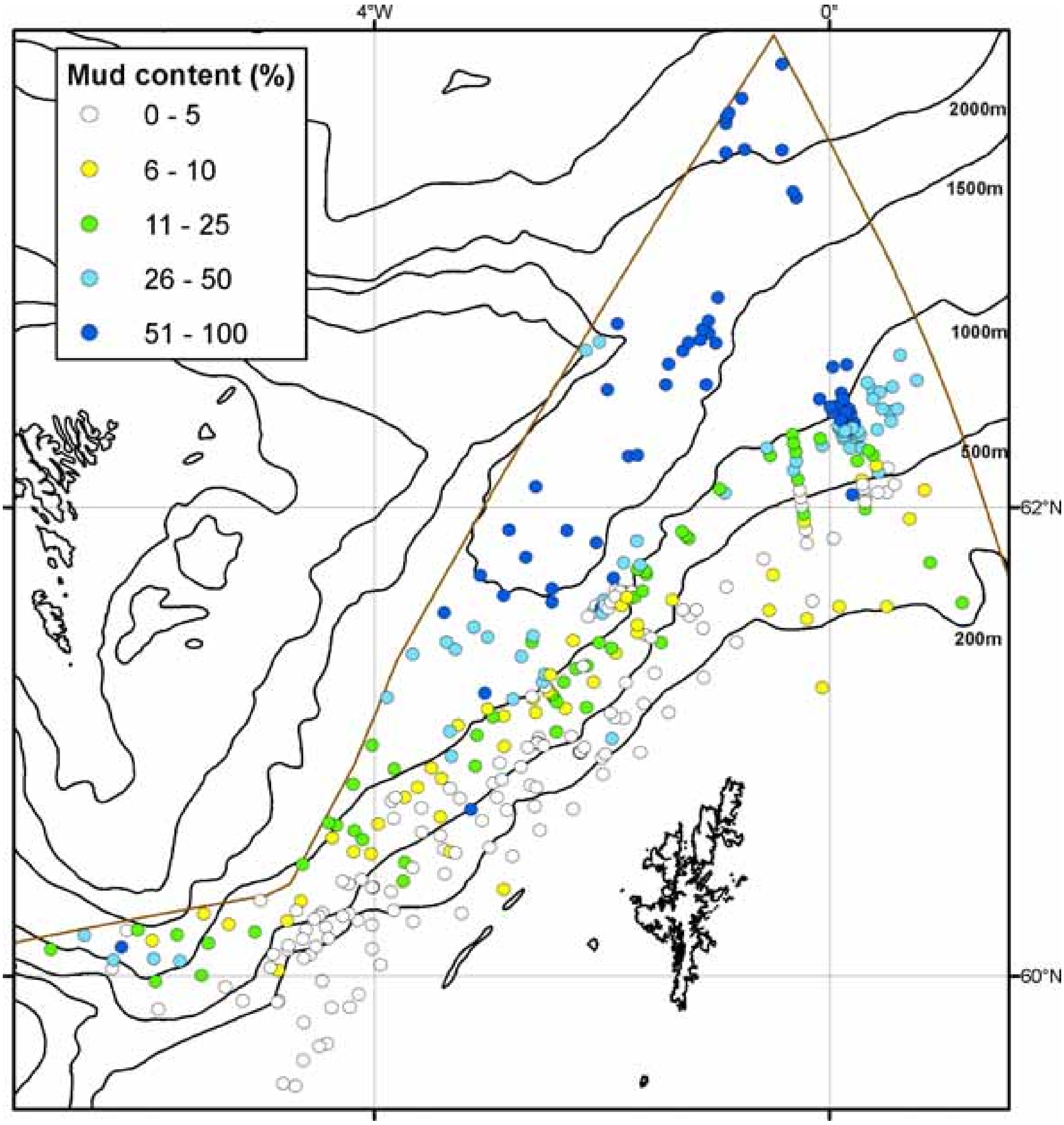

Figure 11. Spatial variation in sediment mud content in the SEA4 area.

3.2 Biological data

The main task of this study is to develop a classification of biological assemblages to serve as the basis of biotope identifications / descriptions. The starting point of these analyses is a matrix of 336 sampled locations and 248 families (or higher taxa) of macrobenthos, the element of the matrix being the density (abundance per unit area) of a given taxon at a particular location. Multivariate statistical techniques were applied to this matrix to reduce its dimensionality, e.g. to group families together where they have a common distribution among locations (classification analysis) or to replace the biological data with derived variables that attempt to summarise common trends in the distribution of the fauna (ordination analysis). Both approaches were employed, classification to produce groups of sites with relatively homogenous faunas, and ordination to examine the potential relationships between those faunas and environmental conditions.

The first technique employed was hierarchical agglomerative clustering, commonly used in marine ecology and generally referred to as cluster analysis. Sites are gathered together on the basis of faunal similarity, the most similar first, the least similar last, producing a hierarchical arrangement of subgroups typically displayed in the form of a dendrogram. Biotope definition requires additional information on environmental conditions, ordination techniques (nMDS, DCA, CCA) were therefore used to examine how faunal composition varied with environmental factors. Finally, a 'hybrid' technique, Two-Way INdicator SPecies Analysis (TWINSPAN), was employed to provide an alternative classification to serve as a test and comparator to the original cluster analysis. TWINSPAN is an ordination-based technique that produces a hierarchical divisive classification, repeatedly dividing the sites into two groups (i.e. 2, 4, 16 groups etc).

3.2.1 Primary classification (cluster) analysis

Cluster analysis was undertaken using the Primer 6 software package (Clarke & Gorley, 2006). The primary sites x families data matrix was log(x+1) transformed prior to calculation of the Bray-Curtis similarity coefficient and a dendrogram formed using a group-average clustering strategy (see Clarke, 1993 for detailed methodology). The resultant dendrogram (see Fig. 12 parts 1 & 2) was subjectively interpreted to identify coherent groups of sites (i.e. clusters). Eleven clusters (1-11) were recognised having broadly comparable levels of faunal similarity (40-55%).

Figures 13 and 14 illustrate the spatial distribution of these clusters. To simplify visualisation some cluster groups have been amalgamated in these plots: groups 3-6 are shown as a common 'upper slope' category, and groups 9 and 10 have been combined to a single 'lower slope north' type. The spatial distribution of clusters exhibits both a clear bathymetric banding and a spatially coherent SE-NW trend in shelf break and lower slope faunal groupings.

The environmental relevance of these clusters was examined in an 'environmental space' plot of depth and sediment mud content within clusters (see Fig. 15). The clusters appear to form coherent depth bands with additional sediment mud content variations. At a higher level they also appear to match general water mass conditions, i.e. groups 1-6 in the warmer, variable upper water masses, groups 7-11 in the more uniform, Arctic, lower water masses. The groups were characterised as follows:

Groups 1 & 2	"shelf break", warm NE Atlantic waters, relative thermal stability; group 2 a North of Shetland variant with increased mud content.
Groups 3-6	"upper slope", highly dynamic, varied water masses, extreme thermal variability.
Groups 8-10	"lower slope", sub-zero Arctic waters, highly stable thermal regime; groups 9 and 10 northern variants with increased mud content.
Group 7	"deep channel", sub-zero Arctic waters, highly stable thermal regime.
Group 11	"Norwegian Basin", sub-zero Arctic waters, highly stable thermal regime, high mud content.

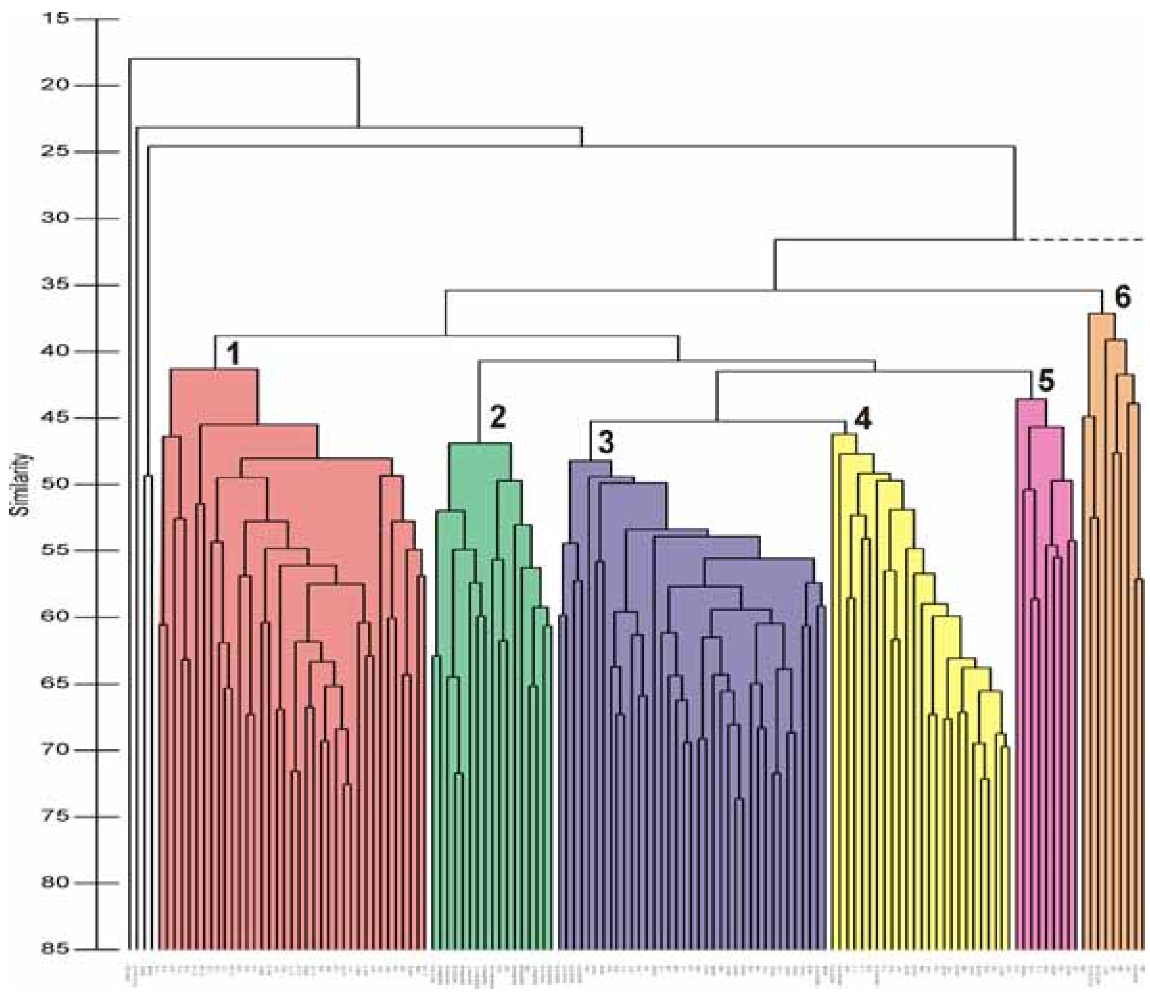

Figure 12 - Part 1. Hierarchical agglomerative cluster analysis of SEA4 area family-level macrobenthos data. Clusters recognised are numbered and colour-coded.

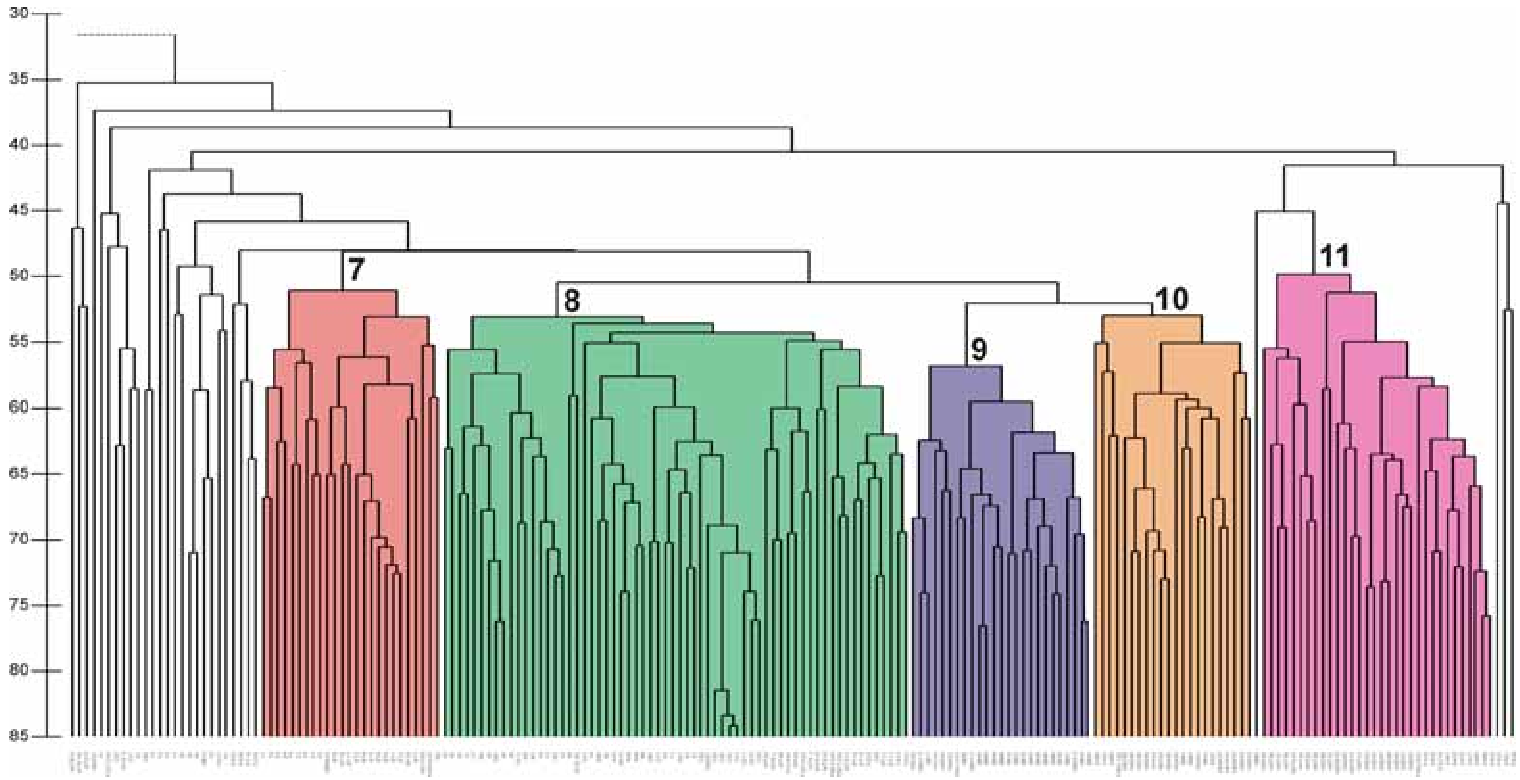

Figure 12 - Part 2. Hierarchical agglomerative cluster analysis of SEA4 area family-level macrobenthos data. Clusters recognised are numbered and colour-coded.

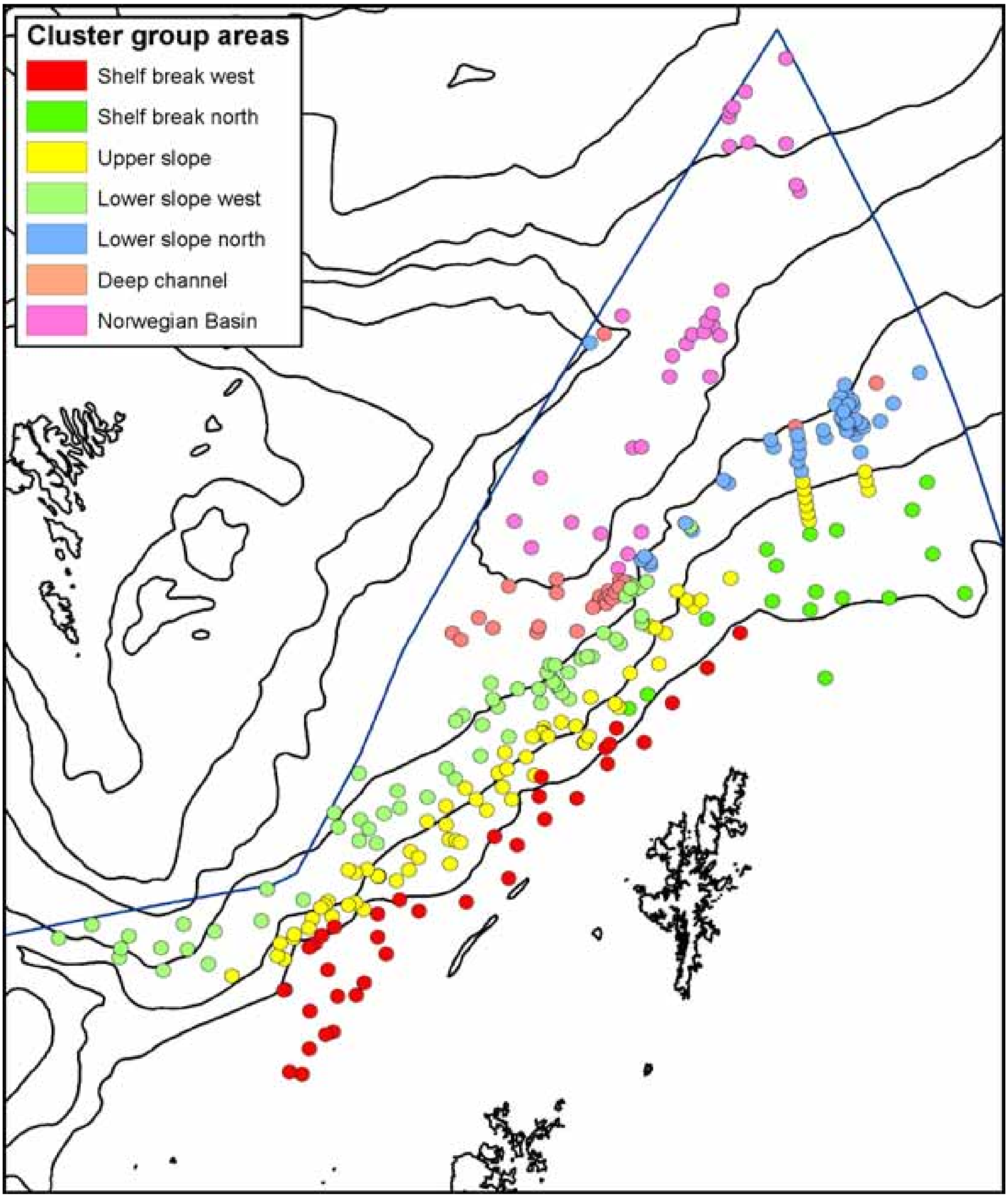

Figure 13. Spatial distribution of hierarchical agglomerative cluster groups of SEA4 area family-level macrobenthos data. (Simplified classification, see text).

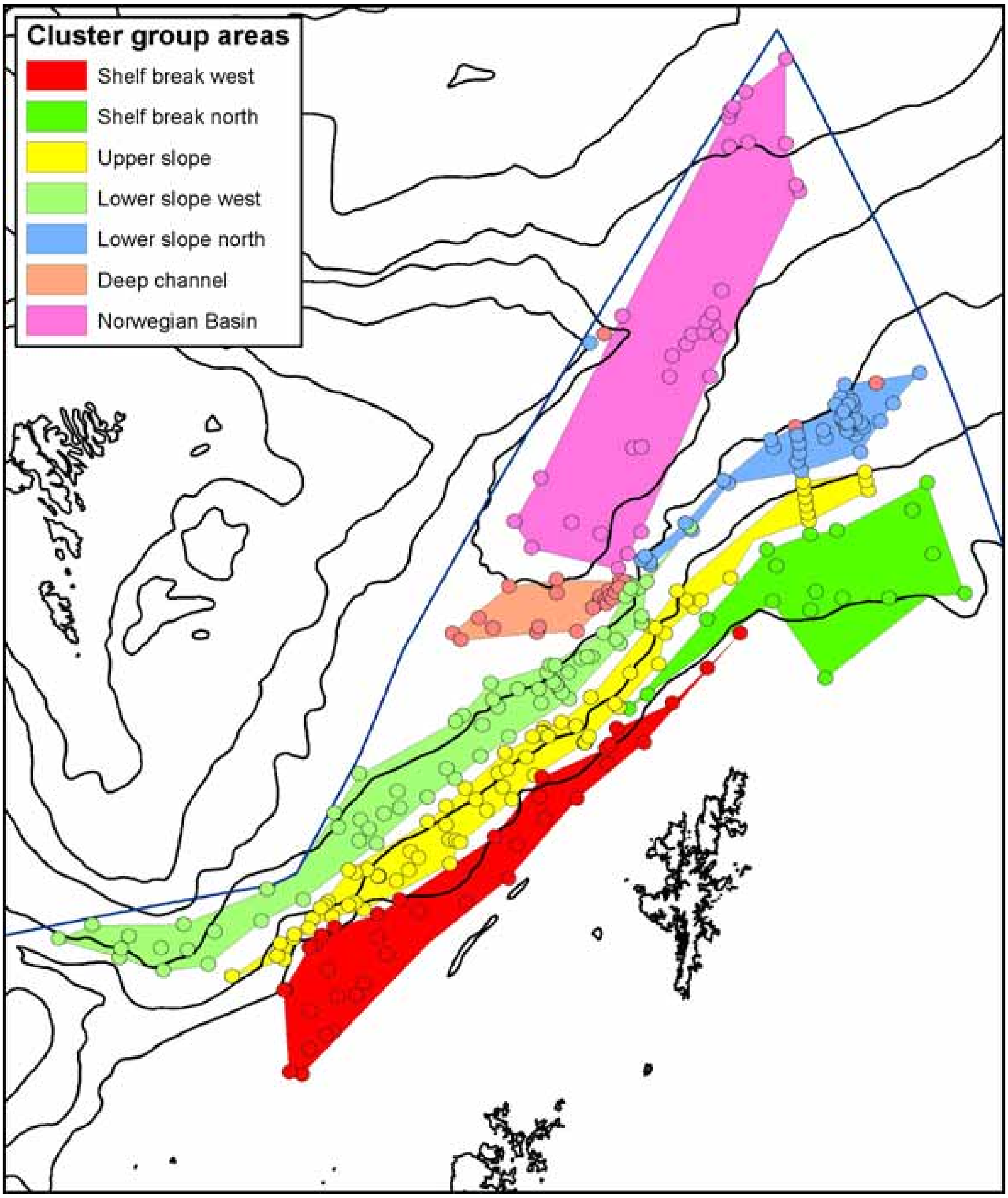

Figure 14. Spatial distribution of hierarchical agglomerative cluster groups of SEA4 area family-level macrobenthos data with areas of extent indicated. (Simplified classification, see text).

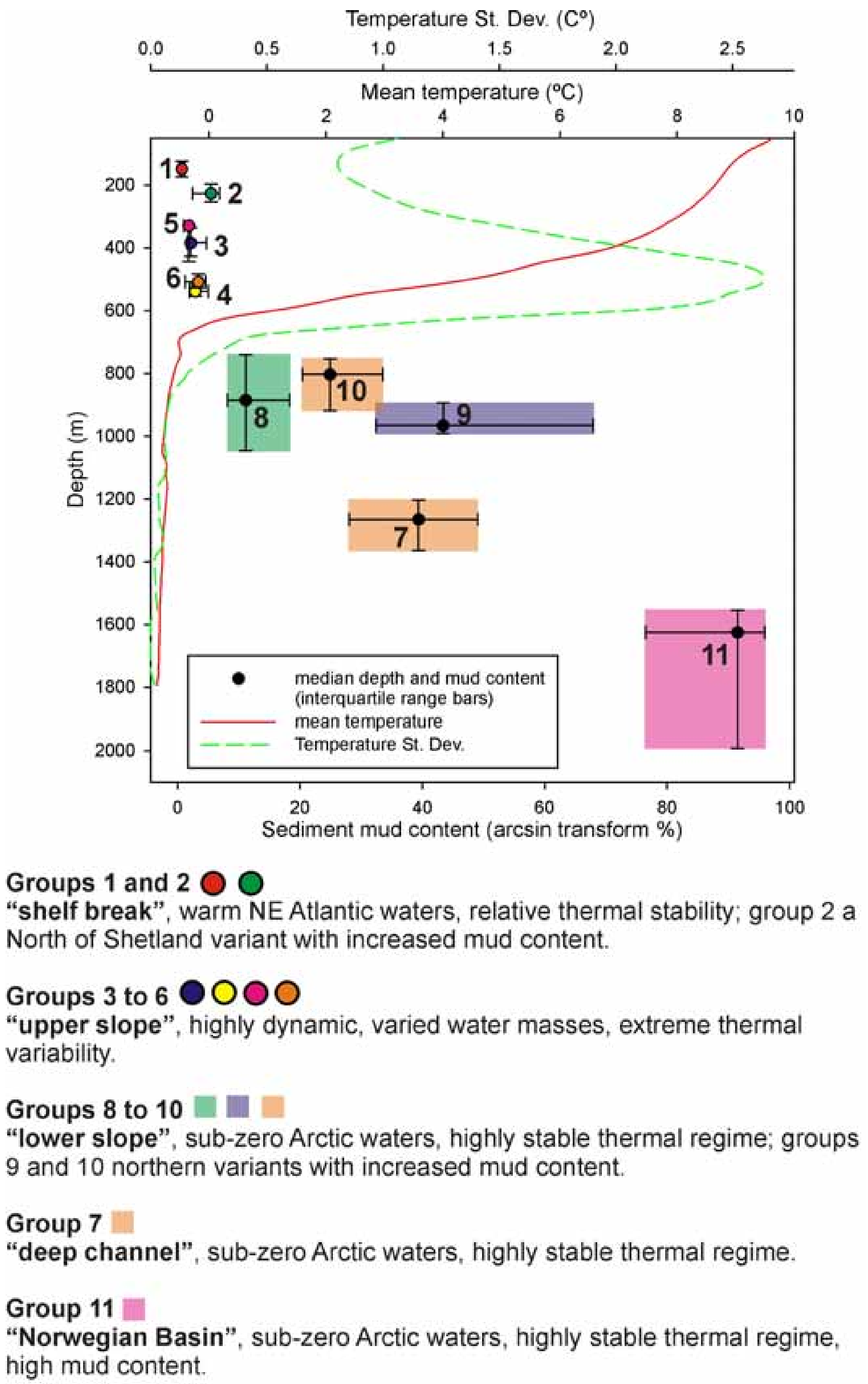

Figure 15. Environmental space plot of SEA4 area family-level macrobenthos clusters 1-11. Depth and sediment mud content of sites within clusters are plotted as median and interquartile range. (Numeric- and colour-coding as per Figure 12).

Biological characterisation of the site groups (clusters) identified above was undertaken using the SIMPER (similarity percentages; Clarke, 1993) routine of the Primer 6 software package. SIMPER assesses the contribution (importance) of individual families to within-group similarity and between-group dissimilarity. To compact the extensive SIMPER output it has been limited as follows:

(a) Only the top ten families contributing to within-group characterisation and between-group discrimination have been listed.

(b) Only spatially and environmentally relevant between-group comparisons are listed (i.e. not all possible between-group assessments are shown). The comparisons included here are illustrated graphically in Fig. 16.

The abbreviated SIMPER output listing is given in Table 1. As an example of its use consider the characterisation and discrimination of 'warm' and 'cold' faunas, i.e. respectively cluster groups 1-6 and 7-11.

The polychaete families Spionidae, Syllidae, Terebellidae, Oweniidae, and Capitellidae are typically abundant and characteristic of the upper slope (150-600m). In deeper waters the polychaete families Cirratulidae, Oweniidae, Amphinomidae and Maldanidae, together with the sipunculid family Golfingiidae are typically abundant and characteristic. Discrimination of the faunas is indicated by switching in the abundance of families from abundant to rare as follows:

Family	**Typical abundance (indiv.m^{-2}) in the 'warm' fauna (Clusters 1-6)**	**Typical abundance (indiv.m^{-2}) in the 'cold' fauna (Clusters 7-11)**
Amphinomidae	2	97
Syllidae	45	0
Golfingiidae	2	71
Maldanidae	2	61
Cirratulidae	7	131

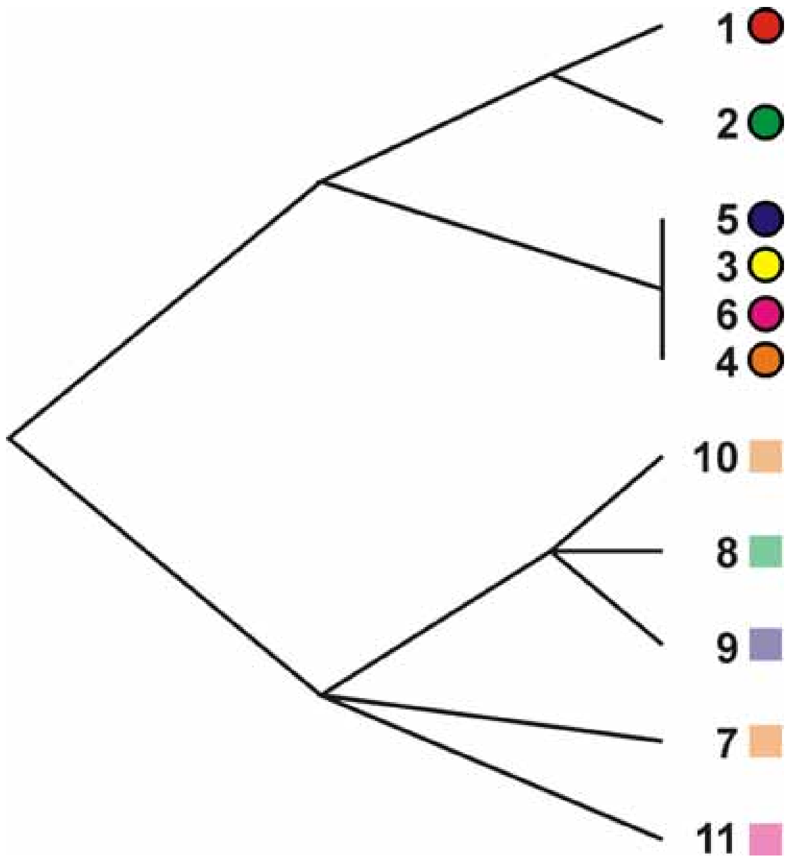

Figure 16. Representational diagram of the SEA4 macrobenthos family-level cluster groups illustrating those nodes that were assessed for biological characterisation (SIMPER analysis). NB this is not a dendrogram, it does not represent the hierarchical structure of the family-level cluster analysis.

Table 1. Characterising and discriminating families for SEA4 area macrobenthos clusters 1-11. Note that a ln(x+1) transformation of faunal density has been used throughout these analyses, "Av.Abund" column in the tables below are transformed units, e.g. a value of 5 corresponds to 400 individuals per square meter, 4 to 150, 3 to 55, 2 to 20, 1 to 2 etc.

	Characterise	G1-6				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
1	Spionidae	5.09	3.56	2.9	8.3	8.3
2	Syllidae	3.83	2.39	1.83	5.57	13.87
3	Terebellidae	3.86	2.37	2.1	5.53	19.4
4	Oweniidae	3.77	2.27	1.91	5.29	24.69
5	Capitellidae	3.31	2.09	1.82	4.87	29.56
6	Glyceridae	3.29	1.98	1.69	4.62	34.18
7	Ampeliscidae	3.47	1.97	1.47	4.58	38.77
8	Paraonidae	3.28	1.87	1.39	4.35	43.12
9	Nemertea	2.68	1.47	1.34	3.42	46.53
10	Sabellidae	2.76	1.4	1.14	3.26	49.79

Discriminate	G1-6	G7-11				
Families	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
Amphinomidae	1.03	4.58	1.6	1.96	2.4	2.4
Syllidae	3.83	0.07	1.58	2.36	2.37	4.77
Golfingiidae	1.12	4.28	1.46	1.72	2.18	6.95
Maldanidae	1.09	4.12	1.44	1.62	2.15	9.11
Cirratulidae	2.07	4.88	1.24	1.54	1.86	10.97
Yoldiidae	1.12	3.37	1.15	1.5	1.72	12.69
Ampeliscidae	3.47	1.99	1.01	1.29	1.51	14.2
Glyceridae	3.29	1.64	0.99	1.33	1.48	15.69
Thyasiridae	2.17	2.87	0.97	1.24	1.45	17.13
Terebellidae	3.86	2.74	0.91	1.17	1.37	18.5

	Characterise	G7-11				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
1	Cirratulidae	4.88	3.94	4.03	7.97	7.97
2	Oweniidae	4.77	3.7	2.39	7.49	15.46
3	Amphinomidae	4.58	3.56	2.72	7.21	22.67
4	Golfingiidae	4.28	3.26	2.15	6.59	29.26
5	Maldanidae	4.12	2.72	1.49	5.51	34.77
6	Paraonidae	4.02	2.69	1.44	5.44	40.21
7	Spionidae	3.97	2.6	1.74	5.25	45.46
8	Yoldiidae	3.37	2.19	1.43	4.43	49.89
9	Capitellidae	3.31	2.13	1.08	4.3	54.19
10	Phoxocephalidae	2.78	1.62	1.13	3.27	57.47

Table 1 continued. Characterising and discriminating families for SEA4 area macrobenthos clusters 1-11.

	Characterise	G1-2				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
1	Spionidae	5.61	4.26	5.26	9.34	9.34
2	Glyceridae	3.73	2.52	2.37	5.52	14.86
3	Syllidae	3.76	2.44	1.71	5.34	20.21
4	Oweniidae	3.69	2.15	1.67	4.72	24.93
5	Terebellidae	3.38	2.13	2.11	4.68	29.6
6	Nemertea	3.01	1.86	1.9	4.08	33.68
7	Paraonidae	3.19	1.66	1.14	3.64	37.33
8	Capitellidae	2.84	1.64	1.28	3.59	40.92
9	Ampeliscidae	2.88	1.55	1.18	3.4	44.32
10	Cirratulidae	2.58	1.36	1.16	2.97	47.3

Discriminate	G1-2	G3-6				
Families	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
Enchytraeidae	0.84	2.97	0.98	1.51	1.62	1.62
Spatangoida	2.52	0.31	0.96	1.35	1.58	3.2
Thyasiridae	1.37	2.71	0.92	1.42	1.52	4.72
Dorvilleidae	2.56	1.57	0.86	1.19	1.43	6.15
Ampharetidae	2.26	2.79	0.82	1.19	1.35	7.5
Tubificidae	0.55	2.2	0.8	1.23	1.33	8.83
Ampeliscidae	2.88	3.87	0.79	1.18	1.31	10.14
Sabellidae	2.22	3.12	0.79	1.23	1.31	11.45
Aoridae	1.59	2.09	0.78	1.19	1.29	12.74
Phoxocephalidae	1.2	2.3	0.78	1.27	1.29	14.03

	Characterise	G3-6				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
1	Spionidae	4.73	3.16	2.45	6.84	6.84
2	Terebellidae	4.19	2.58	2.13	5.57	12.41
3	Capitellidae	3.63	2.42	2.67	5.23	17.65
4	Syllidae	3.88	2.35	1.92	5.08	22.73
5	Oweniidae	3.83	2.34	2.11	5.06	27.79
6	Ampeliscidae	3.87	2.3	1.78	4.96	32.75
7	Paraonidae	3.34	2.01	1.63	4.34	37.09
8	Sabellidae	3.12	1.73	1.46	3.75	40.84
9	Glyceridae	3	1.67	1.45	3.6	44.44
10	Enchytraeidae	2.97	1.57	1.3	3.4	47.84

Table 1 continued. Characterising and discriminating families for SEA4 area macrobenthos clusters 1-11.

	Characterise	G1				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
1	Spionidae	5.75	4.46	5.2	8.96	8.96
2	Syllidae	4.31	3.13	3.15	6.29	15.25
3	Glyceridae	4.06	2.9	3.36	5.81	21.07
4	Dorvilleidae	3.16	1.96	1.46	3.94	25
5	Oweniidae	3.43	1.91	1.4	3.84	28.85
6	Ampeliscidae	3.23	1.86	1.35	3.73	32.58
7	Terebellidae	3.11	1.85	1.75	3.72	36.3
8	Nemertea	3.02	1.82	1.72	3.66	39.96
9	Phyllodocidae	2.87	1.63	1.38	3.28	43.25
10	Polynoidae	2.84	1.56	1.57	3.14	46.38

Discriminate	G1	G2				
Families	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
Thyasiridae	0.51	3.26	1.17	1.52	1.95	1.95
Ampharetidae	1.62	3.67	1.09	1.33	1.82	3.77
Yoldiidae	0.37	2.85	1.09	1.74	1.82	5.6
Paraonidae	2.41	4.88	1.08	1.4	1.8	7.39
Dorvilleidae	3.16	1.27	1.02	1.47	1.71	9.1
Polynoidae	2.84	0.42	0.99	1.74	1.65	10.75
Sabellidae	1.56	3.68	0.97	1.42	1.62	12.37
Ischyroceridae	2.45	0.6	0.89	1.32	1.49	13.86
Ophiuridae	2.3	0.86	0.86	1.21	1.44	15.3
Spatangoida	2.02	3.61	0.86	1.37	1.44	16.73

	Characterise	G2				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*
1	Spionidae	5.32	3.88	6.56	7.57	7.57
2	Paraonidae	4.88	3.49	5.26	6.82	14.39
3	Terebellidae	3.97	2.84	6.69	5.54	19.93
4	Oweniidae	4.25	2.73	3.06	5.34	25.27
5	Capitellidae	3.63	2.63	6.81	5.14	30.41
6	Spatangoida	3.61	2.45	4	4.79	35.2
7	Sabellidae	3.68	2.43	4.72	4.75	39.95
8	Cirratulidae	3.17	2	1.74	3.91	43.86
9	Ampharetidae	3.67	2	1.33	3.9	47.76
10	Nemertea	2.99	1.93	2.51	3.77	51.53

Table 1 continued. Characterising and discriminating families for SEA4 area macrobenthos clusters 1-11.

	Characterise	G8-10					Discriminate	G8-10	G7				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*	*Families*	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
1	Cirratulidae	5.15	3.93	5.98	7.3	7.3	Thyasiridae	3.53	0.94	1.4	1.52	2.73	2.73
2	Maldanidae	4.98	3.73	4.36	6.93	14.24	Capitellidae	2.42	4.89	1.18	1.3	2.3	5.03
3	Amphinomidae	4.86	3.61	3.5	6.71	20.94	Scalibregmatidae	3.08	0.93	1.15	1.52	2.26	7.28
4	Oweniidae	4.49	3.09	2.12	5.75	26.69	Spionidae	4.56	2.7	1.13	1.28	2.21	9.49
5	Spionidae	4.56	3.02	2.23	5.61	32.3	Sphyrapidae	2.37	0.09	1.05	1.19	2.06	11.55
6	Golfingiidae	4.09	2.71	1.85	5.04	37.34	Ophiuridae	2.27	1.54	0.99	1.2	1.93	13.48
7	Yoldiidae	3.85	2.54	1.93	4.73	42.07	Terebellidae	3.27	2.27	0.98	1.21	1.92	15.4
8	Paraonidae	3.59	2.11	1.31	3.93	46	Ampharetidae	3.04	1.65	0.98	1.33	1.91	17.3
9	Thyasiridae	3.53	2.01	1.34	3.73	49.72	Ampeliscidae	2.59	1.56	0.95	1.24	1.85	19.15
10	Scalibregmatidae	3.08	1.85	1.45	3.43	53.16	Glyceridae	2.22	0.88	0.93	1.21	1.81	20.96

	Characterise	G7					Discriminate	G7	G11				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*	*Families*	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
1	Oweniidae	5.71	5.43	8.55	9.82	9.82	Maldanidae	4.52	0.81	2.03	2.16	3.87	3.87
2	Capitellidae	4.89	4.72	4.45	8.53	18.34	Myriotrochidae	0.78	4.05	1.83	1.98	3.49	7.36
3	Cirratulidae	4.74	4.45	4.55	8.05	26.39	Enteropneusta	0.61	3.37	1.55	1.89	2.95	10.31
4	Maldanidae	4.52	4.21	4.85	7.6	33.99	Aspidosiphonidae	0.18	2.71	1.43	1.08	2.72	13.03
5	Golfingiidae	4.48	4.19	4.65	7.58	41.57	Thyasiridae	0.94	2.1	1.1	1.14	2.11	15.14
6	Paraonidae	4.6	4.16	4.23	7.51	49.08	Leptognathiidae	2.49	1.37	1.1	1.28	2.09	17.23
7	Amphinomidae	4.43	3.89	2.81	7.02	56.1	Ophiuridae	1.54	2.02	1.09	1.16	2.09	19.32
8	Yoldiidae	2.76	1.91	1.1	3.46	59.56	Arcidae	0.56	2.21	1.09	1.24	2.08	21.39
9	Spionidae	2.7	1.71	1.12	3.09	62.64	Paraonidae	4.6	5.03	1.08	1.36	2.06	23.45
10	Leptognathiidae	2.49	1.64	1.05	2.96	65.6	Sabellidae	2.06	1.46	1.02	1.18	1.94	25.39

Table 1 continued. Characterising and discriminating families for SEA4 area macrobenthos clusters 1-11.

	Characterise	G11					Discriminate	G8-10	G11				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*	*Families*	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
1	Capitellidae	5.17	5.34	4.73	9.62	9.62	Maldanidae	4.98	0.81	2.03	2.31	3.46	3.46
2	Oweniidae	5	4.91	4.77	8.85	18.47	Myriotrochidae	0.36	4.05	1.8	2.4	3.07	6.54
3	Golfingiidae	4.81	4.76	4.09	8.57	27.04	Enteropneusta	0.5	3.37	1.44	1.99	2.46	9
4	Paraonidae	5.03	4.2	1.58	7.56	34.6	Capitellidae	2.42	5.17	1.35	1.46	2.31	11.31
5	Cirratulidae	4.04	3.76	2.36	6.77	41.37	Scalibregmatidae	3.08	0.39	1.32	1.8	2.25	13.56
6	Myriotrochidae	4.05	3.71	2.33	6.68	48.04	Aspidosiphonidae	0.02	2.71	1.29	1.07	2.2	15.75
7	Amphinomidae	3.75	3.28	1.68	5.9	53.95	Paraonidae	3.59	5.03	1.28	1.28	2.19	17.94
8	Enteropneusta	3.37	3.05	1.95	5.49	59.43	Terebellidae	3.27	1.26	1.22	1.41	2.09	20.03
9	Spionidae	2.92	2.24	1.33	4.03	63.46	Ampharetidae	3.04	0.8	1.2	1.56	2.06	22.08
10	Nemertea	2.52	1.92	1.07	3.46	66.92	Ampeliscidae	2.59	0.27	1.17	1.38	1.99	24.08

Table 1 continued. Characterising and discriminating families for SEA4 area macrobenthos clusters 1-11.

	Characterise	G8					Discriminate	G8	G9				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*	*Families*	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
1	Maldanidae	5.2	3.95	4.19	7.02	7.02	Glyceridae	3.22	0.3	1.4	2.02	2.8	2.8
2	Cirratulidae	5.05	3.93	6.26	6.98	14	Terebellidae	3.99	1.39	1.35	1.6	2.7	5.5
3	Amphinomidae	4.87	3.63	3.73	6.45	20.46	Capitellidae	1.53	3.84	1.19	1.5	2.39	7.89
4	Golfingiidae	4.19	3.07	2.63	5.45	25.91	Ampeliscidae	3.23	1	1.18	1.53	2.37	10.26
5	Spionidae	4.28	2.86	2.06	5.09	31	Oedicerotidae	3.21	0.96	1.18	1.58	2.37	12.63
6	Terebellidae	3.99	2.72	2.11	4.84	35.83	Sphyrapidae	2.6	1.01	1.08	1.29	2.17	14.8
7	Oweniidae	3.89	2.62	1.96	4.66	40.49	Paraonidae	2.81	4.65	1.08	1.15	2.17	16.97
8	Phoxocephalidae	3.53	2.36	1.83	4.2	44.7	Lumbrineridae	0.96	2.82	1.08	1.48	2.16	19.13
9	Yoldiidae	3.65	2.34	1.74	4.15	48.85	Phoxocephalidae	3.53	1.73	1.06	1.35	2.13	21.26
10	Glyceridae	3.22	2.11	1.66	3.75	52.6	Thyasiridae	2.9	4.08	1	1.22	2.01	23.27

	Characterise	G9					Discriminate	G9	G10				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*	*Families*	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
1	Oweniidae	5.86	5.64	7.32	9.22	9.22	Sphyrapidae	1.01	3.22	1.05	1.5	2.22	2.22
2	Cirratulidae	4.68	4.48	7.31	7.33	16.55	Golfingiidae	2.76	5.3	1.04	1.32	2.2	4.43
3	Amphinomidae	4.69	4.39	5.45	7.17	23.72	Terebellidae	1.39	3.31	0.99	1.39	2.09	6.52
4	Maldanidae	4.35	4.2	7.48	6.87	30.59	Onuphidae	0.59	2.47	0.96	1.18	2.05	8.56
5	Paraonidae	4.65	4.09	2.92	6.68	37.27	Ampharetidae	1.99	3.89	0.9	1.3	1.92	10.48
6	Spionidae	4.41	3.66	2.71	5.98	43.26	Sphaerodoridae	0.67	2.46	0.9	1.4	1.9	12.38
7	Thyasiridae	4.08	3.5	2.69	5.71	48.97	Munnopsidae	1.68	3.55	0.87	1.37	1.86	14.24
8	Capitellidae	3.84	3.44	2.73	5.62	54.59	Phoxocephalidae	1.73	3.51	0.87	1.35	1.85	16.09
9	Yoldiidae	3.87	3.42	2.51	5.6	60.18	Ophiuridae	2.96	2.03	0.83	1.3	1.76	17.85
10	Ophiuridae	2.96	2.24	1.43	3.67	63.85	Ampeliscidae	1	2.53	0.81	1.32	1.71	19.57

Table 1 continued. Characterising and discriminating families for SEA4 area macrobenthos clusters 1-11.

	Characterise	G10					Discriminate	G9	G10				
	Families	*Av.Abund*	*Av.Sim*	*Sim/SD*	*Contrib%*	*Cum.%*	*Families*	*Av.Abund*	*Av.Abund*	*Av.Diss*	*Diss/SD*	*Contrib%*	*Cum.%*
1	Cirratulidae	5.99	3.72	7.28	6.41	6.41	Thyasiridae	2.9	4.72	0.92	1.3	1.94	1.94
2	Golfingiidae	5.3	3.21	6.71	5.53	11.94	Lumbrineridae	0.96	2.96	0.89	1.51	1.88	3.82
3	Maldanidae	5.04	2.98	4.53	5.13	17.07	Onuphidae	0.98	2.47	0.86	1.2	1.81	5.63
4	Spionidae	5.56	2.97	2.63	5.12	22.19	Capitellidae	1.53	3.39	0.85	1.43	1.79	7.43
5	Amphinomidae	5.02	2.86	2.77	4.92	27.11	Glyceridae	3.22	1.49	0.84	1.32	1.78	9.21
6	Paraonidae	4.67	2.6	4.28	4.47	31.58	Oedicerotidae	3.21	1.69	0.84	1.34	1.77	10.98
7	Oweniidae	4.64	2.53	2.77	4.36	35.95	Paraonidae	2.81	4.67	0.83	1.18	1.75	12.73
8	Thyasiridae	4.72	2.51	2.6	4.32	40.27	Tubificidae	1.58	1.99	0.82	1.09	1.72	14.46
9	Yoldiidae	4.39	2.32	2.43	3.99	44.26	Sphaerodoridae	0.75	2.46	0.8	1.4	1.7	16.15
10	Ampharetidae	3.89	2.11	2.74	3.63	47.89	Sphyrapidae	2.6	3.22	0.8	1.23	1.68	17.83

3.2.2 Supporting multivariate analyses

3.2.2.1 Non-metric multidimensional scaling

Non-metric multidimensional scaling (MDS) ordination was undertaken using the Primer 6 software package (Clarke & Gorley, 2006). The primary sites x families data matrix was log(x+1) transformed prior to calculation of the Bray-Curtis similarity coefficient and a 2-d ordination plot produced (see Clarke, 1993 for detailed methodology). To simplify visual interpretation sites were grouped in depth order to give n=15 (n=18 in deepest band) and their MDS x- and y-axis coordinates presented as median and interquartile ranges (see Fig. 17a). Both coordinates were also plotted with depth (see Fig. 17b, c). The sites (depth bands) form a U-shaped distribution in ordination space, with the shallowest sites on the left upright and the deepest sites on the right upright. The plots in Fig. 17 have been colour coded to represent general bottom water conditions: 'warm' (>0ºC), 'cold' (<0º), and 'varied' (both positive and negative temperatures experienced, ±0C).

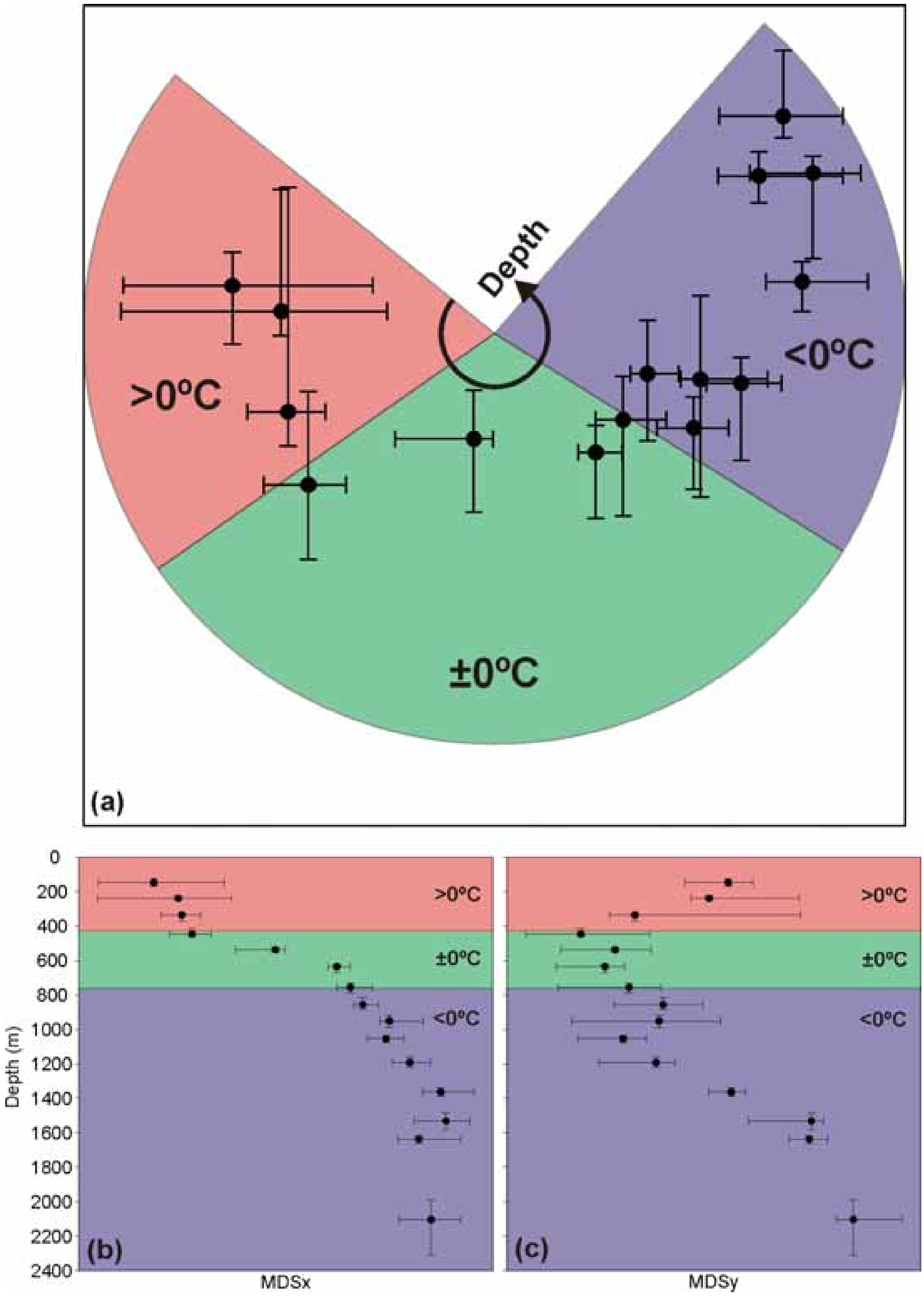

Figure 17. Non-metric multidimensional scaling ordination of SEA4 area family-level macrobenthos data. (a) MDS plot, sites grouped into depth bands (see text) and MDS scores shown as median and interquartile range. (b) MDS x-axis scores plotted with depth, both shown as median and interquartile range. (c) MDS y-axis scores plotted with depth, both shown as median and interquartile range.

3.2.2.2 Detrended correspondence analysis

Detrended correspondence analysis (DCA) ordination was undertaken using the PC-Ord 4 software package (McCune & Mefford, 1999). The primary sites x families data matrix was log(x+1) transformed prior to running the DCA. A secondary matrix of environmental variables (sample depth; sediment mud content; minimum, mean and maximum bottom water temperature; standard deviation of bottom water temperature) was also input to the analysis. PC-Ord 4 default settings were used, for detailed information on this methodology see Jongman *et al* (1995).

Figure 18 illustrates the DCA output, plotting the site scores on the first two axes of the ordination. The distribution of sites in ordination space is somewhat similar to the U-shaped pattern obtained by the corresponding MDS. Environmental variable vectors are superimposed on the DCA plot, the length of the vector representing the significance of the variable in explaining variation in faunal distribution, its direction showing the trend relative to the ordinations axes. Most variables are strongly aligned with the first axis, i.e. varying left to right, with deeper muddier sites to the right and warmer water sites to the left. Variability in bottom water temperature (as standard deviation of temperature) is somewhat offset indicating additional variation on the second axis (top to bottom). These relationships with environmental variables are further presented in Fig. 19 in the form of bubble plots.

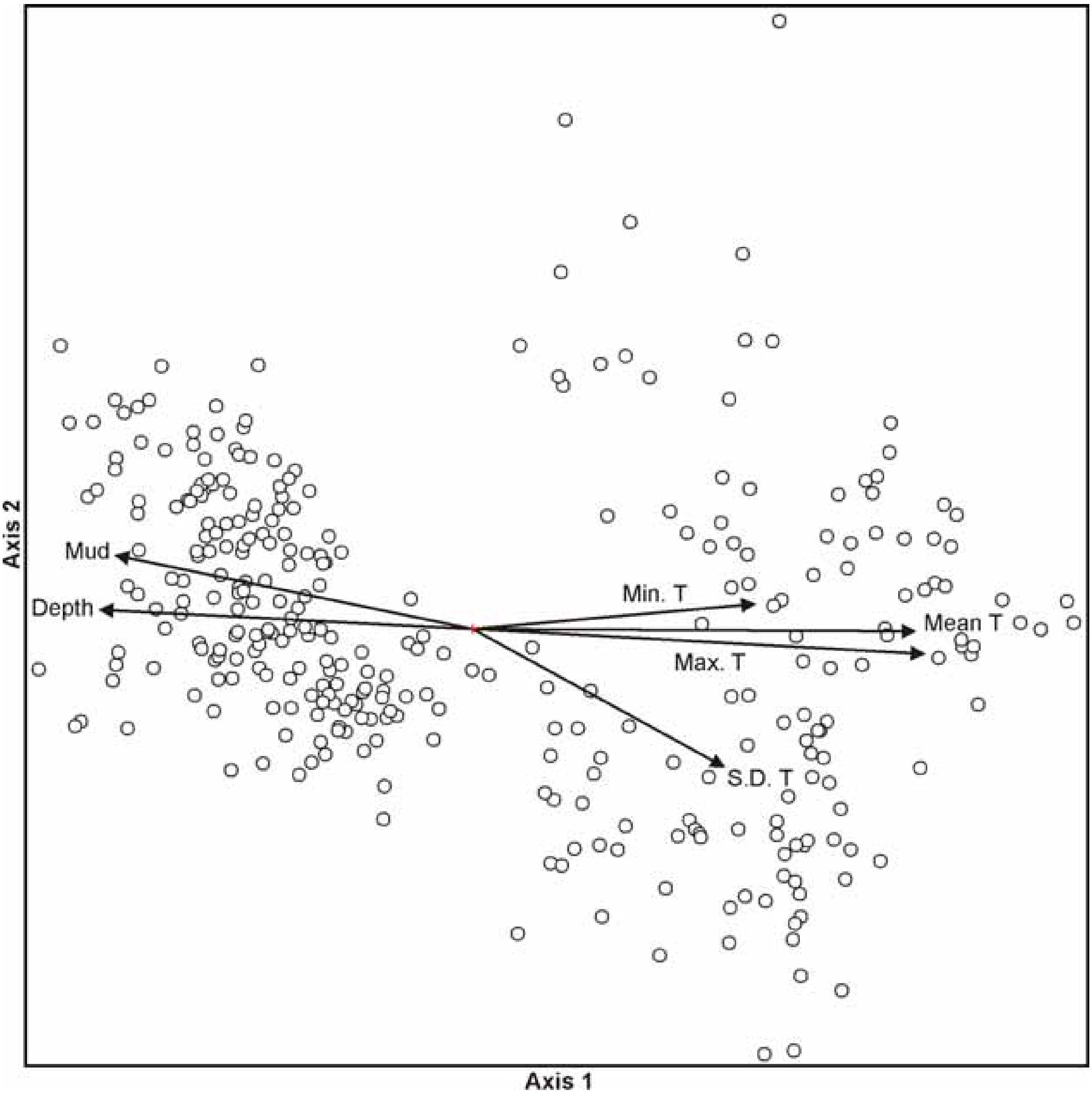

Figure 18. Detrended correspondence analysis ordination of SEA4 area family-level macrobenthos data. Vector representations of relationships with environmental variables are superimposed (Depth, sample depth; Mud, sediment mud content; Min. T, minimum bottom water temperature, Mean T, mean temperature; Max. T, maximum temperature; S.D. T., standard deviation of temperature).

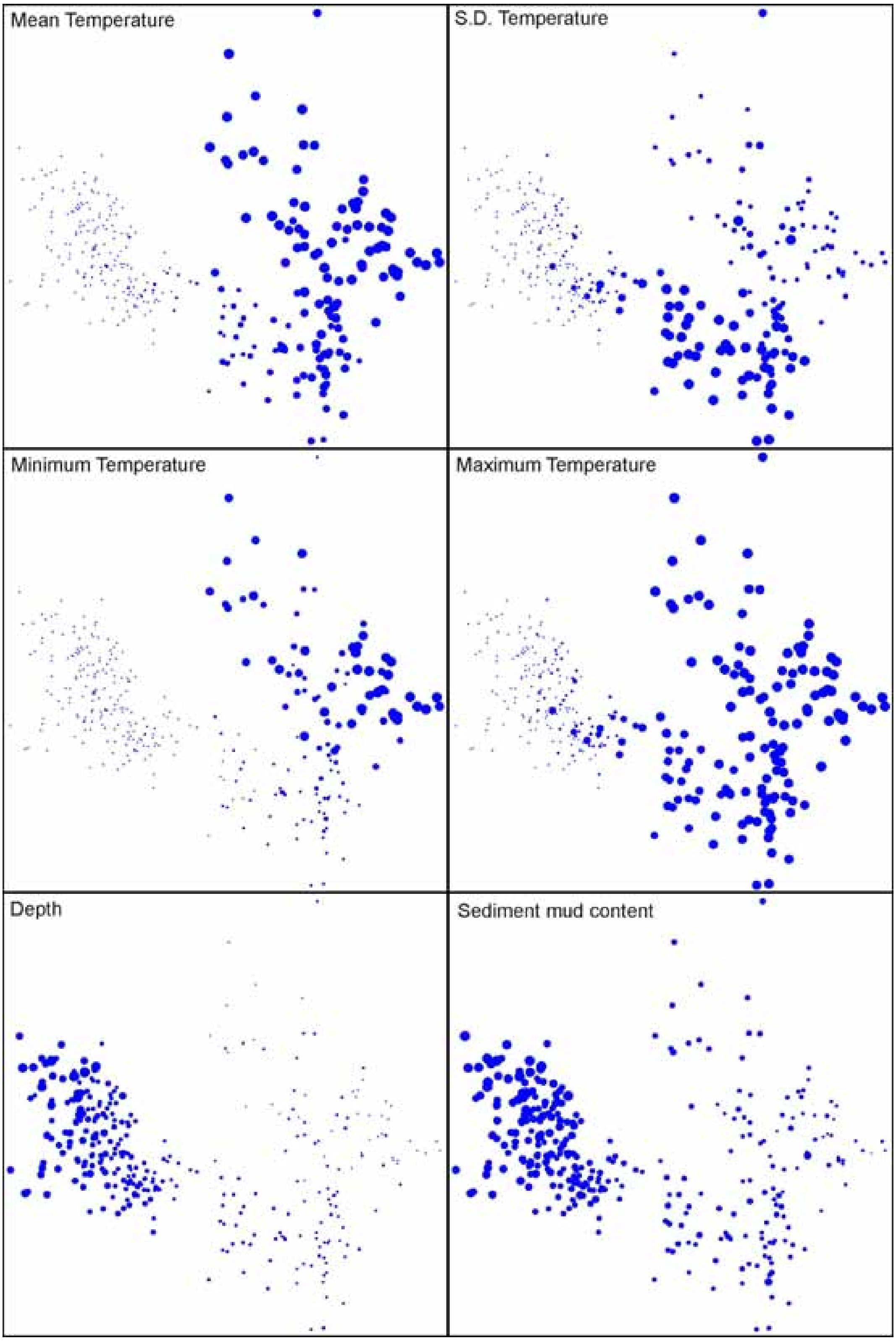

Figure 19. Detrended correspondence analysis ordination of SEA4 area family-level macrobenthos data. Bubble plots of environmental variables (i.e. symbol size proportional to variable value).

3.2.2.3 Canonical correspondence analysis

Canonical correspondence analysis (CCA) ordination was undertaken using the PC-Ord 4 software package (McCune & Mefford, 1999). The primary sites x families data matrix was log(x+1) transformed prior to running the CCA. A secondary matrix of environmental variables (sample depth; sediment mud content; minimum, mean and maximum bottom water temperature; standard deviation of bottom water temperature) was also input to the analysis. PC-Ord 4 default settings were used, for detailed information on this methodology see Jongman *et al* (1995).

Figure 20 illustrates the CCA output, plotting the site scores on the first two axes of the ordination. The distribution of sites in ordination space is broadly an inverted V-shaped pattern, with the deepest sites at the left extremity, the shallowest sites at the right extremity, with intermediate depths at the apex. Environmental variable vectors are superimposed on the CCA plot; sample depth, sediment mud content, mean and maximum bottom water temperature are strongly aligned with the first axis, while minimum temperature and standard deviation of temperature are appreciably offset indicating additional variation on the second axis. These relationships with environmental variables are further presented in Fig. 21 in the form of bubble plots.

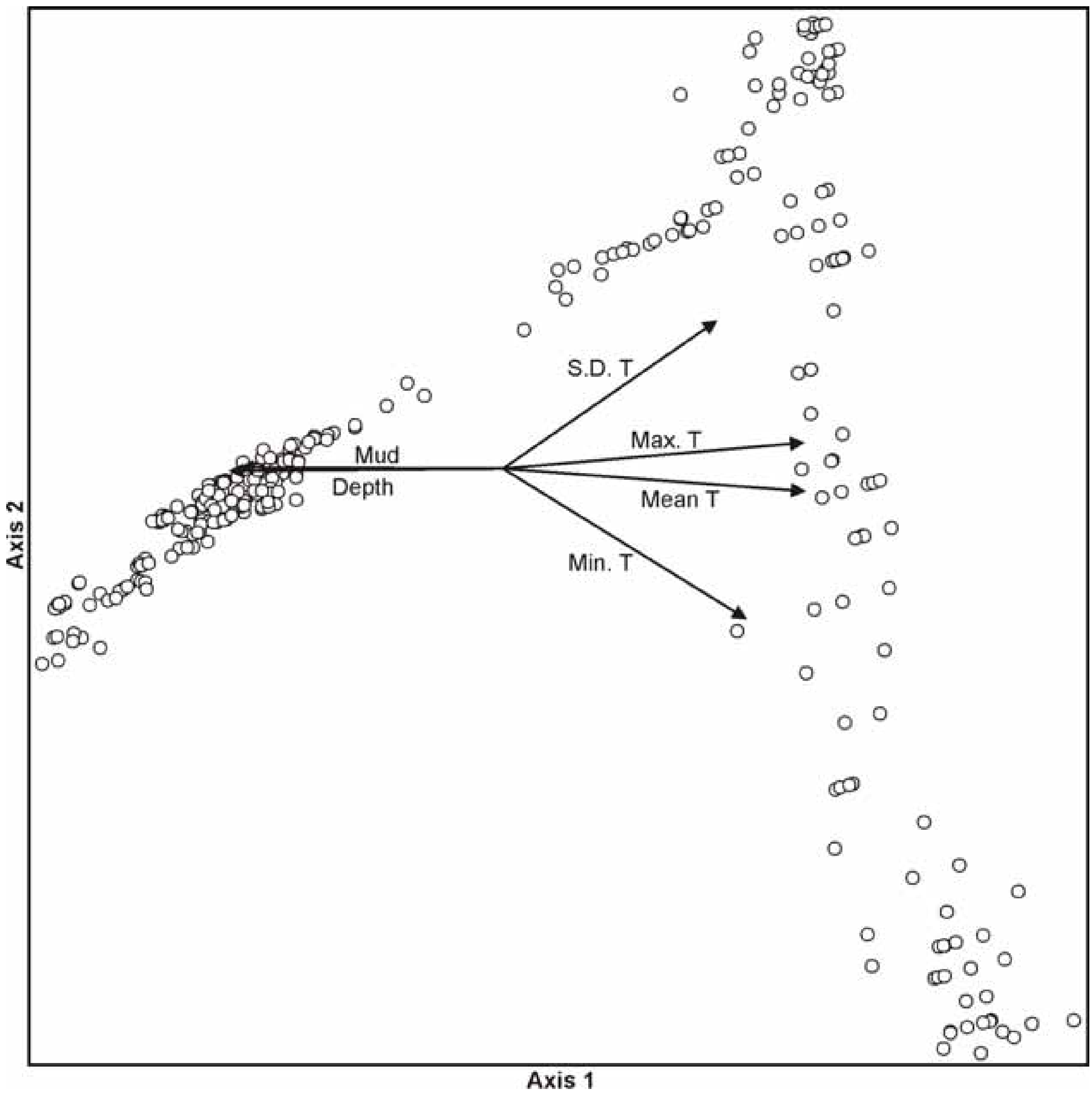

Figure 20. Canonical correspondence analysis ordination of SEA4 area family-level macrobenthos data. Vector representations of relationships with environmental variables are superimposed (Depth, sample depth; Mud, sediment mud content; Min. T, minimum bottom water temperature, Mean T, mean temperature; Max. T, maximum temperature; S.D. T., standard deviation of temperature).

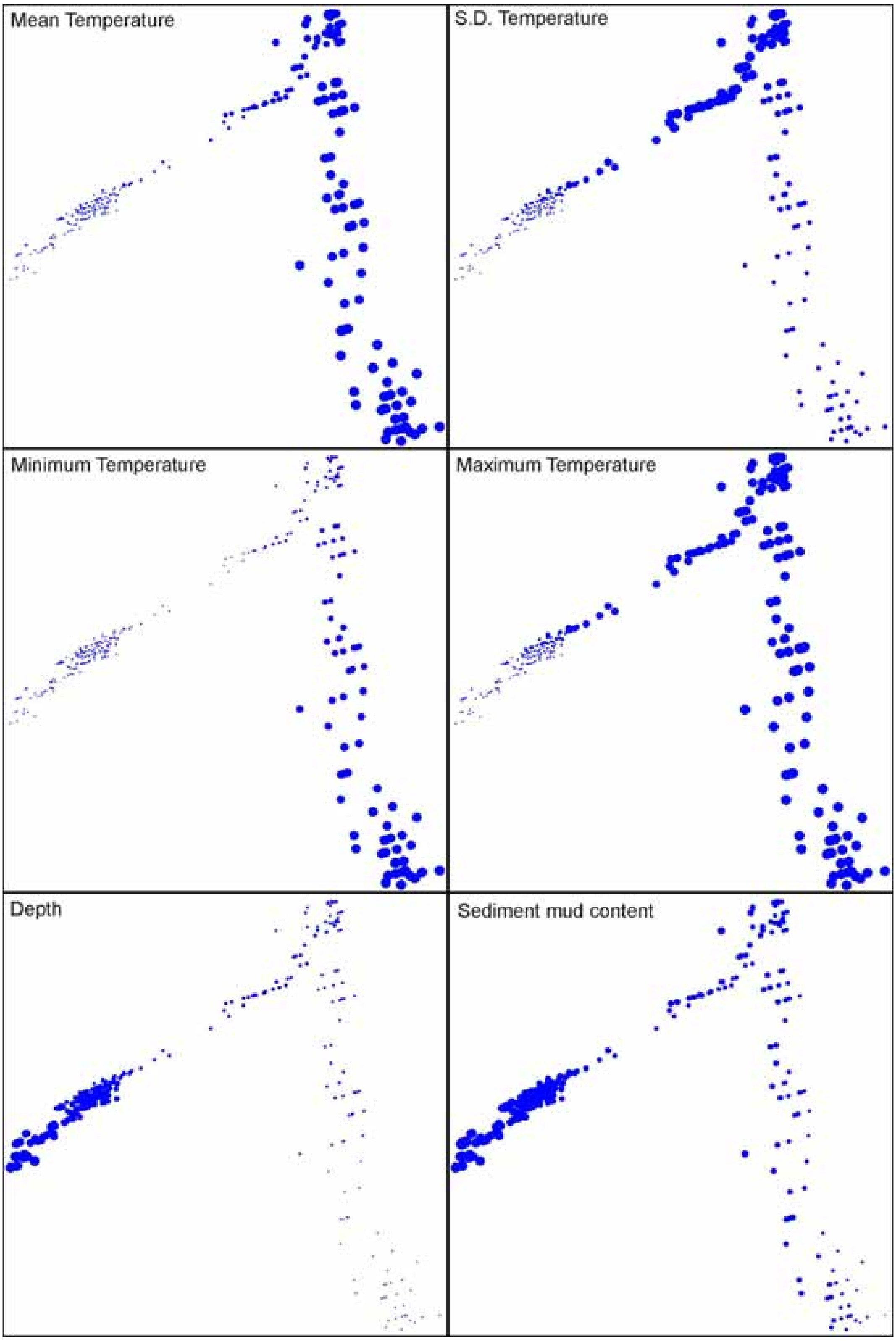

Figure 21. Canonical correspondence analysis ordination of SEA4 area family-level macrobenthos data. Bubble plots of environmental variables (i.e. symbol size proportional to variable value).

3.2.2.4 Comparison of ordinations

All three ordination techniques employed produced broadly similar distributions of sites in 2-dimensional ordination space (Fig.s 17a, 18, 20). All environmental variables tested (see Table 2) were very strongly correlated (p<<0.001) with the first ordination axis, with sample depth and maximum temperature exhibiting the jointly strongest correlations. In all three cases the second axis of ordination was strongly correlated (p<0.001) with bottom water temperature variation, and in two of the three case (MDS y, CCA 2) also strongly correlated (p<0.001) with sediment mud content. These results suggest that biotope characterisation / description should have particular regard for water depth, bottom water temperature variation and sediment mud content.

Table 2. Spearman's rank correlations between ordination axes and environmental variables. (MDS, non-metric multidimensional scaling; DCA, detrended correspondence analysis; CCA, canonical correspondence analysis; * axis inverted to give common direction of trend across ordinations).

	Ordination axis					
Variable	**MDS x**	**DCA 1***	**CCA 1***	**MDS y**	**DCA 2***	**CCA 2**
Sample depth	0.91	0.91	0.92	0.07	-0.10	0.11
Sediment mud content	0.84	0.89	0.88	0.23	0.09	0.20
Mean temperature	-0.89	-0.90	-0.91	-0.08	0.07	-0.11
Temperature standard deviation	-0.82	-0.81	-0.82	-0.28	-0.23	-0.51
Minimum temperature	-0.79	-0.81	-0.82	-0.01	0.11	-0.02
Maximum temperature	-0.91	-0.91	-0.92	-0.07	0.10	-0.11

Significance: p<0.05 (grey); p<0.001 (orange); p<<0.001 (red)

3.2.3 TWINSPAN classification analysis

Two-Way INdicator SPecies Analysis (TWINSPAN) was employed to provide an alternative classification to serve as a test and comparator to the primary cluster analysis (see section 3.2.1.). In terms of the biotoping project this approach offers two useful features:

1. It provides an alternative hierarchical classification scheme for the seabed sites, and
2. It produces 'indicator species' (families in this case) that may be useful in characterising / discriminating biotopes.

Although a long-established technique (Hill, 1979), it does not seem to be widely known or used in the marine science community. Briefly the method operates as follows. TWINSPAN is a divisive classification system, i.e. it begins with all sites then repeatedly divides them into two groups, two, then four, then eight etc. As distinct from agglomerative cluster analysis, which begins with individual sites then gradually groups them into larger and larger groups. TWINSPAN also differs from conventional cluster analysis by being based on an ordination of the sites rather than a similarity matrix of the sites. In essence this ordination (e.g. similar to MDS, DCA, CCA) is split in two at its centre producing two subsets of sites; this process is then repeated for each subset producing four subsets etc.

Indicator species analysis is generally focussed on qualitative data, i.e. the presence / absence of a potential indicator; however, TWINSPAN provides a means to incorporate categorised quantitative data. Fully quantitative data (as are available for the SEA4 area macrobenthos) are dealt with by defining 'pseudo-species' (pseudo-families in this case). These pseudo-species are based on user-selected density (abundance) classes. In the analyses presented below these classes were set to:

Pseudo-family 1 >0	individual m^{-2}
Pseudo-family 2 >11	individual m^{-2}
Pseudo-family 3 >20	individual m^{-2}
Pseudo-family 4 >50	individual m^{-2}

This is a logarithmic scale, set to the values of the quartiles of the full macrobenthos density dataset. As an example of the operation of this method, consider a macrobenthos sample that contains 2 indiv.m^{-2} of Acrocirridae and 60 indiv.m^{-2} of Zeilleriidae, TWINSPAN would interpret those data as:

Acrocirridae	pseudo-family 1	present
Zeilleriidae	pseudo-family 1	present
Zeilleriidae	pseudo-family 2	present
Zeilleriidae	pseudo-family 3	present
Zeilleriidae	pseudo-family 4	present

For more complete details of the TWINSPAN methodology see e.g. Jongman, Ter Braak & Van Tongeren (1995), the technique was implemented using the PC-Ord 4 software package (McCune & Mefford, 1999).

Two levels of TWINSPAN outputs are shown below referred to as 'Level 3' and 'Level 4', these related to the third and forth splits of the site dataset, i.e. respectively producing 8 and 16 subsets of sites (the classifications). Note, however, that those subsets that contained fewer than 10 sites (resulting in 7-groups at Level 3 and 11-groups at level 4) were not further assessed. While these omitted small groups have 'biological reality' they are at a level of detail beyond the broad-scale biotoping objective of this study.

The level 3 hierarchical classification and its potential relationships with environmental variables are illustrated in Fig. 22. The first level split, separating groups A-D from E-F is very closely matched to the bottom water temperature variables, most obviously in the case of maximum temperature, e.g. temperature is >8°C for groups A-D but is <1°C for groups E-F. Similarly there is a clear environmental separation of the second level split between groups A-B and C-D in terms of minimum bottom water temperature and particularly in temperature variation (shown as standard deviation).

In contrast bottom water temperature variables are generally highly consistent among the deep-water groups (E-H). However, sediment mud content increases markedly with depth among these groups providing the best match to the second and third level splits between groups E, G and H.

The Level 3 results are also plotted in water depth versus sediment mud content environmental space in Fig. 23. This illustrates the generally increasing levels of sediment mud content with depth, with the exception of the shelf-edge sites (groups A and B) where there appears to be a systematic difference in mud content despite a broadly common depth range (best viewed on the logarithmic scale shown on the lower plot). This difference in sediment mud content appears to be the key driver of the third level split between groups A and B.

Figures 24 and 25 show similar plots for the level 4 TWINSPAN hierarchical classification. Again there is a very clear correspondence between the first level split (groups K-P vs. R-Y) and bottom water temperature parameters, particularly maximum temperature. The second level split of groups K-L from N-P is also well matched with temperature variation. And as previously, bottom water temperature variables remain generally highly consistent among the deep-water groups (R-Y). Differentiation of the latter groups appears to relate best to a combination of water depth and sediment mud content. For example, the Level 4 lower slope groups (R, S and V) seem to separate on the basis of mud content. Similarly, shelf-edge sites (groups K and L) may have a systematic difference in mud content despite a broadly common depth range (see lower plot of Fig. 25).

'Indicator families' for each of the Level 1 to 4 splits are summarised in Table 3, note that these are 'pseudo-families', i.e. that relative abundance levels are important to their definition.

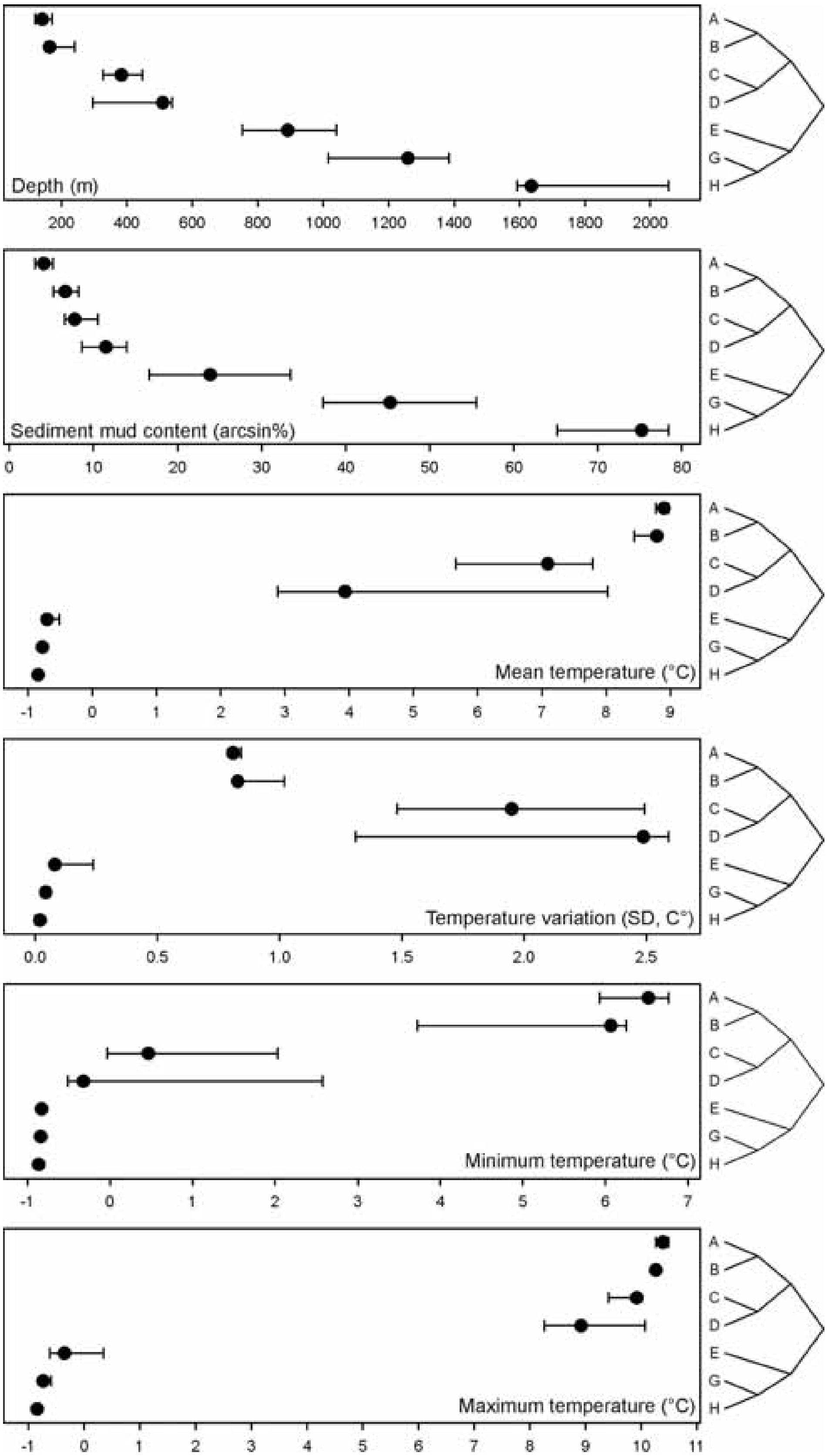

Figure 22. Environmental space plots for TWINSPAN Level 3 classification. Environmental variables are plotted as median and interquartile range encountered among sites within the corresponding TWINSPAN group. (Mud content is shown as arcsin transformed percentage).

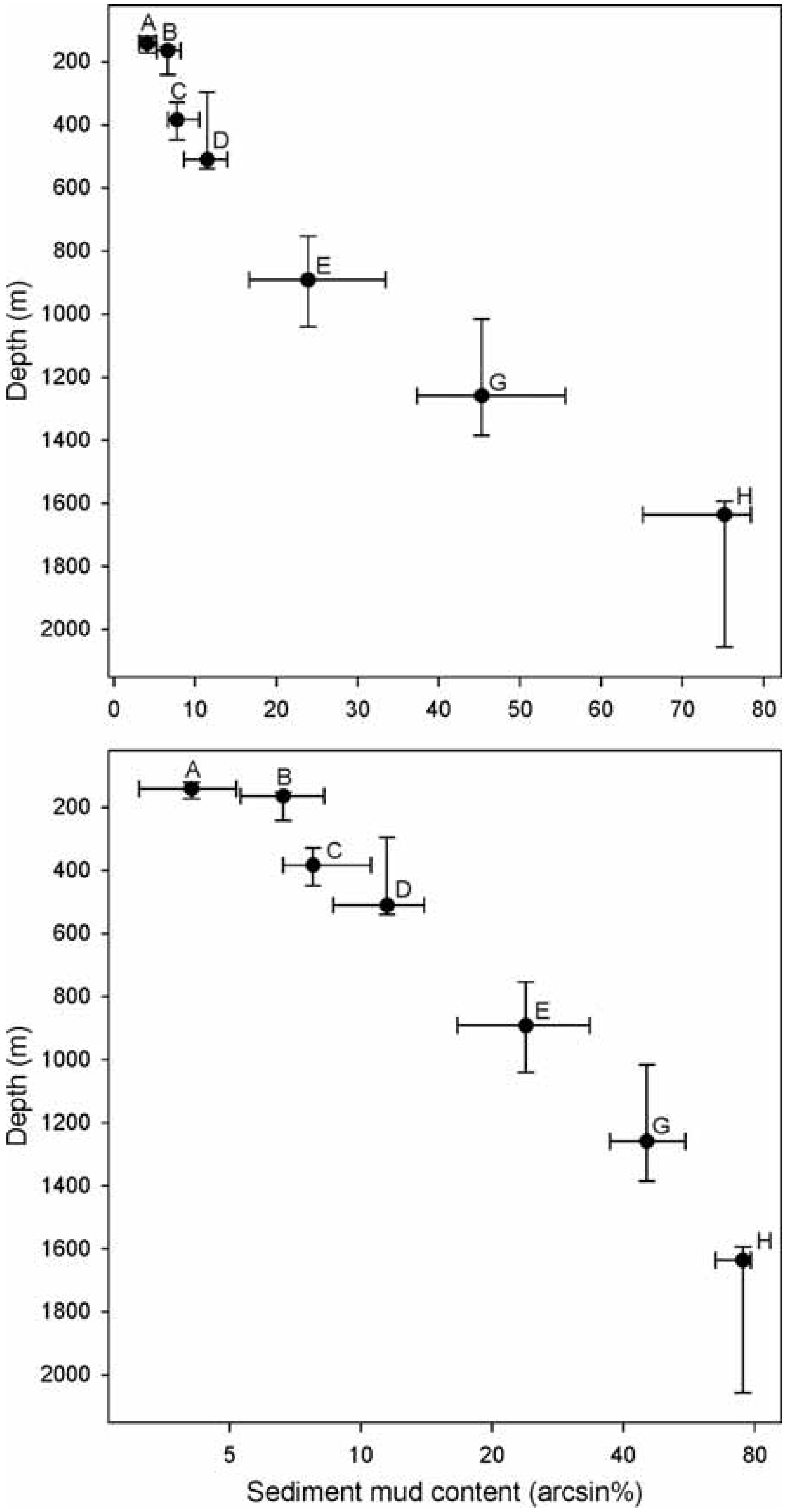

Figure 23. Environmental space plot for TWINSPAN Level 3 classification. Water depth and sediment mud content are plotted as medians and interquartile ranges encountered among sites within the corresponding TWINSPAN group. (Mud content is shown as arcsin transformed percentage; upper panel arithmetic scale, lower panel logarithmic scale).

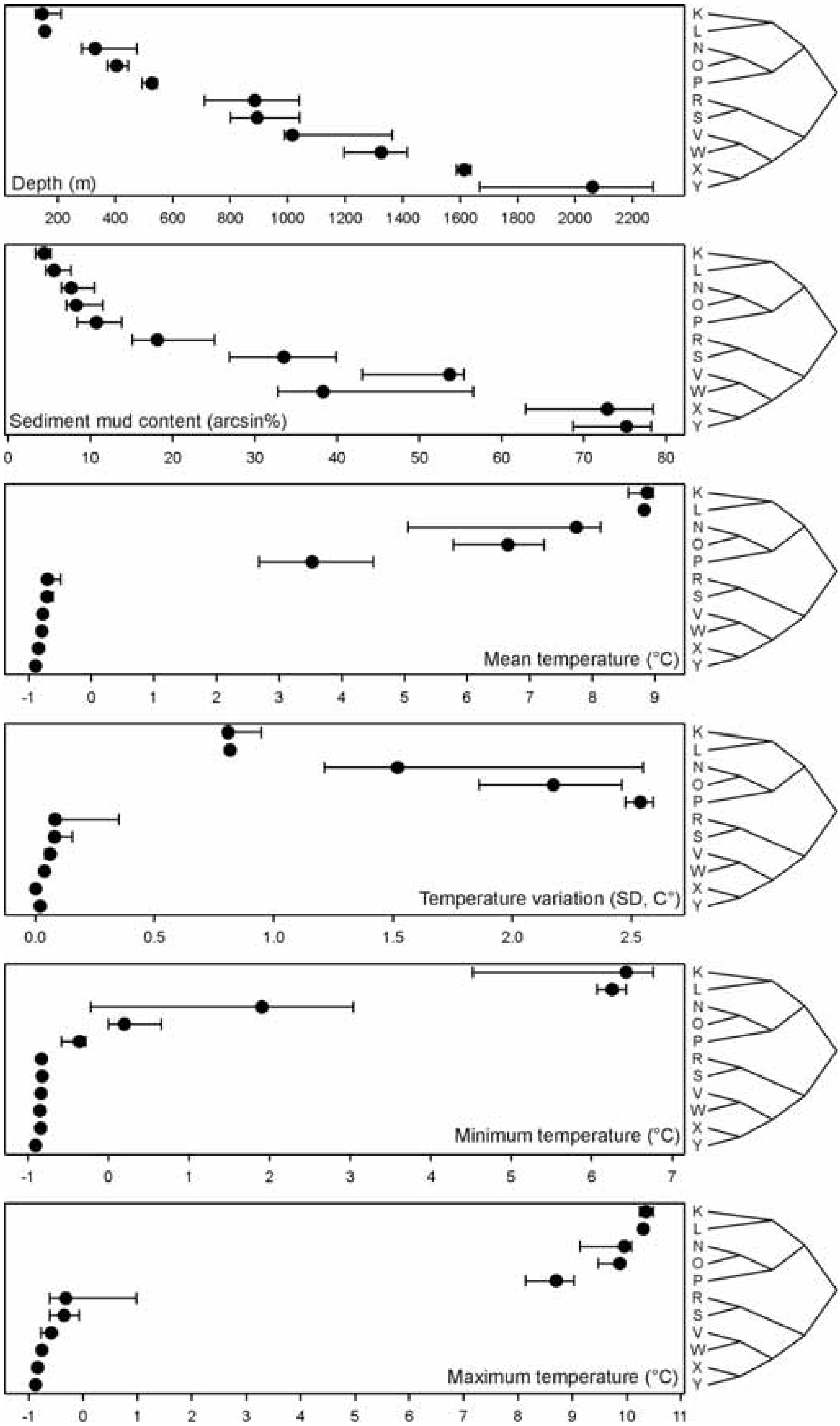

Figure 24. Environmental space plots for TWINSPAN Level 4 classification. Environmental variables are plotted as median and interquartile range encountered among sites within the corresponding TWINSPAN group. (Mud content is shown as arcsin transformed percentage).

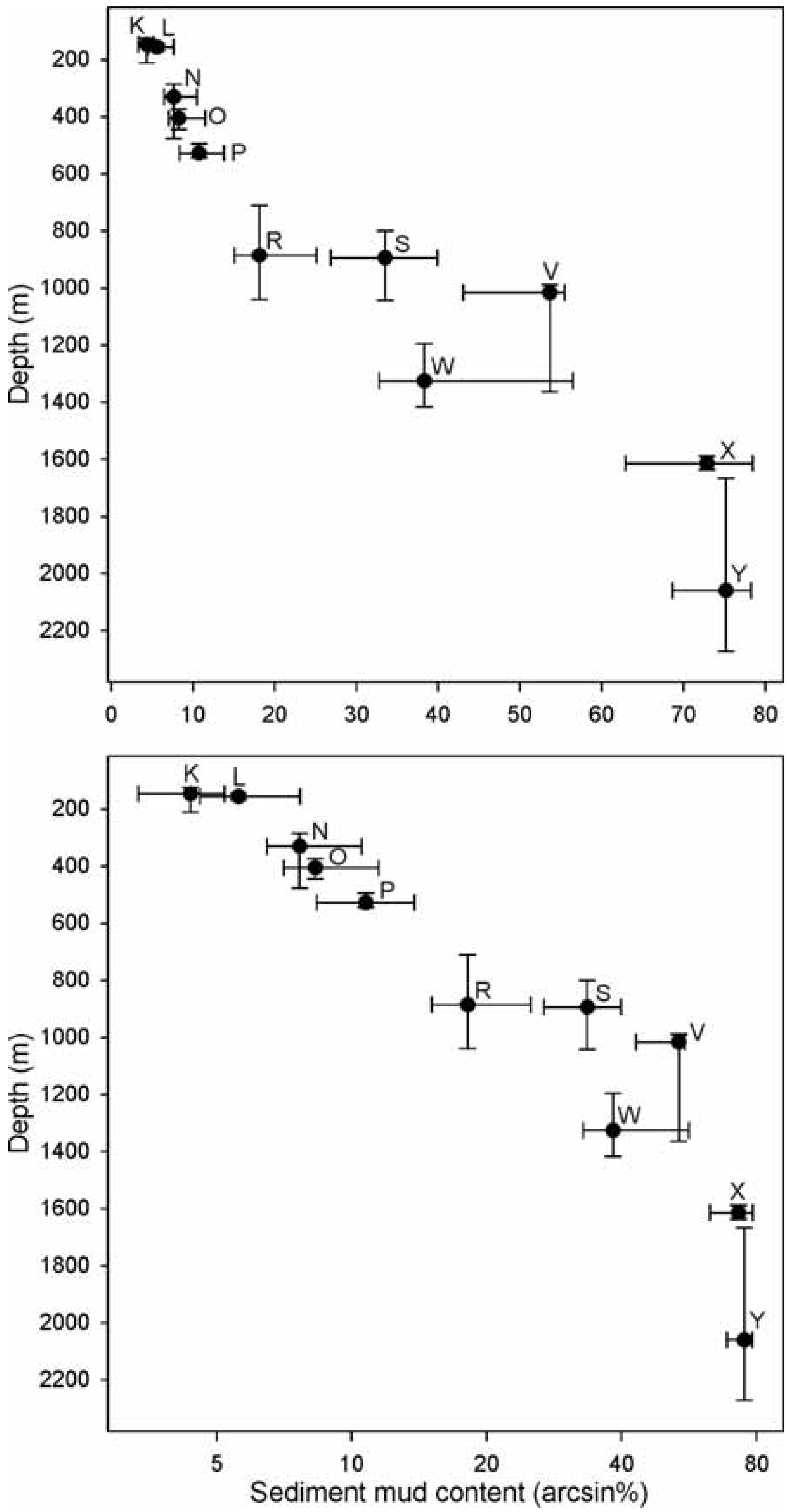

Figure 25. Environmental space plot for TWINSPAN Level 4 classification. Water depth and sediment mud content are plotted as medians and interquartile ranges encountered among sites within the corresponding TWINSPAN group. (Mud content is shown as arcsin transformed percentage: upper panel arithmetic scale, lower panel logarithmic scale).

Table 3. TWINSPAN indicator families for SEA4 area classification (see key below).

	TWINSPAN DIVISION															
	Level 1				Level 2				Level 3				Level 4			
	N	P	T	Indicator family (density class)	N	P	T	Indicator family (density class)	N	P	T	Indicator family (density class)	N	P	T	Indicator family (density class)
SEA4	2	-	0	none	4	-	00	Myriotrochidae (2), Capitellidae (4)	8	H	000	Enteropneusta (2), Myriotrochidae (4)	16	Y	0000	Ischnomesidae (1), Terebellidae (1)
													17	X	0001	Ophiuridae (1)
									9	G	001	Maldanidae (3)	18	V	0010	Thyasiridae (2), Ophiuridae (2), Yoldiidae (3)
													19	W	0011	Macrostylidae (1)
					5	-	01	Scalibregmatidae (2), Maldanidae (4), Terebellidae (3)	10	F	010	Unciolidae (4), Caprellidae (3)	20	U	0100	None
													21	T	0101	Scalibregmatidae (1)
									11	E	011	Oweniidae (1), Paraonidae (3)	22	S	0110	Paraonidae (4), Capitellidae (2), Lumbrineridae (3)
													23	R	0111	Glyceridae (2)
	3	-	1	Syllidae (3)	6	-	10	Thyasiridae (1), Sabellidae (3)	12	D	100	Maldanidae (1), Trichobranchidae (1), Amphinomidae (3)	24	Q	1000	Spatangoida (1)
													25	P	1001	Enchytraeidae (2)
									13	C	101	Limopsidae (1), Dorvilleidae (1)	26	O	1010	Ampeliscidae (4) Munnopsidae (1), Pectinidae (1)
													27	N	1011	None
					7	-	11	Tellinidae (1), Echinocyamidae (1), Thraciidae (1)	14	B	110	Paraonidae (3)	28	M	1100	None
													29	L	1101	Ampeliscidae (1), Lumbrineridae (1), Ophiuridae (1)
									15	A	111	Dorvilleidae (2), Phyllodocidae (3), Pisionidae (1)	30	K	1110	none
													31	J	1111	Dexaminidae (1)

N: simple numeric code of division category; P: letter code used for division category in associated graphic presentations; T: original TWINSPAN binary coding of division category; density classes: (1) >0, (2) >11, (3) >20, and (4) >50 individuals m^{-2}.
Colour coding: ____, category containing fewer than 10 sites; Annelids; Crustaceans; Molluscs; Other taxa.

4 SEA4 area biotopes

The TWINSPAN classification appears to produce coherent groups of sites that relate well to environmental conditions on the seabed and in the water column. Figure 26 provides a comparison of the TWINSPAN and Cluster analysis classifications. In broad terms the two classifications are very similar, despite being derived by very different methodologies. This suggests that there is a strong underlying structure to the biological dataset and that these classifications are relatively robust solutions appropriate to the identification of biotopes.

SHELF BREAK

Both classifications identify two groups in the shelf break zone (see Fig. 26) that appear to be differentiated on the basis of sediment mud content (Cluster groups 1 and 2; TWINSPAN groups K and L). A SW-NE trend in the fauna / environment is suggested (see Fig. 13 and 27).

UPPER SLOPE

Three or four groups are located on the upper slope (see Fig. 26), in the zone of maximal bottom water (temperature) variation. There is some indication that these groups are graded in terms of water depth and sediment mud content though none is particularly distinct. The upper slope realm of the SEA4 area is an extremely complex environment. It is subject to extreme hydrographic variation (e.g. temperature) that is also associated with episodic energetic events (e.g. high bottom current speeds) produced by internal waves / solibores (Hosegood & van Haren, 2004). It is also a region of complex mixed sedimentology, i.e. it broadly equates with the iceberg ploughmark zone. Consequently, high levels of faunal variability are to be expected at local scales, these may be sufficient to mask a regional scale trend.

LOWER SLOPE / CHANNEL FLOOR

Both classifications produce three groups in this depth band (see Fig. 26) that exhibit a consistent trend of increasing sediment mud content. A SW-NE trend in the fauna / environment is suggested (see Fig. 13 and 27).

DEEP CHANNEL FLOOR / NORWEGIAN BASIN

Two groups are recognised in the cluster classification and three in the TWINSPAN assessment (see Fig. 26). A combination of water depth and sediment mud content appears to differentiate the groups in this depth band (see also Fig. 27).

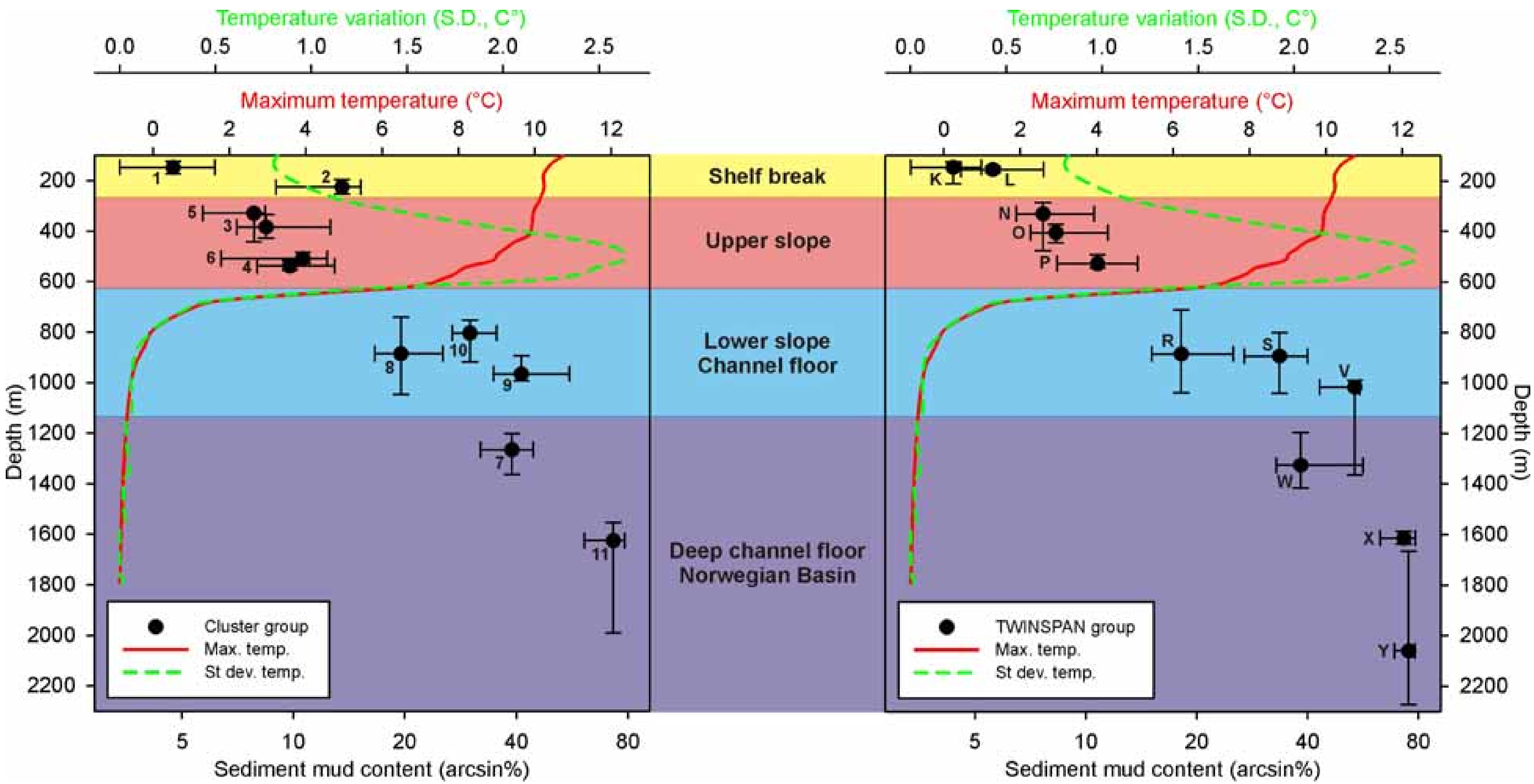

Figure 26. Comparison of Cluster analysis and TWINSPAN Level 4 classifications. Water depth and sediment mud content are plotted as medians and interquartile ranges encountered among sites within the corresponding classification group. (Mud content is shown as arcsin transformed percentage on a logarithmic scale).

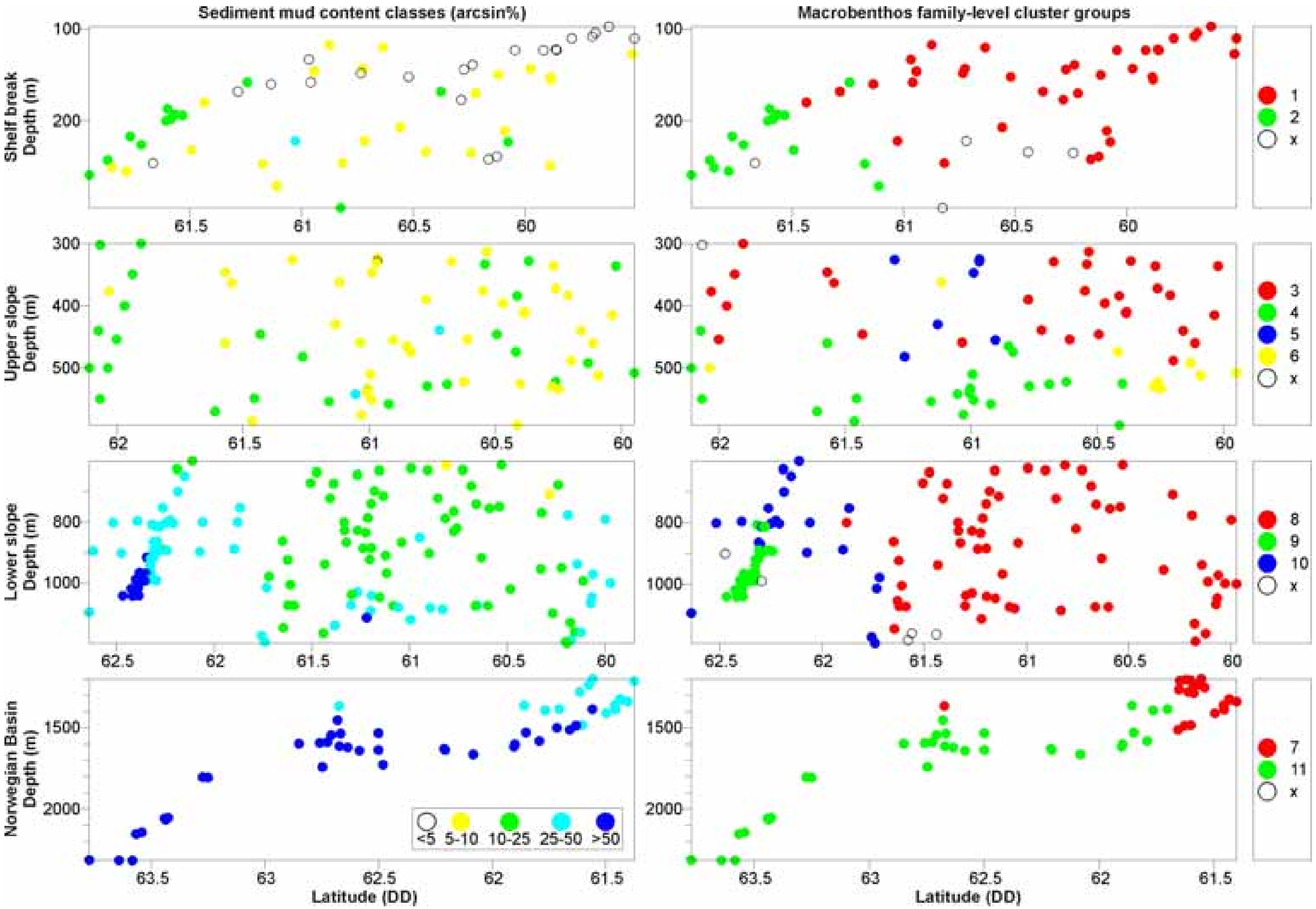

Figure 27. Comparison of sediment mud content classes (left panels) and Cluster groups (right panels) plotted in depth vs. latitude space, by major physiographic / depth bands. (x – other Cluster group).

4.1 Proposed biotopes

Taken together the biological classifications of the SEA4 area (section 3.2.1. cluster analysis; section 3.2.3. TWINSPAN assessment), the available environmental factors (section 3.1.), and their potential controls on the regional ecology (section 3.2.2.4. ordinations) suggest a biotope scheme based on hydrographically relevant depth bands and regional variations in sedimentology (i.e. mud content). Figure 28 provides a representation of the biotopes proposed on these bases.

Hydrographic / water depth boundaries are set at 300 and 600m to reflect three general hydrographic regimes (see Fig. 29):

1. <300m Warm NE Atlantic waters with relative thermal stability,
2. 300-600m Highly dynamic, varied water masses with extreme thermal variability, and
3. >600m Arctic water with highly stable thermal regime

An additional depth boundary is set at 1200m to reflect the continuous variation in faunal composition with depth even within the deep Arctic waters (see e.g. Fig.s 17 and 26).

Superimposed on these depth boundaries is a spatial boundary (see Fig. 28) that reflects the SW-NE variation in the fauna and sedimentary environment, most noticeable in the shelf break and lower slope depth bands (see above). This boundary is drawn to approximate the transition between cluster groups 1 and 2 at the shelf break and cluster groups 8 and 9-10 on the lower slope and the corresponding increase in sediment mud content encountered moving NE alongslope in this area. This boundary is extended along the 1500m depth contour (for convenience) to mark the transition between cluster groups 7 and 11 and corresponding increase in sediment mud content towards the NE.

These boundaries together produce eight proposed biotopes, four in the West of Shetland / Faroe-Shetland Channel area, and four in the North of Shetland / Norwegian Sea area (see Fig.s 28 and 29). A ninth biotope area is identified on Fig 28 (biotope VIII) that may be closely associated with the North Sea Fan and consequent high sediment mud content. However, for the present purposes it is considered as a local variant of biotope VII and amalgamated with it in the considerations that follow.

Table 4 provides an assessment of how well the proposed biotopes reflect the original biological classification of the region provided by the cluster analysis (section 3.2.1). Overall representation is very good, total fidelity ranges from 70-97% among the biotopes, and classified fidelity from 84-100%.

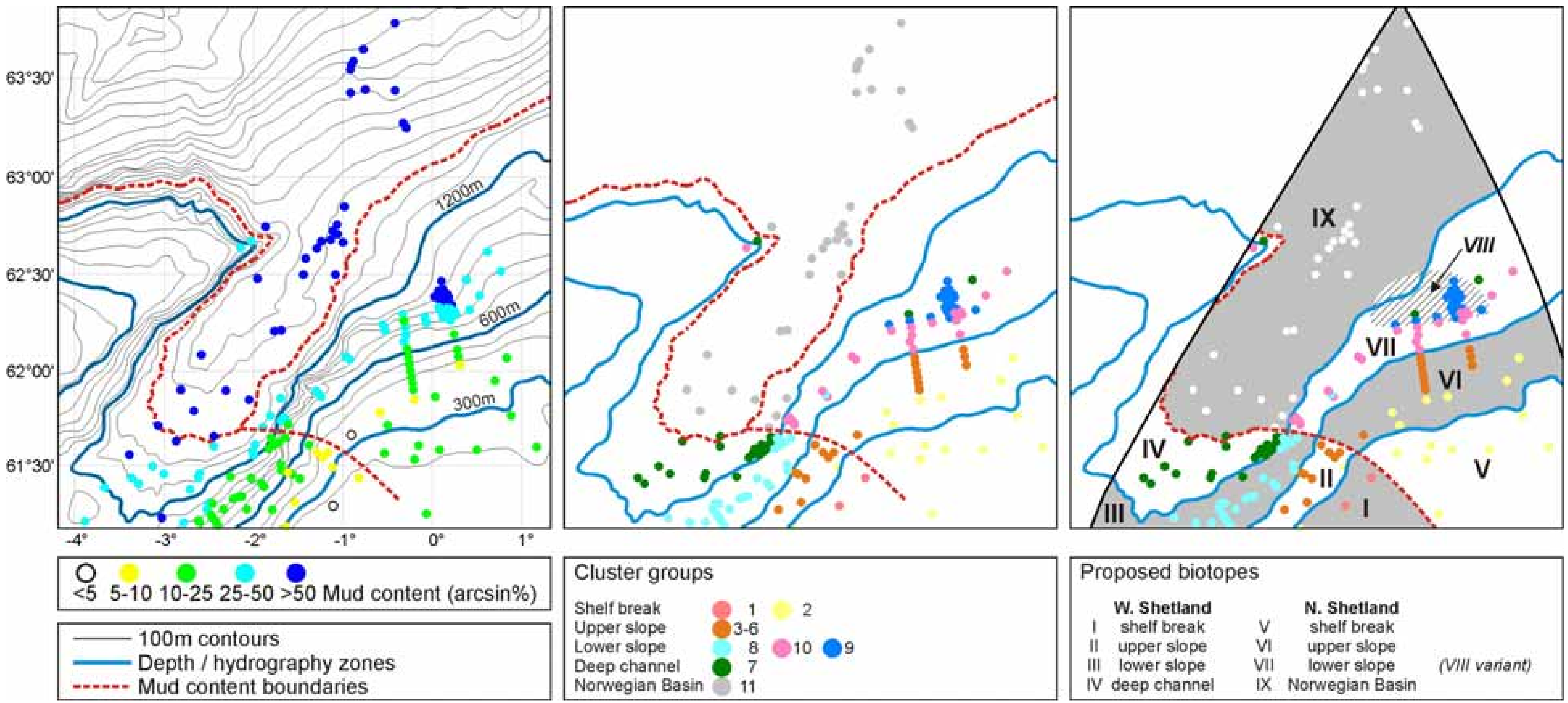

Figure 28. Northern SEA4 area - proposed biotopes. Left panel shows sediment mud content classes with major depth / hydrography zones and suggested mud content boundaries. Centre panel gives corresponding spatial distribution of Cluster groups (family-level classification). Right panel illustrates proposed biotopes, I-IV in West of Shetland area (Faroe-Shetland Channel), and V-IX in North of Shetland area (Norwegian Sea), note that biotope VIII is a local variant that may be associated with the North Sea Fan.

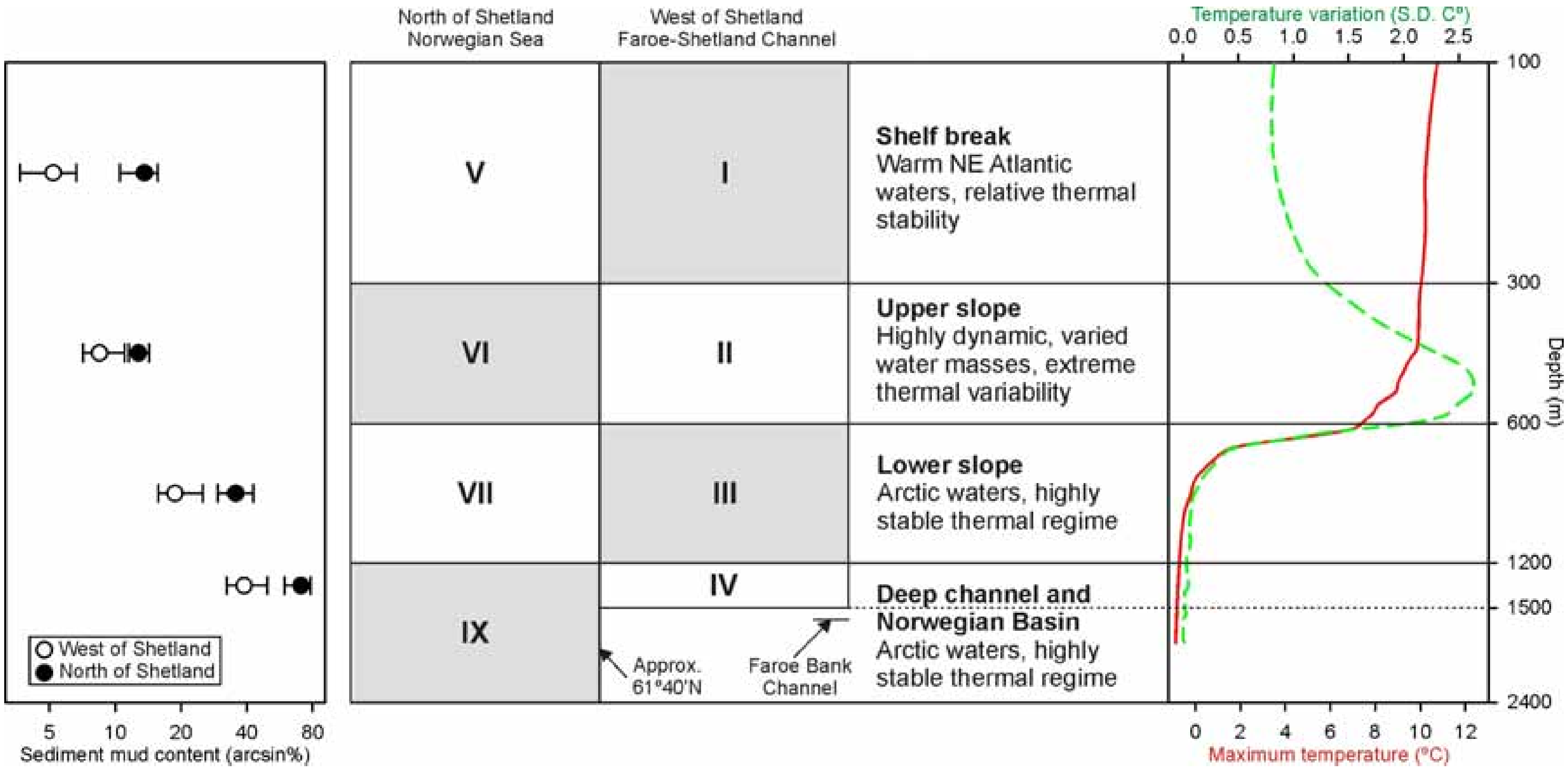

Figure 29. SEA4 area proposed biotopes. Left panel shows sediment mud content as median and interquartile range for each biotope. Right panel provides a schematic representation of biotope boundaries and their link to hydrographic conditions.

Table 4. Comparison of Biotope and Cluster analysis (family-level) site groupings (see key below).

		Cluster group											
		OLs	1	2	3-6	7	8	9-10	11	Total	Total excl. OLs	Total Fidelity (%)	Classified fidelity (%)
Biotope	I	1	37	3	4					45	44	82	84
	II	2			66					68	66	97	100
	III	24				3	63			90	66	70	95
	IV	2				19				21	19	90	100
	V			13	1					14	14	93	93
	VI			1	9					10	10	90	90
	VII	3				2	1	47		53	50	89	94
	IX	2				1			32	35	33	91	97

OLs – outliers, not grouped within identified clusters. Total fidelity = classified sites / total sites.
Classified fidelity = classified sites / (total sites – OLs).

4.2 Biotope characterisation

The biotopes proposed above are essentially delimited by bathymetric contours (300, 600, 1200, 1500m) and a latitudinal separation (at c. 61º 40'N) that divides the SEA4 area into regions North and West of Shetland (see Fig. 28). The following provides a characterisation of these biotopes in terms of both their environmental and biological attributes.

4.2.1 Environmental

Figure 30 provides a graphical summary of the environmental characteristics of the SEA4 area biotopes. Note that hydrographic factors (water temperature) are common to each pair of biotopes within the same depth band (i.e. I and IV, II and V etc). Bottom water hydrographic characteristics will vary spatially and temporally within the SEA4 area (see Turrell *et al* 1999), however, the summary data employed in the present study is highly comparable with more extensive studies of bottom water temperatures in the region (see Westerberg, 1990).

Sedimentology (mud content) provides the key distinction between pairs of biotopes within the same depth band, particularly in the cases of I and V and III and VII (see Fig. 30). Variation in sediment mud content between the West and North of Shetland biotopes may be gradational (i.e. the boundary imposed somewhat arbitrary) driven for example by the northward widening of the Faroe-Shetland Channel into the Norwegian Basin, and shallowing of the seabed slope angle, with a presumed decrease in bottom water current speeds. However, the North of Shetland biotopes may also be directly influenced by, or by proximity to, the North Sea Fan (see e.g. Gafeira *et al* 2010) a potential source of fine grained sediments.

Statistical summaries of sediment mud content and bottom water temperature parameters for each biotope are provided in Table 5.

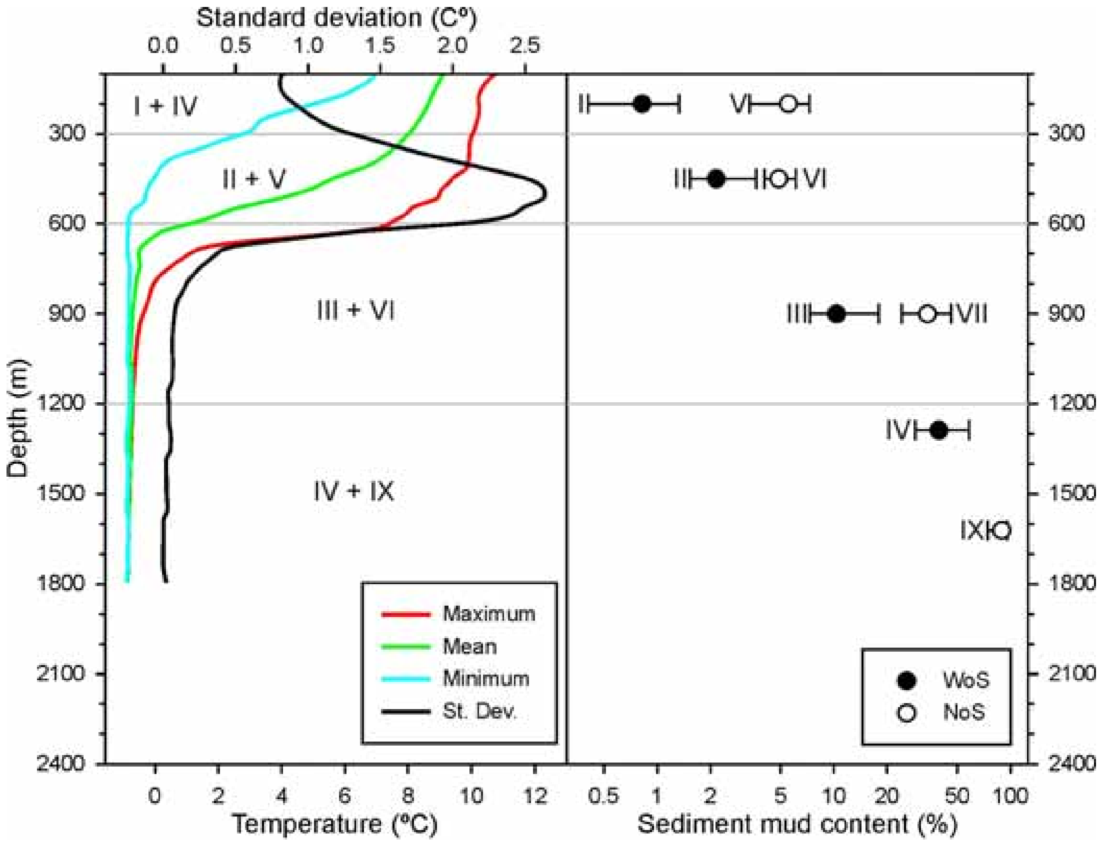

Figure 30. Summary of environmental characteristics of SEA4 area biotopes. Left panel illustrates water temperature parameters across the biotope depth bands, right panel shows sediment mud content for each biotope (as median and interquartile range; WoS, West of Shetland; NoS, North of Shetland).

Table 5. Environmental characterisation of SEA4 area biotopes.

Variable	Statistic	Biotope							
		West of Shetland				North of Shetland			
		100-300m	300-600m	600-1200m	>1200m	100-300m	300-600m	600-1200m	>1200m
		I	II	III	IV	V	VI	VII	IX
Depth (m)	Min.	97	313	615	1200	158	300	602	1363
	Q1	125	373	768	1226	194	337	805	1536
	Med.	**155**	**455**	**928**	**1288**	**209**	**420**	**897**	**1621**
	Q3	223	528	1072	1387	247	500	989	1806
	Max.	295	592	1196	1512	259	550	1192	2315
Mud content (%)	Min.	0.04	0.70	2.22	19.62	0.68	2.50	15.07	30.44
	Q1	0.41	1.53	7.35	28.91	3.35	4.04	24.23	74.29
	Med.	**0.82**	**2.16**	**10.34**	**39.36**	**5.53**	**4.88**	**33.89**	**89.24**
	Q3	1.33	3.64	18.01	58.01	7.25	6.09	46.21	95.91
	Max.	41.50	50.97	59.92	74.35	10.83	11.03	73.32	97.09
Temperature Max. (ºC)	Min.	10.06	7.46	-0.71	-0.82	10.18	8.03	-0.71	-0.88
	Q1	10.23	8.70	-0.64	-0.78	10.20	8.98	-0.56	-0.88
	Med.	**10.30**	**9.35**	**-0.47**	**-0.75**	**10.22**	**9.66**	**-0.35**	**-0.84**
	Q3	10.49	9.93	0.23	-0.72	10.24	9.96	-0.07	-0.82
	Max.	10.85	9.98	7.04	-0.71	10.30	10.02	7.32	-0.78
Temperature mean (ºC)	Min.	8.06	1.26	-0.80	-0.83	8.35	2.36	-0.80	-0.89
	Q1	8.52	3.53	-0.75	-0.80	8.39	4.30	-0.75	-0.89
	Med.	**8.83**	**5.50**	**-0.71**	**-0.77**	**8.60**	**6.24**	**-0.70**	**-0.84**
	Q3	8.98	7.23	-0.54	-0.74	8.67	7.69	-0.61	-0.84
	Max.	9.18	7.88	0.53	-0.73	8.83	7.97	0.90	-0.79
Temperature Min. (ºC)	Min.	2.93	-0.84	-0.87	-0.91	3.36	-0.71	-0.87	-0.90
	Q1	4.19	-0.36	-0.85	-0.88	3.51	-0.31	-0.83	-0.90
	Med.	**6.25**	**-0.09**	**-0.83**	**-0.84**	**4.69**	**0.11**	**-0.83**	**-0.86**
	Q3	6.77	0.66	-0.81	-0.83	5.21	1.83	-0.82	-0.84
	Max.	7.00	2.34	-0.79	-0.82	6.25	2.66	-0.80	-0.83
Temperature st. dev. (Cº)	Min.	0.805	1.406	0.034	0.019	0.816	1.331	0.034	0.000
	Q1	0.808	1.861	0.064	0.024	0.892	1.552	0.064	0.001
	Med.	**0.821**	**2.429**	**0.071**	**0.038**	**0.933**	**2.294**	**0.080**	**0.020**
	Q3	0.974	2.540	0.217	0.043	1.044	2.564	0.155	0.020
	Max.	1.260	2.634	1.628	0.052	1.069	2.634	1.920	0.040
Mud content	n	45	68	83	14	14	10	53	35
All others	n	45	68	90	21	14	10	53	35

4.2.2 Biological

Biological characterisation of the SEA4 area biotopes is provided in several forms below. Table 6 provides a summary of the results of a SIMPER analysis output. For each biotope the top 10 families contributing to the within-group similarity are listed, these can be regarded as the families most typical of the particular biotope. Table 6 also provides listings of the top 10 families contributing to the between-group dissimilarity, these can be regarded as the families most useful in discriminating between the faunas of different biotopes. Note that for brevity Table 6 only includes discriminating families for adjacent biotopes (e.g. biotope I is only contrasted with biotopes II and V, etc), i.e. either alongslope or directly downslope.

Table 7 summarises the average faunal composition of each biotope, listing all those families representing ≥1% of the fauna in at least one biotope. The dominant families are mostly polychaetes, of families representing ≥5% in any one biotope, 11 of the 15 are polychaetes, with sipunculids, amphipods, bivalves and holothurians represented once each. The 'warm water fauna' (biotopes I, II, V, VI) is dominated by the polychaete families Spionidae, Oweniidae, Paraonidae, Terebellidae and Syllidae. The 'cold water fauna' (biotopes III, IV, VII, IX) is dominated by the polychaete families Oweniidae, Paraonidae, Cirratulidae, Maldanidae and Amphinomidae, together with the sipunculid family Golfingiidae.

Tables 8 and 9 provide a graphical summary of the average faunal density of the 10 most abundant families in each of the SEA4 biotopes. The same data is presented in both tables, but in different orientations: 8 is in family x biotope form simplifying within-biotope and latitudinal comparisons; 9 in biotope x family form facilitating between-biotope and bathymetric comparisons. Families have been ordered by depth of predominant occurrence, for example spatangoid urchins and syllid polychaetes occur only in 'warm water areas' (biotopes I, II, V, VI), in contrast to enteropneusts (acorn worms) and myriotrochid sea cucumbers that occur only in northern 'cold water areas' (biotopes VII, IX).

Finally, Figure 31 illustrates some general biological community characteristics for the average fauna of each biotope. Median faunal density ranges between 1,500 and 2,500 individual m^{-2} across the SEA4 biotopes with no indication of significant differences between biotopes within the same depth band (i.e. I vs. V; II vs. VI etc). There is some suggestion of a general increase in faunal density with depth, however, this trend is not statistically significant (Spearman's rank correlation, $p>0.05$). Standard text books (Gage & Tyler, 1991) and recent global syntheses (Wei *et al* 2010) indicate that faunal density 'should' decline logarithmically with depth in response to a corresponding decline in the availability of organic matter. Clearly this is not the case in the SEA4 area (see Bett, 2001 for additional discussion). Similarly, the faunal diversity-depth trend observed does not conform to 'standard expectation' for the deep sea (Gage & Tyler, 1991), where a diversity maximum is expected to occur in the deep bathyal realm (2000-3000m). Again, clearly this is not the case in the SEA4 area where there is an obvious diversity maximum in the 300-600m depth band (biotopes II and VI). This diversity maximum is likely driven by a number of inter-linked factors: (a) extreme thermal variability, preventing competitive exclusion and promoting species co-existence; (b) an 'ecotone' fauna consisting of elements of both the 'warm' and 'cold' water faunas; and (c) enhanced seafloor habitat heterogeneity characteristic of the iceberg ploughmark zone (Masson, 2001) that broadly corresponds with the 300-600m depth band (biotopes II and VI). These factors will tend to both increase species richness and reduce species dominance for this depth band as a whole (see Bett, 2001 for additional discussion).

There are perhaps two important conclusions to be drawn from the above:

1. The SEA4 area in general, and the 300-600m depth band (biotopes II and VI) in particular, is a highly atypical deep-sea environment. It is a boundary region between temperate NE Atlantic and Arctic conditions. Unlike more familiar biogeochemical or biogeographic province boundaries it is not expressed at the sea surface but at depth. Moreover, it is a highly dynamic boundary that is mobile between 300 and 700m water depth. In global terms it is rare, occurring only on the north side of the Greenland-Iceland-Faroe-Scotland ridge system and part of the Norwegian Continental Margin. It is important that text book generalisations about the deep sea are not applied to the SEA4 area.

2. The 300-600m depth band (biotopes II and VI) has conservation value in terms of (i) "rocky reef habitat", i.e. iceberg ploughmark terrain; (ii) the occurrence (if sporadic and already impacted) of 'cold-water corals' (*Lophelia*); and (iii) the occurrence of demosponge aggregations. Note that it also supports the highest diversity of macrobenthos in the SEA4 area – a diversity maximum that occurs at a much shallower depth (e.g. 400m) than text book generalisations would predict (e.g. 2,500m).

Table 6. Characterising and discriminating families (top 10) for SEA4 area biotopes. SIMPER analysis results, note that abundance (Abund) values are shown as ln(x+1) transformations.

	Characterise	Biotope I				
	Family	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
1	Spionidae	5.75	4.48	5.14	9.22	9.22
2	Syllidae	4.29	3.15	3.37	6.48	15.7
3	Glyceridae	4.06	2.83	2.79	5.82	21.53
4	Oweniidae	3.48	2.02	1.52	4.16	25.69
5	Dorvilleidae	3.25	2.02	1.49	4.15	29.83
6	Terebellidae	3.18	2.01	1.92	4.13	33.97
7	Phyllodocidae	2.84	1.69	1.55	3.49	37.45
8	Ampeliscidae	3.01	1.64	1.20	3.37	40.82
9	Nemertea	2.83	1.61	1.43	3.30	44.12
10	Capitellidae	2.59	1.42	1.12	2.92	47.05

	Discriminate	Biotope I	Biotope II				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Dorvilleidae	3.25	1.44	0.98	1.32	1.61	1.61
2	Enchytraeidae	1.08	2.96	0.96	1.45	1.59	3.2
3	Thyasiridae	0.75	2.74	0.95	1.45	1.58	4.78
4	Veneridae	2.57	0.89	0.89	1.33	1.47	6.25
5	Phyllodocidae	2.84	1.21	0.88	1.34	1.45	7.7
6	Sabellidae	1.81	3.02	0.86	1.29	1.42	9.11
7	Ampeliscidae	3.01	3.88	0.84	1.11	1.39	10.51
8	Tubificidae	0.63	2.24	0.83	1.23	1.38	11.88
9	Echinocyamidae	2.09	0.36	0.81	1.27	1.34	13.23
10	Spatangoida	1.98	0.15	0.79	1.13	1.31	14.54

	Discriminate	Biotope I	Biotope V				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Thyasiridae	0.75	3.43	1.20	1.56	1.97	1.97
2	Dorvilleidae	3.25	0.66	1.16	1.71	1.92	3.88
3	Ampharetidae	1.87	3.81	1.14	1.38	1.88	5.76
4	Paraonidae	2.61	4.83	1.02	1.30	1.68	7.44
5	Sabellidae	1.81	3.97	1.00	1.34	1.65	9.09
6	Syllidae	4.29	2.09	0.96	1.38	1.58	10.67
7	Yoldiidae	0.54	2.54	0.95	1.40	1.56	12.23
8	Phyllodocidae	2.84	0.83	0.95	1.58	1.56	13.79
9	Spatangoida	1.98	3.65	0.91	1.38	1.49	15.28
10	Urothoidae	1.14	2.67	0.90	1.39	1.48	16.76

Table 6 continued. Characterising and discriminating families for SEA4 area biotopes.

	Characterise	Biotope II				
	Family	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
1	Spionidae	4.61	3.23	2.19	7.03	7.03
2	Capitellidae	3.56	2.46	2.54	5.34	12.37
3	Terebellidae	4.11	2.45	1.73	5.32	17.69
4	Oweniidae	3.76	2.42	2.14	5.25	22.94
5	Syllidae	3.83	2.40	1.91	5.22	28.16
6	Ampeliscidae	3.88	2.32	1.65	5.03	33.19
7	Paraonidae	3.30	2.08	1.54	4.53	37.72
8	Glyceridae	2.98	1.79	1.50	3.90	41.62
9	Sabellidae	3.02	1.65	1.35	3.58	45.2
10	Enchytraeidae	2.96	1.62	1.31	3.53	48.73

	Discriminate	Biotope II	Biotope III				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Maldanidae	1.38	4.91	1.66	1.67	2.56	2.56
2	Syllidae	3.83	0.13	1.59	2.38	2.45	5.02
3	Amphinomidae	1.44	4.62	1.55	1.63	2.39	7.41
4	Cirratulidae	1.56	4.87	1.47	1.77	2.27	9.68
5	Golfingiidae	1.37	3.68	1.25	1.43	1.93	11.61
6	Enchytraeidae	2.96	0.22	1.22	1.76	1.88	13.49
7	Yoldiidae	1.09	3.38	1.18	1.47	1.81	15.3
8	Oedicerotidae	0.65	2.83	1.10	1.41	1.70	17
9	Capitellidae	3.56	1.47	1.07	1.47	1.65	18.66
10	Scalibregmatidae	1.06	2.79	0.99	1.32	1.52	20.18

	Discriminate	Biotope II	Biotope VI				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Amphinomidae	1.44	2.43	1.00	0.99	1.75	1.75
2	Aoridae	2.25	1.62	0.86	1.19	1.51	3.26
3	Limopsidae	1.80	1.31	0.78	0.99	1.38	4.64
4	Polyplacophora	0.04	2.21	0.76	1.42	1.35	5.99
5	Ampeliscidae	3.88	3.32	0.73	0.98	1.29	7.28
6	Photidae	1.41	2.12	0.72	1.19	1.27	8.55
7	Yoldiidae	1.09	1.79	0.71	1.04	1.26	9.8
8	Cirratulidae	1.56	2.72	0.71	1.21	1.25	11.05
9	Phyllodocidae	1.21	2.37	0.71	1.26	1.24	12.3
10	Scalibregmatidae	1.06	2.39	0.71	1.25	1.24	13.54

Table 6 continued. Characterising and discriminating families for SEA4 area biotopes.

	Characterise	Biotope III				
	Family	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
1	Cirratulidae	4.87	4.15	5.03	8.16	8.16
2	Maldanidae	4.91	3.92	2.71	7.72	15.88
3	Amphinomidae	4.62	3.63	2.54	7.14	23.02
4	Terebellidae	3.71	2.62	1.59	5.16	28.18
5	Spionidae	3.88	2.61	1.47	5.14	33.32
6	Golfingiidae	3.68	2.58	1.53	5.08	38.4
7	Yoldiidae	3.38	2.27	1.42	4.47	42.87
8	Oweniidae	3.49	2.24	1.30	4.40	47.27
9	Phoxocephalidae	3.22	2.14	1.36	4.22	51.48
10	Ampharetidae	2.95	1.96	1.35	3.85	55.33

	Discriminate	Biotope III	Biotope IV				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Capitellidae	1.47	4.99	1.84	1.75	3.34	3.34
2	Paraonidae	2.34	4.42	1.39	1.24	2.52	5.86
3	Spionidae	3.88	2.12	1.33	1.25	2.42	8.28
4	Terebellidae	3.71	1.85	1.26	1.28	2.30	10.58
5	Glyceridae	2.91	0.78	1.25	1.46	2.28	12.86
6	Scalibregmatidae	2.79	0.69	1.24	1.45	2.25	15.11
7	Oweniidae	3.49	5.50	1.18	1.15	2.14	17.25
8	Ampharetidae	2.95	1.26	1.12	1.35	2.03	19.28
9	Sphyrapidae	2.20	0.10	1.11	1.09	2.03	21.31
10	Ampeliscidae	2.77	1.68	1.04	1.26	1.88	23.19

	Discriminate	Biotope III	Biotope VII				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Thyasiridae	2.08	4.34	1.31	1.38	2.52	2.52
2	Paraonidae	2.34	4.62	1.20	1.25	2.30	4.83
3	Capitellidae	1.47	3.54	1.13	1.40	2.17	6.99
4	Glyceridae	2.91	0.94	1.10	1.39	2.11	9.11
5	Terebellidae	3.71	2.29	1.08	1.26	2.09	11.2
6	Oweniidae	3.49	5.20	1.06	1.13	2.04	13.24
7	Lumbrineridae	0.72	2.65	1.04	1.38	2.00	15.24
8	Oedicerotidae	2.83	1.26	1.02	1.32	1.97	17.2
9	Sphyrapidae	2.20	1.96	0.97	1.19	1.88	19.08
10	Ampeliscidae	2.77	1.59	0.96	1.25	1.85	20.93

Table 6 continued. Characterising and discriminating families for SEA4 area biotopes.

	Characterise Family	Biotope IV Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
1	Oweniidae	5.50	5.37	6.37	9.98	9.98
2	Capitellidae	4.99	5.25	4.34	9.75	19.73
3	Cirratulidae	4.73	4.56	2.66	8.47	28.2
4	Maldanidae	4.59	4.50	4.26	8.36	36.56
5	Golfingiidae	4.45	4.43	4.68	8.22	44.78
6	Amphinomidae	4.35	4.04	2.46	7.50	52.28
7	Paraonidae	4.42	3.80	1.92	7.06	59.34
8	Leptognathiidae	2.62	1.92	1.21	3.56	62.9
9	Yoldiidae	2.46	1.68	0.95	3.11	66.01
10	Phoxocephalidae	2.22	1.41	0.84	2.62	68.63

	Discriminate Family	Biotope IV Av.Abund	Biotope IX Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Maldanidae	4.59	0.85	2.16	2.07	4.05	4.05
2	Myriotrochidae	0.48	3.98	2.02	2.08	3.79	7.83
3	Enteropneusta	0.59	3.08	1.52	1.64	2.84	10.68
4	Aspidosiphonidae	0.00	2.60	1.43	1.03	2.68	13.36
5	Paraonidae	4.42	4.99	1.24	1.06	2.31	15.67
6	Ophiuridae	1.64	2.24	1.17	1.15	2.19	17.87
7	Leptognathiidae	2.62	1.41	1.14	1.31	2.13	19.99
8	Arcidae	0.80	2.22	1.11	1.22	2.08	22.08
9	Thyasiridae	0.50	2.02	1.09	1.08	2.04	24.12
10	Spionidae	2.12	2.87	1.09	1.15	2.04	26.16

Table 6 continued. Characterising and discriminating families for SEA4 area biotopes.

	Characterise	Biotope V				
	Family	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
1	Spionidae	5.24	3.84	8.42	7.48	7.48
2	Paraonidae	4.83	3.35	4.43	6.53	14.01
3	Terebellidae	4.11	2.99	5.45	5.82	19.83
4	Capitellidae	3.73	2.75	6.05	5.35	25.18
5	Sabellidae	3.97	2.66	4.03	5.18	30.37
6	Oweniidae	4.26	2.58	1.98	5.02	35.39
7	Spatangoida	3.65	2.33	2.07	4.54	39.93
8	Ampharetidae	3.81	1.98	1.18	3.86	43.79
9	Lumbrineridae	2.90	1.90	2.24	3.70	47.49
10	Nemertea	2.97	1.89	2.30	3.67	51.16

	Discriminate	Biotope V	Biotope VI				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Enchytraeidae	0.39	3.22	1.12	1.78	1.89	1.89
2	Spatangoida	3.65	1.26	1.07	1.52	1.80	3.69
3	Amphinomidae	1.04	2.43	0.94	1.04	1.59	5.28
4	Ampharetidae	3.81	2.81	0.90	1.13	1.51	6.79
5	Syllidae	2.09	3.95	0.86	1.39	1.45	8.24
6	Thyasiridae	3.43	2.21	0.86	1.26	1.44	9.68
7	Yoldiidae	2.54	1.79	0.81	1.26	1.37	11.05
8	Urothoidae	2.67	1.67	0.80	1.25	1.35	12.4
9	Lumbrineridae	2.90	1.13	0.79	1.32	1.33	13.73
10	Polyplacophora	0.00	2.21	0.76	1.46	1.28	15.01

Table 6 continued. Characterising and discriminating families for SEA4 area biotopes.

	Characterise	Biotope VI				
	Family	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
1	Spionidae	5.11	3.03	4.79	7.14	7.14
2	Terebellidae	4.07	2.49	4.27	5.86	13
3	Syllidae	3.95	2.17	1.74	5.11	18.11
4	Capitellidae	3.85	2.04	1.80	4.80	22.91
5	Paraonidae	3.79	2.03	1.59	4.79	27.7
6	Oweniidae	4.08	2.02	1.62	4.77	32.47
7	Enchytraeidae	3.22	1.82	1.57	4.28	36.75
8	Nemertea	3.29	1.67	1.81	3.93	40.68
9	Ampeliscidae	3.32	1.46	1.22	3.44	44.11
10	Sabellidae	2.70	1.22	1.15	2.87	46.98

	Discriminate	Biotope VI	Biotope VII				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Syllidae	3.95	0.00	1.51	2.46	2.37	2.37
2	Enchytraeidae	3.22	0.09	1.26	2.00	1.98	4.36
3	Maldanidae	1.37	4.64	1.20	2.13	1.89	6.25
4	Golfingiidae	1.13	3.89	1.18	1.73	1.85	8.1
5	Amphinomidae	2.43	4.77	1.14	1.46	1.79	9.89
6	Yoldiidae	1.79	4.04	1.07	1.40	1.68	11.57
7	Cirratulidae	2.72	5.22	1.03	1.21	1.63	13.2
8	Thyasiridae	2.21	4.34	0.97	1.21	1.53	14.73
9	Ampeliscidae	3.32	1.59	0.93	1.42	1.47	16.2
10	Ophiuridae	1.03	2.42	0.88	1.22	1.38	17.59

Table 6 continued. Characterising and discriminating families for SEA4 area biotopes.

	Characterise	Biotope VII				
	Family	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
1	Cirratulidae	5.22	3.95	5.26	7.14	7.14
2	Oweniidae	5.20	3.89	2.35	7.03	14.17
3	Amphinomidae	4.77	3.60	3.24	6.50	20.68
4	Maldanidae	4.64	3.58	4.71	6.46	27.14
5	Paraonidae	4.62	3.40	2.93	6.13	33.28
6	Spionidae	4.93	3.35	2.65	6.05	39.32
7	Thyasiridae	4.34	2.94	2.22	5.32	44.64
8	Yoldiidae	4.04	2.80	2.15	5.05	49.69
9	Capitellidae	3.54	2.53	1.94	4.56	54.25
10	Golfingiidae	3.89	2.31	1.36	4.17	58.42

	Discriminate	Biotope VII	Biotope IX				
	Family	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1	Maldanidae	4.64	0.85	1.87	2.18	3.35	3.35
2	Myriotrochidae	0.68	3.98	1.68	1.92	3.02	6.38
3	Thyasiridae	4.34	2.02	1.34	1.39	2.40	8.78
4	Enteropneusta	0.70	3.08	1.30	1.57	2.34	11.12
5	Scalibregmatidae	3.01	0.46	1.29	1.67	2.31	13.43
6	Aspidosiphonidae	0.05	2.60	1.25	1.02	2.24	15.67
7	Spionidae	4.93	2.87	1.18	1.34	2.13	17.8
8	Ampharetidae	2.90	0.89	1.15	1.43	2.07	19.87
9	Yoldiidae	4.04	2.26	1.09	1.24	1.96	21.83
10	Arcidae	0.05	2.22	1.07	1.24	1.92	23.75

Table 6 continued. Characterising and discriminating families for SEA4 area biotopes.

	Characterise	Biotope IX				
	Family	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
1	Capitellidae	5.16	5.45	4.71	10.05	10.05
2	Oweniidae	5.02	5.06	4.58	9.32	19.37
3	Paraonidae	4.99	4.28	1.64	7.89	27.25
4	Golfingiidae	4.54	4.22	2.28	7.78	35.04
5	Cirratulidae	4.02	3.82	2.44	7.04	42.08
6	Myriotrochidae	3.98	3.59	2.00	6.62	48.7
7	Amphinomidae	3.81	3.41	1.75	6.28	54.98
8	Enteropneusta	3.08	2.54	1.39	4.68	59.66
9	Spionidae	2.87	2.19	1.27	4.04	63.7
10	Nemertea	2.30	1.60	0.90	2.95	66.65

Table 7. Average faunal composition (%) within SEA4 area biotopes. Only those families representing ≥1% of the fauna in at least one biotope are tabulated. (Composition values ≥5% and ≥10% have been shaded).

	Biotope							
	West of Shetland				North of Shetland			
	I	II	III	IV	V	VI	VII	IX
Spionidae	39.0	16.2	6.1	0.7	21.1	20.8	11.0	1.9
Oweniidae	3.9	6.9	4.1	25.0	7.8	7.3	14.5	17.1
Paraonidae	1.6	4.2	1.2	8.3	14.0	5.5	8.1	16.6
Capitellidae	1.5	5.6	0.4	14.9	4.6	5.8	2.7	19.8
Cirratulidae	1.1	0.6	16.5	11.5	2.3	1.8	14.8	6.3
Maldanidae	0.1	0.5	17.4	10.0	0.5	0.4	8.2	0.2
Amphinomidae	0.0	0.5	13.0	7.8	0.2	1.3	9.4	5.0
Terebellidae	2.9	9.8	5.1	0.5	6.8	7.3	0.7	0.3
Golfingiidae	0.2	0.5	5.0	8.7	0.0	0.3	3.9	10.6
Syllidae	9.0	7.4	0.0	0.0	0.8	6.5	0.0	0.0
Ampeliscidae	2.4	7.7	1.9	0.4	1.1	3.4	0.3	0.1
Glyceridae	7.1	3.0	2.2	0.1	1.7	1.5	0.1	0.0
Thyasiridae	0.1	2.4	0.9	0.1	3.3	1.0	6.1	0.7
Ampharetidae	0.7	2.2	2.3	0.3	4.9	2.0	1.4	0.2
Sabellidae	0.6	3.2	1.0	0.3	5.8	1.7	0.9	0.4
Yoldiidae	0.1	0.3	3.6	1.1	1.3	0.6	4.5	1.0
Nemertea	2.0	1.6	0.4	0.4	2.1	3.3	0.9	1.0
Phoxocephalidae	0.2	1.3	3.1	0.8	1.1	1.2	0.9	0.6
Enchytraeidae	0.2	3.0	0.0	0.0	0.1	3.1	0.0	0.0
Myriotrochidae	0.0	0.0	0.0	0.1	0.0	0.0	0.1	6.0
Scalibregmatidae	0.0	0.3	2.0	0.1	0.5	1.3	1.5	0.1
Spatangoida	0.8	0.0	0.0	0.0	4.2	0.3	0.0	0.0
Lumbrineridae	0.6	0.2	0.1	0.1	1.9	0.3	1.1	0.6
Dorvilleidae	3.1	0.5	0.0	0.0	0.1	0.5	0.2	0.0
Oedicerotidae	0.4	0.1	2.0	0.7	0.5	0.1	0.2	0.2
Phyllodocidae	2.0	0.4	0.2	0.1	0.1	1.2	0.1	0.0
Astartidae	1.0	1.1	0.1	0.0	0.6	0.6	0.1	0.0
Polynoidae	1.6	0.7	0.1	0.0	0.1	0.6	0.1	0.1
Tubificidae	0.1	1.4	0.4	0.1	0.1	0.8	0.2	0.1
Leptognathiidae	0.1	0.2	0.7	1.3	0.2	0.1	0.2	0.4
Enteropneusta	0.0	0.0	0.1	0.1	0.0	0.0	0.1	2.4
Aoridae	0.7	1.4	0.0	0.0	0.0	0.5	0.0	0.0
Urothoidae	0.3	0.2	0.1	0.0	1.5	0.5	0.0	0.0
Veneridae	1.5	0.2	0.0	0.0	0.2	0.1	0.0	0.0
Sphyrapidae	0.0	0.2	1.0	0.0	0.0	0.0	0.5	0.0
Aspidosiphonidae	0.0	0.0	0.0	0.0	0.0	0.2	0.0	1.4
Polyplacophora	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0

Table 8. Graphical representation of average faunal density (indiv.m^{-2}) within SEA4 area biotopes. Horizontal form comparing relative abundance of families. Only the top ten most abundant families in each biotope are tabulated. (See inset key for faunal density levels illustrated).

	Biotope							
	West of Shetland				North of Shetland			
	I	II	III	IV	V	VI	VII	IX
Spatangoida	+				+++	+		
Dorvilleidae	+++	+				+	+	
Syllidae	++++	+++			++	+++		
Phyllodocidae	++	+	+		+	++	+	
Glyceridae	++++	++	++	+	++	++	+	
Spionidae	+++++	++++	+++	++	+++++	+++++	++++	++
Sabellidae	+	++	++	+	+++	++	++	+
Terebellidae	+++	++++	+++	+	++++	++++	++	+
Ampharetidae	+	++	++	+	+++	++	++	+
Enchytraeidae	+	++				+++		
Ampeliscidae	++	+++	++	+	++	+++	+	
Nemertea	++	++	+	+	++	+++	++	++
Thyasiridae	+	++	+		+++	++	++++	+
Phoxocephalidae	+	++	+++	++	++	++	++	+
Paraonidae	++	+++	++	++++	++++	+++	++++	++++
Yoldiidae		+	+++	++	++	+	++++	++
Oweniidae	+++	+++	+++	+++++	++++	++++	+++++	++++
Cirratulidae	++	+	++++	++++	+++	++	+++++	+++
Maldanidae		+	++++	++++	+	+	++++	+
Capitellidae	++	+++	+	++++	+++	+++	+++	+++++
Amphinomidae		+	++++	++++	+	++	++++	+++
Leptognathiidae		+	+	++	+	+	+	+
Aspidosiphonidae						+		++
Golfingiidae	+	+	+++	++++		+	+++	++++
Enteropneusta							+	+++
Myriotrochidae								+++

Key	
Density (indiv.m^{-2})	
1-6	+
7-19	++
20-55	+++
56-155	++++
>156	+++++

Table 9. Graphical representation of average faunal density (indiv.m^{-2}) within SEA4 area biotopes. Vertical form comparing bathymetric distribution of families. Only the top ten most abundant families in each biotope are tabulated. (See inset key in Table 8 for faunal density levels illustrated).

Biotope		Spatangoida	Dorvilleidae	Syllidae	Phyllodocidae	Glyceridae	Spionidae	Sabellidae	Terebellidae	Ampharetidae	Enchytraeidae	Ampeliscidae	Nemertea	Thyasiridae	Phoxocephalidae	Paraonidae	Yoldiidae	Oweniidae	Cirratulidae	Maldanidae	Capitellidae	Amphinomidae	Leptognathiidae	Aspidosiphonidae	Golfingiidae	Enteropneusta	Myriotrochidae
West of Shetland	I	+	+++	++++	++	++++	+++++	+	+++	+	+	++	++	+	+	++		+++	++		++				+		
	II		+	+++	+	++	++++	++	++++	++	++	+++	++	++	++	+++	+	+++	+	+	+++	+	+		+		
	III				+	++	+++	++	+++	++		++	+	+	+++	++	+++	+++	++++	++++	+	++++	+		+++		
	IV					+	++	+	+	+		+	+		++	++++	++	+++++	++++	++++	++++	++++	++		++++		
North of Shetland	V	+++		++	+	++	+++++	+++	++++	+++		++	++	+++	++	++++	++	++++	+++	+	+++	+	+				
	VI	+	+	+++	++	++	+++++	++	++++	++	+++	+++	+++	++	++	+++	+	++++	++	+	+++	++	+	+	+		
	VII		+		+	+	++++	++	++	++		+	++	++++	++	++++	++++	+++++	+++++	++++	+++	++++	+		+++	+	
	IX						++	+	+	+			++	+	+	++++	++	++++	+++	+	+++++	+++	+	++	++++	+++	+++

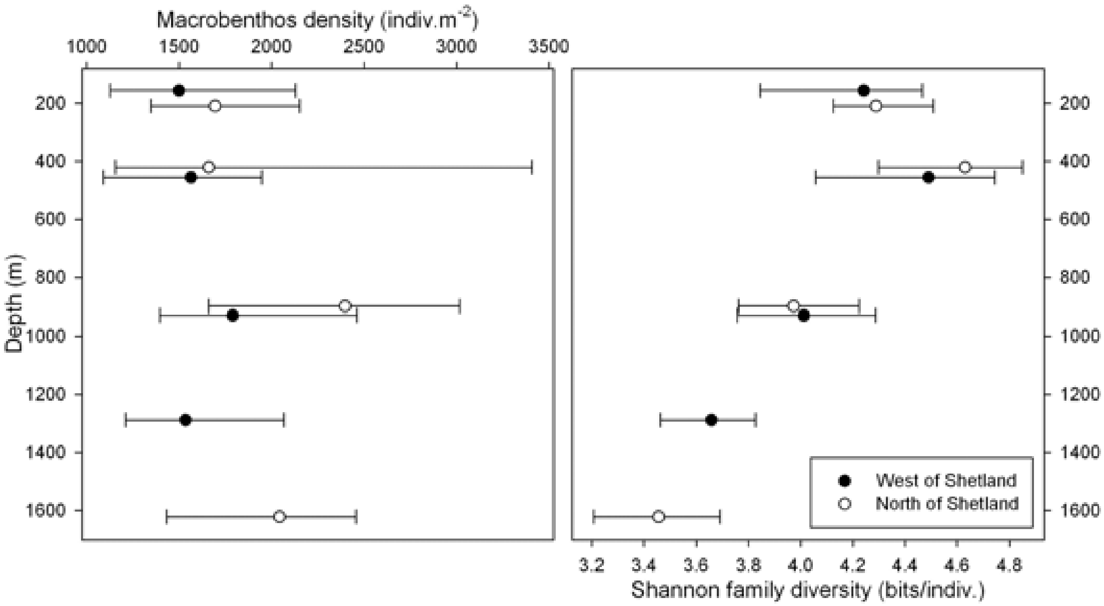

Figure 31. General ecological characteristics of the SEA4 area biotopes. Left panel – faunal density, right panel – faunal diversity, both parameters are illustrated as median and interquartile range.

4.3 Biotope names and descriptions

Biotope descriptions are here based on high-level biological characterisation and broad-scale environmental characteristics. The biological characterisation is based on identification of those families of macrobenthos most characteristic of a given biotope (e.g. see Table 6) and those families that are most distinctive (i.e. discriminating between biotopes) of that biotope. These distinctive families were identified by an additional SIMPER analysis contrasting all samples from one biotope with all samples from all other biotopes (note that Table 6 above provides similar contrasts for adjacent biotopes). The distinctive family for a particular biotope was then taken to be the family contributing most to the dissimilarity between that biotope and all others in a positive manner (i.e. where its abundance was greater in the biotope of interest). Table 10 identifies the most distinctive family for each of biotopes I-IX.

The environmental characteristics considered are those that most drive the ecology of the region: (i) water depth; (ii) water mass; and (iii) sediment type (see section 3.2.2.4 above). To characterise sediment type, sediment mud content was referenced to the Folk classification scheme and a simplified version of that classification (Fig. 32; McBreen & Askew, 2010). For simplicity it is assumed that sediment gravel content is <5% throughout. It is, however, clear that gravel, cobble and boulder sized material may be encountered anywhere in the SEA4 area and indeed may provide 100% seabed cover in some areas (see section 4.4 below). Such areas can not be quantitatively sampled for macrobenthos by conventional means and so have been 'self-excluded' from this study. This does not impact the results presented here but must be borne in mind if comparison is made with visual (photo / video) assessments of sediment type.

Table 11 provides a compilation of the biological and environmental characterisations of each biotope. Two elements of terminology in this table require clarification:

1. In the water mass category the term 'Atlanto-Arctic' is introduced to refer to the dynamic boundary region between temperate NE Atlantic waters and Arctic waters, a zone of exceptional thermal variability.

2. The term 'trinomen' (cf. taxonomic nomenclature) is introduced to refer to the compilation of characterising and discriminating families. The trinomen consists of the names of the two most characteristic families (Table 6) and the most distinctive family (Table 10): characteristic 1-charcteristic 2-distinctive 1.

The biotope 'name' or descriptor is then derived as:

'trinomen' in 'water mass' 'sediment type' '(water depth range)'

For example, Biotope I:

"Spionidae-Syllidae-Syllidae in Atlantic sand and muddy sand (100-300m)"

The biotope names and descriptions are given as follows:

SEA4 BIOTOPE I
SPIONIDAE-SYLLIDAE-SYLLIDAE IN ATLANTIC SAND AND MUDDY SAND (100-300M)
Deep-water biotope (100-300m) of the Faroe-Shetland / Faroe Bank Channels (West of Shetland); temperate Atlantic waters; sand and muddy sand substratum (predominantly S); macrobenthos characterised by Spionidae and Syllidae, distinguished from other UK SEA area 4 biotopes by abundance of Syllidae.

SEA4 BIOTOPE II
SPIONIDAE-CAPITELLIDAE-SYLLIDAE IN ATLANTO-ARCTIC SAND AND MUDDY SAND (300-600M)
Deep-water biotope (300-600m) of the Faroe-Shetland / Faroe Bank Channels (West of Shetland); mixed Atlantic and Arctic waters; sand and muddy sand substratum (predominantly S); macrobenthos characterised by Spionidae and Capitellidae, distinguished from other UK SEA area 4 biotopes by abundance of Syllidae.

SEA4 BIOTOPE III
CIRRATULIDAE-MALDANIDAE-MALDANIDAE IN ARCTIC SAND AND MUDDY SAND (600-1200M)
Deep-water biotope (600-1200m) of the Faroe-Shetland / Faroe Bank Channels (West of Shetland); Arctic waters; sand and muddy sand substratum (predominantly S/mS); macrobenthos characterised by Cirratulidae and Maldanidae, distinguished from other UK SEA area 4 biotopes by abundance of Maldanidae.

SEA4 BIOTOPE IV
OWENIIDAE-CAPITELLIDAE-MALDANIDAE IN ARCTIC MUD AND SANDY MUD (>1200M)
Deep-water biotope (>1200m) of the Faroe-Shetland / Faroe Bank Channels (West of Shetland); Arctic waters; mud and sandy mud substratum (predominantly mS/sM); macrobenthos characterised by Oweniidae and Capitellidae, distinguished from other UK SEA area 4 biotopes by abundance of Maldanidae.

SEA4 BIOTOPE V
SPIONIDAE-PARAONIDAE-SPATANGOIDA IN ATLANTIC SAND AND MUDDY SAND (100-300M)
Deep-water biotope (100-300m) of the Norwegian Basin (North of Shetland); temperate Atlantic waters; sand and muddy sand substratum (predominantly S); macrobenthos characterised by Spionidae and Paraonidae, distinguished from other UK SEA area 4 biotopes by abundance of Spatangoida.

SEA4 BIOTOPE VI
SPIONIDAE-TEREBELLIDAE-SYLLIDAE IN ATLANTO-ARCTIC SAND AND MUDDY SAND (300-600M)
Deep-water biotope (300-600m) of the Norwegian Basin (North of Shetland); mixed Atlantic and Arctic waters; sand and muddy sand substratum (predominantly S); macrobenthos characterised by Spionidae and Terebellidae, distinguished from other UK SEA area 4 biotopes by abundance of Syllidae.

SEA4 BIOTOPE VII
CIRRATULIDAE-OWENIIDAE-THYASIRIDAE IN ARCTIC MUD AND SANDY MUD (600-1200M)
Deep-water biotope (600-1200m) of the Norwegian Basin (North of Shetland); Arctic waters; mud and sandy mud substratum (predominantly mS); macrobenthos characterised by Cirratulidae and Oweniidae, distinguished from other UK SEA area 4 biotopes by abundance of Thyasiridae.

SEA4 BIOTOPE IX
CAPITELLIDAE-OWENIIDAE-MYRIOTROCHIDAE IN ARCTIC MUD AND SANDY MUD (>1200M)
Deep-water biotope (>1200m) of the Norwegian Basin (North of Shetland); Arctic waters; mud and sandy mud substratum (predominantly sM/M); macrobenthos characterised by Capitellidae and Oweniidae, distinguished from other UK SEA area 4 biotopes by abundance of Myriotrochidae.

Table 10. Discriminating families (top 5) for SEA4 area biotopes – named biotope contrasted with all others. SIMPER analysis results, note that abundance (Abund) values are shown as ln(x+1) transformations. The highest ranked positive (i.e. is most abundant in the named biotope) discriminating family is indicated (shading).

Discriminate Family	Biotope I Av.Abund	Others Av.Abund	Contrib%
Amphinomidae	0.04	3.54	2.24
Syllidae	4.29	1.19	2.15
Maldanidae	0.34	3.25	1.96
Dorvilleidae	3.25	0.70	1.79
Golfingiidae	0.96	3.09	1.75

Discriminate Family	Biotope II Av.Abund	Others Av.Abund	Contrib%
Syllidae	3.83	1.04	2.11
Amphinomidae	1.44	3.49	2.01
Cirratulidae	1.56	4.21	1.97
Maldanidae	1.38	3.23	1.90
Golfingiidae	1.37	3.16	1.81

Discriminate Family	Biotope III Av.Abund	Others Av.Abund	Contrib%
Maldanidae	4.91	2.10	2.35
Capitellidae	1.47	3.75	2.01
Amphinomidae	4.62	2.50	2.00
Paraonidae	2.34	3.90	1.88
Golfingiidae	3.68	2.48	1.80

Discriminate Family	Biotope IV Av.Abund	Others Av.Abund	Contrib%
Spionidae	2.12	4.47	2.30
Maldanidae	4.59	2.74	2.06
Golfingiidae	4.45	2.69	1.87
Amphinomidae	4.35	2.99	1.85
Thyasiridae	0.50	2.47	1.83

Discriminate Family	Biotope V Av.Abund	Others Av.Abund	Contrib%
Spatangoida	3.65	0.36	2.32
Golfingiidae	0.22	2.91	1.96
Amphinomidae	1.04	3.16	1.93
Ampharetidae	3.81	2.39	1.78
Maldanidae	1.66	2.91	1.72

Discriminate Family	Biotope VI Av.Abund	Others Av.Abund	Contrib%
Syllidae	3.95	1.53	1.85
Amphinomidae	2.43	3.09	1.74
Enchytraeidae	3.22	0.89	1.73
Maldanidae	1.37	2.90	1.57
Golfingiidae	1.13	2.85	1.55

Discriminate Family	Biotope VII Av.Abund	Others Av.Abund	Contrib%
Thyasiridae	4.34	1.97	2.13
Maldanidae	4.64	2.52	1.99
Amphinomidae	4.77	2.75	1.87
Golfingiidae	3.89	2.60	1.86
Yoldiidae	4.04	2.07	1.83

Discriminate Family	Biotope IX Av.Abund	Others Av.Abund	Contrib%
Myriotrochidae	3.98	0.22	2.87
Enteropneusta	3.08	0.29	2.18
Maldanidae	0.85	3.09	2.18
Paraonidae	4.99	3.31	2.09
Golfingiidae	4.54	2.60	1.98

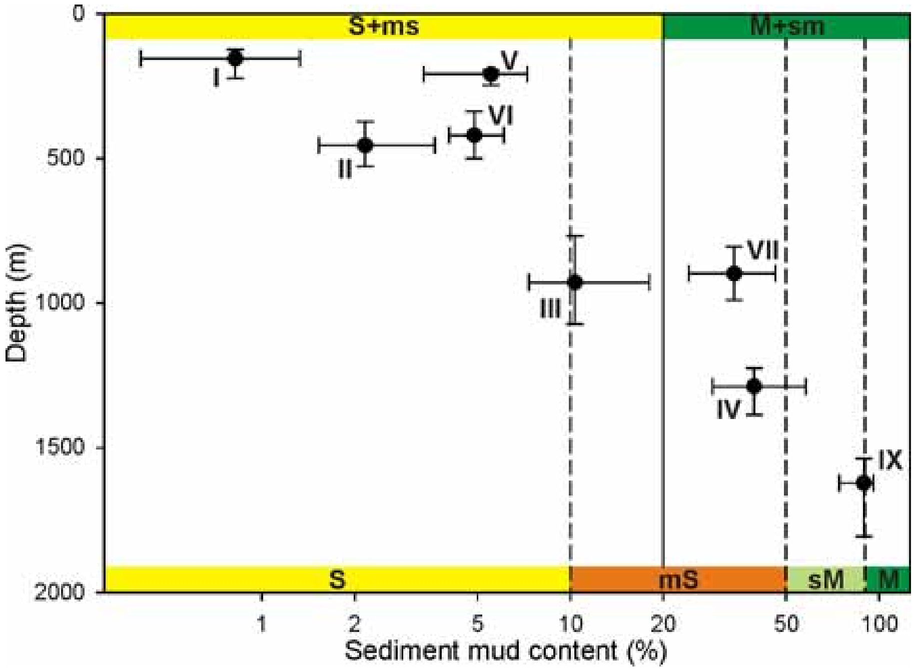

Figure 32. Sediment mud content of Biotopes I-IX referenced to standard and simplified Folk classification schemes (m, mud; ms, muddy sand; s, sand; sm, sandy mud; McBreen & Askew, 2010). Biotope values are plotted as median and interquartile range with depth.

Table 11. Proposed primary biotopes for Scotland's northern deep seas, Strategic Environmental Assessment area 4 (SEA4).

1	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**IX**
2	West of Shetland				North of Shetland			
3	Faroe-Shetland / Faroe Bank Channels				Norwegian Basin			
4	100-300m	300-600m	600-1200m	>1200m	100-300m	300-600m	600-1200m	>1200m
5	Atlantic	Atlanto-Arctic	Arctic	Arctic	Atlantic	Atlanto-Arctic	Arctic	Arctic
6	sand and muddy sand	sand and muddy sand	sand and muddy sand	mud and sandy mud	sand and muddy sand	sand and muddy sand	mud and sandy mud	mud and sandy mud
7	S	S	S/mS	mS/sM	S	S	mS	sM/M
8	Spionidae-Syllidae-Syllidae	Spionidae-Capitellidae-Syllidae	Cirratulidae-Maldanidae-Maldanidae	Oweniidae-Capitellidae-Maldanidae	Spionidae-Paraonidae-Spatangoida	Spionidae-Terebellidae-Syllidae	Cirratulidae-Oweniidae-Thyasiridae	Capitellidae-Oweniidae-Myriotrochidae
9	Spionidae-Syllidae-Syllidae in Atlantic sand and muddy sand (100-300m)	Spionidae-Capitellidae-Syllidae in Atlanto-Arctic sand and muddy sand (300-600m)	Cirratulidae-Maldanidae-Maldanidae in Arctic sand and muddy sand (600-1200m)	Oweniidae-Capitellidae-Maldanidae in Arctic mud and sandy mud (>1200m)	Spionidae-Paraonidae-Spatangoida in Atlantic sand and muddy sand (100-300m)	Spionidae-Terebellidae-Syllidae in Atlanto-Arctic sand and muddy sand (300-600m)	Cirratulidae-Oweniidae-Thyasiridae in Arctic mud and sandy mud (600-1200m)	Capitellidae-Oweniidae-Myriotrochidae in Arctic mud and sandy mud (>1200m)

1. Biotope coding used in this report
2. Geographic classification
3. Oceanographic classification
4. Water depth range
5. Water masses: Atlanto-Arctic (dynamic boundary zone between Atlantic and Arctic waters)
6. Sediment types: simplified Folk classification (McBreen & Askew, 2010)
7. Sediment types: conventional Folk classification (McBreen & Askew, 2010)
8. Characterising and discriminating families trinomen (see text for details)
9. Biotope descriptor ('name')

4.3.1 Biotopes in the European (EUNIS) context

The European Nature Information System (EUNIS) is a framework for the classification of all European habitat types (Davies *et al* 2004). In the EUNIS system, a '*habitat*' is defined as: '*a place where plants or animals normally live, characterized primarily by its physical features and secondarily by the species of plants and animals that live there*'. Many, but not all, EUNIS habitats are also '*biotopes*' - '*areas with particular environmental conditions that are sufficiently uniform to support a characteristic assemblage of organisms*'. The deep-sea component of EUNIS is rather poorly developed, at present it is an eclectic, non-hierarchical admixture of physiographic and biogeographic elements with highly varied levels of detail.

Table 12 lists the EUNIS deep-sea habitat classification system, relating its various elements to the proposed SEA4 area biotopes and other habitats in the area. Many EUNIS types are present (or likely to occur) in the SEA4 area, however, as a predominantly low-relief sedimentary environment the region is likely best classified by sediment type, e.g. A6.3, A6.4 and A6.5, respectively deep-sea sand, muddy sand, and mud. The entirety of the SEA4 area, certainly biotopes I-VII, could be regarded as a 'mixed substratum' environment (A6.2). However, the fauna show a very clear response (see section 3.2.2 above) to variations in the fine sediment (sand and mud) fraction and this seems to offer the most efficient means of classifying these biotopes / habitats.

Table 13 details a suggested expansion of the EUNIS deep-sea habitat classification system to incorporate the SEA4 area biotopes. All SEA4 biotopes are suggested as Level 5 EUNIS habitats in keeping with existing bathyal mud habitats of the Mediterranean (e.g. A6.511-6.514). It is therefore also necessary to propose additional Level 4 habitats to accommodate the SEA4 biotopes:

Atlantic bathyal sand (added to parent A6.3)
Atlanto-Arctic bathyal sand (added to parent A6.3)
Arctic bathyal muddy sand (added to parent A6.4)
Arctic bathyal mud (added to parent A6.5)

Again this is in keeping with the existing '*Mediterranean bathyal mud*' Level 4 habitat (A6.51).

Table 12. EUNIS deep-sea habitat classification system[3], with notes on EUNIS habitat occurrence in Scotland's northern deep seas, Strategic Environmental Assessment area 4 (SEA4).

Code	Level 3	Level 4	Level 5	Level 6	SEA4
A6.1	Hard substratum				Present in all Biotopes I-IX
A6.11		Bedrock			May occur in the Judd Deeps (abutting Biotope III; Bulat & Long, 2001)
A6.12		Anthropogenic			Extensive occurrence of oil industry seabed infrastructure
A6.13		Manganese nodule			
A6.14		Boulder			Present in all Biotopes I-IX
A6.2	Mixed substratum				Present in all Biotopes I-IX
A6.21		Lag deposit			Present in all Biotopes I-IX
A6.22		Biogenic gravel			
A6.23		Calcareous pavement			
A6.24		Allochthonous material			(Likely to occur in all Biotopes I-IX)
A6.241			Macrophyte debris		(Likely to occur in all Biotopes I-IX)
A6.3	Sand				Dominant sediment type of Biotopes I, II, V and VI
A6.31		Bathyal detritic sand			
A6.4	Muddy sand				Dominant sediment type of Biotopes III, IV and VII
A6.5	Mud				Dominant sediment type of Biotope IX
A6.51		Mediterranean bathyal mud			
A6.511			Sandy mud		
A6.512			Fluid mud		
A6.513			Soft mud		
A6.514			Compact mud		
A6.52		Abyssal mud			
A6.6	Bioherm				Present, predominantly within Biotopes II and VI
A6.61		Coral			Present, predominantly within Biotopes II and VI
A6.611			Lophelia reef		Present, predominantly within Biotopes II and VI, but probably not in "reef" quantities
A6.62		Sponge			Present, predominantly within Biotopes II and VI, also notable in Biotope III
A6.621			Pheronema aggregation		
A6.7	Raised feature				(Wyville Thomson Ridge – Biotope II)
A6.71		Oceanic island			
A6.72		Seamount / knoll / bank			
A6.721			Euphotic zone summit		
A6.722			Mesopelagic zone summit		
A6.723			Deeper summit		
A6.724			Flank		
A6.725			Base		
A6.7251				Moat	

[3] http://eunis.eea.europa.eu/

A6.73		Ridge			(Wyville Thomson Ridge – Biotope II)
A6.731			Flank		
A6.732			Axial trough		
A6.733			Non-hydrothermal		(Wyville Thomson Ridge – Biotope II)
A6.74		Abyssal hill			
A6.75		Carbonate mound			
A6.8	Varia				
A6.81		Canyons / channels / slope failures and slumps			Variously present
A6.811			Active channel		
A6.812			Inactive channel		Present in Biotope III (Masson, 2001)
A6.813			Alongslope channel		
A6.814			Turbidite / fan		Various occurrences, e.g. the "AFEN Slide" in Biotope III[78], the North Sea Fan in Biotopes V-IX (Gafeira *et al* 2010)
A6.82		Trenches			
A6.9	Vent / reducing environment				
A6.91		Reducing environment			
A6.911			Seep		(Possible occurrence, see Section 4.4 below)
A6.9111				Hadal seep	
A6.912			Gas hydrate		(Are known from the abutting Norwegian continental margin; Bunz *et al* 2003)
A6.913			Carcass		(Could occur in all Biotopes I-IX)
A6.92		Hypoxic water column			
A6.93		Seamount (etc) hypoxic water column			
A6.94		Vent			
A6.941			Active field		
A6.942			Inactive field		
A6.95		Black Sea anoxic mud			

Table 13. Suggested expansion of the EUNIS deep-sea habitat classification system[4] to incorporate biotopes proposed for Scotland's northern deep seas, Strategic Environmental Assessment area 4 (SEA4). (Grey shading indicates all existing EUNIS components in A6.3-6.5).

Code	Level 3	Level 4	Level 5	SEA4 biotope
A6.3	Sand			
A6.31		Bathyal detritic sand		
A6.32		***Atlantic bathyal sand***		
A6.321			***Spionidae-Syllidae-Syllidae in Atlantic sand and muddy sand (100-300m)***	***I***
A6.322			***Spionidae-Paraonidae-Spatangoida in Atlantic sand and muddy sand (100-300m)***	***V***
A6.33		***Atlanto-Arctic bathyal sand***		
A6.331			***Spionidae-Capitellidae-Syllidae in Atlanto-Arctic sand and muddy sand (300-600m)***	***II***
A6.332			***Spionidae-Terebellidae-Syllidae in Atlanto-Arctic sand and muddy sand (300-600m)***	***VI***
A6.4	Muddy sand			
A6.41		***Arctic bathyal muddy sand***		
A6.411			***Cirratulidae-Maldanidae-Maldanidae in Arctic sand and muddy sand (600-1200m)***	***III***
A6.412			***Cirratulidae-Oweniidae-Thyasiridae in Arctic mud and sandy mud (600-1200m)***	***VII***
A6.413			***Oweniidae-Capitellidae-Maldanidae in Arctic mud and sandy mud (>1200m)***	***IV***
A6.5	Mud			
A6.51		Mediterranean bathyal mud		
A6.511			Sandy mud	
A6.512			Fluid mud	
A6.513			Soft mud	
A6.514			Compact mud	
A6.52		***Arctic bathyal mud***		
A6.521			***Capitellidae-Oweniidae-Myriotrochidae in Arctic mud and sandy mud (>1200m)***	***IX***
A6.52		Abyssal mud		

[4] http://eunis.eea.europa.eu/

4.3.2 Biotopes in the UK (EUNIS) context

The additions to the EUNIS system proposed above suggest a mechanism for the more general incorporation of other UK deep-sea biotopes, and indeed for European deep-sea habitats in general. The UK's deep-water territory spans four major water mass types. In the SEA4 area the types 'Arctic', 'Atlanto-Arctic' and 'Atlantic' have already been detailed above. The entirety of the SEA7 area would fall within the 'Atlantic' type, as would the bulk of the SEA8 area. However, the SEA8 area is also influenced by Mediterranean Outflow Water (MOW). There is some debate (e.g. Bozec *et al* 2011) as to whether, and to what extent, MOW enters and influences the Rockall Trough (e.g. SEA7 area). It is nevertheless clear that its primary 'impact' has its northern limit at around the Porcupine Bank. This water mass has its core at c. 1000m water depth and may occupy the depth range 500-1500m. It is thought to influence the ecology of the benthic fauna of the Iberian Continental Margin (Schonfeld, 1997) and the Porcupine Seabight (Howell *et al* 2002) and therefore by inference the intervening SEA8 area. This region of MOW influence is here referred to as 'Atlanto-Mediterranean'.

The deep-sea areas of the Mediterranean itself are highly distinct as a result of their exceptionally high temperatures and general oligotrophy (Danovaro *et al* 2010). Certainly justifying their distinction at Level 4 in the EUNIS system (A6.51 *Mediterranean communities of bathyal muds*). Similarly, the uniquely high temperature, low oxygen, and high sulphide deep-sea environment of the Black Sea (Tomczak & Godfrey, 1994) equally warrants a Level 4 distinction (A6.95 *Pontic anoxic H2S black muds …*).

This water mass-based classification of UK and European deep-sea areas is closely paralleled by the 'Marine Ecoregions of the World' (MEOW) biogeographic system developed for coastal and shelf seas (Spalding *et al* 2007). Fig. 33 illustrates the MEOW Provinces of the European region and indicates those locations where subducting water masses may modify this classification in the bathyal realm, i.e. at depths greater than the MEOW system was intended to represent. This is amplified further in Fig. 34, where the MEOW Provinces have been re-drawn to reflect water mass conditions in the bathyal realm. Specifically, the Lusitanean Province ('*Atlanto-Mediterranean*') has been extended northwest to the Porcupine Bank area and the Arctic Province has been extended south to the Iceland-Faroe-Scotland Ridge. An interface zone has been added between the Northern European Seas and Arctic Provinces to represent the '*Atlanto-Arctic*' water mass type.

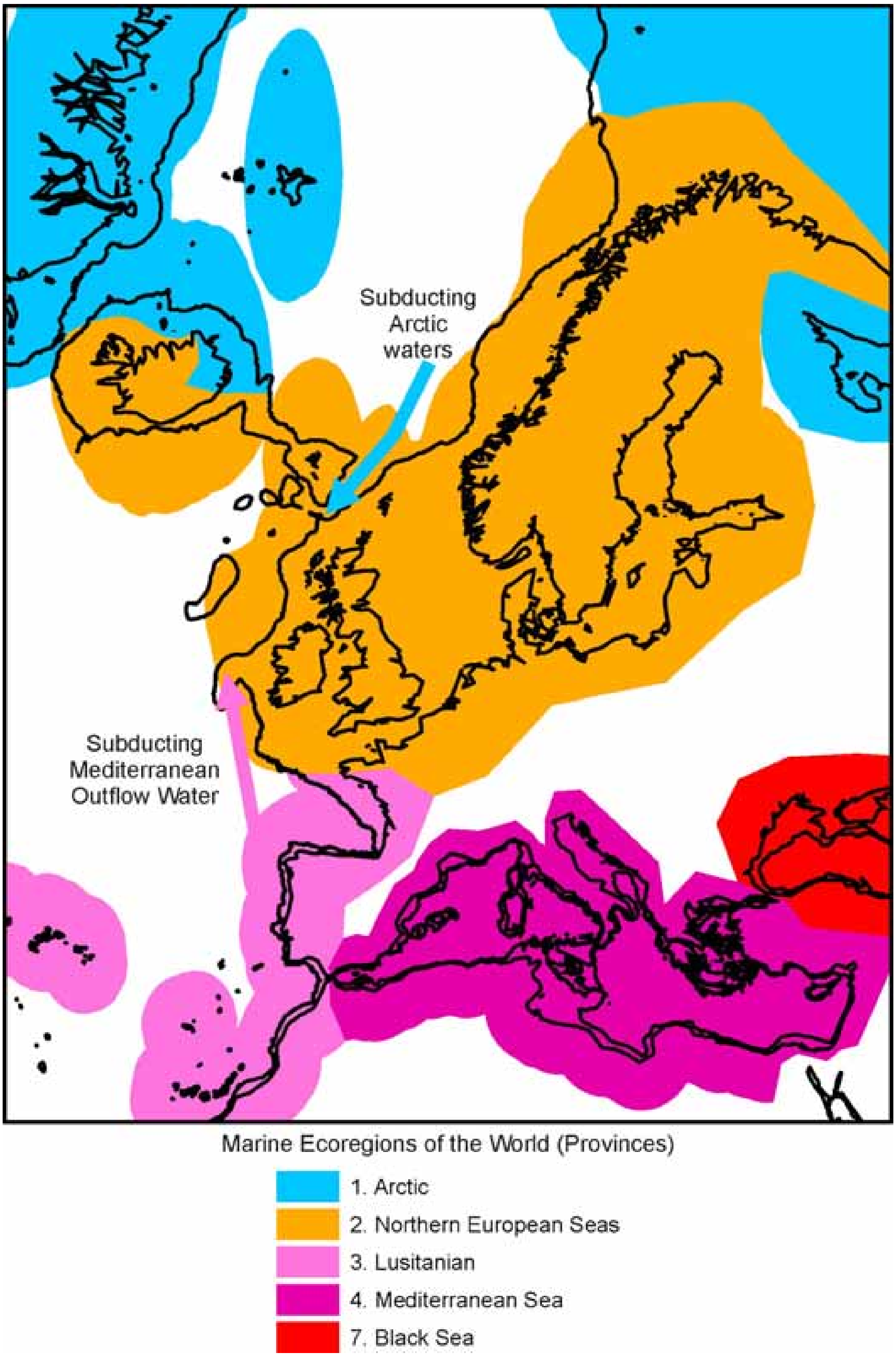

Figure 33. Marine Ecoregions of the World (from Spalding *et al* 2007) shown with areas where subducting deep and intermediate water masses may modify this classification in the bathyal realm. (Shown with coastline and 500m bathymetric contour).

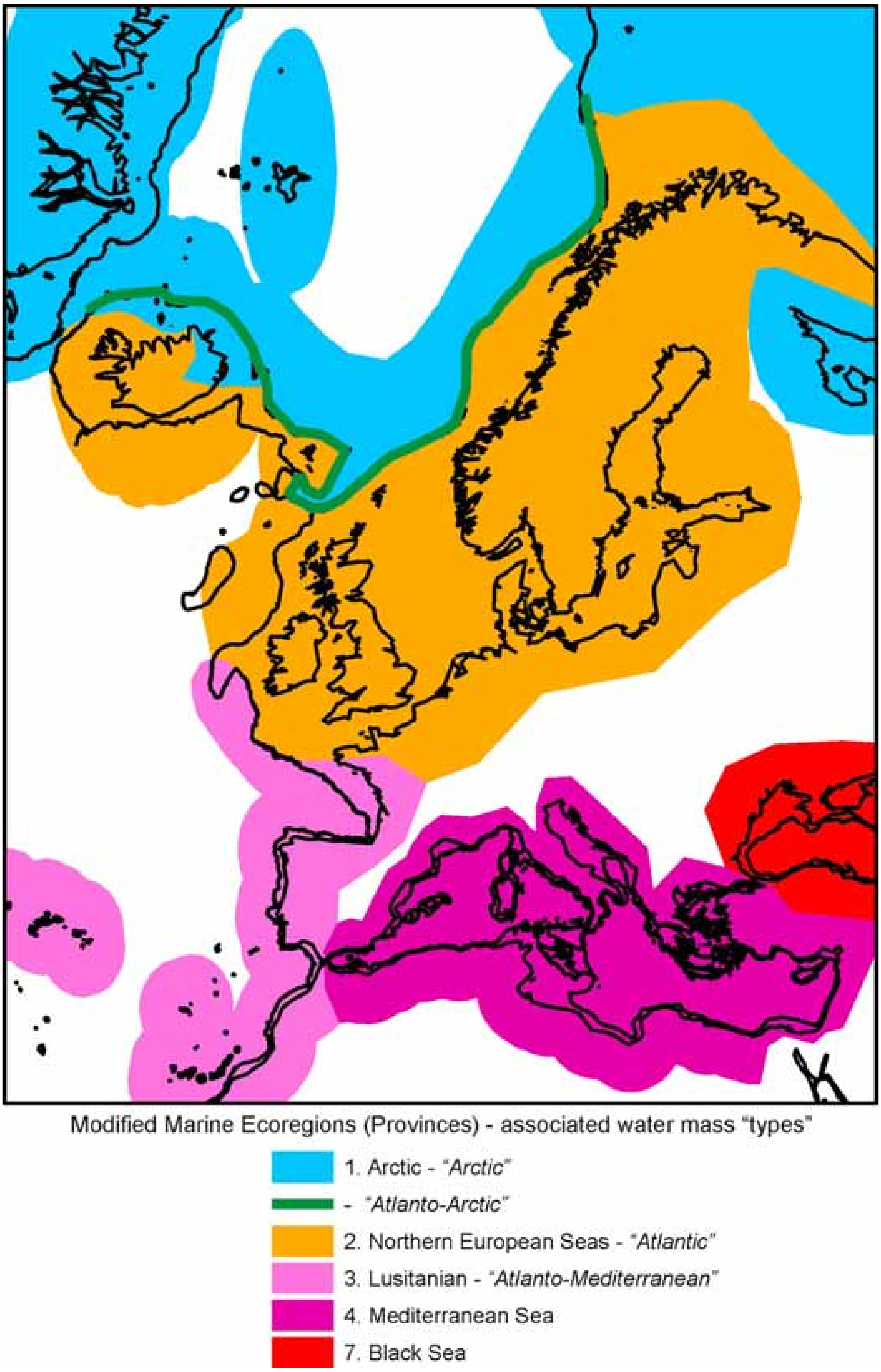

Figure 34. Marine Ecoregions of the World (from Spalding *et al* 2007) modified to reflect a water mass-based classification of deep-sea (bathyal) areas. (Shown with coastline and 500m bathymetric contour).

A simplified schematic of this water mass-based classification of European deep-sea areas is shown in Fig. 35. The diagram encompasses all European deep-sea areas, dividing them on a water mass basis. UK Strategic Environmental Assessment (SEA) areas 4, 7 and 8 are also indicated together with known and potential biotopes, arranged within SEA and water mass boundaries. SEA4 Biotopes I-IX are shown together with three similar 'biotopes' from the SEA7 area identified by Bett (2001) (see Fig. 36).

These SEA7 biotopes were determined by species-level cluster analysis of the AFEN 1998 survey macrobenthos data, and are here simply identified as A-C, corresponding to depth bands 200-500m, 500-1200m, and >1200m respectively. SEA4 area cluster groups D, E, and F of Bett (2001) correspond directly with Biotopes III, VII, and IX respectively. Note that biotope 'A' likely has considerable faunal similarity with SEA4 Biotopes I and V (see Fig 36), and conversely that biotope 'B' has little or no faunal similarity with Biotopes II, III, VI and VII, nor does biotope 'C' have similarity with Biotopes IV and IX (see Fig. 36).

The shelf edge biotope of SEA8 (indicated as '?A') may well share fauna with SEA7 biotope 'A', as may well the lower slope of SEA8 ('?C') and SEA7 biotope 'C'. However, the intrusion of Mediterranean Outflow Water (Atlanto-Mediterranean) at mid-slope depths in SEA8 may well make the fauna more-or-less distinct from the corresponding SEA7 biotope ('B').

Needless to say, all UK deep-sea biotopes will be highly distinct from those of the Mediterranean and Black Seas.

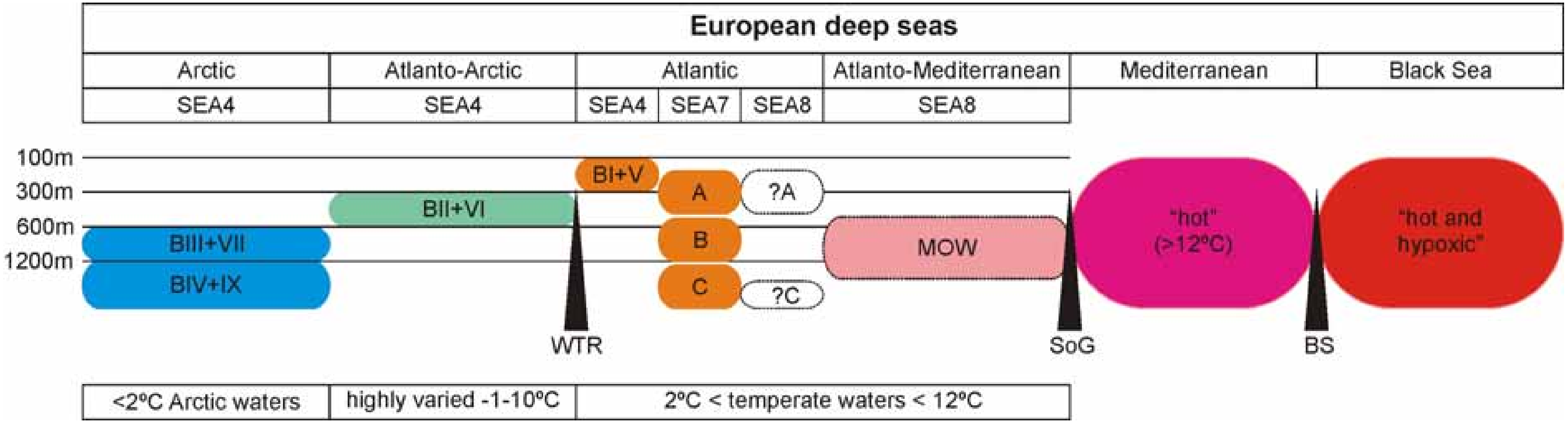

Figure 35. Schematic representation of water mass-based classification of UK, and wider European, deep-sea habitats (biotopes). (SEA, strategic environmental assessment area; BI-IX, proposed SEA4 biotopes [this report]; A-C macrobenthos cluster groups [af. biotopes] identified by Bett, 2001 in SEA7; MOW, Mediterranean Outflow Water). Note physical barriers: WTR – Wyville Thomson Ridge; SoG – Strait of Gibraltar; BS - Bosphorus Strait.

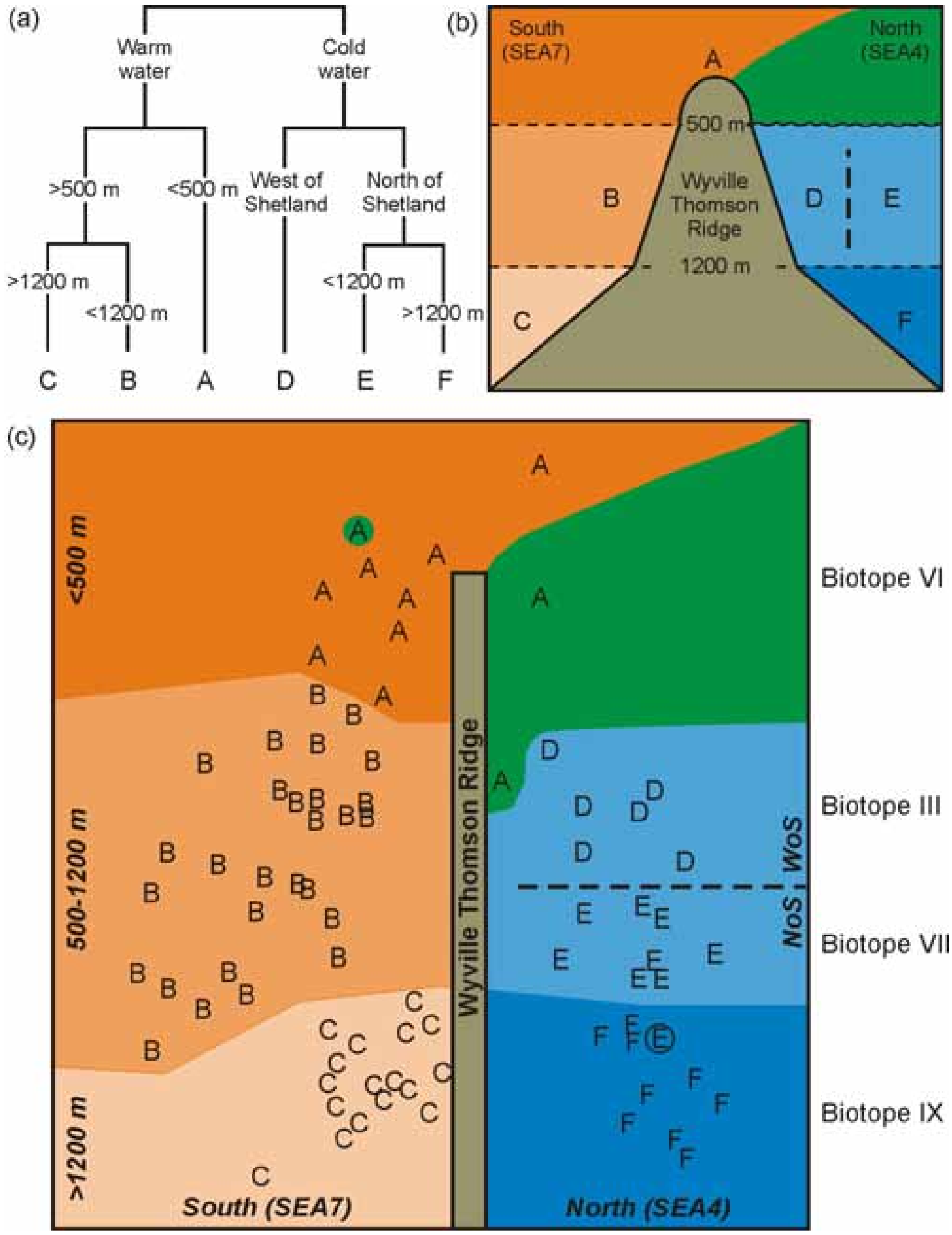

Figure 36. Revised version of Fig. 15. of Bett (2001) reflecting the SEA4 area biotopes identified in the present study. Species-level multivariate analyses of the AFEN 1998 survey macrobenthos dataset. (a) Simplified dendrogram indicating the likely environmental controls defining the six main faunal cluster groups. (b) Schematic representation of the environmental setting of the six main cluster groups. (c) Interpreted 2-d non-metric multidimensional scaling ordination of the same data, with individual sample sites coded by cluster group (circled sites are 'mis-classified'; NoS, north of Shetland; WoS, west of Shetland).

4.4 Sub-biotopes (-habitats and -features)

The primary biotopes described above characterise the regional scale variation in the fauna and environment of the SEA4 area. Below are listed a set of sub-biotopes, -habitats and seabed features that introduce additional variation to local faunas and environmental characteristics (see also Fig. 37).

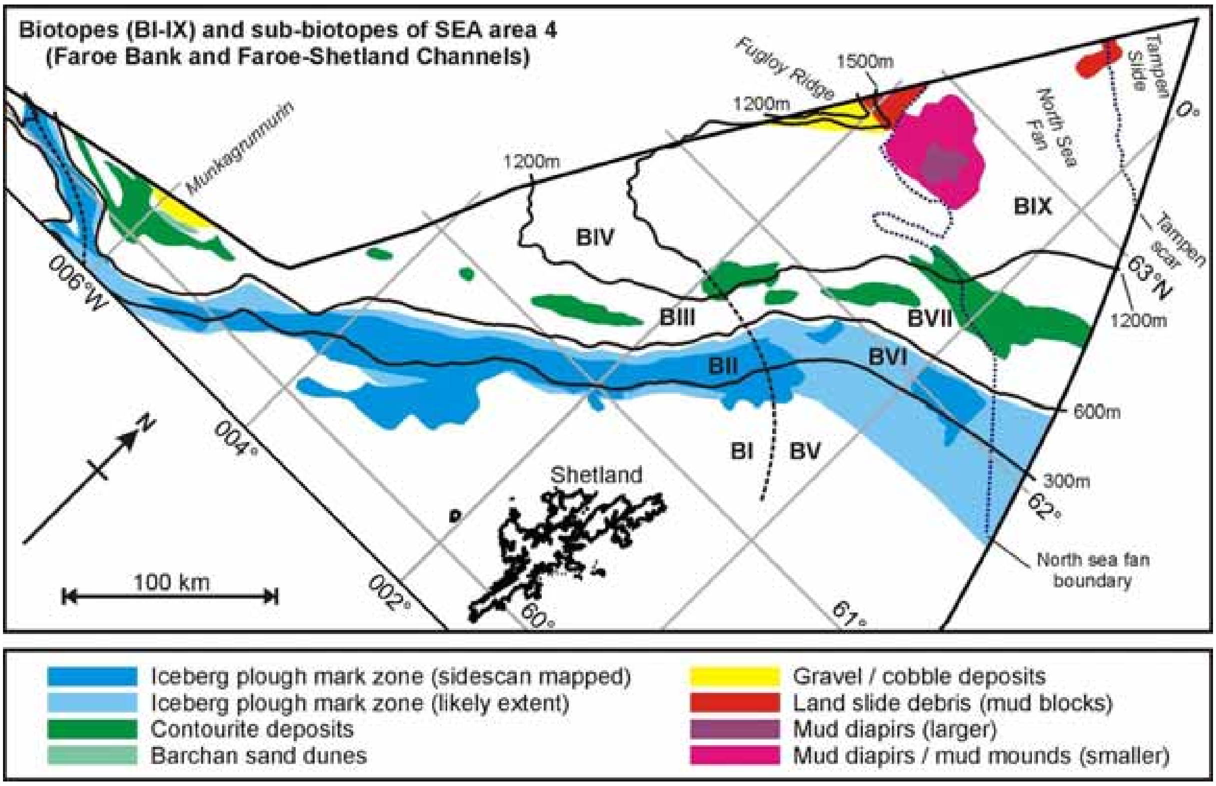

Figure 37. Distribution of sub-biotopes (-habitats and -features) in the deep-water SEA 4 area. Mapping derived from various sources cited in the accompanying text.

STONY REEFS / ICEBERG PLOUGH MARK ZONE

Iceberg plough mark terrain (predominantly Biotopes II and VI) has been equated with 'stony reef' habitat (Irving, 2009) as a result of the common presence of ice-rafted and redistributed cobble- to boulder-sized rocks (i.e. particle diameters >64mm). The formalised definition of what does and does not constitute a 'stony reef' (see Table 3 of Irving, loc. cit.) has, perhaps, been rather overworked – requiring a knowledge of rock size distribution, elevation above seabed, areal coverage of seabed (both relative and absolute), to the extent that formal mapping of presence / absence of 'stony reef' along the UK Atlantic Margin would require a 100% coverage photographic survey. Better perhaps to say that iceberg plough mark terrain occurs throughout the UK Atlantic margin, including its offshore banks and ridges, to water depths of about 600m. Present day seabed expression of iceberg plough mark terrain may vary from sand streaks between low gravel ridges, to continuous cobble pavements variably overlain by large boulder fields. In the SEA4 area, Biotopes II and VI will contain areas of 'stony reef' but not uniformly so. There may be a north-south trend in the extent of 'stony reef'; certainly there is a higher 'reefiness' (Irving, loc. cit.) on the Wyville Thomson Ridge and at the southern extremity of the Faroe-Shetland Channel. Nevertheless, areas of seabed of sufficient 'reefiness' to qualify as 'stony reef' may occur throughout Biotopes II and VI (see also deep gravel and cobble pavements further below). The presence of iceberg drop stones throughout the SEA4 area, particularly in Biotopes II and VI is of direct significance to the occurrence corals, sponges and other encrusting fauna.

COLD-WATER CORALS / *LOPHELIA PERTUSA*

Note that the standard phrase 'cold-water corals', referring to azooxanthellate corals, is perhaps best not used in connection with the SEA4 area, i.e. *Lophelia* forms part of the 'warm-water fauna' not the 'cold-water fauna'. During the planning and conduct of the AFEN surveys (1996 and 1998) there was considerable concern for the occurrence of *Lophelia* in the area. This was influenced by records from fishermen's charts (e.g. Kingfisher charts), knowledge of the mass occurrence of *Lophelia* on the Sula Ridge, a somewhat similar environment, offshore Norway (Freiwald *et al* 1999), occurrence around Faroe (Frederiksen *et al* 1992), and extraordinarily exaggerated claims of the occurrence of vast *Lophelia* reefs offshore Scotland in the UK press at the time.

The reality was rather more mundane. The extensive 1996 West of Shetland survey recorded only two instances of living *Lophelia*: (a) fragments in a seabed sample (Site G3, 330m, Biotope II), and (b) a single small (c. 25cm) colony photographed (Site CORAL-A, 550m, Biotope II; see photo Fig. 12g in Bett, 2001). Similarly the 1998 survey encountered only two small colonies, photographed north of Shetland (Site 3BA350, 350m, Biotope VI; see photo Fig. 12f in Bett, loc. cit.). *Lophelia* does grow abundantly West of Shetland – on oilfield infrastructure (e.g. *Schiehallion* field, Jones, *et al* 2009), including very extensive growths ('hanging reefs') on risers to the *Foinaven* FPSO (see Fig. 38). It is possible that *Lophelia* <u>should</u> be common and widespread in the iceberg plough mark zone (Biotopes II and VI) but has been practically eradicated by demersal trawling outside the areas now protected by oilfield installations. The impact of trawling on 'cold-water corals' is generally discussed as a modern phenomenon (Wheeler *et al* 2005), however, major trawler impact on coral habitat has a 100+ year history on the European Atlantic Margin (i.e. early 1900s onwards; see Tietchert, 1958).

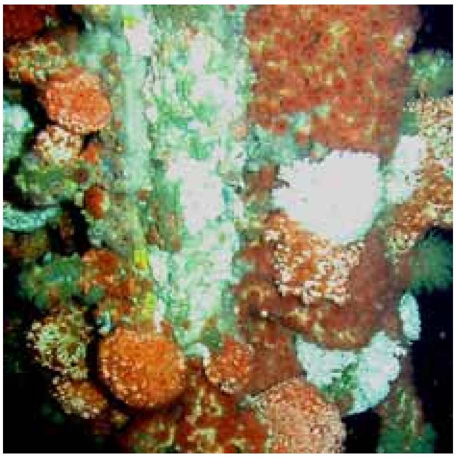

Figure 38. Extensive *Lophelia* growths on West of Shetland oilfield infrastructure (http://www.serpentproject.com/).

DEMOSPONGE AGGREGATIONS / *OSTEBUND*

Deep-sea sponge aggregations are regarded as an important habitat (Christiansen, 2010), a form of 'biogenic reef' that is thought to support an appreciable associated diversity of other fauna (Klitgaard, 1995). The occurrence of sponge aggregations in the Northeast Atlantic is comprehensively reviewed by Klitgaard & Tendal (2004), they recognise two forms: (i) boreal "*ostur*" characterised by *Geodia barretti, G. macandrewi, G. atlantica, Isops phlegraei, Stryphnus ponderosus* and *Stelletta normani* (Faroe, Norway, Sweden, western Barents Sea, south of Iceland); and (ii) cold-water ''*ostur*'' characterised by *G. mesotriaena, Isops phlegraei pyriformis* and *Stelletta rhaphidiophora* (north of Iceland, Denmark Strait, East Greenland, north of Spitzbergen). As the authors note, the taxonomic / morphological differences between the con-generic species of these two groups can be small and variable and have been variously interpreted as species, subspecies or cold- and warm-water forms by other workers. Klitgaard & Tendal (loc. cit.) nevertheless regard the differences as useful in that they are biogeographically coherent and possibly reflect environmental distinctions, with the boreal "*ostur*" seldom occurring where bottom water temperatures are less than 3ºC.

Mass occurrences of demosponges (boreal "*ostur*") are widespread around Faroe, including the western margin of the Faroe-Shetland Channel (Klitgaard *et al* 1997). Similar occurrences of large and / or abundant demosponges are known from Biotopes II and VI (see e.g. Fig.s 12b and 12c, from Biotope II, and Fig. 12e, from Biotope VI, in Bett, 2001). These are presumed to correspond with the boreal "*ostur*". As with the related occurrence of 'stony reef' habitat, when 'some sponges' become an 'aggregation' or 'mass occurrence' is more a political than ecological point. 'Sponginess' (cf. 'reefiness' above) does vary through Biotopes II and VI, some areas on and in the vicinity of the Wyville Thomson Ridge will have a high 'sponginess', as does the deeper northern part of Biotope II (c. 500m, Bett, loc.cit.). It is also worth noting again, as with *Lophelia* occurrence, that the apparent present day distribution of "*ostur*" in the SEA4 area may have already been impacted by demersal trawling. Klitgaard & Tendal (2004) report the loss of known "*ostur*" grounds to trawling and recount fishermens' admissions to '*improving*' their trawl grounds by deliberate destruction of sponge and coral aggregations. Note also that attempts to model the distribution of sponges and corals based on their present day distributions may be flawed for this same reason.

DEEP GRAVEL AND COBBLE PAVEMENTS

In addition to the iceberg plough mark zone with its potential 'stony reefs', there are two other deep-water areas in the SEA4 region with appreciable seabed cover by cobbles and boulders. The first is on the northeast extremity of the Faroe Plateau (Fugloy Ridge), corresponding with the small disjunct areas of Biotopes III and IV in that location (approximately 1000-1500m). Gravel is common at the seabed, cobbles may be frequent and boulders may be present. Where such hard substratum is present, well developed epifaunas also occur (e.g. octocorals, sponges and echinoderms), camera runs in these areas show indications of current scour behind boulders and cobbles, as well as direct forced movement of the fauna in response to current flow (Bett, 2007a). This promontory-like location appears to experience elevated near-bottom current speeds, exposing ice-rafted rocks at the seabed. Whether these locations qualify as 'stony reefs' is a matter for political judgement, they can certainly support well developed deep-water epifaunal communities.

The second area is the southern extremity of the Faroe Plateau (i.e. south of Munkagrunnurin), water depths approximately 800-1200m (Biotope III), that also appears to experience elevated near-bottom current speeds (Masson *et al* 2004). The seabed in this area has near-100% gravel cover, areas of 100% cobble pavement and variable occurrence of boulders, and a correspondingly well developed epifauna (e.g. echinoderms, sponges and octocorals; Bett, 2007a). Parts of this deep-water area would certainly meet the 'reefiness' criteria of Irving (2009), i.e. complete seabed cover by cobble-sized rocks. Designation of the wider area is again a matter for political judgement.

CONTOURITES AND OTHER DEEP SAND FEATURES

A variety of deep-water sandy habitats are present in the SEA4 area. The most widespread of these are sandy contourites that occur more-or-less throughout the UK extents of the Faroe Bank and Faroe-Shetland Channels in water depths of approximately 800-1200m (Biotopes III and VII) (Masson, 2001; Masson *et al* 2004, 2010). The contourite deposits of Biotope III are the best developed / best examples, those of Biotope VII (fringing into Biotope IX) are perhaps more silty (i.e. higher mud content of Biotope VII compared to III) with a less distinctly characteristic fauna. Bett (2001) noted an unusual community of surface-dwelling enteropneusts (acorn worms) on the 'West of Shetland Contourite' (centred 61º10'N 002º30'W). Abundant surface-dwelling enteropneusts may also be present on the contourite deposits at the southern end of Biotope III (Bett, 2007a). The southern contourites are also notable for abundant populations of small stalked sponges, and in some areas very abundant populations of sabellid polychaetes (Bett, loc. cit.). These variations in the fauna associated with the contourite deposits may relate to near bottom current speeds, with lowest flows on the open slope north of Shetland, and highest flows where bottom waters are steered round into the Faroe Bank Channel.

These accelerated bottom water currents entering the Faroe Bank Channel also form another deep-water sand feature – barchan sand dunes (Wynn *et al* 2002). The barchan field lies in a band between the contourite deposit to the south and the deep gravel / cobble area of the Faroe Plateau to the north. The northern part of the band has large scattered barchans with horizontal dimensions of up to 120m, in the south the dunes are smaller (20m horizontal dimensions), more numerous and more closely spaced (Wynn *et al* loc. cit.). The fauna associated with the dunes varies with position on the dune, the strongly rippled seabed immediately adjacent to the dunes appears near barren, while the slopes of the barchan may have abundant seston feeders (sea pens, *Halcampa*-type anemones). These deep-water sand features (contourites and barchans), are in deep-sea terms at least, relatively high energy habitats, of limited occurrence and rather poorly known. Consequently, they may warrant some degree of conservation status.

PILOT WHALE DIAPIRS AND SIMILAR SEABED TERRAIN

The Pilot Whale Diapirs appear to have been first identified / named by Haflidason *et al* (1996). Good TOBI sidescan imagery of part of the diaper field was obtained during the 1999 DTI survey (Bett & Jacobs, 2007) along with some seafloor photography. Full multi-beam bathymetry was obtained during the 2002 DTI survey (Masson, 2002) as was additional seafloor photography and sampling (Bett, 2007c). The geological setting and formation of these diapirs is reviewed by Holmes *et al* (2003).

Lying in the otherwise rather featureless level-bottom soft muddy environment of Biotope IX, these upthrust blocks of ancient muds are a rather unusual habitat. They have complex and steep topography with local elevations in excess of 100m. However, as reported by Bett (2007a), "although these are rather impressive features, they do not appear to support any distinct fauna". The presence of 'scree slopes' and 'rock filled gullies' among these features does introduce otherwise rare hard substratum to the Norwegian Basin area, which consequently may modify the fauna to a limited extent. The diapiric features appear to be principally of geological rather than biological interest. The mud blocks themselves have a 'plasticine-like' consistency that, while clearly resistant to erosion, does not appear suitable for colonisation by attached fauna. However, winnowing of fine surficial sediments within and around the mud blocks has revealed iceberg drop stones that are otherwise rarely exposed at the seabed in Biotope IX, permitting the development of an epistratum fauna (e.g. octocorals and tubular sponges; Bett, loc. cit.).

In addition to the diapiric structures, very similar seabed terrain (based on sidescan sonar, multibeam and photography during the cruises noted above) was encountered at two other locations in Biotope IX: (i) base of the northeast extremity of the Faroe Plateau (Fugloy Ridge); and (ii) at the edge of the Tampen Slide Scar. Although visually (at the seabed) and biologically more-or-less identical to the Pilot Whale Diapir habitat, the mud blocks in these locations are landslide debris and not the result of diapirism (see e.g. Masson *et al* 2003). Again these mud blocks do not appear to be suitable for colonisation by attached fauna but have promoted the exposure of iceberg drop stones enabling the development of an epistratum fauna.

Although no unusual faunas were encountered on or around the Pilot Whale Diapirs during the DTI surveys they remain a site of potential interest. The underlying geological structures are potential conduits for fluid escapes from the seafloor, i.e. seeps. Holmes *et al* (2003) suggest that a seismic profile adjacent to the SW group of large diapirs could indicate fluid ascent, though note that other interpretations are possible. They also indicate that areas of shallow sub-seabed acoustic scatter with small diapirs and mud mounds, an area more widespread than the large diapirs themselves, have perhaps the highest potential for modern fluid escape.

A COLD SEEP?

Diapiric structures and proven hydrocarbon reservoirs are present in the SEA4 area; it would therefore not be entirely surprising if cold seep biological communities were to be discovered in the region. Cold-water (Arctic) cold-seep communities are known from the Norwegian Basin, perhaps best exemplified by the bacterial mats and siboglinid tubeworm populations found on the Haakon Mosby Mud Volcano (Niemann *et al* 2006). A single observation during the period of the 2000 DTI survey suggested the possible occurrence of a small tubeworm patch at the southwest extremity of Biotope IX. This observation occurred during a period of operation on behalf of a commercial operator (Texaco) and as such has been treated as commercial in confidence (Bett *et al* 2007). The observation amounts to little more than a single seabed photograph and the corresponding few seconds of video. Three further camera runs were made targeting the same location but no further records of the possible tubeworm patch were obtained. In total four-hours of seabed observations revealed only the one small putative tubeworm patch. If this was a cold seep, it was very small and very rare. The SERPENT Project, carrying out seafloor observations via opportunistic use of industry ROVs, has undertaken a number of missions in the deep axis of the Faroe-Shetland Channel (Biotopes III and IV; *Tornado*, *Rosebank, Rosebank North*, and *South Uist* fields) but has not encountered any cold seep-type communities. Similarly, SERPENT missions at the *Lagavulin* field (Gates, 2011) in the Pilot Whale Diapir province have not observed any unusual biological communities that might be associated with fluid escape from the seabed.

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