

Distribution and diversity of desmosomatid and nannoniscid isopods (Crustacea) on the Greenland–Iceland–Faeroe Ridge

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Abstract The distribution and diversity of isopods (Crustacea, Isopoda; families Desmosomatidae Sars, 1897 and Nannoniscidae Hansen, 1916) was examined in Icelandic waters where a diversity of water masses (temperature range -0.9 to 12°C) occurs and the topography is characterized by the large and shallow Greenland–Iceland–Faeroe (GIF) Ridge extending across the North Atlantic in an east-west direction. Both families were species rich in the area, in total occurring with 34 species in 20 genera. Most of the species were restricted either to the north (10) or to the south (14) of the GIF Ridge, occurring either in cold (-0.8 to 2.8°C) or warm ($>2^{\circ}\text{C}$) water masses. Five species were found on both sides of the Ridge, occurring at a wide range of temperatures (-0.9 to $>4^{\circ}\text{C}$), while another five species extend across the GIF Ridge. Most species occurred in two and more water masses and the species north of the Ridge occurred usually within narrower temperature range than the species living south of the Ridge. The water masses in association with the Ridge seem to limit distribution of most species. Despite similar number of species occurring in the areas north and south of the Ridge, the areas differ considerably in diversity pattern with depth.

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Introduction

A variety of factors shape species distributions, both historic and ecological, and these are often difficult to separate. Temperature has for a long time been recognized as one of the most important factors shaping distributions, not at least in the polar and sub-polar marine regions, where subzero temperatures dominate in large areas. The shallow and deep waters of the Arctic Ocean and the Nordic Seas (Greenland, Iceland and Norwegian Seas) hold a unique diversity of water masses, with temperatures of different ranges from -0.9°C to approximately 12°C (Hansen and Østerhus 2000). The northernmost part of the North Atlantic is further characterized by having a Ridge of shallow depth, the Greenland–Iceland–Faeroe (GIF) Ridge, extending across the Atlantic in an east-west direction and separating the Nordic Seas and the Arctic Ocean from the North Atlantic proper. Due to the deepest sill depth at about 860 m depth between the Faeroe Islands and Scotland, the deep water basins ($>4,000$ m) to the north and to the south of the GIF Ridge are largely separated from each other (Hansen and Østerhus 2000). The average sill depth in the region of the study area is 620 m in the Denmark Strait and 480 m between Iceland and the Faeroe Islands.

Extensive information on distribution on benthic invertebrates in the GIF Ridge area indicates that many species have their distributional limits in the vicinity of the Ridge. Furthermore, there are considerable differences in the species composition between the cold areas north of the Ridge and the warm areas south of the Ridge (e.g. Hansen

1916; Stephensen 1937, 1943; Svavarsson et al. 1993; Negoescu and Svavarsson 1997; Gudmundsson 1998; Weissshappel 2000, 2001; Schuchert 2000; Stransky and Svavarsson 2006; Dijkstra et al. 2009). It is not clear what shapes the species distribution at the Ridge, if it is the topography of the area, i.e. the physical presence of the Ridge itself, or the environmental parameters, i.e. temperature, sediments, food availability, etc., at the Ridge and the overlying waters.

The Desmosomatidae Sars, 1897 (Isopoda, Asellota) are among the most diverse families of deep-sea isopods. The members of the Desmosomatidae and the Nannoniscidae Hansen, 1916 are benthic species dwelling in the uppermost centimetre of the bottom (Hult 1941; Hessler and Strömberg 1989). Like all asellote isopods these are brooders, so their dispersal abilities are suspected to be poor compared to other macrofaunal taxa with pelagic larvae. Copulatory males may, however, enter the water column in search for females. Actually, one has to think about the speed of bottom currents as both asellote families treated here are epifaunal. Valsangkar (2004) mentions a transport of sediment in the deep sea may reach a distance of 15 km within 6 days. The families are closely related (see Hessler 1970a; Siebenaller and Hessler 1977, 1981; Svavarsson 1984; Wilson 2008a). Combined, the families are represented by about 207 described species in the world oceans, and they are frequently collected from the deep sea (Wolff 1962; Poore et al. 1994; Brandt et al. 2004, 2007; Brix 2006a, b, 2007, Kaiser and Brix 2005, 2007; Schotte et al. 2009; Wilson 2008b). They are well represented in the North Atlantic Ocean and the Nordic Seas, being commonly found in shallow waters at high latitudes and at bathyal and abyssal depths in the Nordic Seas and the Arctic Ocean (Hansen 1916; Wolff 1962; Hessler 1970a; Svavarsson 1988). The Desmosomatidae can be regarded as a true deep-sea family, considering that upper limit of the bathymetrical distributions of >50% of known species in below 1,000 m (Svavarsson et al. 1993). Polar emergence has been postulated for the family (Hessler 1970b). Isopods in general have been studied for more than a century in the Nordic Seas, the Arctic Ocean and the northernmost part of the North Atlantic (Sars 1899; Hansen 1916; Gurjanova 1946; Menzies and Mohr 1962; Just 1970, 1980; Paul and George 1975; Svavarsson 1982, 1984, 1988, 1997; Svavarsson et al. 1990, 1993), the most extensive information of the isopods at the GIF Ridge being gathered by during the Danish Ingolf Expedition in 1895 and 1896 (Hansen 1916).

The BIOICE project (Benthic invertebrates in Icelandic waters) was designed to investigate the faunal composition and species distribution in the northernmost part of the North Atlantic and the Nordic Seas. Here, we evaluate the distribution, faunal composition and diversity of the

Desmosomatidae and Nannoniscidae in Icelandic waters. We evaluate the following:

Do the isopods occur at wide or narrow ranges in the temperature and are they restricted to any specific water mass or masses (water bodies with certain temperature and salinity characteristics) found in the area?

Does the topography of the GIF Ridge shape the distribution of asellote isopods or do other abiotic factors, like temperature, salinity, sediment or depth, limit the species distribution in the area?

Materials and methods

Study area (Fig. 1)

The study area comprises the northernmost part of the North Atlantic and the south-western part of the Nordic Seas (i.e. the Iceland, Greenland and Norwegian Seas). This area is characterized by a prominent topographic feature, the GIF Ridge. The Ridge is generally shallow, with a maximum sill depth of 620 m in the Denmark Strait between Greenland and Iceland, a maximum sill depth of 480 m between Iceland and the Faeroes and a maximum sill depth of 840 m between the Faeroes and Scotland (Hansen and Østerhus 2000). Generally, the Ridge is considerably shallower than the sill depths and most of the Denmark Strait is shallower than 300 m.

The hydrography of the area is complicated and diverse, with several primary water masses often overlying each other (Stefánsson 1962; Hansen and Østerhus 2000; Malmberg and Valdimarsson 2003). All water masses occur also at the bottom. For the BIOICE stations observed during this study the intersections of the water masses with the benthic boundary layer are known and shown in Fig. 2. The water masses dominating the study area are Modified North Atlantic Waters (MNAW; 7.0–8.5°C, salinity 35.10–35.30), Labrador Sea Water (LSW; 3–4°C, salinity 34.90–34.95), Iceland Sea Overflow Water (ISOW; 2–3°C, salinity 34.85–35.00); Modified East Icelandic Water (MEIW; 1–3°C, salinity 34.70–34.90), Norwegian Sea Deep Water (NSDW; <–0.5°C, salinity <–34.40), Norwegian Sea Arctic Intermediate Water (NSAIW; –0.5 to 0.5°C, salinity 34.85–34.90), Arctic/Polar Water (A/PW; 0–2°C, salinity 34.30–34.90) and Coastal Water (CW; 5–12°C, salinity <34.50) all differing in salinity (total range 34.30–35.45) and temperature (total range –0.9 to 12°C). Individual stations were assigned to water masses using Stefánsson (1962), Hansen and Østerhus (2000) and Malmberg and Valdimarsson (2003).

The area south of the Ridge is characterised by warm waters (e.g. MNAW; LSW), while the area north of the Ridge is characterised by cold waters (e.g. NSDW). Most of the shallower parts of the Ridge are influenced by warm

Fig. 1 BIOICE stations used in this study

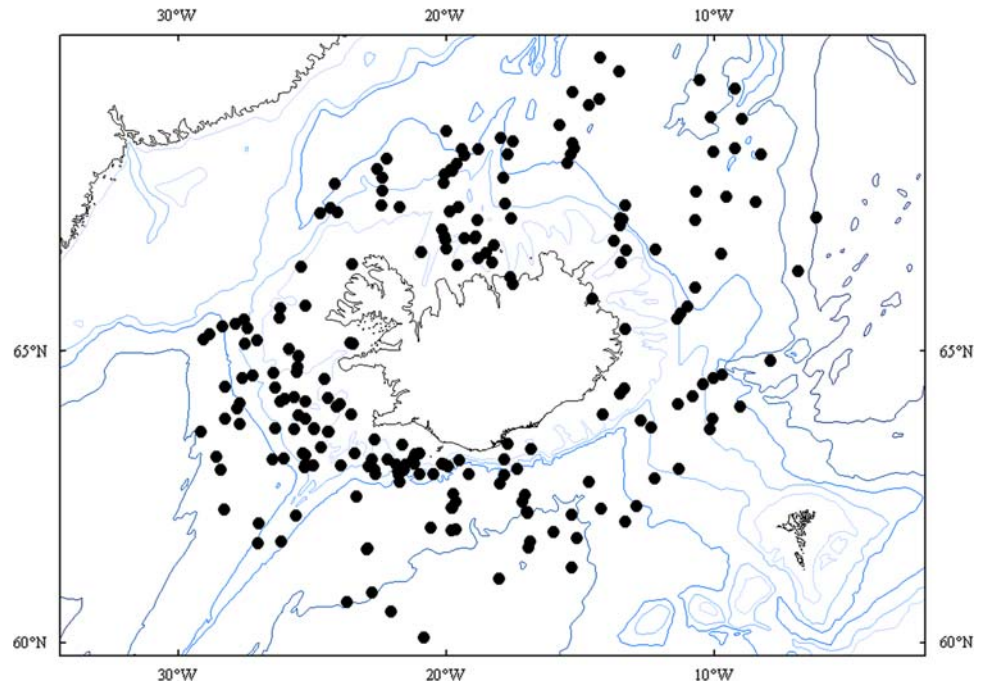
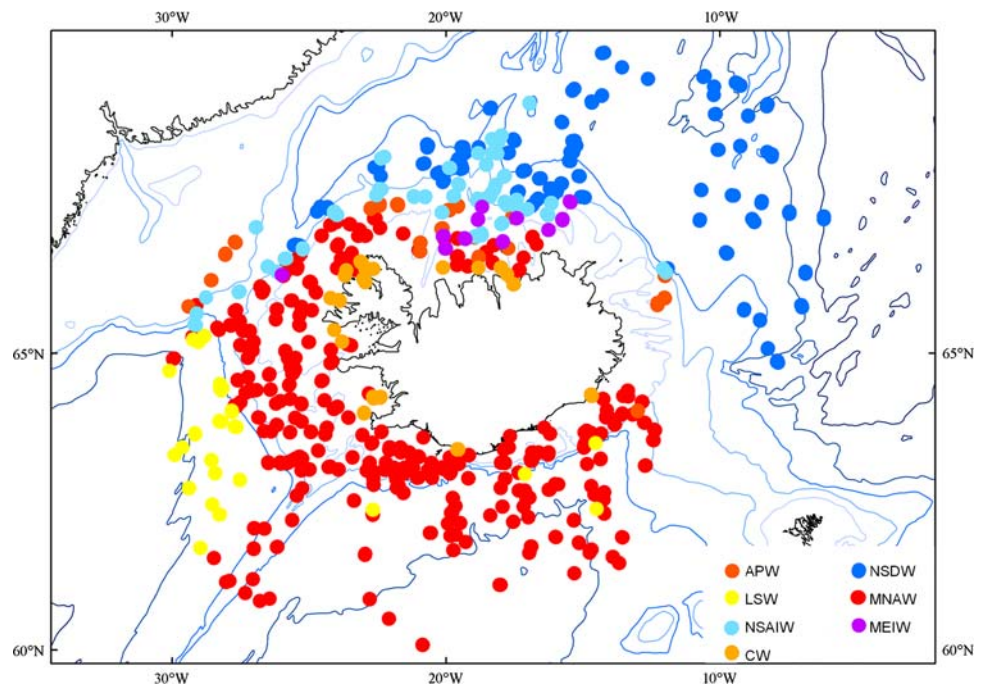


Fig. 2 Intersections of the water masses with the benthic boundary layer for the RP sledge stations: Modified North Atlantic Waters (*MNAW*), Labrador Sea Water (*LSW*), Iceland Sea Overflow Water (*ISOW*); Modified East Icelandic Water (*MEIW*), Norwegian Sea Deep Water (*NSDW*), Norwegian Sea Arctic Intermediate Water (*NSAIW*), Arctic/Polar Water (*A/PW*) and Coastal Water (*CW*)



waters (e.g. MNAW, MEIW, CW), while the deepest channels and some Ridge depressions hold cold waters, either constantly or intermittently (e.g. NSAIW). Cold waters from the north partly flow along the East Greenland current into the North Atlantic as surface waters (A/PW) or as overflow across the Denmark Strait and the Iceland–Scotland Ridge (e.g. NSAIW). The Iceland–Faeroe Ridge overflow may occur in five branches along depressions between Iceland and the Faeroes. In contrast to the eastern branches, the western branches of this overflow are presumably

continuous, but the overflow water is highly variable, both spatially and temporally. A major amount of water flows through the Faeroe–Shetland channel. Accordingly, there are bands of warm and cold waters across the Ridge and in some places these bands vary in character. A detailed overview is given in Hansen and Østerhus (2000).

At each station, except stations taken on cruise with the RV *Magnus Heinason*, temperature and salinity were measured. Based on these data, stations were assigned to the water masses (Fig. 2).

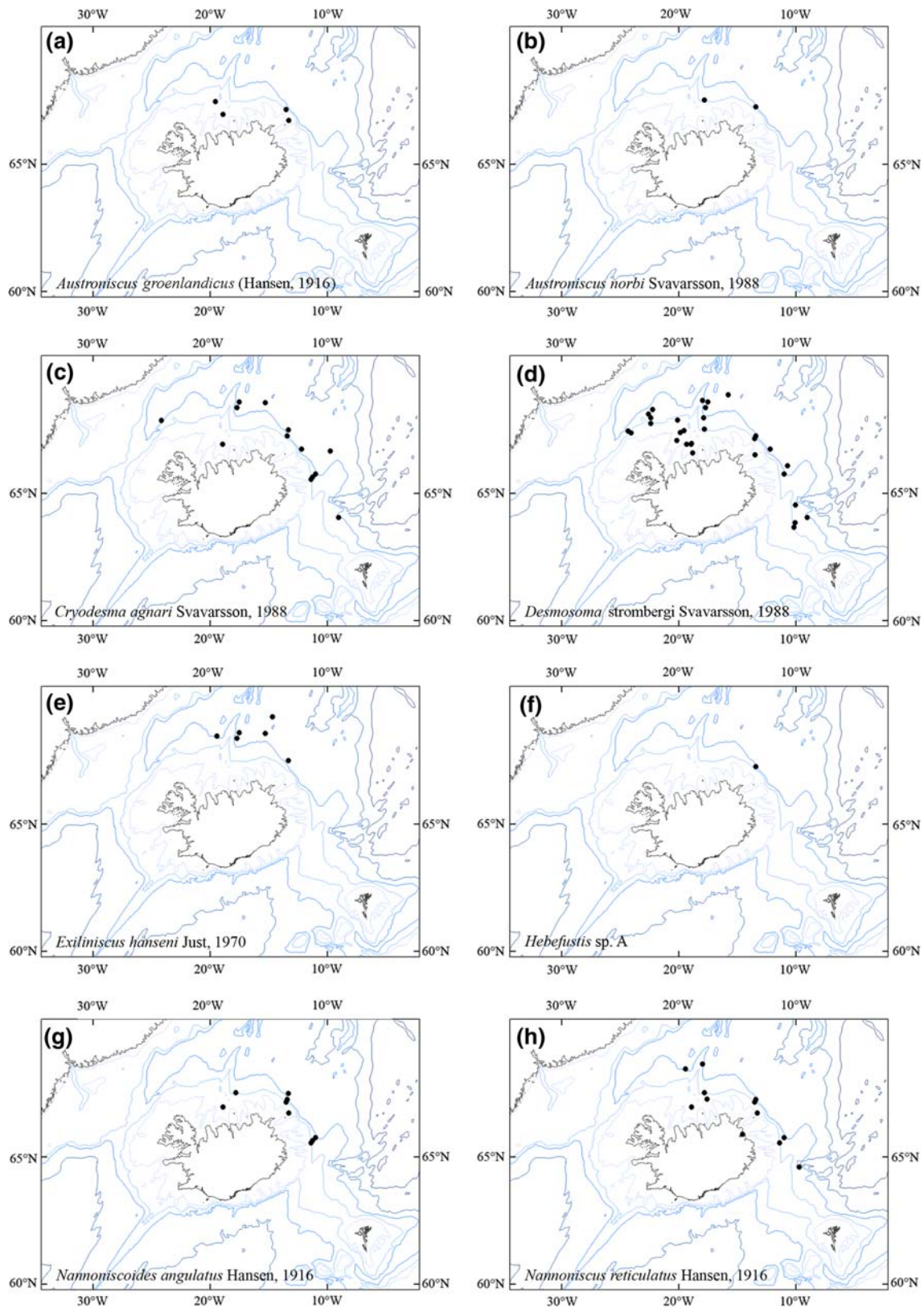


Fig. 3 Distribution of species in the sampling area. Northern species. **a** *Austroniscus groenlandicus* Hansen, 1916; **b** *A. norbi* Svarrsson, 1988; **c** *Cryodesma agnari* Svarrsson, 1988; **d**

Desmosoma strombergi Svarrsson, 1988; **e** *Exilinisicus hanseni* Just, 1970; **f** *Hebefustis* sp. A; **g** *Nannoniscoides angulatus* Hansen 1916; **h** *Nannoniscus reticulatus* Hansen 1916

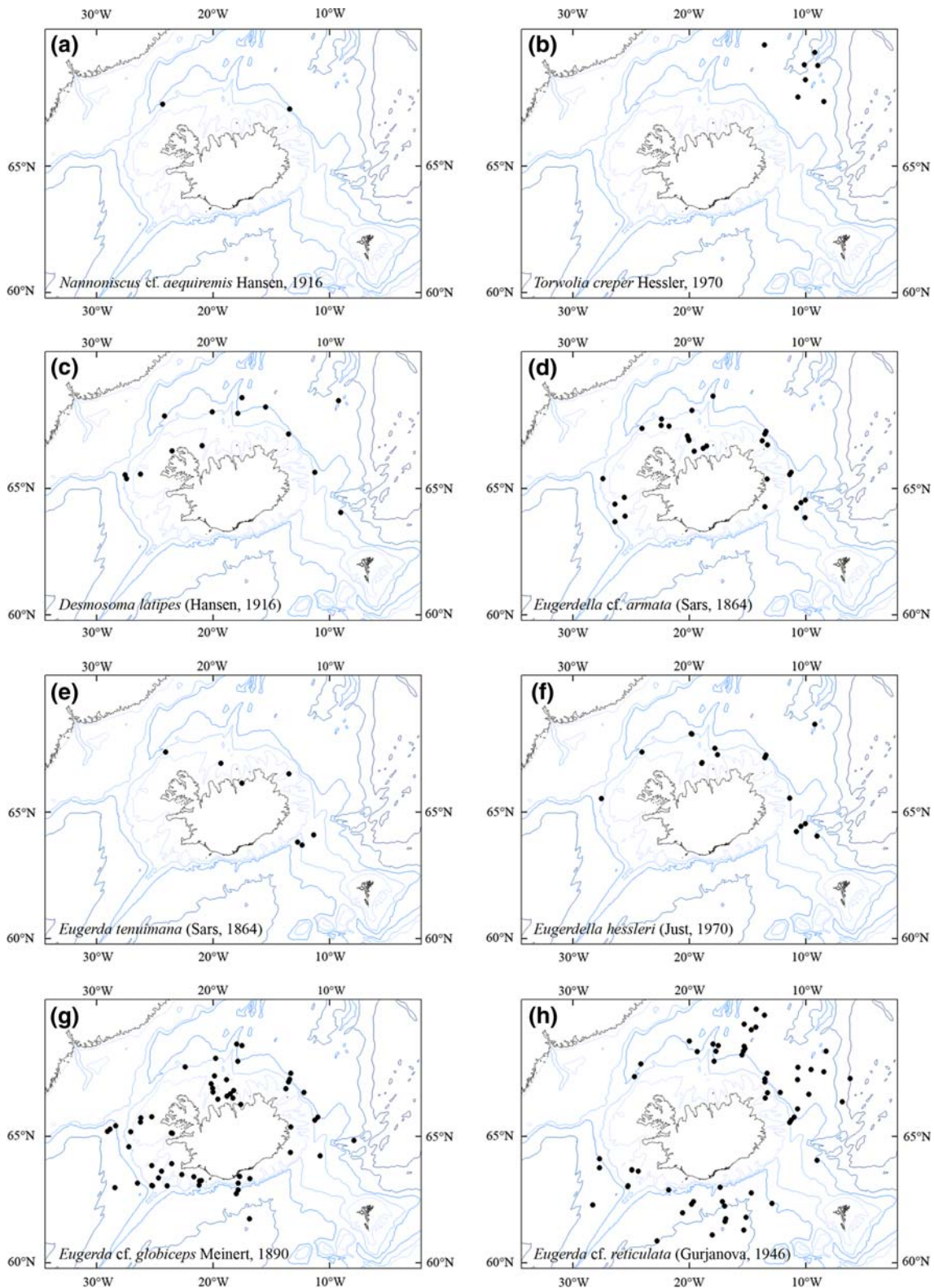


Fig. 4 Distribution of species in the sampling area. **a, b** northern species. **a** *Nannoniscus* cf. *aequiremis* Hansen, 1916; **b** *Torwolia creper* Hessler, 1970. **c–f** northern species with tendency to cross the Ridge southwards. **c** *Desmosoma latipes* (Hansen, 1916); **d** *Eugerdella* cf.

armata (Sars, 1864); **e** *Eugerda tenuimana* (Sars, 1864); **f** *Eugerdella hessleri* (Just, 1979). **g, h**, northern and southern species. **g** *Eugerda* cf. *globiceps* Meinert, 1890; **h** *Eugerda* cf. *reticulata* (Gurjanova, 1946)

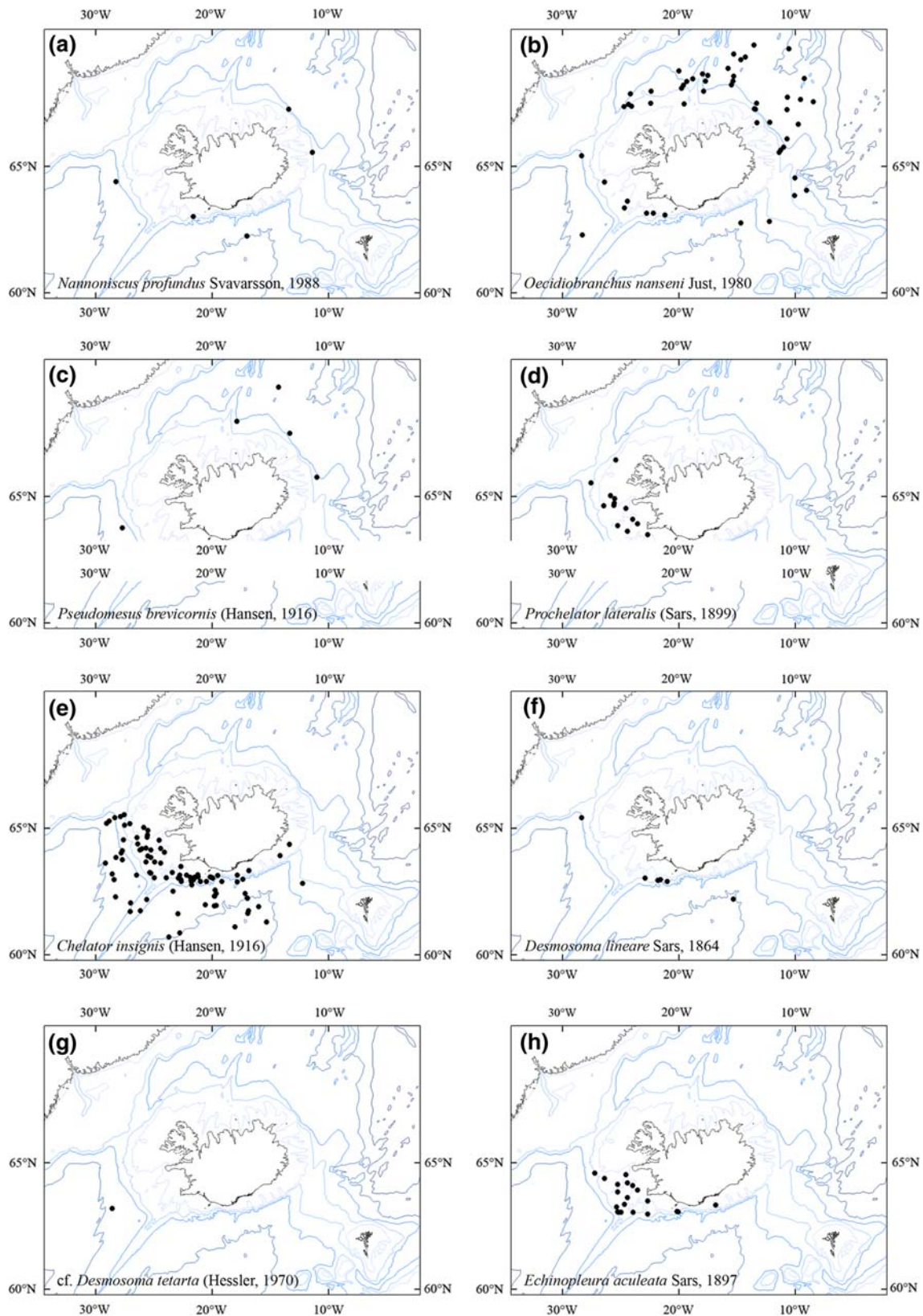


Fig. 5 Distribution of species in the sampling area. **a–c** Northern and southern species. **a** *Nannoniscus profundus* Svavarsson, 1988; **b** *Oecidiobranchius nansenii* Just, 1980; **c** *Pseudomesus brevicornis* (Hansen, 1916). **d** Southern species with tendency to cross the Ridge

northwards: *Prochelator lateralis* (Sars, 1899). **e–h** Southern species. **e** *Chelator insignis* (Hansen, 1916); **f** *Desmosoma lineare* Sars, 1864; **g** *cf. Desmosoma tetarta* (Hessler, 1970); **h** *Echinopleura aculeata* Sars, 1897

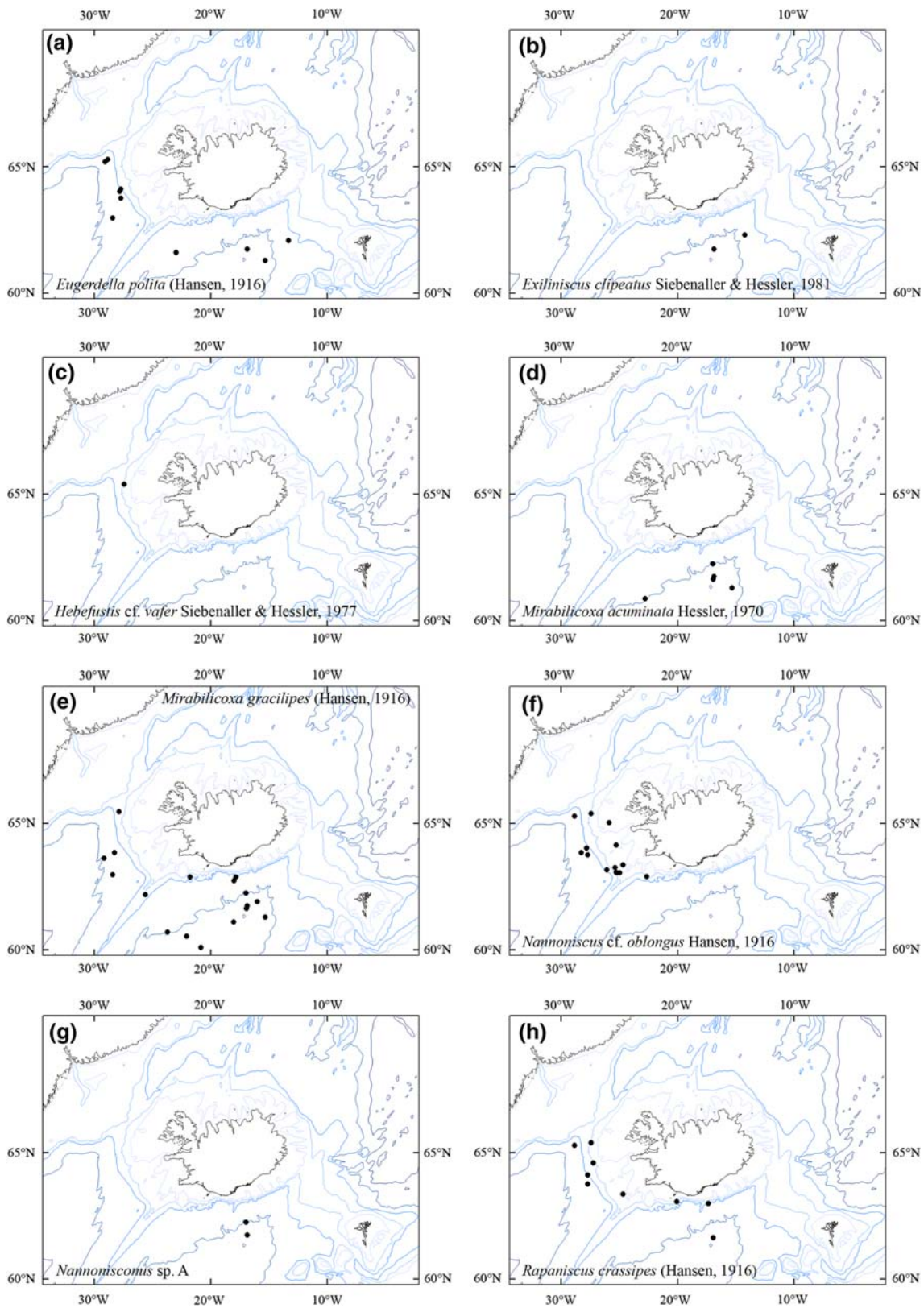


Fig. 6 Distribution of species in the sampling area. **a–h** southern species. **a** *Eugerdella polita* (Hansen, 1916); **b** *Exilinisca clipeatus* Siebenaller and Hessler, 1981; **c** *Hebefustis cf. vafer* Siebenaller and

Hessler, 1977; **d** *Mirabilicoxa acuminata* Hessler, 1970; **e** *Mirabilicoxa gracilipes* (Hansen, 1916); **f** *Nannoniscus cf. oblongus* Sars, 1870; **g** *Nannoniscus* sp. A; **h** *Rapaniscus crassipes* (Hansen, 1916)

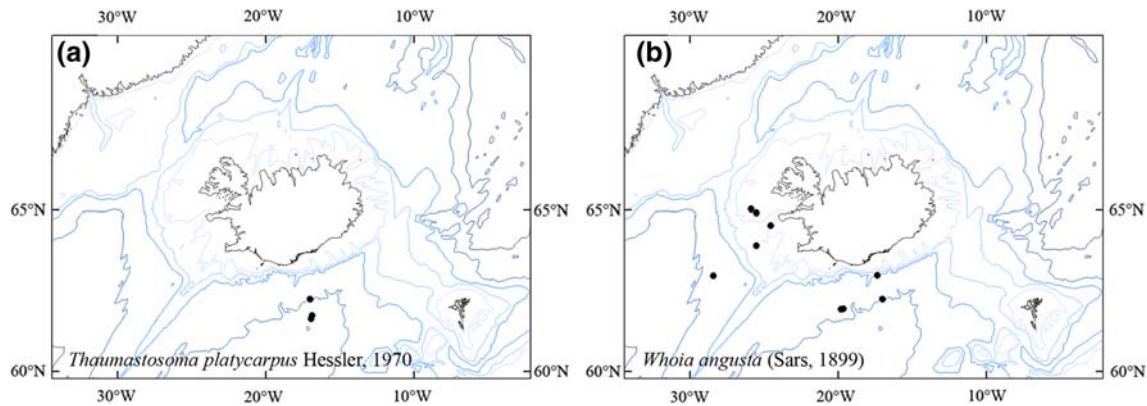


Fig. 7 Distribution of species in the sampling area. **a–b** Southern species. **a** *Thaumastosoma platycarpus* Hessler, 1970; **b** *Whoia angusta* (Sars, 1899)

Sampling and analysing

Samples were taken during the BIOICE project from 1991 to 2004. In total, 1,411 samples were collected with various instruments during the BIOICE cruises on the research vessels *Bjarni Sæmundsson*, *Håkon Mosby* and *Magnus Heina-son*. The present study is based on 223 samples taken with a modified Rothlisberg–Pearcy epibenthic sled (RP sled; Rothlisberg and Pearcy 1977; Brattegard and Fosså 1991) with 0.5 mm mesh in the cod end (Fig. 1; complete species by sample matrix is available as electronic supplement; ES1).

The samples were decanted through a series of sieves, the smallest mesh size being 0.5 mm. The specimens were then preserved in 10% buffered formalin and later transferred to 80% ethanol. Samples were sorted at the BIOICE facilities in Sandgerði where all specimens were sorted to family. The authors determined a total of 13,425 specimens of the Desmosomatidae and Nannoniscidae from 223 samples on species level. For species, which appeared to be similar, but not identical with the original description (holotype) of the species, a “cf.” was put in front of the species name. The term diversity refers here to ‘local diversity’ or ‘alpha diversity’.

Shipek grab samples were taken at some of the same station as the RP sled samples. These were analysed for sediment composition. The sediments were defined by the percentage of grain size (percentage of sand, muddy sand, sandy mud and gravel).

Maps were generated using ArcGIS 9.0. The Primer package (Clarke and Warwick 2001) version 6 was used for non-metric multidimensional scaling (nMDS) and cluster analysis to visualize faunal similarities. Abundance data were transformed by fourth root. Bray–Curtis similarity was used for the similarity matrix. Only species occurring at more than five stations were included in the data matrix. Four variables (Table 1) were analysed using BIOENV

(rank correlation method: Spearman, resemblance measure: D1 Euclidean distance) to measure which abiotic factor has the strongest influence (Clarke and Ainsworth 1993). Differences between groups (defined a priori), using permutation/randomisation methods on resemblance matrix was tested with a one way designed “analysis of similarities” (ANOSIM, Clarke and Warwick 2001). To compare differences between groups, data were analyzed using the chi-square test with the statistical software package Sigma Stat version 3.5.

Results

In total, 13,425 specimens of desmosomatid and nannoniscid isopods were collected on the 223 analysed stations. These have been assigned to 20 genera and 34 species (Table 2), 12 desmosomatid (*Chelator*, *Cryodesma*, *Desmosoma*, *Echinopleura*, *Eugerdella*, *Mirabilicoxa*, *Oecidiobrancus*, *Prochelator*, *Thaumastosoma*, *Torwolia* and *Whoia*) and 8 nannoniscid (*Austroniscus*, *Exilinisca*, *Hebefustes*, *Nannoniscoides*, *Nannonisconus*, *Nannoniscus*, *Pseudomesus* and *Rapaniscus*) genera.

The most common species was *Chelator insignis* comprising 6,100 specimens collected at 94 stations (i.e. 43% of the stations; Table 2). *Eugerdella reticulata* was the second most abundant species occurring at 63 stations (28.3% of the stations) with the total number of 1,943 specimens. The third and the fourth most frequently occurring species were *Eugerdella* cf. *globiceps* and *Oecidiobrancus nanseni*, occurring on 56 stations, respectively. Nine of the 34 species occurred at fewer than five stations, and three species occurred at a single station only. Most species were well represented and only five species had fewer than ten specimens each.

Nineteen species had a fairly wide depth range (>1,000 m, Table 2; Fig. 8). There was a tendency for a

Table 1 Result of the BIOENV analysis, correlations of the abiotic factors (1, sediment; 2, depth; 3, temperature; 4, salinity)

No. of variable	Correlations	Selections
3	0.983	2–4
2	0.899	3, 4
4	0.875	All
2	0.783	2, 3
3	0.779	1, 3, 4
3	0.699	1–3
2	0.687	2, 4
1	0.680	3
3	0.563	1, 2, 4
2	0.556	1, 3

wide bathymetric range in species with a wide geographic range, i.e. seen in species found at several stations. Twelve of the 19 species with a depth range of >1,000 m were found at ten or more stations (Fig. 8; Table 2).

Only a few ubiquitous species (occurring at ≥ 7 stations) were restricted to shallow water, i.e. *Echinopleura aculeata*, *Eugerdella tenuimana* and *Eugerdella* cf. *armata*. In all, 13 species occurred in relatively shallow waters (≤ 300 m) towards considerable depths (>1,000 m). Eight species occurred only at depths greater than 840 m, deeper than the deepest sill depth of the Ridge.

Distributional patterns

In all, ten species were only found north of the Ridge. Some of the species, e.g. *Austroniscus groenlandicus* (Fig. 3a) and *Austroniscus norbi* (Fig. 3b) occurred only in fairly shallow waters (347–552 and 539–831 m, respectively) north of Iceland, both in water masses typical of the intermediate and deeper waters (NSAIW and NSDW), but *A. groenlandicus* also occurred in the A/PW. Two species, i.e. *Hebefustis* sp. A (Fig. 3f) and *Nannoniscus* cf. *aequiremis* (Fig. 4a) were only rarely observed north of the Ridge, but at intermediate depths. The remaining six species occurred either in shallow or deep waters of the Nordic Seas, i.e. at temperatures between <0 and $<2.2^\circ\text{C}$ and were found in at least two types of water masses; *Cryodesma agnari* (Fig. 3c), *Desmosoma strombergi* (Fig. 3d), *Nannoniscoides angulatus* (Fig. 3g) and *Nannoniscus reticulatus* (Fig. 3h), or were restricted to deeper cold waters (NSDW only; $<0^\circ\text{C}$; *Exilinisca hanseni* 1,130–1,648 m; Fig. 3e; and *Torwolia creper*, 1,642–2,069 m; Fig. 4b). Despite that *E. hanseni* and *T. creper* both occurred in deep waters and both at the same temperatures, their distributions differed considerably. *E. hanseni* occurred only to the north of Iceland, while *T. creper* occurred only in the deep waters northeast of Iceland, i.e. the former in the Iceland Sea, while the latter in the Norwegian Sea.

The largest group of species (14) was restricted to the south of the Ridge. The most common species, *C. insignis* (Fig. 5e), was found in shallow and deep waters southeast, south and southwest of Iceland (Table 2). This species was restricted to the warm waters masses found south of the Ridge, i.e. MNAW, LSW and ISOW and only found at temperatures from 2.07 to 7.6°C . Despite being present considerably shallower (about 40 localities more shallow than 600 m) than the sill depth (620 m) of the Greenland–Iceland Ridge, the species does not enter the cold waters north of the Ridge. Four species followed quite a similar pattern, i.e. occurring from quite shallow (upper ranges at 163–296 m) to deep waters, but not passing the channels of the Ridge, i.e. *Nannoniscus* cf. *oblongus* (Fig. 6f), *Whoia angusta* (Fig. 7b), *Desmosoma lineare* (Fig. 5f) and *Rapaniscus crassipes* (Fig. 6h), all occurring at temperature $>2.3^\circ\text{C}$ in MNAW, ISOW or LSW. *E. aculeata* (Fig. 5h) occurred only at shallow depths mainly southwest of Iceland between 200 and 300 m, with occasional findings from 136–778 m, at temperatures above 5.5°C and only in MNAW.

Several species occurred in deep water south and southwest of the Ridge and all but *Mirabilicoxa gracilipes* (upper limits 769 m; Fig. 6e) below the maximum sill depth of the GIF Ridge, i.e. 840 m), i.e. *Eugerdella polita* (Fig. 6a), *Exilinisca clipeatus* (Fig. 6b), cf. *Desmosoma tetarta* (Fig. 5g), *Mirabilicoxa acuminata* (Fig. 6d), *Nannoniscus* sp. A (Fig. 6g), and *Thaumastosoma platycarpus* (Fig. 7a). Some of these species did not occur often in the samples, such as *D. tetarta*. *M. gracilipes* and *E. polita* occurred in all three water masses south of the Ridge (MNAW, LSW, ISOW), while the other species occurred in either ISOW or LSW.

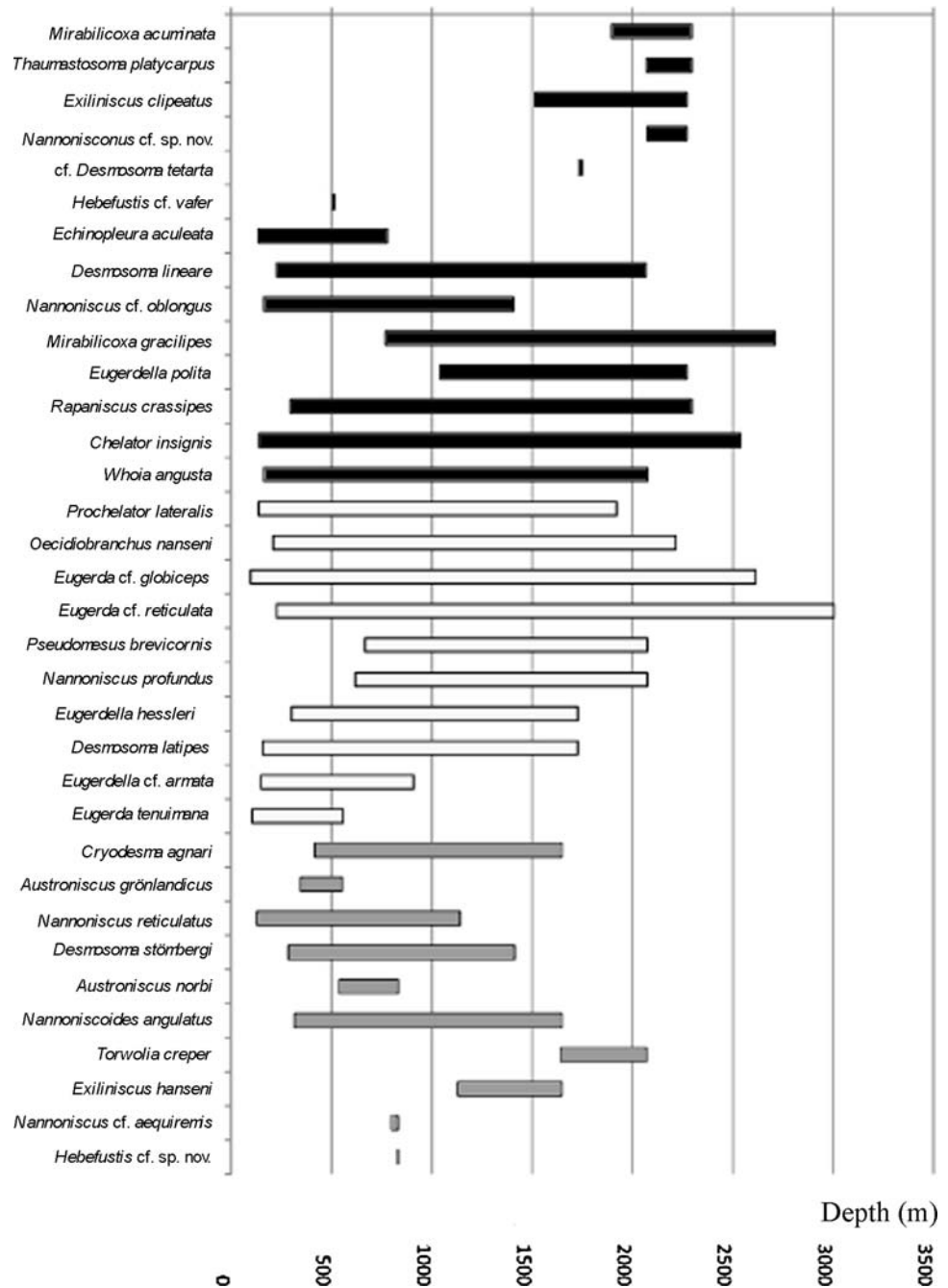
Among the species occurring only to the south of the Ridge, patterns in the regional distribution differed. *N. oblongus* differed from other species in this group by occurring only to the west of the deep Reykjanes Ridge. On the other hand, *M. acuminata* and *T. platycarpus* occurred only to the east of the Reykjanes Ridge.

Only three species, i.e. *Eugerdella* cf. *globiceps* (Fig. 4g), *E. reticulata* (Fig. 4h) and *O. nanseni* (Fig. 5b) were commonly found both north and south of the GIF Ridge. All of them had a wide bathymetrical distribution both north and south of the Ridge and occurred accordingly at a wide range of temperatures (*Eugerdella* cf. *globiceps*, north: 97–2,613 m, south: 120–2,270 m, -0.86 to 8.04°C ; *O. nanseni*, north: 209–1,558 m, south: 317–2,215 m, -0.86 to 7.12°C ; *E. reticulata*, north: 227–3,003 m, south: 544–2,295 m, -0.9 to 4.57°C ; Fig. 8) and in all seven water masses (i.e. MNAW, LSW, ISOW, MEIW, A/PW, NSAIW and NSDW). No significant differences ($p > 0.05$) were found in the depth occurrences of these common species (occurrences at stations shallower than 350 m compared to

Table 2 List of desmosomatid and nannoniscid species occurring in the area, including information about the number of stations, number of specimens, minimum and maximum depth (m), minimum and maximum temperature (°C) and water masses (Modified North Atlantic Waters *MNAW*; Labrador Sea Water *LSW*; Iceland Sea Overflow Water *ISOW*; Modified East Icelandic Water *MEIW*; Norwegian Sea Deep Water *NSDW*; Norwegian Sea Arctic Intermediate Water *NSAIW*; Arctic/Polar Water *A/PW* and Coastal Water *CW*)

Species	No. of stations	No. of individuals	Min. depth (m)	Max. depth (m)	Area	Min. temp. (°C)	Max. temp. (°C)	Water masse(s)
Desmosomatidae								
<i>Desmosoma latipes</i> (Hansen, 1916)	14	48	157	1,727	N(S)	-0.82	6.66	MNAW, A/PW, NSAIW, NSDW
<i>Desmosoma lineare</i> Sars, 1864	7	31	227	2,067	S	2.78	6.74	MNAW, ISOW, MEIW
<i>Desmosoma tetarta</i> (Hessler, 1970)	1	9	1,744		S		3.7	LSW
<i>Desmosoma strombergi</i> Svavarsson, 1988	31	662	284	1,413	N	-0.86	2.11	MEIW, A/PW, NSAIW, NSDW
<i>Chelator insignis</i> (Hansen, 1916)	94	6,100	139	2,537	S	2.07	7.60	MNAW, LSW, ISOW
<i>Cryodesma agnari</i> Svavarsson, 1988	13	85	417	1,648	N	-0.78	0.58	A/PW, NSAIW, NSDW
<i>Echinopleura aculeata</i> Sars, 1897	20	180	136	778	S	5.50	7.30	MNAW
<i>Eugerda</i> cf. <i>reticulata</i> (Gurjanova, 1946)	63	1,943	227	3,003	NS	-0.9	4.57	MNAW, LSW, ISOW MEIW, A/PW, NSAIW, NSDW
<i>Eugerda</i> cf. <i>globiceps</i> Meinert, 1890	56	508	97	2,613	NS	-0.86	8.04	MNAW, LSW, ISOW MEIW, A/PW, NSAIW, NSDW
<i>Eugerda tenuimana</i> (Sars, 1864)	7	30	104	558	N(S)	-0.47	5.4	MNAW, MEIW, NSAIW, CW
<i>Eugerdella</i> cf. <i>armata</i> (Sars, 1864)	32	491	149	910	N(S)	-0.57	7.48	MNAW, MEIW, A/PW, NSAIW, NSDW
<i>Eugerdella hessleri</i> Just, 1970	16	85	300	1,727	N(S)	-0.82	5.97	MNAW, A/PW, NSAIW, NSDW
<i>Eugerdella polita</i> (Hansen, 1916)	9	40	1,042	2,270	S	2.37	4.2	MNAW, LSW, ISOW
<i>Mirabilicoxa acuminata</i> Hessler, 1970	5	20	1,897	2,295	S	2.34	3.29	ISOW
<i>Mirabilicoxa gracilipes</i> (Hansen, 1916)	17	247	769	2,709	S	2.07	6.5	MNAW, LSW, ISOW
<i>Oecidiobranthus nanseni</i> Just, 1980	55	1,125	209	2,215	NS	-0.86	7.12	MNAW, LSW, ISOW MEIW, A/PW, NSAIW, NSDW
<i>Prochelator lateralis</i> (Sars, 1899)	19	39	136	1,921	(N)S	2.93	7.3	MNAW, ISOW
<i>Torwolia creper</i> Hessler, 1970	7	24	1,642	2,069	N	-0.8	-0.84	NSDW
<i>Whoia angusta</i> (Sars, 1899)	9	28	163	2,074	S	2.34	7.43	MNAW, LSW, ISOW
Nannoniscidae								
<i>Austroniscus groenlandicus</i> (Hansen, 1916)	4	140	347	552	N	-0.54	1.41	A/PW, NSAIW, NSDW
<i>Austroniscus norbi</i> Svavarsson, 1988	2	10	539	831	N	-0.44	0.55	NSAIW, NSDW
<i>Exilinisca clipeatus</i> Siebenaller & Hessler, 1981	2	2	1,514	2,270	S	2.37	2.57	ISOW
<i>Exilinisca hansenii</i> Just, 1970	6	32	1,130	1,648	N	-0.52	-0.78	NSDW
<i>Hebefustis</i> cf. sp. nov.	1	2	831		N		-0.55	NSDW
<i>Hebefustis</i> cf. <i>vafer</i> Siebenaller & Hessler, 1977	1	1	513		S		6.24	MNAW
<i>Nannoniscus</i> cf. <i>oblongus</i> Hansen, 1920	14	146	163	1,407	S	3.71	6.97	MNAW, LSW
<i>Nannoniscus reticulatus</i> Hansen, 1916	12	801	129	1,141	N	-0.58	2.8	MEIW, A/PW, NSAIW, NSDW
<i>Nannoniscus profundus</i> Svavarsson, 1988	5	29	619	2,074	NS	-0.36	6.09	MNAW, LSW, ISOW, NSAIW, NSDW
<i>Nannoniscus</i> cf. <i>aequiremis</i> Hansen, 1916	2	25	800	831	N	-0.53	-0.55	NSDW
<i>Nannoniscoides angulatus</i> Hansen, 1916	9	455	317	1,648	N	-0.76	1.41	NSAIW, NSDW
<i>Nannonisconus</i> cf. sp. nov.	2	2	2,074	2,270	S	2.34	2.37	ISOW
<i>Pseudomesus brevicornis</i> (Hansen, 1916)	7	36	666	2,074	NS	-0.8	6.09	MNAW, LSW, ISOW, NSAIW, NSDW
<i>Rapaniscus crassipes</i> (Hansen, 1916)	9	32	296	2,295	S	2.60	6.92	MNAW, LSW, ISOW
<i>Thaumastosoma platycarpus</i> Hessler, 1970	3	12	2,070	2,295	S	2.34	2.60	ISOW

Fig. 8 Bathymetric range of individual species. *Filled bars* southern species, *open bars* northern and southern circum-micelandic species, *gray bars* northern species



occurrences at stations >350 m). In addition, *Nannoniscus profundus* (Fig. 5a) and *Pseudomesus brevicornis* (Fig. 5c) were found at both sides of the Ridge, but only at a few or several deep locations (Fig. 8).

A few species were found on both sides of the GIF Ridge, but in different patterns. *Desmosoma latipes* (Fig. 4c), *Eugerdella armata* (Fig. 4d) and *Eugerdella hessleri* (Fig. 4f) had most of their sites north of the Ridge. All these species were found from shallow to intermediate or deep waters, i.e. *Eugerdella* cf. *armata* at 149–910 m, *D. latipes* at 157–1,727 m and *E. hessleri* at 300–1,727 m

and occurred accordingly in several water masses and at considerable temperature range (<0 to $\geq 6^{\circ}\text{C}$). *E. tenuimana* (Fig. 4e) was mainly found at the northern side of the Greenland–Iceland Ridge, but with additional localities south of the Iceland–Faeroe Ridge. This is a species occurring in quite shallow waters (104–558 m), but at a fairly wide temperature range (–0.47 to 5.4°C) and in four water masses. *Prochelator lateralis* (Fig. 5d) was mainly found south of the Ridge, but stretching into cold waters having been found at one location northwest of Iceland and to the north of the Greenland–Iceland Ridge.

Temperature ranges and water masses

Most of the species occurred in more than a single water mass. Only 11 species were restricted to single water mass (Table 2). Several of these were, however, found at only a few locations. Only four of the species found at more than four stations were restricted to single water mass, i.e. *T. creper* and *E. hanseni* in NSDW, *M. acuminata* in ISOW and *E. aculeata* in MNAW.

Some species occurred in several water masses. Most often, individual species occurred in water masses that were similar in temperature and salinity. In all, 15 species were “warm water species” occurring either in a single warm water mass or combinations of either one or two warm water masses (i.e. MNAW, LSW or ISOW) with temperatures above 2°C, some at a narrow range (range about 2°C), while others had a fairly wide range (range about 5°C). The occurrence of species depending on temperature (°C) in water mass was tested for warm (>3°C) and cold (<3°C). The test showed that the two groups were not significantly related ($p = 0.647$).

Despite the fact that the ISOW is formed north of the Ridge, its temperatures are above zero. Four species occurred in this water mass only (*E. clipeatus*, *M. acuminata*, *Nannoniscus* sp. and *T. platycarpus*), while seven species occurred in combinations of MNAW, LSW and ISOW (temperatures >2.07°C), and five species occurred in a ISOW as well as warm and cold water masses.

Only eight species were confined to purely arctic water masses (A/PW, NSAIW or NSDW) ranging in temperatures from <0°C to maximally 1.41°C. Of these only four species were restricted to temperatures below 0°C (*E. hanseni*, *Hebefustis* sp. A, *Nannoniscus* cf. *aequiremis* and *T. creper*). All four species occurred in the deep Nordic Seas.

Patterns of species composition

The MDS plot distinguished the northern stations and the southern stations (Fig. 9a). The MDS plot did further distinguish the stations with warm water masses from the stations with cold water masses (Fig. 9b). The ANOSIM analysis revealed that the regions north and south of the Ridge were different from each other (Global $R = 0.44$, $p < 0.001$) and that stations with cold and warm temperatures were different from each other (Global $R = 0.474$, $p < 0.001$). Individual water masses were, however, poorly distinguished from each other in the MDS plot. Depth and sediment types were not found to be important in explaining observed patterns. A few stations located both north and south of the Ridge were distinguished in both plots from the bulk of the stations (Fig. 9a, b). These stations are located at various depths and with different water masses, i.e. NSDW, MNAW or CW. Four stations were northern stations below

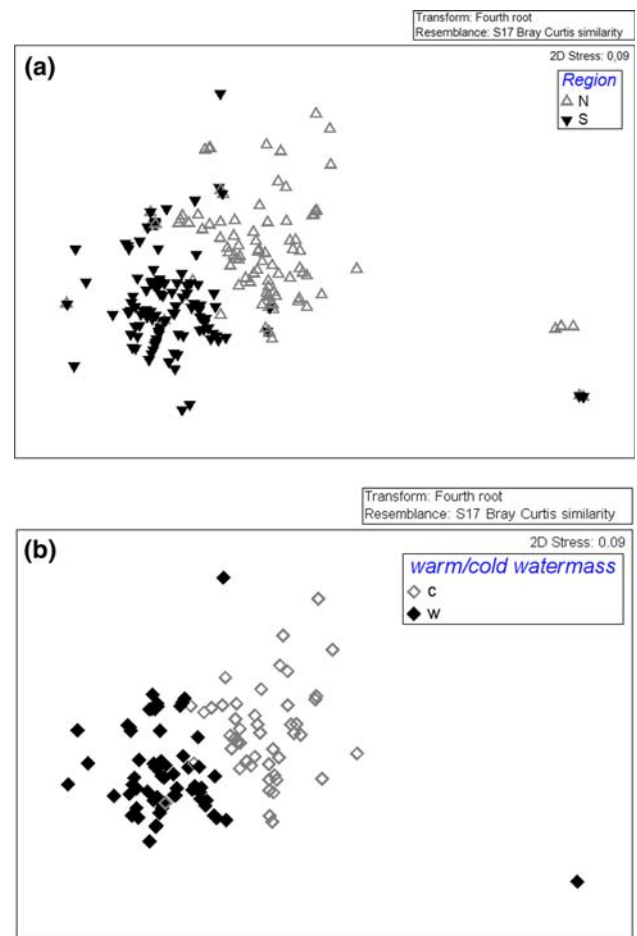


Fig. 9 Multivariate analyses of the species composition of all sites: Two-dimensional MDS configuration based on Bray–Curtis similarities. **a** Species abundance plotted with the factor of the region; **b** species abundance plotted with the factor water mass

1,844 m and the deepest one being at 2,069 m in NSDW. Stations with MNAW were at depths of 425 and 558 m, and the station with CW was at 104 m depth.

Species richness patterns

The number of desmosomatid and nannoniscid species collected varied considerably (by an order of magnitude) between samples, ranging from one to 12 species per sample. The patterns in number of species per sled with increasing depth differed considerably between the areas north and south of the Ridge (Fig. 10). North of the Ridge the number of species ranged from one to 12, with several stations having ≥ 6 species at the depth range from about 300 to about 1,700 m. Below 1,800 m only a single species occurred at each of the stations. South of the Ridge, species numbers were similar at all depths, while the two stations with the highest species richness occurred at depths below 2,000 m.

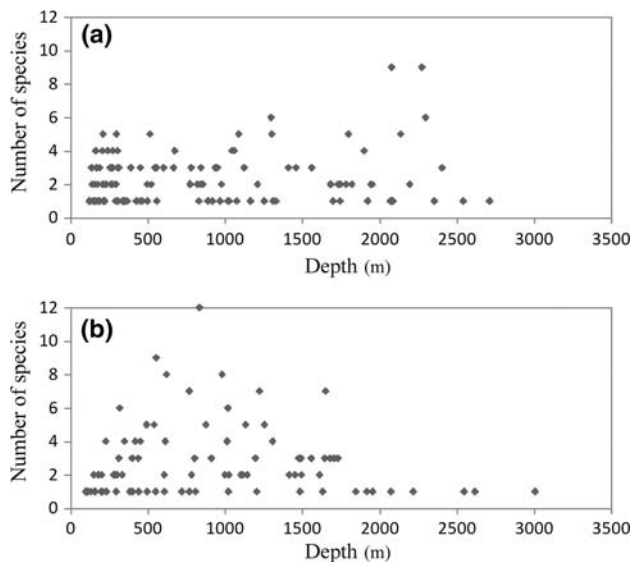


Fig. 10 Number of species with depth (m). **a** South of the GIF Ridge; **b** north of the GIF Ridge

Discussion

The Nordic Seas and the Arctic Ocean are in a way semi-isolated from other oceans. Only the shallow Bering Strait connects the Arctic Ocean and the North Pacific, while the shallow GIF Ridge separates the deep basins of the Nordic Seas and the Arctic Ocean from the North Atlantic proper. The topographical evolution of the GIF Ridge is related to the development of the oceanic circulation of the North Atlantic (Bott 1983). Today, the GIF Ridge plays a decisive role in separating water masses of different climatological origin: the Atlantic waters with high salinities and high temperatures and the Polar waters with low temperatures and low salinities (Meincke 1983; Hansen and Østerhus 2000). The GIF Ridge was formed in the time interval 57–16 m.y. ago (Larsen 1983), the youngest part being at the spreading axis through Iceland (Bott 1983). In times of a lower sea level, the western part of the GIF Ridge was apparently a continuous land bridge and has probably interrupted the water exchange between the Atlantic proper and the Nordic Seas (Thiede 1983; Larsen 1983). The Iceland–Faeroe Ridge has probably subsided below sea level 24–14 m.y. ago (Berggren and Schnitker 1983).

The Nordic Seas and the Arctic Ocean have undergone large changes in the temperatures, changing from fairly high temperatures in the past to cold waters at the beginning of the glaciations 2.5 m.y. ago. The structure and the development of the GIF Ridge may explain the patterns observed today for the isopod fauna around Iceland. The pattern seen may partly be historical and partly due to present ecological conditions. The northernmost part of the

North Atlantic and the Nordic Seas, where the Atlantic proper meets the Nordic Seas and the Arctic Ocean, holds a diverse component of the desmosomatid and nannoniscid isopods, with an even dispersal of the species. This may indicate that the distributional pattern of the species around Iceland is more due to present ecological conditions rather than historical events. The deep water basins of the Nordic Seas and the Arctic Ocean may, have been strongly influenced by glaciations during the last few million years (Dahl 1972). Indeed one of the strongest signals in these and other data is the considerable drop in diversity with increasing depth north of the GIF Ridge, whereas south of it and elsewhere in the open Atlantic (Svavarsson 1997; Wilson 1998). Bouchet and Warén (1979) concluded though that a part of the molluscs fauna of the Norwegian Sea was a reminiscence of the old Pacific fauna that lived in the Polar Basin before it was disconnected from the North Pacific by the formation of the Bering Strait.

Pronounced differences were seen in the distributions of the isopods in the area, and most of the species were restricted either to the cold waters north of the Ridge or to the warm waters south of the GIF Ridge. This indicates that the distributions are not only shaped by the temperature (ANOSIM: R 0.474, p 0.001), also by the actual presence of the Ridge itself (ANOSIM: Global R 0.44, p 0.001). This is supported by the fact that several of the species occur shallower than the actual sill depths of the Ridge and could pass the Ridge if the temperatures were suitable. Therefore, the physical presence of the Ridge itself may act secondarily as barrier, having though in mind that the Ridge shapes the temperatures of the area. Similar argumentation has been provided for the isopod *Astacilla boreaphilis* Stransky and Svavarsson 2006, which occurs only in the waters to the south of the Ridge, but the species occurs considerably shallower than the sill depths of the Ridge (Stransky and Svavarsson 2006). Numerous other studies have shown pronounced limits in species distributions at the Ridge (e.g. Negoescu and Svavarsson 1997; Gudmundsson 1998; Weissshappel 2000, 2001; Dijkstra et al. 2009).

Most of the isopod species occurred in several water masses, and only a few common species were restricted to single water mass. The physical differences between several of the water masses are quite small and even though occurring in more than one water mass, a species may be adapted to a narrow range of temperatures as the small differences are not sufficient to limit distributions. Most species were, however, restricted to either cold or warm water masses, while a few species, i.e. the species occurring on both sides of the Ridge, were able to deal with a wide range of temperatures. The presence of cryptic species cannot be excluded for such species occurring within so wide ranges of temperatures, e.g. *Eugerda* cf. *globiceps* and *O. nanseni*.

Differences were observed in the distribution of several species within the Nordic Seas (e.g. *E. hanseni* vs. *T. creper*) and for some species in the Atlantic proper (e.g. *M. acuminata* vs. *Nannoniscus* cf. *oblongus*). These differences are most likely due to ecological conditions, other than the temperature. Sediment had not much influence on the distributions (BIOENV analysis). Weisshappel and Svavarsson (1998) showed that the sediment structure shaped the distribution of amphipods only when the temperature was excluded. Other plausible explanations for these differences are differences in the food supply, competition, disturbance, etc., which can act at local scales (Gray 1974; Pearson and Rosenberg 1987; Thrush et al. 2005).

With most of the species occurring to the south of the Ridge, the desmosomatids and nannoniscids are similar to most other studied groups in the area, showing the same pattern, e.g. anthurid isopods (Negoescu and Svavarsson 1997) and eusirid amphipods (Weisshappel 2000). Calliopiid amphipods have, however, a different pattern with most of their species occurring to the north of the Ridge (Weisshappel 2001).

A low regional diversity has been demonstrated for several groups of invertebrates, e.g. echinoderms (Sibuet 1979) and molluscs (Bouchet and Warén 1979), of the Arctic deep water. A low regional diversity has previously been shown for the asellote isopods of the deep Arctic Ocean (Gurjanova 1938) and the deep Nordic Seas (Svavarsson et al. 1990; Svavarsson 1997). The low diversity of the deep waters of the Nordic Seas has been partly explained due to the presence of the Ridge itself, i.e. isolation of the deep basins of the Nordic Seas and the Arctic Ocean from the basins of the North Atlantic (e.g. Svavarsson et al. 1993; Rex et al. 1993, 2000; Wilson 1998).

This is based on the argument that various groups of invertebrates are differently represented in the Nordic Seas/Arctic Ocean and the North Atlantic south of the Ridge (Svavarsson et al. 1993). Despite being a deep-sea family the Desmosomatidae has a fair amount of their known species (46) occurring in the Nordic Seas. However, some of the other deep-sea asellote isopod families seem to have much lesser representation in the Nordic Seas, despite being species rich just south of the Ridge. Only two species of the Haploniscidae, a family with over 100 known species worldwide, occur in the Nordic Seas (Svavarsson et al. 1993) while several species of this family were collected at the RP sledge stations on the GIF Ridge during the BIOICE project. The highest number of haploniscid specimens per station collected was 4,259 specimens of *Haploniscus bicuspis* (Sars 1877) (BIOICE station 2014, North of Iceland). However, this may not fully explain the low diversity and a lack of adaptation towards subzero temperatures needs to be addressed.

A decline in diversity with depth has been shown for asellote isopods in the eastern and western part of the Nordic Seas (Svavarsson et al. 1990; Svavarsson 1997). In the present study, the pattern seen in species richness differed considerably between the areas south and north of the Ridge. North of the Ridge the highest numbers of species per station (5–12 species/sled) were at shallow and intermediate depths (around 300 to >1,600 m) and the species richest stations were either in shallow warm (>0°C) or intermediate cold (−0.51 to −0.76°C) waters. Below depths of around 1,700 m only a single species occurred per station north of the Ridge. Similar pattern (high diversity at cold temperatures, but low diversity in the basins of the Arctic Ocean and the Nordic Seas) has also been shown for the amphipods (Weisshappel 2000, 2001). Renaud et al. (2006) found, however, no changes in nematode diversity with depth in the central Arctic Ocean. As fairly high diversity occurs at those cold temperatures, this implies that the low regional diversity of the deep Arctic Ocean and the Nordic Seas may not be caused by a lack of adaptations to subzero temperatures. Extinction events in the past may play a role and other environmental factors, such as food availability, may shape the diversity patterns.

Interestingly, few species that occur on the Norwegian coast, e.g. *N. oblongus* and *R. crassipes*, are found only on the Atlantic side of Iceland. These species are shallow water species which are also recorded from the Greenland shelf. In the case of *N. oblongus*, we speak of a species with a wide distribution from Greenland over the south of Iceland, the Faroes, the southern part of Norway to the northern part of Norway. Most probably temperature is the limit for distribution at the GIF Ridge while the coastal waters in Norway offer the species good conditions.

In all, 13 species occurred between relatively shallow waters (≤ 300 m) and considerable depths (>1,000 m). Only a few ubiquitous species, i.e. *E. aculeata*, *E. tenuimana* and *Eugerdella* cf. *armata*, were restricted to shallow water while eight species occurred only at depths greater than 840 m. While shallow waters were more frequently sampled than the deep waters and thus shallow water species seem to be ubiquitous, they are actually no more common than species in deep waters.

Some desmosomatid species occur in bathyal waters south-east of the Greenland–Iceland–Faeroe Ridge although being usually found in shallower waters in other subarctic regions. The circumciclandic species *Eugerdella* cf. *globiceps* extends deeper north of the Ridge as well as *E. reticulata* and *O. nanseni*. For these three circumciclandic species (showing a wide bathymetric range and occurring at more than 50 stations) it was tested if there is no difference of occurrence in depth (“shallow” <350 m; “deep” >350 m). No difference was found. Although bathymetrical distribution of water masses and hence temperature may differ

considerably within the Arctic Ocean and the Nordic Seas and hence lead to shallow occurrences of a species in some areas but deeper occurrences of the same species in other areas, this is not the case for *Eugerdella* cf. *globiceps*, *E. reticulata* and *O. nanseni*.

In the deep-sea basins south of Iceland, i.e. the North Atlantic proper, species were found that were recorded by Hessler (1970a) and Siebenaller and Hessler (1977, 1981) from the Bermuda Transect (in the Irminger Basin *D. tetarta* and *Hebefustis* cf. *vafer*; in the Iceland Basin *E. clipeatus*, *M. acuminata*, *Nannonisconus* cf. sp. nov. and *T. platycarpus*), indicating that some of the species having their northern limits of distribution at the GIF Ridge may extend their distribution far south. Meland and Brattegard (2007) found mysid species south of Iceland previously reported from the Antarctic and close resemblance of Antarctic and North Atlantic species. Such wide distribution raises a question of presence of cryptic species. Brökeland and Raupach (2008) showed for species of Haploniscidae that genetic distances in mitochondrial markers go along with morphological characters in a complex of sibling species.

In particular, the observation above suggests that the ecological differences between the Atlantic and Arctic sectors may be influencing the distributions. Answering the questions from the beginning, we can conclude:

Most isopod species around Iceland are restricted to water masses of a certain temperature and salinity. The topography of the GIF Ridge does not shape the distribution of asellote isopods as much as the abiotic factors temperature and salinity. Sediment or depth were not found to limit the species distribution in the area.

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