Megafauna from sublittoral to abyssal depths along the Mid-Atlantic Ridge south of Iceland

Mid-ocean ridge
Megafauna
Reykjanes Ridge
Bathymetric zonation
Water mass structure

Dorsale médio-océanique
Mégafaune
Dorsale de Reykjanes
Bathymétrie faunistique
Structure des masses d'eau

Jonathan T.P. COPLEY[a], Paul A. TYLER[a], Martin SHEADER[a], Bramley J. MURTON[b] and Christopher R. GERMAN[b]

[a] Department of Oceanography,
[b] Challenger Division for Seafloor Processes,
Southampton Oceanography Centre, University of Southampton, European Way, Southampton SO14 3ZH, UK.

Received 10/04/95, in revised form 01/02/96, accepted 06/02/96.

ABSTRACT

101 species were identified from 102 biological samples obtained between 225 and 2600 m depth on the Reykjanes Ridge, extending the biogeographic records for several species. Multivariate analysis of between-sample species similarity reveals a two-zone bathymetric faunal distribution with the transition at 800-1000 m. A hydrographic survey of the ridge axis suggests that this faunal zonation is influenced by the water mass structure. Despite the limitations of a sampling programme not designed *a priori* for biological sampling, the recovery and preservation of the samples and the insight that they provide serves to reinforce that every effort should be made to capitalise on the opportunities for obtaining samples afforded by non-biological sampling programmes.

RÉSUMÉ

Mégafaune du domaine sublittoral à abyssal sur la dorsale médio-Atlantique au sud de l'Islande.

Le prélèvement de 102 échantillons sur la dorsale de Reykjanes, entre 225 et 2 600 m de profondeur, a permis d'identifier 101 espèces et de compléter les enregistrements biogéographiques dans plusieurs cas. L'analyse multivariée de la similarité entre les stations révèle une répartition bathymétrique de la faune en deux régions, la transition se faisant entre 800 et 1000 m. Une campagne hydrologique sur la dorsale suggère que cette répartition faunistique pourrait être liée à la structure des masses d'eau. Malgré les limites du programme d'échantillonnage, qui *a priori* n'était pas consacré à la biologie, les échantillons récoltés et préservés, ainsi que les résultats obtenus soulignent l'importance des prélèvements effectués au cours de campagnes d'échantillonnage non biologiques.

Oceanologica Acta, 1996, **19**, 5, 549-559.

INTRODUCTION

Although soft sediments dominate the seabed in the deep-sea, the seafloor of the ocean basins is punctuated by areas of exposed rock along the continental slope, and at seamounts and mid-ocean ridges where newly-formed seafloor has yet to be covered by sediment. Compared to our knowledge of the soft-sediment fauna of the deep-sea (Gage, Tyler, 1991), comparatively little is known of the fauna of these rocky areas. There have been studies of the fauna on the rocky areas of seamounts (Genin *et al.*, 1986; Kaufmann *et al.*, 1989; Chave, Jones, 1991) and continental slopes (Grasshoff, 1985; Roux, 1985; Zibrowius, 1985; Tyler, Zibrowius, 1992). Faunas at hydrothermal vents have been proportionally well documented (Grassle, 1986; Tunnicliffe, 1991; Van Dover, 1995), but the fauna of non-vent areas of the mid-ocean ridge is poorly known and generally only studied peripherally to hydrothermal vents

(Arquit, 1990; Carey *et al.*, 1990; Milligan, Tunnicliffe, 1994; Sudarikov, Galkin, 1995). In 1993 a large number of biological samples were incidentally recovered during a rock sampling programme along the Reykjanes Ridge, providing a rare opportunity to describe the fauna of a long section of mid-ocean ridge.

The Reykjanes Ridge is one of four geographical areas chosen by the British Mid-Ocean Ridge Initiative (BRIDGE) as a focus for multidisciplinary studies of the processes associated with the formation of new oceanic crust, and forms an 800 km segment of the Mid-Atlantic Ridge (MAR) from the southwest margin of Iceland to the Charlie Gibbs Fracture Zone. North of the Bight Fracture Zone at 57° N (Fig. 1), the ridge exhibits several unique features: it is the longest obliquely spreading mid-ocean ridge in the world (Talwani *et al.*, 1971) with the ridge axis oriented at 036° compared to the 099° vector of plate separation (Minster, Jordan, 1978), and is devoid of transform faults. The ridge axis also shows a depth gradient from effectively 0 m at the Icelandic coast to ~3000 m at the Bight Fracture Zone and high temperature hydrothermal activity has only been detected at one site along its length (Steinahóll 63° 06' N, Olaffson *et al.*, 1991; German *et al.*, 1994).

The axis of the Reykjanes Ridge is bathed in Upper North Atlantic Deep Water (potential temperature 2 to 4 °C) at its deeper southern end and warmer Sub-Polar Mode Water (potential temperature 4 to 7 °C) at the shallower northern end (McCartney, 1992). The eastern shoulder of the ridge is swept by the southerly flow of the Western Boundary Undercurrent but data on currents at the ridge axis are scarce. Results from one autonomous benthic station (60° 59.7' N, 27° 47.7' W, 960 m; Dietrich, Kontar, 1990) show tidal fluctuation between axis-parallel SW currents up to 0.17 m s^{-1} and northerly currents of a similar magnitude; this current regime is modified near the bottom (< 2.5 m altitude).

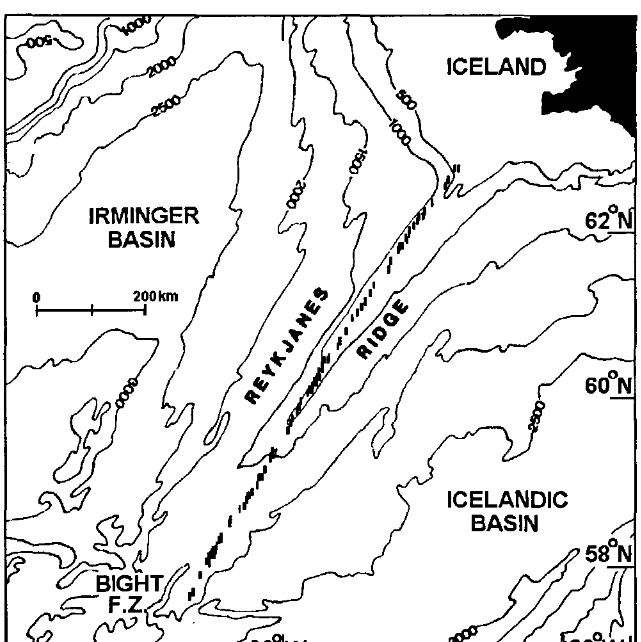

Figure 1

Location map of CD80 stations (▮) where megafauna were recovered (after Parson et al., *1993).*

Pillow lavas and sheet flows are a major component of the substrata available to benthic fauna at the ridge axis. These lavas are erupted from volcanic seamounts that form en echelon Axial Volcanic Ridges (AVRs), which exhibit a range of morphologies from narrow ridges with linear seamounts, through broader ridges with flat-topped seamounts, to more sedimented regions with split seamounts (Murton, Parson, 1993). This results in a varied topography at the ridge axis, with local sediment ponds and thin blankets in some regions. These sediments are dominated by remains of the pelagic foraminiferan *Globigerina bulloides*, with brown (basaltic) volcanic glass and autochthonous sponge spicules occasionally present; clay-rich sediments were found at stations situated in topographic lows within the ridge axis (Wallrabe-Adams, Lackschewitz, 1994).

MATERIALS AND METHODS

The PETROS (PETRogenesis of Oblique Spreading) rock sampling programme took place during cruise CD80 of the *RRS Charles Darwin* (BRIDGE Cruise No. 10, September 1993; Murton *et al.*, 1993) and occupied 169 dredge stations between 57° N and 63° N on the Reykjanes Ridge. Biological samples were recovered at 102 of these stations (Fig. 1), the positions and depths of which are given in Table 1.

Care was taken in the PETROS sampling programme not to preferentially sample seamounts or non-seamount sites. Sampling targets were identified from side-scan sonar images and Hydrosweep multibeam bathymetric charts of the ridge made during cruise EW9008 of the *RV Maurice Ewing* in 1990 (Parson *et al.*, 1993). As the objective of the PETROS programme was rock sampling, areas with a high probability of bare rock exposure were preferred to those with probable sediment cover. The SIMRAD EM12 multibeam swath bathymetry system was used to fine-tune the positioning of sample stations in poorly-charted areas of the ridge.

A pinger was deployed with the dredge to confirm station depth and the dredges had less than 20 minutes bottom time. Rock samples were analysed to give an indication of geological age in the form of an alteration index and the presence or absence of sediment in the dredge bucket was noted at the stations where this occurred. Biological samples were frozen to –20 °C onboard the *RRS Charles Darwin* and stored in a freezer until April 1994, when they were transferred to 4 % seawater formaldehyde and allowed to thaw. Specimens were identified to species level or as close to this as possible, with the assistance of taxonomic specialists sought for several groups.

To examine the potential influence of the different bathymetric distributions of individual species on the faunal distribution as a whole and to see if any distinct faunal zonation was present, the data set was subject to cluster analysis. This multivariate technique works by grouping samples on the basis of some measure of similarity between them. Traditional measures of similarity in benthic ecology, such as minimum % similarity (Whittaker, Fairbanks, 1958) and Normalised Expected Species Shared (NESS; Grassle, Smith, 1976), require information concerning species relative abundance in samples. These indices cannot therefore be

Table 1

Details of CD80 dredge stations where megafauna were recovered.

Station number	Depth (m)	Latitude	Longitude
2	1575	57° 44.20' N	32° 41.60' W
12	1796	57° 28.00' N	33° 00.50' W
13	1805	57° 31.17' N	32° 54.30' W
14	-	57° 31.17' N	32° 54.30' W
16	1850	57° 53.08' N	32° 24.70' W
17	1725	57° 53.20' N	32° 25.80' W
18	2600	57° 54.75' N	32° 30.80' W
19	1625	57° 55.15' N	32° 25.45' W
22	1600	57° 58.69' N	32° 27.30' W
23	1600	57° 58.25' N	32° 24.60' W
27	1610	57° 59.16' N	32° 22.40' W
28	1625	57° 59.30' N	32° 20.10' W
29	1575	57° 59.51' N	32° 16.50' W
32	1890	58° 01.56' N	32° 21.00' W
33a	1700	58° 02.41' N	32° 17.47' W
35	1650	58° 02.80' N	32° 14.35' W
37	1600	58° 04.00' N	32° 14.00' W
39	1575	58° 05.30' N	32° 12.55' W
40	1625	58° 06.70' N	32° 12.10' W
43	1900	58° 10.35' N	32° 07.40' W
44	1650	58° 11.00' N	32° 04.00' W
45	1600	58° 12.05' N	32° 04.55' W
58	1450	58° 22.59' N	31° 49.40' W
59	1550	58° 23.29' N	31° 47.80' W
60	1425	58° 25.29' N	31° 47.50' W
62	1170	58° 33.30' N	31° 32.30' W
65	1400	58° 35.00' N	31° 24.70' W
66	1175	58° 39.60' N	31° 20.70' W
67	1200	58° 42.30' N	31° 19.00' W
68	1800	58° 43.10' N	31° 15.40' W
70	1450	58° 45.60' N	31° 11.00' W
72	1375	58° 49.50' N	31° 07.00'W
75	1125	58° 50.50' N	31° 01.00' W
78	999	58° 56.20' N	30° 58.20' W
79	1275	58° 56.60' N	30° 53.70' W
83	1125	59° 02.20' N	30° 48.00' W
89	1079	59° 12.32' N	30° 33.30' W
91	1056	59° 15.50' N	30° 34.50' W
96	1000	59° 29.80' N	30° 06.68' W
97	1000	59° 30.70' N	30° 05.08' W
98	800	59° 35.80' N	30° 02.20' W
99	900	59° 39.25' N	29° 58.90' W
100	900	59° 40.30' N	29° 52.62' W
102	725	59° 43.68' N	29° 51.30' W
103	800	59° 46.65' N	29° 50.45' W
104	925	59° 47.87' N	29° 47.20' W
107	925	59° 51.43' N	29° 43.80' W
111	950	59° 57.20' N	29° 31.45' W
112	875	59° 59.95' N	29° 29.10' W
113	950	59° 59.53' N	29° 25.00' W
115	775	60° 02.30' N	29° 23.30' W
116	1000	60° 04.94' N	29° 15.60' W
117	925	60° 05.57' N	29° 19.18' W
118	900	60° 06.77' N	29° 20.48' W
120	625	60° 08.90' N	29° 15.80' W
121	825	60° 08.90' N	29° 11.40' W
124	500	60° 15.13' N	29° 06.35' W
127	750	60° 21.90' N	29° 02.55' W
128	850	60° 22.45' N	28° 56.30' W
129	650	60° 24.06' N	28° 54.30' W
132	575	60° 32.16' N	28° 39.35' W
133	600	60° 35.94' N	28° 36.30' W
134	608	60° 40.70' N	28° 27.60' W
135	752	60° 43.25' N	28° 24.80' W
138	691	60° 56.70' N	28° 05.60' W
139	870	61° 00.10' N	28° 03.00' W
140	562	61° 01.45' N	27° 57.30' W
141	590	61° 05.30' N	27° 51.20' W

Table 1 *(continued).*

Station number	Depth (m)	Latitude	Longitude
142	540	61° 11.00' N	27° 42.60' W
143	595	61° 15.75' N	27° 35.80' W
144	534	61° 17.50' N	27° 36.20' W
149	650	61° 29.60' N	27° 10.80' W
150	650	61° 36.00' N	27° 06.35' W
153	600	61° 43.79' N	26° 54.10' W
154	725	61° 46.20' N	26° 51.60' W
155	575	61° 46.80' N	26° 46.45' W
157	775	61° 50.58' N	26° 38.70' W
158	639	61° 52.93' N	26° 41.15' W
160	600	61° 55.62' N	26° 35.20' W
161	575	61° 57.89' N	26° 34.02' W
164	575	62° 01.63' N	26° 27.00' W
165	600	62° 04.31' N	26° 21.07' W
166	525	62° 08.05' N	26° 18.28' W
167	575	62° 08.87' N	26° 11.00' W
168	420	62° 11.91' N	26° 07.80' W
169	405	-	-
171	650	62° 18.10' N	25° 55.30' W
172	500	62° 21.95' N	25° 53.00' W
173	700	62° 24.20' N	25° 51.20' W
174	600	62° 26.08' N	25° 42.70' W
176	650	62° 30.45' N	25° 31.95' W
177	550	62° 35.00' N	25° 28.20' W
178	500	62° 38.60' N	25° 23.30' W
179	493	62° 41.48' N	25° 17.86' W
180	500	62° 43.60' N	25° 10.20' W
181	500	62° 43.70' N	25° 17.10' W
183	550	62° 52.05' N	25° 03.30' W
184	350	62° 55.85' N	24° 47.25' W
185	233	62° 55.73' N	24° 47.21' W
186	225	62° 55.79' N	24° 46.97' W

applied to non-quantitative samples such as dredges, so Jaccard's Index (C_j; Jaccard, 1900) was used:

$$C_j = \frac{j}{a + b - j}$$

where j represents the number of species in common between two samples and $a + b$ is the total number of species present in the two samples.

Jaccard's Index values were calculated for each element in a samples-by-samples matrix, and converted into dissimilarity values (D) as follows:

$$D = 1 - C_j.$$

Classification was then carried out on the samples-by-samples dissimilarity matrix using the software package UNISTAT. The technique used was hierarchical polythetic agglomerative clustering by the unweighted pair-groups method using arithmetic averages (UPGMA). This technique is recognised in maximising the cophenetic correlation between input dissimilarities in the dissimilarity matrix and output dissimilarities in the resulting dendrogram, and is therefore recommended when there is no specific reason for choosing another technique (Sneath, Sokal, 1973).

Hydrographic information was provided by 175 CTD casts along the ridge axis during cruise BS8 of the *RV Bjarni Saemundsson* whilst prospecting from hydrothermal plumes (BRIDGE Cruise No. 9, July 1993; German *et al.*, 1994).

RESULTS

An inventory of the fauna is shown in Table 2. The common groups in the samples and the occurrence of species beyond previous records or thought be previously undescribed are presented below.

Porifera

Class Hexactinellida

This class is represented by nine species from six families, recovered from 31 stations. This amounts to about 50 % of the species recorded in the area (Ole Tendal, pers. comm.). Owing to the fragmentation and, in the case of the many dictyonines, being dead for a long time with the subsequent loss of non-fused spicules, not all specimens could be identified.

Aphrocallistes beatrix, represented by samples from 20 stations, is common in the NE Atlantic in a number of "forms". All samples were dead skeletons, but if one can judge from their presence, the species has a rather wide bathyal bathymetric distribution on the Reykjanes Ridge.

Asconema setubalense is commonly distributed in the upper bathyal of the Norweigan-Greenland Seas and the adjacent parts of the North Atlantic. It is a soft species, and this may be the reason why it was only recovered in one sample.

Chonelasma sp. is new to the northern part of the North Atlantic, and represented in samples from five stations. The material is in poor condition and further identification is not possible without more material for comparison. Lower bathyal to abyssal *Chonelasma* species are known from the central North Atlantic.

Hexactinellid sp.1 is a species separate from the others, but owing to the poor condition of the material further identification was not possible.

Pheronema carpenteri, represented in samples from two stations, is widely distributed in the NE Atlantic, mainly in the upper bathyal (Rice *et al.*, 1990). From west of the Faroes and south of Iceland it has been taken from 820-1160 m (O. Tendal, pers. comm.), and the present record at 500 m (station 178) is, accordingly, the shallowest known from the area.

Class Demospongiae

This class is represented by at least 30 species of 19 families from seven orders, amounting to about 20 % of the shelf and slope sponge species known south of Iceland (O. Tendal, pers. comm.). Most of the species present in the samples are of large size and robust morphology, and it is therefore likely that the collection method influenced the species composition of the samples. It is obvious that several orders, especially the Hadromerida, Poecilosclerida and Haplosclerida are underrepresented.

Alectona millari and *Aka labyrinthica* are the most common boring sponges in *Lophelia* and *Madrepora* in deep water off the Norweigan coast and around the Faroes and Iceland (Tendal, unpublished). In the CD80 samples they

Table 2

Systematic résumé of fauna collected from Reykjanes Ridge during Cruise CD80.

PORIFERA	**CD80 STATIONS**
Class Hexactinellida	
Aphrocallistes beatrix Gray	37, 60, 113, 120, 121, 132, 139, 149, 153, 154, 157, 158, 160, 165, 169, 171, 173, 178, 179, 180
Asconema setubalense Kent	178
Chonelasma sp.	33, 45, 83, 100, 117, 118
Euplectella sp.	45
Farrea fecunda Schmidt	12
Farrea sp.	33a
Farreid sp.	13
Hexactinellid sp. 1	174, 185
Pheronema carpenteri (Thomson)	116, 178
Class Demospongiae	
Aka labyrinthica (Hancock)	83
Alectona millari Carter	138
Bubaris ?flagelliformis van Soest & Stentoft	18
Bubaris vermiculata (Bowerbank)	178
Chondrosia sp.	62
Geodia macandrewi Bowerbank	178
Geodia sp.	113
Haliclona sp.	185
Halicondria sp. 1	13, 153
Halicondria sp. 2	115, 160
Hamacantha implicans Lundbeck	83
Hamacantha sp.	118
Isops phlegraei Sollas	18, 91
Jaspis sp.	2
Lissodendoryx diversichela Lundbeck	160
Mycale sp.	183
Pacastrella monilifera Schmidt	83
Pacastrellid sp.	18
Petrosia crassa (Carter)	83
Phakellia bowerbanki Vosmaer	149, 153, 160, 166, 168, 169
Phakellia ventilabrum (Johnston)	179, 183
Plakortis sp.	13
Poecillastra compressa (Bowerbank)	83, 115, 134, 138, 150, 174, 178, 180
Pseudosuberites sp.	150
Stelletta normani (Sollas)	32
Tetilla cranium (Mueller)	116
Tetilla cf. longipilis Topsent	79, 89, 149
Thenea levis Ledenfeld	178, 185
Thenea valiviae Ledenfeld	179
Timea sp.	139
CNIDARIA	
Subclass Zoantharia	
Actinian sp. A	132
Actinian sp. B	149
Actinian sp. C	14
Zoanthid sp.	18, 23
Subclass Octocorallia Order Alcyonacea	
Eunephthya sp.	96, 121
Pachyclavularia sp.	129
Xenia sp.	2, 22, 97
Order Gorgonacea	
Acanthogorgia granulata (Stueder)	97
Muricedes kuekenthali (Broch)	132
Muricedes sceptrum (Stueder)	132, 142
Paragorgia arborea (Linnaeus)	97, 122, 132, 171, 177, 180, 183

Table 2 *(continued).*

Paragorgia ?johnsoni Gray	99
Paramuricea placomus (Linnaeus)	106, 122, 142, 149
Placogorgia sp.	132
Primnoa resedaeformis (Gunnerus)	96, 102, 132, 133, 167
Order Scleractinia	
Desmophyllum cristagalli M-Edwards & Haime	12, 16, 17, 18, 27, 32, 70, 72, 96, 99, 102, 112, 115, 116, 128
Leptosammia britannica (Duncan)	143, 149, 150, 153, 157, 158, 160, 161, 164, 166, 169, 172, 173, 177, 178, 179, 181
Lophelia pertusa (Linnaeus)	112, 124, 128, 132, 133, 138, 140, 142, 144, 149, 160, 166, 167, 172, 183, 177, 178, 171, 183
Madrepora oculata Linnaeus	120, 128, 133, 135, 138, 142, 143, 155, 157, 167, 174, 179
Solenosmilia variabilis (Duncan)	27, 28, 40, 43, 44, 45, 58, 59, 62, 66, 67, 70, 72, 78, 83
Stephanocyathus nobilis (Moseley)	29
Vaughanella concinna Gravier	99, 100, 139
ANNELIDA	
Class Polychaeta	
Eunice norvegica (Gunnerus)	19, 22, 45, 62, 70, 83, 120, 124, 135, 144, 155
?Iphione sp.	153, 166
?Micronephtys sp.	45
Polynoid sp.	83
MOLLUSCA	
Class Polyplacophora	
Hanleya nagelfar (Loven)	141
Class Gastropoda	
Buccinum sp.	127
Buccinid sp.	58
Calliostoma carolii Dautzenberg	121
Calliostoma grimaldii Dautzenberg & Fisher	62, 83
Ektonos turbonilloides	127
Fissurellid sp.	134, 139
Laiocochlis sinistrata	171, 180
Metzgeria gagei Bouchet & Warén	45, 58, 65, 72, 127, 138
Trichotropis borealis Broderip & Sowerby	45
Triphorid sp.	180
Volutomitra cf. groenlandica (Beck in Möller)	153
Class Bivalvia	
Acesta excavata (Fabricius)	18, 39, 58, 62, 102, 129, 132, 134, 140, 158, 176, 177, 179
Astarte sulcata (da Costa)	124, 140, 141, 143, 150, 153, 166, 171, 172, 173, 177, 178, 179, 180, 186
CHELICERATA	
Class Pycnogonida	
Nymphon sp.	153
CRUSTACEA	
Class Cirripedia	
Arcoscalpellum cf. michelottianum (Pilsbury)	35
Bathylasma hirsutum (Hoek)	78, 103

Table 2 *(continued).*

Class Malacostraca order Decapoda	
Caridean sp. A	102, 177, 180
Galathea sp.	122, 177, 179, 180
Munida sp.	75, 116
Rochinia crassus Milne-Edwards	104
Order Isopoda	
Cirolana sp.	132, 183
BRYOZOA	
Order Cyclostomata	
Bicrisia ?abyssicola Kluge	12, 65, 70
BRACHIOPODA	
Macandrevia cf. cranium Mueller	186
SIPUNCULA	
Aspidosiphon (?Akrikos) sp.	127
ECHINODERMATA	
Class Crinoidea	
Hathrometra sarsii Clark	128
Class Asteroidea	
Brisinga endecacnemos Asbjörnsen*	
Ceramaster granularis (O. F. Müller)	158, 160, 180
Henricia pertusa (O. F. Müller)	22, 153, 177
Leptychaster arcticus (M. Sars)	153, 180
Class Ophiuroidea	
Asteronyx loveni Mueller & Troschel	97
Ophiacantha abyssicola G. O. Sars	62, 132, 140, 141, 142, 143, 153, 179
Ophiacantha anomala G. O. Sars	83, 96, 124, 140, 167
Ophiacantha aristata Koehler	13, 83, 149
Ophiacantha bidentata (Retzius)	22, 113, 138
Ophiacantha spectabilis G. O. Sars	112, 121, 124, 140, 174, 183
Ophiactis abyssicola (M. Sars)	12, 16, 17, 18, 33, 37, 45, 67, 72, 83, 96, 97, 106, 107, 111, 112, 115, 116, 118, 121, 122, 128, 135, 138, 140, 149, 150, 153, 161, 166, 167
Ophiomusium lymani Wyville-Thomson	68
Ophiomyxa serpentaria Lyman	13, 124, 142, 149, 150, 153, 158, 166, 178, 179, 180
Ophiopholis aculeata (Linnaeus)	180
Ophiura carnea M. Sars	45
Class Echinoidea	
Cidaris cidaris (Linnaeus)	115
Echinus affinis Mortensen	13, (132)
Echinus elegans Düben & Koren	166
Class Holothuroidea	
Chiridota sp.	184
Laetmogone violacea Théel	166
CHORDATA	
Class Ascidiacea	
Ascidiid sp.	177

* collected from the ridge on an instrument during CD81.

were associated with *Lophelia pertusa* and *Solenosmilia variabilis* respectively.

Isops phlegraei is a widely distributed species in the NE Atlantic, with a large bathymetric range from about 100 to 1500 m. Therefore the record of 2600 m (station 18) is unusually deep and should perhaps be considered with hesitation.

Petrosia crassa is a massive species found widely distributed at outer shelf and upper bathyal depths around the Faroes and parts of Iceland (Tendal, unpubl.). The present record (station 83) is the deepest known and most westerly.

Poecillastra compressa is, in its typical form, known from many parts of the North Atlantic and Norweigan and Greenland Seas, at outer shelf and upper slope depths.

Tetilla cf. longipilis is new to the area. The identification must be considered as tentative, because the North Atlantic species of the family are not fully revised. It was described from the Azores, from about 1860 m depth; the somewhat shallower distribution of 650 to 1275 m here is in accordance with the experience that many species are found deeper further to the south.

Cnidaria

Order Gorgonacea

Specimens of several well-known and frequently found northern ocean species were present in the samples, such as *Paramuricea placomus*, *Primnoa resedaeformis* and *Muriceides kuekenthali*. *Muricedes sceptrum* was represented in samples from two stations; this species is previously recorded from the Mid-Atlantic Ridge SW of the Azores, Mauretania, Morocco, the Bay of Biscay and Ireland (Grasshoff, 1977).

Paragorgia arborea was represented by both its white and red variants. A specimen of *Paragorgia* was recovered from station 99 resembling *Paragorgia johnsoni*, with more delicate branches and growing more in one plane than *P. arborea; P. johnsoni* is previously recorded from Madiera and the Bay of Biscay at 4100 m (Grasshoff, 1977).

A specimen of *Placogorgia* unlike any of the species of the North Atlantic revised by Grasshoff (1977) was recovered from station 132. *Acanthogorgia granulata* was recovered from WP97 (800 m); the species is previously recorded from the Azores with a depth range of 600-1500 m (Grasshoff, 1973).

Order Scleractinia

Scleractinians were the most abundant group represented in the samples in terms of the number of stations: 60 out of 106 stations with biota, which may reflect their probable greater resistance to destruction during dredging compared to other groups. Occurrences of species reported here are for specimens that were of a fresh appearance.

Desmophyllum cristagalli was recovered from 15 stations with a depth range of 725-2600 m (Fig. 2) Dead specimens of this solitary species were also recovered at other stations at the southern end of the ridge, coated in a crust of manganese oxide. The species is previously recorded SW of Iceland (Zibrowius, 1980) and is represented in the BIOICE (Biology of Iceland) collection (H. Zibrowius, pers. comm.).

Leptosammia britannica was represented at 17 stations towards the shallower northern end of the ridge (Fig. 2) with several specimens recovered attached to basalts. The species is common in the BIOICE collection.

Lophelia pertusa was recovered from 19 stations towards the shallower northern end of the ridge (Fig. 3). This colonial species is widespread in the NE Atlantic (Wilson, 1979) with a very wide bathymetric distribution: living branches have been collected from 50-60 m in Norwegian waters and the deepest record is 3430-3530 m from 26° N on the Mid-Atlantic Ridge (BRAVEX/94 Scientific Team, 1994). Carlgren (1939) reported specimens from a station S.W. of Iceland and *L. pertusa* is also present in the BIOICE collection.

Madrepora oculata was recovered from 12 stations with a depth range of 493-850 m, similar to that of *Lophelia pertusa* (Fig. 3). Carlgren (1939) also reported this species SW of Iceland in the same area as *Lophelia pertusa. Solenosmilia variabilis* was recovered from 15 stations with depths >1000 m (Fig. 3) and *M. oculata* and *S. variabilis* are both represented in the BIOICE collection.

A single specimen of *Stephanocyathus nobilis* was recovered from station 29. Fragments of this species are recorded from further south (56° 01' N) on the Mid-Atlantic Ridge (Zibrowius, 1980).

Vaughanella concinna was represented at three stations by eroded specimens, included here as there were no fresh specimens in any of the samples. The species is previously

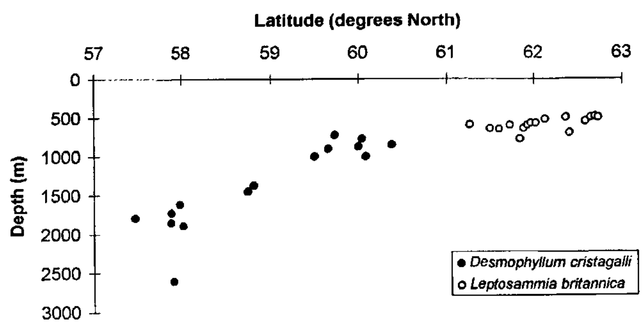

Figure 2

Spatial distribution of common solitary scleractinian species among CD80 samples.

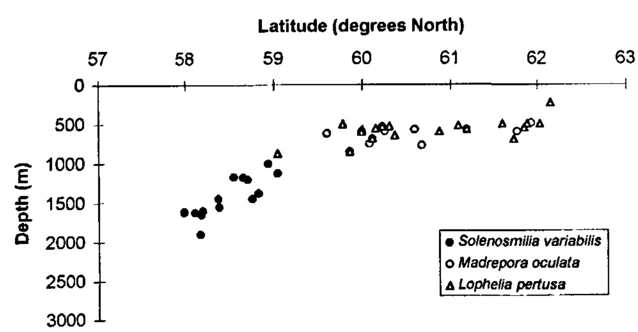

Figure 3

Spatial distribution of colonial scleractinian species among CD80 samples.

reported from the Celtic Sea and the Azores (Zibrowius, 1980).

Annelida

Class Polychaeta

Eunice norvegica was recovered from eleven stations along the ridge, associated with *Solenosmilia variabilis, Lophelia pertusa* and *Madrepora oculata* at nine of those stations; at the other stations it is possible that specimens had been separated from their host during dredging. Specimens of the genus are previously recorded from south of Iceland in this association (Wesenberg-Lund, 1951), although they were assigned to the species *E. floridiana.* Taxonomy within the genus, however, has been revised by Fauchald (1992).

Mollusca

Class Gastropoda

A specimen of the Buccinidae was recovered from station 58, and a shell of a *Buccinum* sp. was found in the sample from station 127; both are thought to be previously undescribed (A. Waren, pers. comm.). Topshells were represented in the samples by *Calliostoma carolii* and *C. grimaldii,* both of which are previously recorded from the Azores and are known from there only (A. Waren, pers. comm.).

Class Bivalvia

Acesta excavata was recovered from 13 stations along the length of the ridge; *Astarte sulcata* was recovered from 15 stations at the shallower northern end (Fig. 4).

Sipuncula

A sipunculan specimen was found associated with a shell of *Ektonos turbonilloides* from station 127. The specimen was identified as either an *Aspidosiphon* or *Akrikos* species, but does not fit the descriptions for either and could therefore be new (P. Gibbs, pers. comm.).

Echinodermata

Echinoderms representing all five classes were found at 52 of the 106 stations where biota were recovered. A single crinoid specimen was recovered from station 128 and identified as *Hathrometra sarsii* although the specimen was quite damaged. The delicacy of these organisms and potential for damage during dredging is perhaps the cause of their perceived paucity of this group amongst the samples. A specimen of *Brisinga endecacnemos* was recovered on an ocean bottom seismometer that was deployed on the ridge during Cruise CD80 (57° 42.96' N, 32° 36.00' W, 1238 m) and recovered during Cruise CD81 (Sinha, 1993).

Ophiuroids were present in samples from 46 of the 52 stations where echinoderms were found. Within the ophiuroids, the Suborder Ophiurida dominated with the Suborder Euryalida being represented by a single specimen of *Asteronyx loveni,* found entwined around a branch of *Acanthogorgia granulata* from station 97.

Ophiactis abyssicola was the most ubiquitous ophiuroid, being recovered from 31 stations along the whole length of the ridge (Fig. 5). This species was associated with living and dead colonial scleractinians in twelve samples; 32 individuals were found on a single piece of coral approximately 30 cm diameter recovered from station 83. Specimens show considerable variation in the occurrence of spines and pattern of scales on the dorsal side of the disk (Mortensen, 1933).

Ophiomyxa serpentaria was found in samples from eleven stations all along the ridge, although it was more common at the shallower northern stations (Fig. 5). The minimum depth among the samples here (493 m) is shallower than the bathymetric distribution recorded for the N. E. Atlantic as a whole (600-1200 m; Paterson, 1985).

Ophiacanthids were represented in the samples by five species, recovered from a total of 22 stations. *Ophiacantha aristata* was recovered from stations with a depth range of 650-1805 m; Mortensen (1927) reports the species from S.W. Ireland, the Bay of Biscay and the Azores with a narrower depth range of 890-1740 m. The specimens of *Ophiacantha bidentata,* recovered from three stations along the ridge, show morphological similarites to the warm water variety *fraterna* (Verrill) recognised by Mortensen (1933) and are therefore likely to be protandric her-

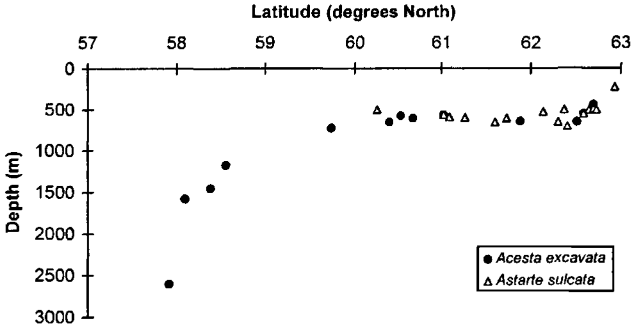

Figure 4

Spatial distribution of common bivalve species among CD80 samples.

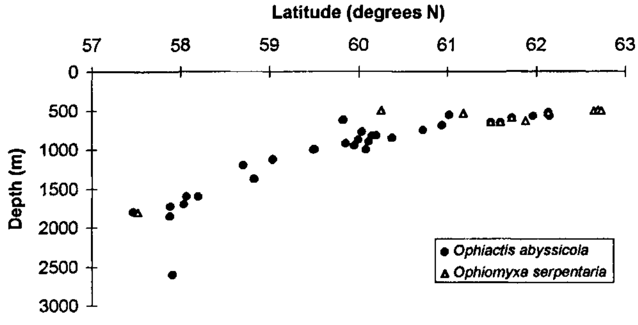

Figure 5

Spatial distribution of common ophiuroid species among CD80 samples.

maphrodites from the North Atlantic population of this species (Tyler, Gage, 1982).

A single specimen of *Ophiopholis aculeata* was found at station 180 (500 m). The species is circumpolar with the British south coast denoting its southern limit in the Atlantic. Mortensen (1927) further reports it to be rare below 300 m, but this may be based on Arctic specimens displaying the characteristic shallowing of recognised faunal provinces described by Menzies *et al.* (1973).

Echinus affinis was found at stations 13 (1805 m) and 132 (575 m); the species is previously recorded south of Iceland with a bathymetric distribution of 770-2230 m (Gage *et al.*, 1985). However, the specimen from our shallower station was badly damaged and may have been the shallower species *Echinus acutus* Lamark variety *norvegicus* Düben, Koren.

DISCUSSION

One of the key problems in biology lies in correctly choosing the scale of sampling or analysis to fit the scale of the feature or process that is to be investigated. Failure to do so correctly can produce results that are artefacts of the sampling programme or analysis rather than being "real" phenomena. This consideration must be foremost in interpreting the faunal distribution shown through the samples here, as fundamentally the absence of a species from a particular area cannot strictly be inferred from the absence of that species in a sample from that area. Furthermore, the predominance of the more robust groups within the samples is likely to be a function of their relative resistance to the rigours of dredge sampling.

However, despite these limitations, it is apparent from the spatial distributions of individual species in the samples shown in Figures 2 - 5 that certain species such as *Ophiactis abyssicola* and *Acesta excavata* are comparatively eurybathic, whilst others are more stenobathic and restricted towards either the shallower northern (*e.g. Leptosammia britannica, Lophelia pertusa, Madrepora oculata*) or deeper southern end of the ridge (*e.g. Desmophyllum cristagalli*). Some species, such as *Ophiomyxa serpentaria*, are distributed along the length of the ridge but are more common amongst samples from shallower northern stations.

Considering the effects of the differences in bathymetric distribution between individual species on the faunal distribution as a whole by multivariate analysis, two major clusters of stations are produced in the resulting dendrogram (Fig. 6) at a Dissimilarity Index of 0.95. Plotting the spatial distribution of stations belonging to these two clusters, it is apparent that the two clusters separate fairly well on the basis of their station bathymetries (Fig. 7). This analysis therefore suggests a two-zone bathymetric faunal zonation along the ridge, with the transition between them at 800 to 1000 m, equivalent to around 60° N. The zonation is somewhat coarse, reflecting the summation of step-wise zonations from the presence or absence of individual species perceived through the classification analysis with the lack of relative abundance information preventing the distinction of finer rates of faunal change. However, the zonation is similar to the North Atlantic pattern first recognised by Le Danois (1948) in the Bay of Biscay, and that of Menzies *et al.* (1973) on the continental slope of the eastern USA from the Carolinas to Georgia.

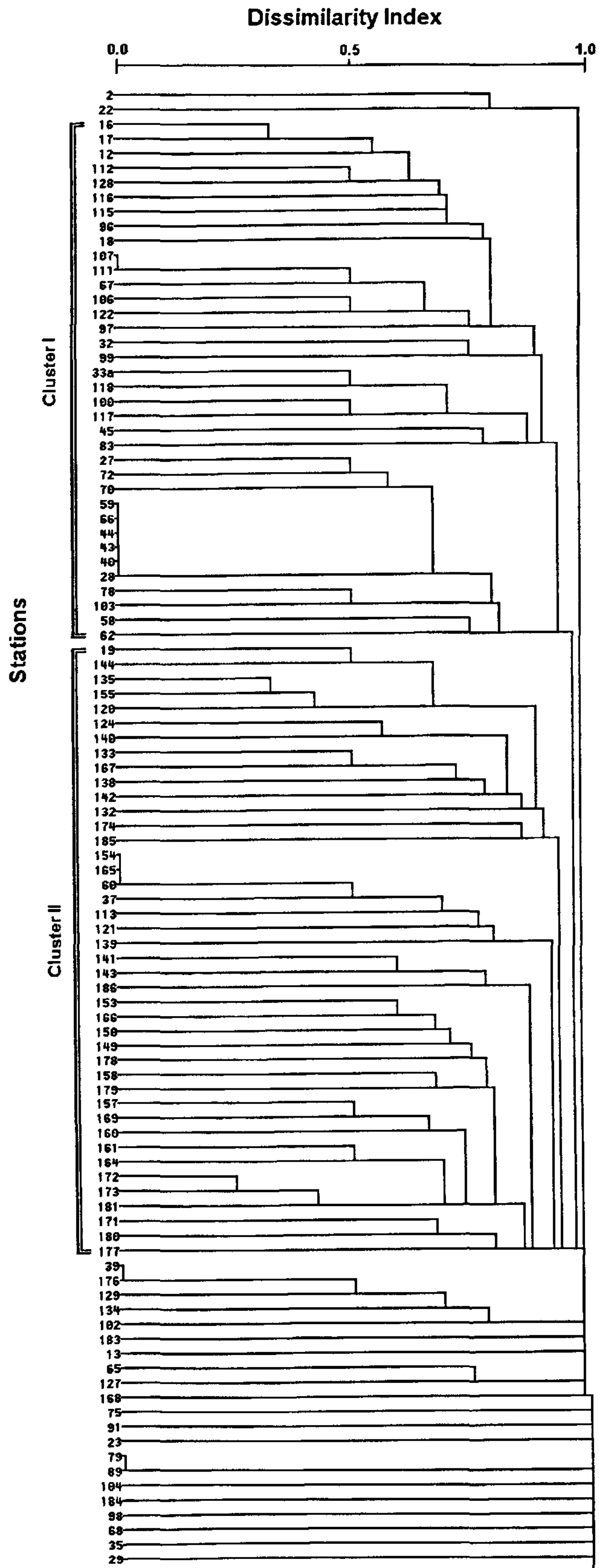

Figure 6

Classification of CD80 stations by cluster analysis.

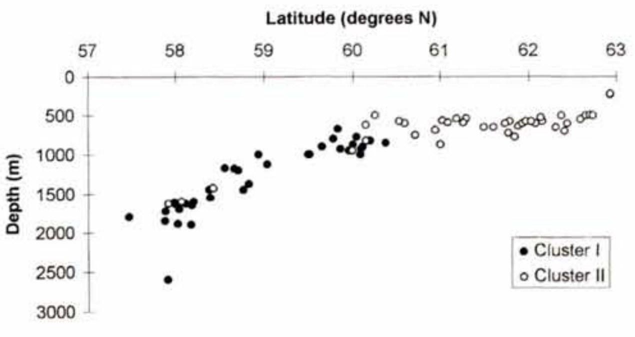

Figure 7

Spatial distribution of CD80 stations belonging to the two main clusters recognised by multivariate analysis.

Bathymetry can influence faunal distribution "directly", through differences in physiological tolerance of pressure (Siebenaller, Somero, 1978) and through high pressure being a prerequiste for successful larval development in some species (Young, Tyler, 1993), or "indirectly" by representing covariance with another environmental variable, such as temperature of water mass. Gage, Tyler (1991) recognised a deeply embedded but largely untested view in the deep-sea literature that the effects of temperature override those of the hydrostatic pressure gradient.

Hydrographic information from BS8 (Fig. 8) indicates the presence of two water masses on the ridge axis. A warmer, more saline water mass covers the northern end of the ridge, with a cooler, less saline water mass at the southern end. The warmer water mass corresponds to Subpolar Mode Water (SPMW) and the cooler water mass to Upper North Atlantic Deep Water (UNADW; Schmitz, McCartney, 1993), with the salinity minimum showing the influence of Labrador Sea Water (LSW; Read, Gould, 1992; Tsuchiya *et al.*, 1992). The transition between these water masses occurs at 800-1000 m, matching the transition between the faunal zones recognised by our analysis. This suggests that the faunal zonation may reflect the water mass structure, an observation previously made on the continental slope SW of Ireland (Tyler, Zibrowius, 1992).

In classification analysis it is important that samples are sufficiently large to minimise the stochasticity in the representation of fauna at the different stations. As our samples were obtained incidentally through a rock sampling programme it was not possible to ensure that this was the case. Multivariate analysis also recognises several outlier stations and minor station clusters at a Dissimilarity Index of 0.95. The minor clusters are not distinct in their bathymetric range, nor are they consistent in the presence of sediment in their dredges or the alteration index of their rocks. Whilst our environmental data are limited and the species composition of these minor cluster stations may be related to unmeasured variables such as local hydrodynamics, undersampling could also account for these minor clusters and the outlier stations, as their sample composition generally comprises only species that are rare or unique in the samples, or species that are more eurybathic without any of the more stenobathic species found in the same area.

Data on substrata at CD80 stations were recorded by the presence of sediment in the dredge bucket and by analysis of the rocks recovered to determine their alteration index. A rock index of 1 indicates fresh "young" rocks and an index of 4 indicates weathered "older" rocks. There are, however, problems of both temporal and spatial scale when investigating the influence of substratum expressed by these variables. A rock alteration index of 1 denotes youth in geological terms, representing an age of 0-10000 years, whilst the processes involved with biological colonisation operate on far shorter timescales. For the sediment data, it is likely that the dredge integrates fauna from small-scale patches of sediment and bare rock within an area, and therefore the presence of sediment in the dredge at one station does not imply that the fauna collected were living on or in the sediment at that station. However, this latter effect can only serve to mask any preference of bare rock as a substratum, as it can only reduce the number of stations at which a species is found with no sediment. There was evi-

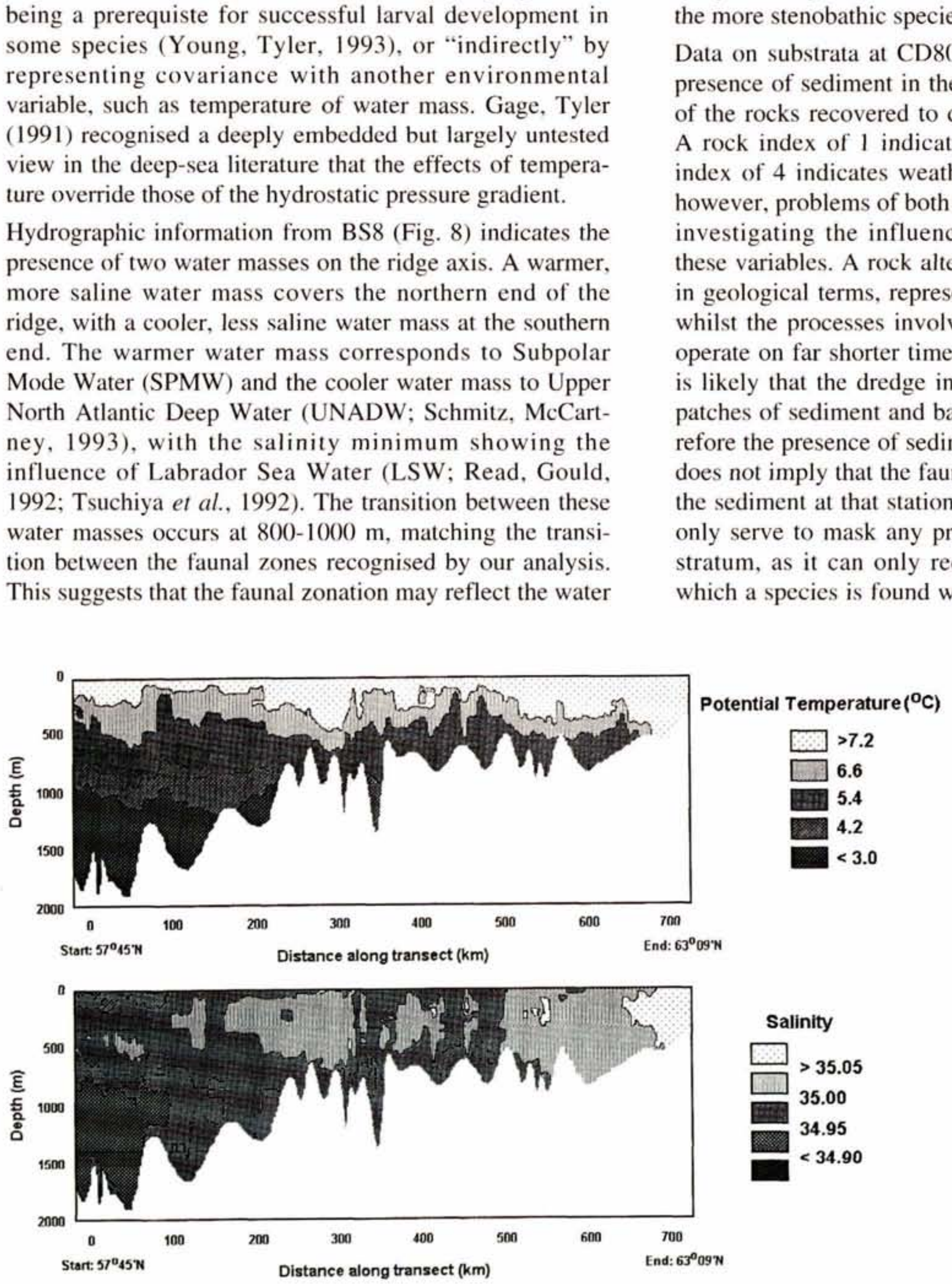

Figure 8

Vertical section of the hydrography of the Reykjanes Ridge axis from BS8.

dence that *Lophelia pertusa* and *Ophiactis abyssicola* were recovered from more sediment-free stations than would be expected by chance alone (*L. pertusa* $\chi^2 = 9.29$, $v = 1$, $p < 0.05$; *O. abyssicola* $\chi^2 = 5.14$, $v = 1$, $p < 0.01$).

CONCLUSION

The biological samples obtained during CD80 extend the biogeographic records of many species and provide a collection of megafauna from the length of the Reykjanes Ridge. Several of the species recovered are previously only recorded from further south in deeper water. Whilst the predominance of more robust groups in the samples is likely to be a result of the sampling technique, multivarate analysis of the samples suggests a two-zone bathymetric zonation in megafauna along the ridge, corresponding to the water mass structure at the ridge axis shown by hydrographic data from BS8. These results should highlight the opportunities for obtaining specimens and data that are afforded by non-biological sampling programmes (Tunnicliffe, 1994). Other factors such as local topography and substratum are also likely to influence the faunal distribution on a smaller scale, but the limitation imposed by dredging on the information that can be gained from samples precludes their investigation here.

Acknowledgements

Cruise CD80 of the *RRS Charles Darwin* and Cruise BS8 of the *RV Bjarni Saemundsson* were funded by NERC through the British Mid-Ocean Ridge Initiative (BRIDGE). JTC was supported during this work by a NERC Advanced Course Studentship and Endowment Fund sponsorship from the Society for Underwater Technology, which are gratefully acknowledged.

We are grateful to colleagues who have given their time in identifying species in the samples: Ole Tendal, Anne Klitgaard, Michelle Kelly-Bourges and Clare Valentine (sponges); Manfred Grasshoff (gorgonians and alcyonians); Anders Waren (gastropods); Peter Gibbs (sipunculans) and Howard Brunton (brachiopods).

Ole Tendal and Helmut Zibrowius are thanked for their helpful comments on the manuscript. Mark Rudnicki, Richard Miller and Phillipe Guyard are thanked respectively for producing vertical profiles of temperature and salinity from BS8, topographic maps from CD80 EM12 data and the French translation of the abstract.

REFERENCES

Arquit A.M. (1990). Geological and hydrothermal controls on the distribution of megafauna in Ashes Vent Field, Juan de Fuca Ridge. *J. Geophys. Res.* **95**, 12947-12960.

BRAVEX/94 Scientific Team (1994). BRAVEX/94: a joint British-Russian expedition to the Broken Spur (29° N) and TAG (26° N) hydrothermal vent sites on the Mid-Atlantic Ridge. *BRIDGE Newsletter* **7**, 6-9.

Carey Jr. A.G., D.L. Stein, P.L. Rona (1990). Benthos of the Gorda Ridge axial valley (NE Pacific Ocean): taxonomic composition and trends in distribution. *Progr. Oceanogr.* **24**, 47-57.

Carlgren O. (1939). Actiniaria, Zoantharia and Madreporaria. *Zoology of Iceland* **2**, 8, 20 p.

Chave E.H., A.T. Jones (1991). Deep water megafauna of the Kohala and Hakeakala slopes, Alenuihaha Channel, Hawaii. *Deep-Sea Res.* **38**, 781-803.

Dietrich P.G., E.A. Kontar (1990). Ermittlung aktuo-fazieller Bedingungen am Meeresboden mit Hilfe autonomer Bodenstationen. *Zeitschrift für angewandte Geologie* **36**, 292-296.

Faulchald K. (1992). A review of the Genus *Eunice* (Polychaeta: Eunicidae) based on type material. *Smithsonian Contributions to Zoology* **523**, 1-422.

Gage J.D., P.A. Tyler (1991). *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor.* Cambridge University Press, 504 p.

Gage J.D., M. Pearson, A.M. Clark, G.L.J. Paterson, P.A. Tyler (1983). Echinoderms of the Rockall Trough and adjacent areas I: Crinoidea, Asteroidea and Ophiuroidea. *Bulletin of the British Museum Natural History (Zoology)*, **45**, 5, 263-308.

Gage J.D., D.S.M. Billett, M. Jensen, P.A. Tyler (1985). Echinoderms of the Rockall Trough and adjacent areas II: Echinoidea and Holothuroidea. *Bulletin of the British Museum Natural History (Zoology)*, **48**, 4, 173-213.

Genin A., P.K. Dayton, P.F. Lonsdale, F.N. Spiess (1986). Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. *Nature* **322**, 59-61.

German C.R., J. Briem, C. Chin, M. Danielsen, S. Holland, R. James, A. Jónsdóttir, E. Ludford, C. Moser, J. Olafsson, M.R. Palmer, M.D. Rudnicki (1994). Hydrothermal activity on the Reykjanes Ridge: the Steinahöll vent-field at 63° 06' N. *Earth and Planetary Science Letters* **121**, 647-654.

Grasshoff M. (1973). Die Gorgonarien des östlichen Nordatlantik und des Mittelmeeres II: Die Gattung Acanthogorgia (Cnidaria, Anthozoa). *Meteor Forschungsergebnisse Reihe D*, **13**, 1-10.

Grasshoff M. (1977). Die Gorgonarien des östlichen Nordatlantik und des Mittelmeeres III: Die Familie Paramuriceidae (Cnidaria, Anthozoa). *Meteor Forschungsergebnisse Reihe D*, **27**, 5-76.

Grasshoff M. (1985). Die Gorgonaria, Pennatularia und Antipatharia des Tiefwassers der Biskaya (Cnidaria, Anthozoa). Ergebnisse der französischen Expeditionen *Biogas, Polygas, Géomanche, Incal, Noratlante* und Fahrten der Thalassa. III Ergänzungen, *in: Peuplements profonds du Golfe de Gascogne*. Campagnes Biogas, L. Laubier, C. Monniot eds. IFREMER, Brest, 299-310.

Grassle J.F. (1986). The biology of deep-sea hydrothermal vent communities. *Adv. Mar. Biol.* **23**, 301-362.

Grassle J.F., W. Smith (1976). A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologica* **25**, 13-22.

Jaccard P. (1900). Contribution au problème de l'immigration post-glaciaire de la flore alpine. *Bulletin de la Société Vaudoise des Sciences Naturelles* **36**, 87-130.

Kaufmann R.S., W.W. Wakefield, A. Genin (1989). Distribution of megafauna and lebenspurren on two central North Pacific seamounts. *Deep-Sea Res.* **32**, 859-874.

Le Danois E. ed. (1948). *Les profondeurs de la mer. Trente ans de recherches sur la faune sous-marine au large des côtes de France.* Paris: Payot, 303 p.

McCartney M.S. (1992). Recirculating components to the deep boundary current of the northern North Atlantic. *Progr. Oceanogr.* **29**, 283-383.

Menzies R.J., R.Y. George, G.T. Rowe (1973). *Abyssal environment and ecology of the world oceans.* New York: Wiley Interscience, 488 p.

Milligan B.N., V. Tunnicliffe (1994). Vent and nonvent faunas of the Cleft segment, Juan de Fuca Ridge, and their relations to volcanic age. *J. Geophys. Res.* **99**, B3, 4777-4786.

Minster J.B., T.H. Jordan (1987). Present day plate motions. *J. Geophys. Res.* **83**, 5331-5354.

Mortensen T. (1927). *Handbook of the Echinoderms of the British Isles.* Oxford University Press, 471 p.

Mortensen T. (1933). Ophiuroidea. *Danish Ingolf Expedition* **4**, 8, 121 p.

Murton B.J., L.M. Parson (1993). Segmentation, volcanism and deformation of oblique spreading centres: a quantitative study of the Reykjanes Ridge. *Tectonophysics* **222**, 237-257.

Murton B.J., J. Evans, J. Forster, R. Owens, L.M. Parson, L. Redbourne, D. Sauter, L. Slater, R.N. Taylor, C.L. Walker (1993). The PETROS programme (PETRogenesis of Oblique Spreading): a report from CD80 (BRIDGE Cruise No. 10), 1-29 September 1993, Barry, South Wales to Reykjavik, Iceland. *BRIDGE Newsletter* **5**, 22-26.

Olaffson J., K. Thors, J.R. Cann (1991). A sudden cruise off Iceland. *RIDGE Events*, **2/2**, 35-38.

Parson L.M., B.J. Murton, R.C. Searle, D. Booth, J. Evans, P. Field, J. Keetoin, A. Laughton, E. McAllister, N. Millard, L. Redbourne, I. Roude, I. Shor, D. Smith, S. Spencer, C. Summerhayes, C.L. Walker (1993). En echelon axial volcanic ridges at the Reykjanes Ridge: a life cycle of volcanism and tectonics. *Earth and Planetary Science Letters* **117**, 73-83.

Paterson G.L.J. (1985). The deep-sea Ophiuroidea of the North Atlantic Ocean. *Bulletin of the British Museum (Natural History)*, **49**, 1-162.

Read J.F., W.J. Gould (1992). Cooling and freshening of the subpolar North Atlantic Ocean since the 1960s. *Nature* **360**, 55-57.

Rice A.L., M.H.Thurston, A.L. New (1990). Dense aggregations of a hexactinellid sponge, *Pheronema carpenteri*, in the Porcupine Seabight (NE Atlantic Ocean), and possible causes. *Progr. Oceanogr.* **24**, 179-196.

Roux M. (1985). Les Crinoïdes pédonculés (échinodermes) de l'Atlantique NE: inventaire, écologie et biogéographie, *in: Peuplements profonds du Golfe de Gascogne.* Campagnes Biogas, L. Laubier, C. Monniot eds. IFREMER, Brest, 479-489.

Schmitz W.J., M.S. McCartney (1993). On the North Atlantic circulation. *Reviews of Geophysics* **31**, 29-49.

Siebenaller J., G.N. Somero (1978). Pressure-adaptive differences in lactate dehydrogenases of congeneric fishes living at different depths. *Science* **201**, 255-257.

Sinha M. (1993). A geophysical survey of the Reykjanes Ridge: CD81 Cruise Progress Report. *BRIDGE Newsletter* **5**, p. 27.

Sneath P.H.A., R.R. Sokal (1973). *Numerical taxonomy.* San Fransisco: W. H. Freeman, 290 p.

Sudarikov S.M., S.V. Galkin (1995). Geochemistry of the Snake Pit vent field and its implications for vent and non-vent fauna, *in: Hydrothermal Vents and Processes*, L.M. Parson, C.L. Walker, D.R. Dixon eds. Geological Society, London, Special Publication, **87**, 319-328.

Talwani M., C.C. Windisch, M. Langseth (1971). Reykjanes Ridge crest: a detailed geophysical study. *J. Geophys. Res.* **76**, 473-577.

Tsuchiya M., L.D. Talley, M.S. McCartney (1992). An eastern Atlantic section from Iceland southward across the equator. *Deep-Sea Res.* **39**, 1885-1917.

Tunnicliffe V. (1991). The biology of hydrothermal vents: ecology and evolution. *Oceanogr. Mar. Biol. Ann. Rev.* **29**, 319-407.

Tunnicliffe V. (1994). A letter to the InterRidge Community: What to do with the slimy stuff. *InterRidge News* **3**, 1, p. 12.

Tyler P.A., J.D. Gage (1982). The reproductive biology of *Ophiacantha bidentata* (Echinodermata: Ophiuroidea) from the Rockall Trough. *J. Mar. Biol. Association of the UK* **62**, 45-56.

Tyler P.A., H. Zibrowius (1992). Submersible observations of the invertebrate fauna on the continental slope southwest of Ireland (NE Atlantic Ocean). *Oceanologica Acta* **15**, 211-226.

Van Dover C.L. (1995). Ecology of Mid-Atlantic Ridge hydrothermal vents, *in: Hydrothermal Vents and Processes*, L.M. Parson, C.L. Walker, D.R. Dixon, eds.Geological Society, London, Special Publication **87**, 257-294.

Wallrabe-Adams H.J., K.S. Lackschewitz (1994). The *R/V Professor Logachev* Research Cruise 09 to the Reykjanes Ridge near 59° N: Sediment Distribution on the Reykjanes Ridge (August-September 1993). *InterRidge News* **3**, 1, 8-11.

Wesenberg-Lund E. (1951). Polychaeta. *The Zoology of Iceland* **II, 19**, 1-182.

Whittaker R.H., C.W. Fairbanks (1958). A study of plankton copepod communities in the Columbia basin, southeastern Washington. *Ecology* **54**, 46-65.

Wilson J.B. (1979). The distribution of the coral *Lophelia pertusa* (L.) [*L. prolifera* (Pallas)] in the North-East Atlantic. *J. Mar. Biol. Association of the UK* **59**, 149-164.

Young C.M., P.A. Tyler (1993). Embryos of the deep-sea echinoid *Echinus affinis* require high-pressure for development. *Limnol. Oceanogr.* **38**, 178-181.

Zibrowius H. (1980). Les scléractinaires de la Méditerranée et de l'Atlantique nord-oriental. *Mémoires de l'Institut océanographique, Monaco* **11**, 284 p., 107 pl.

Zibrowius H. (1985). Les scléractinaires bathyaux et abyssaux de l'Atlantique nord-oriental, *in: Peuplements profonds du Golfe de Gascogne. Campagnes* Biogas, L. Laubier, C. Monniot eds. IFREMER, Brest, 311-324.