Distributional patterns of isopods (Crustacea) in Icelandic and adjacent waters

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Distributional patterns of isopods (Crustacea) in Icelandic and adjacent waters

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Abstract

Since the 1990s, the marine benthos of the Greenland–Iceland–Faeroe (GIF) Ridge has been sampled through the BIOICE (Benthic Invertebrates of Icelandic waters) and subsequent IceAGE (Icelandic Marine Animals: Genetics and Ecology) projects. Isopod crustaceans formed one of the prominent macrofaunal groups. Most isopod families occurred on both sides of the ridge, but showed side-specific abundance patterns reflecting known distribution from the literature. Our results from 35,536 isopod specimens from 55 epibenthic sled stations show a depth pattern at the family level indicating typical shallow water families like, for example, Paramunnidae or typical deep-water families like, for example, Haploniscidae and Ischnomesidae, while other families did not show a clear depth trend. We hypothesize that the ridge influences the distribution of the families through its effects on the hydrography and sediment characteristics. Total organic carbon (TOC) and mud content significantly explained isopod family distributions, possibly reflecting different habitat use and lifestyle (e.g., infaunal, epifaunal). Our analysis of a subset of 27 selected BIOICE and IceAGE stations and 100 isopod species (22,574 specimens), mostly covering the upper 1000 m depths between Iceland and Norway along the Iceland–Faeroe Ridge (IFR), resulted in four main species assemblages differing in species diversity. Whereas north of the IFR, we found 76 species; south of the IFR, we found 52 species; 40 species occurred both north and south of the IFR. Although the subset of selected stations is limited to a comparably small portion of the IceAGE sampling grid and to a comparably restricted depth range of the upper 1000 m, our result shows the slope area of Northeast Iceland and around the Faeroes and the Norwegian Channel with the highest number of species, especially stations in the thermocline between 400 and 800 m depth, where we observed the turnover from shallow to deep-water faunal elements.

Keywords Subpolar · Benthos · Isopoda · Depth · Gradient · Thermocline · Diversity · Biogeography

Introduction

Unique environmental conditions render the oceanic waters around the Greenland–Iceland–Faeroe Ridge (GIF Ridge; also termed the GIS Ridge, Greenland–Iceland–Scotland Ridge) in the northernmost Atlantic and the European Northern Seas, an interesting region for studies of biogeography, ecology, genetics, and evolution of the Arctic and subarctic marine fauna. This shallow ridge extends across the North Atlantic in an east-west direction and is the only significant east-west ridge

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crossing the Atlantic Ocean. It separates the deep oceanic basins (> 4000 m) of the Nordic Seas (Greenland, Iceland, and Norwegian Seas) and the Arctic Ocean (collectively often termed the Arctic Mediterranean) from the North Atlantic proper. It has a mean depth of less than 500 m and the deepest sill depth at 840 m between the Faeroe Islands and Scotland (Hansen and Østerhus 2000).

The region is unique in having a diverse and complicated hydrography with at least seven primary water masses, i.e., water bodies with characteristic temperatures, salinities, and densities, often overlying each other (Stefánsson 1962; Hansen and Østerhus 2000) and various currents (see figure 1 in Schnurr et al. 2014 for currents). A sharp gradient is seen in the temperatures from − 0.9 (north) to 12 °C (south) and in bottom temperatures with increasing depths (Jochumsen et al. 2016). Extensive exchange of water masses occurs through the channels of the ridge. Warm and saline Atlantic water (> 5 °C, > 35.1 ppm) flows in near-surface layers northwards over the ridge (Hansen and Østerhus 2000; Jochumsen et al. 2015, 2016). This transport of heat into the northern regions is mainly responsible for comparatively high surface temperatures in the seas north of the ridge, as waters at similar latitudes are usually much colder. From the Nordic Seas, cold (< 0 °C) and low-saline (< 34.9 ppm) waters return southwards partly as near-surface layers near Greenland and partly in deeper waters overflowing the ridge.

There is increasing evidence that the GIF Ridge, as a physical barrier, has a significant impact on the distributions of the marine, benthic fauna in the region (e.g., Svavarsson et al. 1993; Brix and Svavarsson 2010; Stransky and Svavarsson 2010). Abiotic factors (e.g., depth, temperature, salinity, sedimentary characteristics) are important variables to explain faunal distributions in Icelandic waters (Brix and Svavarsson 2010; Meißner et al. 2014); the ridge also influences these parameters.

Exploration of the marine fauna of Icelandic and adjacent waters dates back to the Danish Ingolf Expedition, which sampled the waters around Iceland, the Faeroe Islands, and parts of Greenland during the summers of 1895 and 1896 (Wandel 1899). The BIOFAR (Biology of the Faeroes) project in the late 1970s (Nørrevang et al. 1994) and the BIOICE (Benthic Invertebrates of Icelandic waters) project 1992–2004 extensively augmented knowledge of the benthic fauna. The aim of BIOICE was to investigate the faunal composition and species distributions around Iceland. The IceAGE (Icelandic marine Animals: Genetics and Ecology) project was a follow-up of BIOICE with the objectives of enhancing the understanding of the ecosystems around Iceland, combining classical taxonomic methods with modern approaches of biodiversity research (Brix et al. 2012, 2013, 2014), like DNA barcoding (Jażdżewska et al. 2018; Riehl et al. 2014a). The first IceAGE expedition in August and September 2011 on board the RV *Meteor* (Cruise M85/3, IceAGE1) sampled the northernmost part of the North Atlantic

Ocean and the southwestern part of the Nordic Seas, while the RV *Poseidon* (POS456, IceAGE2) sampled the Iceland–Faeroe Ridge in 2013 (Fig. 1). In total, the stations of both expeditions are partitioned into several depth transects (named during the expeditions following our sampling design): Denmark Strait (DS), Iceland Basin (IceB), Irminger Basin (IrmB), Norwegian Sea (NS), Faeroe–Shetland Channel (FSC), Iceland–Faeroe Ridge (IFR), and the Norwegian Channel (NC).

Isopoda Latreille, 1817 is a diverse order of peracarid crustaceans with a worldwide distribution. There are over 10,000 described species (Ahyong et al. 2011) with marine, freshwater, brackish water, and terrestrial forms (Naylor 1972). Most isopods are small epibenthic marine species. Among those, Asellota Latreille et al., 1802 is the most common isopod taxon of the deep-sea fauna and the most species-rich isopod group in the region (Svavarsson 1997). Asellotes comprise diverse forms, e.g., extended stick-like animals (Ischnomesidae Hansen, 1916), acanthous species (e.g., Acanthaspidiidae Menzies, 1962; Janirellidae Menzies, 1956, Mesosignidae Schultz, 1969), burrowing dozer-like animals (e.g., Hansen, 1916, Hansen, 1916), and secondarily highly modified swimmers within the Lilljeborg, 1864. One of the main characteristics of peracarid crustaceans is that they are brooders and for the most part do not have planktonic larvae. Marine asellote isopods are probably either detritus feeders (Wolff 1962) or feed on foraminiferans and other protists (Guðmundsson et al. 2000; Brökeland et al. 2010; Riehl et al. 2016). In shallower waters, non-asellotan isopods in particular also form an important component of the benthos (Poore and Bruce 2012). However, their diversity is decisively lower in the temperate North Atlantic and subarctic region when compared to similar southern latitudes and depths (Brey et al. 1994; Clarke 2008). Among these, the Anthuroidea Leach, 1814 are often minute and some species are of almost meiofauna size. They are vermiform isopods that are capable of building tubes in the sediment. They are probably predators of other crustaceans (see Wägele 1981, 1989). Much more dominant in the North Atlantic towards the Arctic is the valviferan family Arcturidae Dana, 1849. Arcturids are filter feeders (e.g., Wägele 1987; Poore 2001) yet remain poorly understood, including their role in the food web (Poore and Bruce 2012).

Isopod research in this region has a long tradition with extensive studies by Sars (1899) in particular around Norway, and Hansen (1916), who determined and described the rich collections of the Danish Ingolf expedition around the Faeroe Islands, Iceland, and Southern Greenland. The descriptions and species lists provided by those two authors are still the major source for information about isopods of the deep waters of the Arctic Ocean, the Nordic Seas, and the northernmost part of the North Atlantic. While there are several studies dealing with the Icelandic isopod species distributions (e.g., Negoescu and Svavarsson 1997; Svavarsson 1997; Brix and Svavarsson 2010; Schnurr et al. 2014), an overview of isopod
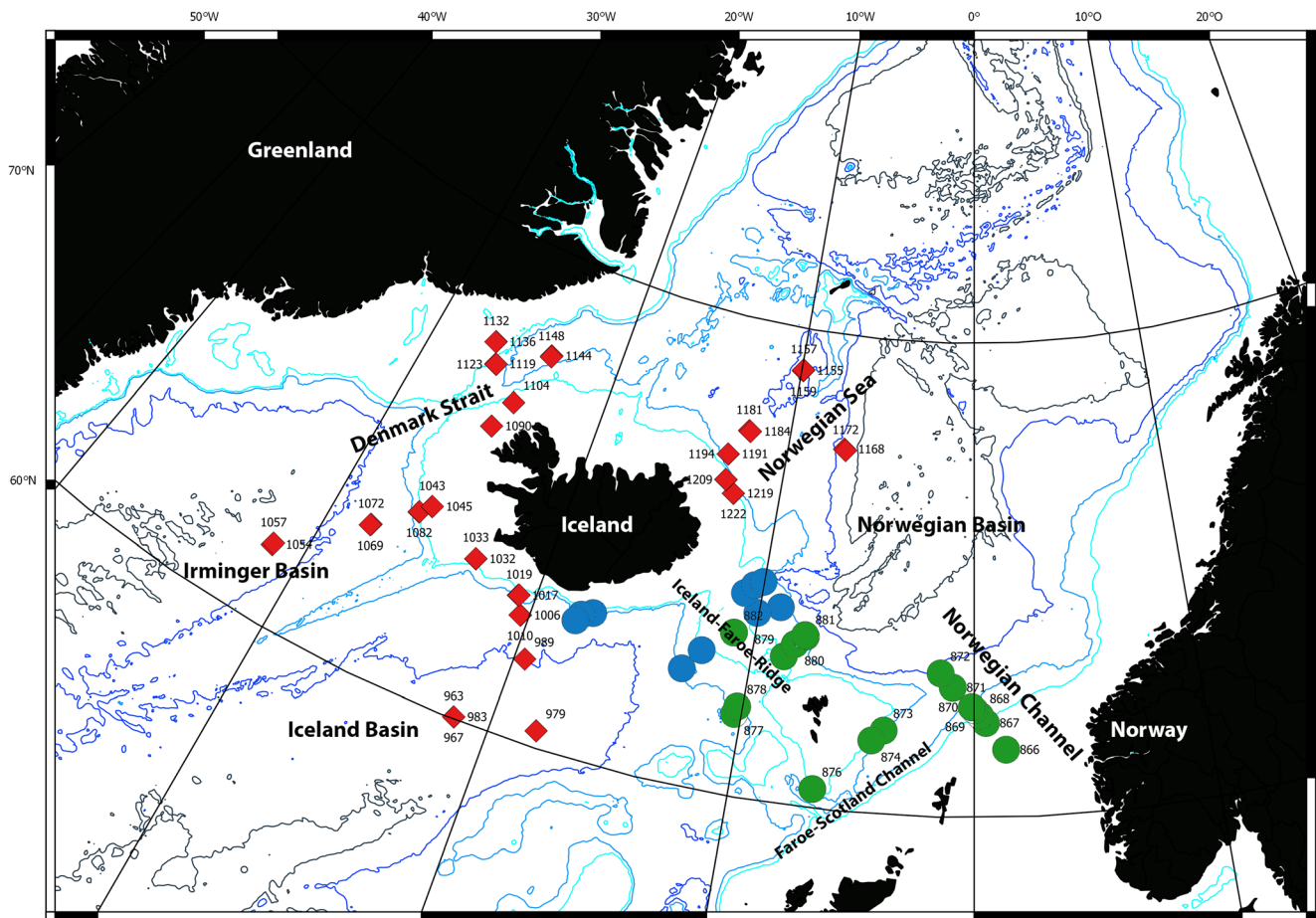
Fig. 1 Overview map. All IceAGE stations plus selected BIOICE stations used for the analyses in the present study: Red squares: IceAGE1, green dots: IceAGE2, blue dots: BIOICE. For IceAGE1 and 2, the distribution maps were created on family level. Isopod species distribution was analyzed only for IceAGE2 and the selected BIOICE stations along the Iceland–Faeroe Ridge, Faeroe–Shetland, and Norwegian Channel

family distributions is still missing. As the primary goal of this contribution, we want to present an overview of isopod family distributions in the IceAGE sampling area. Additionally, this study evaluates the distribution of isopod species along the Iceland–Faeroe Ridge (IFR) addressing the specific questions:

How is species distribution affected in the overflow region along the IFR? At which depth can we observe a faunal turnover from shallow to deep-water fauna (along the Norwegian Channel)? How species rich are the upper 1000 m North and South of the IFR and along the Norwegian Channel?

Material and methods

Sampling

The samples used in this study were collected during the BIOICE (1991–2004) and the IceAGE (ongoing since 2011) projects. A detailed description of the sampling design is given in Brix et al. (2014). Samples (Table 1) were taken with a

modified Rothlisberg–Pearcy epibenthic sled (RP sled; Rothlisberg and Pearcy 1977; Brattegard and Fosså 1991) which had a 0.5-mm mesh in the cod end and with different types of epibenthic sleds (EBS: Brenke 2005), partly equipped with a camera system (Brandt et al. 2013).

On deck, the samples were either fixed with pre-cooled 96% undenatured ethanol or with 4% formalin. Later, the macrofauna from the formalin samples was sorted to taxonomic order at the Sandgerði Marine Center, Sandgerði, Iceland. Ethanol-fixed macrofauna samples were sorted at the DZMB in Hamburg, Germany. Isopods too damaged for identification were not considered in the analyses. Handling of the ethanol-preserved material available for molecular genetic work was described by Riehl et al. (2014a). Species identification either took place in Sandgerði, Iceland (University of Iceland) or at the DZMB in Hamburg using Leica MZ12.5 and Leica MZ8 dissection microscopes. All family and species identifications as well as the abiotic factors were entered into a Microsoft Access 2010 database. Final storage for all IceAGE isopod material is planned in two museums:

Table 1 Station lists of all EBS stations used for analyses from BIOICE and IceAGE1 and 2 including all available abiotic information (depth [m], water temperature ground [°C], salinity ground, O2 saturation ground, and sediment parameters like median—Md 50 [mm], skewness—SkI, sorting coefficient—QDI)

Project	Station	Depth	Region	Watertemp ground	Salinity ground	O2-saturation ground	Water content [%]	TOC	Md 50 [mm]	SkI	QDI	Mud	Sand	Gravel
IceAGE1	963	2749	South Iceland	2.5253	34.9916	5.85461	70.56	9.25	0.033	0.857	2.311	74.47	25.53	0
	967	2750	South Iceland	2.5253	34.9916	5.85461	70.56	9.25	0.033	0.857	2.311	74.47	25.53	0
	979	2567	South Iceland	2.6581	34.9955	258.389	60.36	5.68	0.064	0.929	2.561	56.57	43.41	0.02
	983	2749	South Iceland	2.6581	34.9955	258.389	60.99	6.73	0.033	0.929	2.561	54.24	45.76	0
	989	1912	South Iceland	2.7443	34.9866	258.5425	44.21	4.86	0.033	0.929	2.561	60.32	39.48	0.2
	1006	1386	South Iceland	3.8804	35.02456	254.57	53.69	5.8	0.002	0.857	2.311	78.31	21.69	0
	1010	1384	South Iceland	3.8804	35.02456	254.57	53.69	5.8	0.003	0.857	2.311	78.31	21.69	0
	1017	891	South Iceland	5.29	35.08	242.79	57.64	5.97	0.002	1	2.409	71.93	28.07	0
	1019	913	South Iceland	5.29	35.08	242.79	57.64	5.97	0.002	1	2.409	71.93	28.07	0
	1032	289	South Iceland	8.01	35.22	241.44	42.36	4.51	0.157	−0.563	2.962	24.48	73.24	2.28
	1033	288	South Iceland	8.01	35.22	241.44	42.36	4.51	0.157	−0.563	2.962	24.48	73.24	2.28
	1043	213	South Iceland	7.42	35.19	246.74	44.2	7.23	0.126	−0.227	3.667	26.21	66.58	7.21
	1045	218	South Iceland	7.42	35.19	246.74	44.2	7.23	0.126	−0.227	3.667	26.21	66.58	7.21
	1054	2537	South Iceland	3.16	34.94	254.17	53.16	4.74	0.126	0.938	2.962	59.64	38.32	2.04
	1057	2504	South Iceland	3.16	34.94	254.17	53.16	4.74	0.126	0.938	2.962	59.64	38.32	2.04
	1069	1588	South Iceland	4.28	34.99	245.53	35.66	3.34	0.188	−0.167	1.864	12.54	83.48	3.99
	1072	1593	South Iceland	4.28	34.99	245.53	35.66	3.34	0.188	−0.167	1.864	12.54	83.48	3.99
	1082	724	South Iceland	6.19553	35.09964	231.5267	50.88	4.85	0.157	−0.389	3.364	19.73	78.35	1.93
	1086	698	South Iceland	6.19553	35.09964	231.5267	50.88	4.85	0.157	−0.389	3.364	19.73	78.35	1.93
	1090	742	West Iceland	7.87818	35.12831	228.812	17.68	3.05	0.75	−0.375	0.856	2.06	82.05	15.89
	1104	118	Northwest Iceland	7.32249	35.1535	237.1402	30.4	3.22	0.625	0	1.909	4.28	74.56	21.16
	1119	696	East Greenland	0.07	34.907	292.966	33.11	2.36	0.033	0.833	2.864	56.48	39.21	4.31
	1123	716	East Greenland	0.07	34.907	292.966	33.11	2.36	0.033	0.833	2.864	56.48	39.21	4.31
	1132	318	East Greenland	0.706	34.625	290.9	51.07	3.6	0.064	0.833	2.864	52.91	43.63	3.46
	1136	315	East Greenland	0.706	34.625	290.9	51.07	3.6	0.064	0.833	2.864	52.91	43.63	3.46
	1144	1281	East Greenland	−0.66561	34.91109	278.7728	51.23	4.16	0.064	0.938	2.962	61.28	35.91	2.81
	1148	1248	East Greenland	−0.66561	34.91109	278.7728	51.23	4.16	0.064	0.938	2.962	61.28	35.91	2.81
	1155	2203	Northeast Iceland	−0.7518	34.91	266.74	55.06	6.69	0.064	0.929	2.561	57.39	42.05	0.56
	1159	2202	Northeast Iceland	−0.7518	34.91	266.74	55.06	6.69	0.064	0.929	2.561	57.39	42.05	0.56
	1168	2372	Northeast Iceland	−0.82	34.91	271.26	55.01	7.71	0.064	0.929	2.561	58.95	41.05	0
	1172	2422	Northeast Iceland	−0.82	34.91	271.26	55.01	7.71	0.064	0.929	2.561	58.95	41.05	0
	1181	1827	Norwegian Sea	−0.8511	34.91	0	58.73	8.37	0.048	0.929	2.561	70.31	29.69	0
	1184	1819	Norwegian Sea	−0.8511	34.91	0	58.73	8.37	0.048	0.929	2.561	70.31	29.69	0
	1191	1574	Northeast Iceland	−0.74403	34.90862	269.2512	62.51	9.26	0.033	0.875	2.712	71.04	28.77	0.19

Table 1 (continued)

Project	Station	Depth	Region	Watertemp ground	Salinity ground	O2-saturation ground	Water content [%]	TOC	Md 50 [mm]	Skl	QDI	Mud	Sand	Gravel
	1194	1573	Northeast Iceland	− 0.74403	34.90862	269.2512	62.51	9.26	0.033	0.875	2.712	71.04	28.77	0.19
	1209	315	Northeast Iceland	1.36103	34.8472	291.8144	NA	NA	NA	NA	NA	NA	NA	NA
	1212	317	Northeast Iceland	1.36103	34.8472	291.8144	NA	NA	NA	NA	NA	NA	NA	NA
	1219	579	East Iceland	− 0.40217	34.90286	283.581	53.05	3.77	0.126	− 0.222	3.114	35.06	60.68	4.26
	1222	610	East Iceland	− 0.40217	34.90286	283.581	53.05	3.77	0.126	− 0.222	3.114	35.06	60.68	4.26
IceAGE2	866	169	Norwegian Channel	8.50471	35.311	265.602	NA	NA	NA	NA	NA	NA	NA	NA
	867	302	Norwegian Channel	8.065	35.265	278.043	NA	NA	NA	NA	NA	NA	NA	NA
	868	587	Norwegian Channel	− 0.65	34.92	302.21	21.93	1.28	2.03	− 0.0910	4.4167	27.41	31.72	40.86
	869	846	Norwegian Channel	− 0.78667	34.916	300.029	NA	NA	NA	NA	NA	NA	NA	NA
	870	1058	Norwegian Channel	− 0.78667	34.916	299.957	NA	NA	NA	NA	NA	NA	NA	NA
	871	1577	Norwegian Channel	− 0.79	34.92	298.34	62.52	1.66	0.0020	0.8670	2.0091	86.2700	13.7300	0.0000
	872	1858	Norwegian Channel	− 0.80	34.92	295.35	64.84	1.84	0.0020	0.8670	2.0090	86.2000	13.8000	0.0000
	873	833	Faröer Channel	− 0.70	34.92	303.51	46.72	1.41	0.1260	− 0.3290	2.5606	60.7300	37.7100	1.5100
	874	901	Faröer Channel	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	876	554	Faröer Channel	0.30	34.92	310.95	21.14	0.97	0.25	− 0.1670	3.3636	47.1600	49.6000	3.1900
	877	1087	F I Ridge	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	878	781	F I Ridge	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	879	510	F I Ridge	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	880	686	F I Ridge	− 0.43	34.91	306.23	42.05	1.07	0.0640	− 0.5000	2.5606	37.2500	62.5100	0.2300
	881	1043	F I Ridge	− 0.58	34.91	303.95	61.50	1.10	0.0210	0.8670	2.0091	84.3200	15.6800	0.0000
	881	1056	F I Ridge	− 0.58	34.91	303.95	64.13	1.32	0.0210	1.0000	2.0076	83.9600	16.0400	0.0000
	882	440	F I Ridge	0.27	34.91	311.94	47.03	1.76	0.0330	− 0.4670	2.4091	52.5000	47.5000	0.0400
BIOICE	2317	996	NW FIR	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2323	623	NW FIR	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2332	550	NW FIR	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2337	1099	NW FIR	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2360	391	NW FIR	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2362	495	South FIR	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2364	605	South FIR	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2844	1085	SW FIR	4.48	35.01	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2846	947	SW FIR	3.48	34.98	NA	NA	NA	NA	NA	NA	NA	NA	NA
	2849	976	SW FIR	3.26	34.98	NA	NA	NA	NA	NA	NA	NA	NA	NA

NA not available

Zoological Museum Hamburg (all families except Munnopsidae) and Senckenberg Crustacean Collection in Frankfurt (Munnopsidae). Presently, all IceAGE isopod specimens and the BIOICE munnopsids used in this study are available via DZMB HH numbers and stored in the material archive hosted at the DZMB. All remaining BIOICE isopods determined during this study are hosted at the University of Iceland under the responsibility of Jörundur Svavarsson. Sediment and TOC data used in the analysis with Primer7 were extracted from Ostmann et al. (2014) and Meißner et al. (2014).

Data analysis

In all, 55 samples were used in the multivariate analysis based on family-level data. Species abundance data were standardized (abundance in each sample was turned into relative percentage) before analysis because epibenthic sleds are a "semi-quantitative" sampling gear (see Schnurr et al. 2014). The data were then square root transformed (Clarke and Gorley 2015), and hierarchical agglomerative clustering based on Bray–Curtis similarity formula was used with the group average method. A SIMPROF test with 1% significance level was performed in order to check multivariate structure within groups (Clarke and Gorley 2015). We also analyzed similarity among the 27 samples for which isopods were identified to the species level (seven of those samples were collected during the BIOICE project). All analyses were done in Primer 7 (Clarke and Warwick 1994).

Detrended correspondence analysis (DCA) allowed us to choose the appropriate method to analyze family-level abundance and available environmental factors (depth; water temperature; salinity; oxygen saturation; water content in the sediments; organic matter content (TOC); median—Md 50 [mm]; skewness—SkI; sorting coefficient—QDI; and mud, sand, and gravel content). In total, 46 samples with a full set of the abovementioned environmental conditions were used in this analysis. To recognize factors that significantly shape isopod assemblages, Redundancy analysis (RDA) was performed (data were square root transformed). Factor significance was tested by Monte Carlo unrestricted permutation with automatic selection and permutation under the full model. Because of autocorrelation, Md 50 [mm] was excluded from the further RDA analysis. Statistics were computed with Canoco 4.5 software (Ter Braak and Smilauer 2002; Legendre and Legendre 2012). The full set of environmental data was available only for eight out of the 27 samples identified to the species level (part of the abiotic data: depth, water temperature, salinity, oxygen saturation was available also for seven BIOICE samples). Therefore, we did not perform RDA on this set of samples.

Results

Isopod distribution on family level

A total of 35,536 isopod specimens from 55 sled stations was determined to family level. The individuals were assigned to 23 families belonging to the suborders Asellota, Cymothoida Wägele, 1989 and Valvifera Sars, 1883. The family composition varied considerably between individual stations (Fig. 2).

The asellote families Munnopsidae, Desmosomatidae Sars, 1897, Haploniscidae, Ischnomesidae, and Macrostylidae each occurred north as well as south of Iceland (Figs. 3, 4, and 5), at depths from 118 to 2750 m. The most common family was the Munnopsidae, found in every sample collected, often comprising around 50% of the total number of collected isopod specimens. The munnopsid share was particularly high in the Iceland Basin and Norwegian Sea and Irminger Basin but lower in the Denmark Strait.

Whereas the Paramunnidae Vanhöffen, 1914, Munnidae Sars, 1897, Nannoniscidae Hansen, 1916, Thambematidae Stebbing, 1912 and Janiridae Sars, 1897 (Figs. 3, 4, and 5), as well as Acanthaspidiidae and Dendrotionidae Vanhöffen, 1914 (Figs. 3 and 4), were also found on both sides of the GIF Ridge and at various depths, Haplomunnidae Wilson, 1976 was only collected at one upper slope station (~ 1400 m) south of Iceland. The family Mesosignidae was found at two slope stations in the southern deep sea of the Iceland Basin (2572 and 2744 m depth). Katianiridae Svavarsson, 1987a were present at several northern stations and at a single station southwest (2435 m depth) of the ridge. At northern stations down to 900 m shelf depth, Paramunnidae constituted one of the largest fractions of the family composition. Generally, the Norwegian Sea transect was dominated by the families Munnopsidae and Paramunnidae, whereas the Munnidae, Macrostylidae, Ischnomesidae, Gnathiidae Leach, 1814, Desmosomatidae, and the other families formed much smaller fractions.

In approximately half of the stations in the Iceland and Irminger Basins, the Arcturidae occurred in remarkable numbers (Fig. 2). The Desmosomatidae were encountered more frequently and in higher proportion in the Iceland Basin compared to the other areas. While the Iceland Basin was dominated by the Munnopsidae, the Arcturidae and the Desmosomatidae, the families Macrostylidae and Ischnomesidae occurred also in substantial numbers. In the Irminger Basin, it is noticeable that many families occurred in equal numbers and their numbers were comparably low compared to the other transects, namely Nannoniscidae, Macrostylidae, Janiridae, Ischnomesidae, Gnathiidae, Desmosomatidae, Dendrotionidae, and Arcturidae. Some families, like Ischnomesidae, seem to prefer specific depths. While most stations containing the Ischnomesidae were located below 1000 m depth, most families, however, did not follow a clear depth trend.
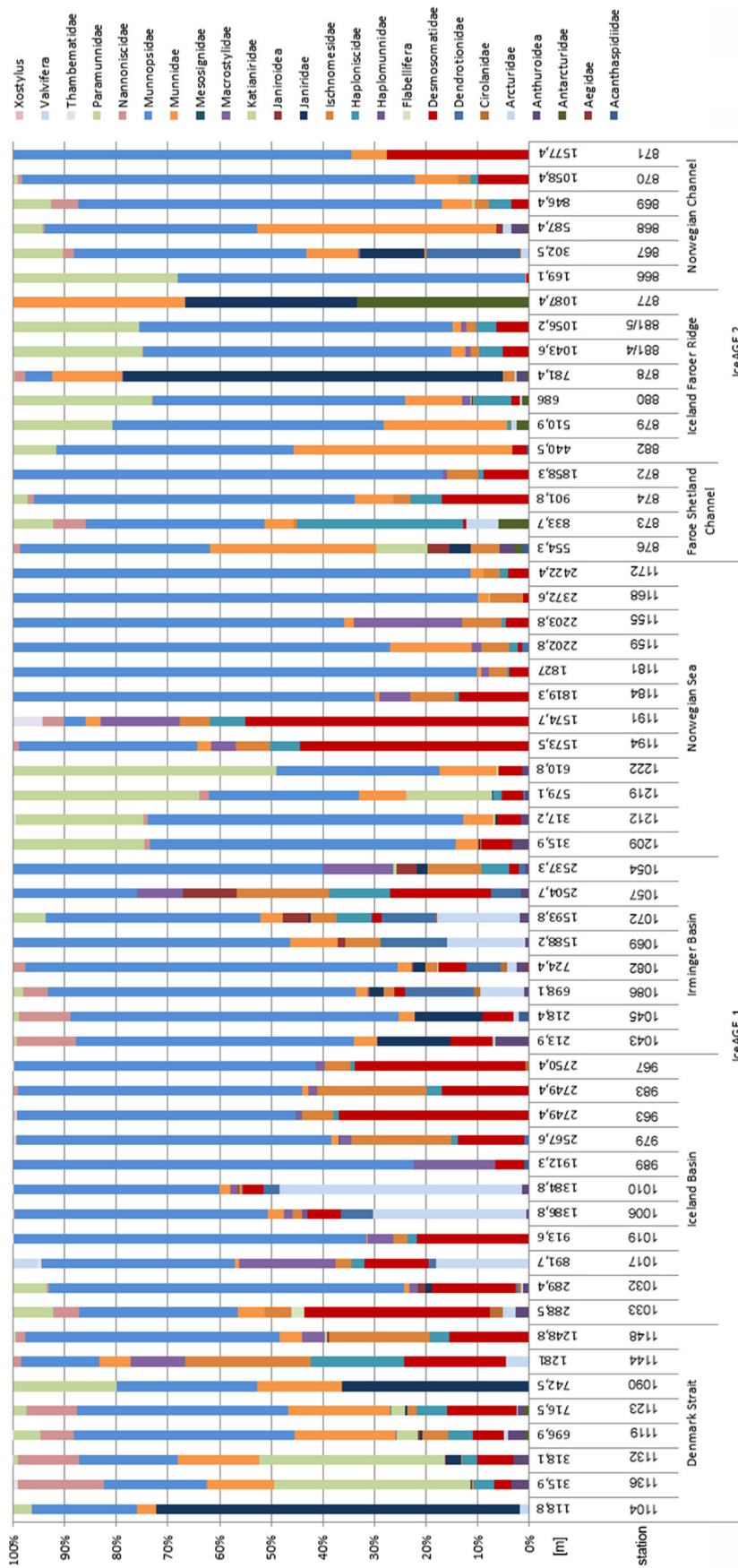
Fig. 2 Percentage of isopod families at the stations listed by transects. Within each transect (DS Denmark Strait, IceB Iceland Basin, IrmB Irminger Basin, NS Norwegian Sea, FSC Faeroe–Shetland Channel, IFR Iceland–Faeroe Ridge, and the NC Norwegian Channel), stations are ordered by depth
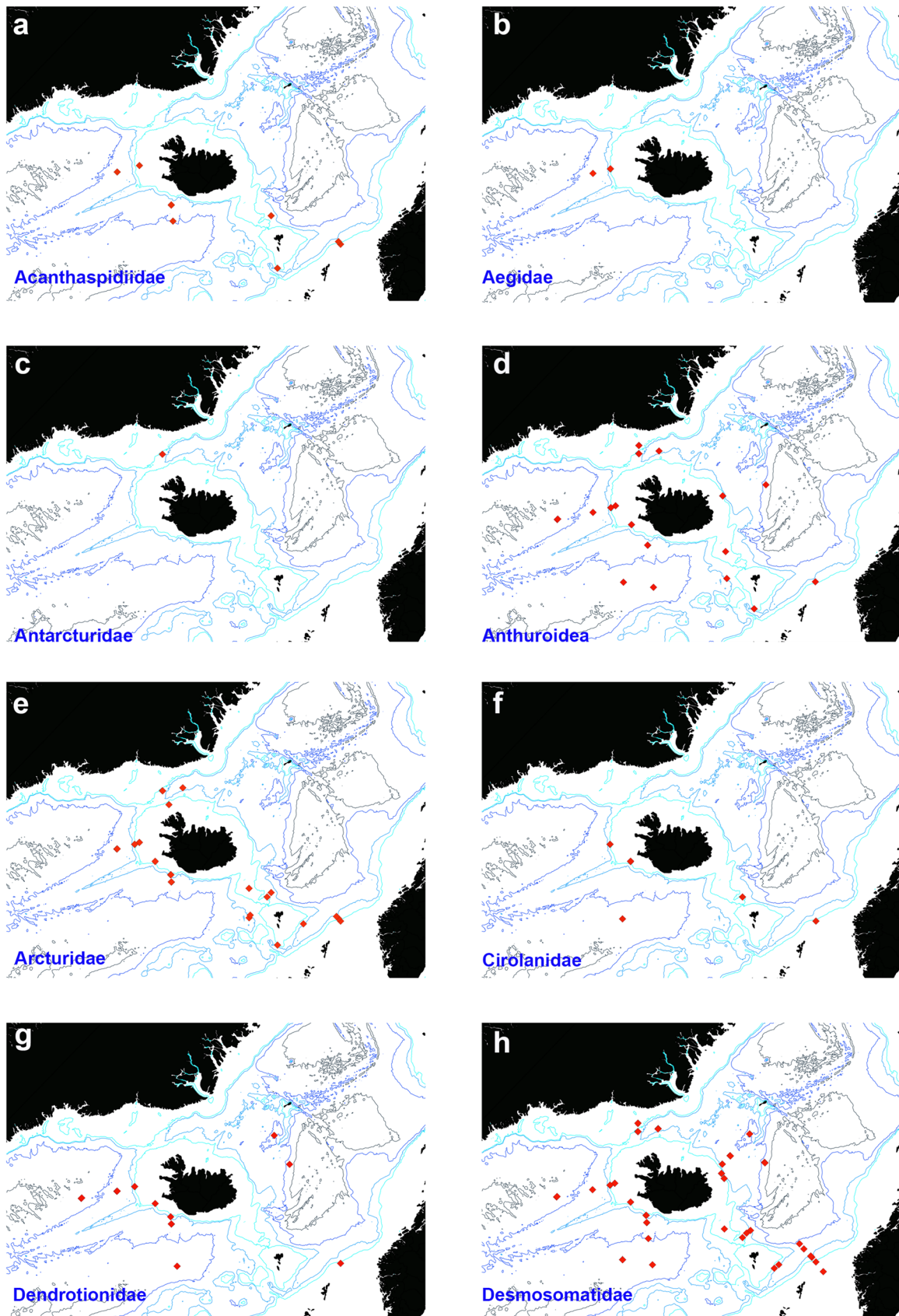
Fig. 3 Occurrence of the families **a** Acanthaspidiidae, **b** Aegidae, **c** Antarcturidae, **d** Anthuroidea, **e** Arcturidae, **f** Cirolanidae, **g** Dendrotionidae, and **h** Desmosomatidae at the stations in distribution maps (one map per family ordered alphabetically)
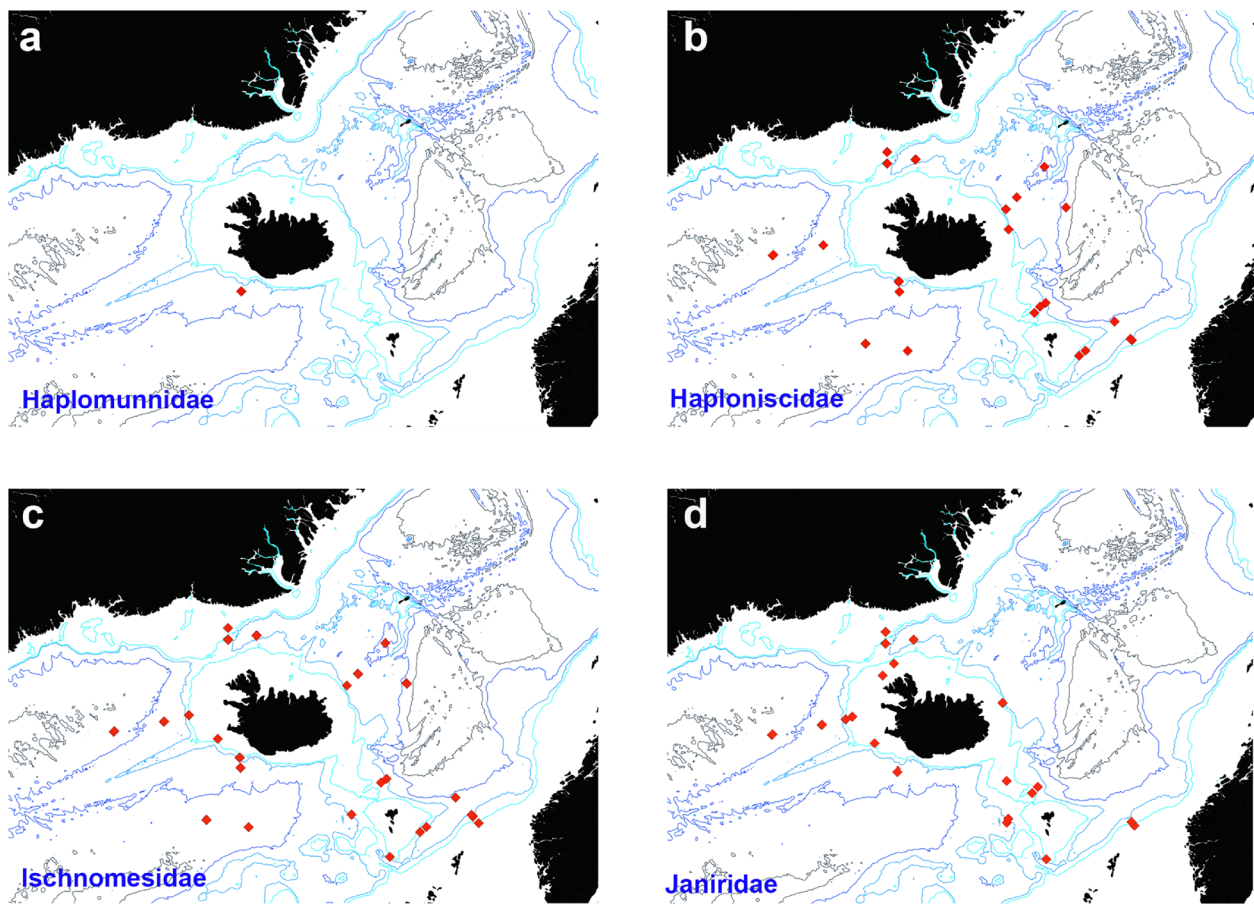
Fig. 4 Occurrence of the families **a** Haplomunnidae, **b** Haploniscidae, **c** Ischnomesidae, and **d** Janiridae

Similarity analysis showed three larger groups of samples (Figs. 6 and 7 clusters B, D, and E) and four other smaller groups at a relatively high level of similarity (about 60%), although not all were significantly differentiated by the SIMPROF. Two clusters (B and E) grouped mostly shallower samples collected between 200 and 800 m in the region of the Faeroe Islands and Norwegian Sea, while group D comprised mainly deep-sea samples (1500–2500 m) from Norwegian Sea and Iceland Basin. The shallower clusters were both dominated by the Munnopsidae, Munnidae, Paramunnidae, and Desmosomatidae. In group E, the Nannoniscidae were also a constant and an abundant element of the community. In the deep sea (cluster D), the isopod fauna was dominated by the Munnopsidae and Desmosomatidae followed by the Ischnomesidae, Macrostylidae, and Haploniscidae.

The RDA (Fig. 8) indicated a relation between abundance of isopod families and environmental factors. Only two environmental factors (TOC—10% and mud content—5%) significantly explained assemblage composition ($\alpha < 0.05$). Both factors were negatively correlated with the x axis, showing a group of samples collected mainly in the region of the Faeroe Islands (sample numbers 871 to 882) characterized by a low value of TOC, and samples collected in the Iceland Basin, the

Irminger Basin and the Norwegian Sea characterized by higher values of TOC.

Isopod distributions at the species level

A number of 22,574 isopod specimens were identified to species level. The analysis of 27 samples (100 species) yielded four large clusters at 20–45% similarity (Figs. 9 and 10 clusters G, H, I, and J). There was no clear spatial or depth-related pattern visible, although most of the samples used in this analysis were collected in the region of the Faeroe Islands and on a more restricted depth range, with most samples in the upper 1000 m. The dataset allows, however, for more detailed insight into the community structure, but on a smaller spatial scale than what was attempted with the family-level analysis.

There were differences in species richness and species composition between the groups observed (Fig. 12, Table 5). Group G had a low number of species per sample (16.0 ± 6.8; min = 3, max = 25) and was dominated by *Astacilla boreaphilis* Stransky and Svavarsson, 2006 and *Janira maculosa* Leach, 1814, although *A. boreaphilis* was recorded only in three samples collected during BIOICE project.
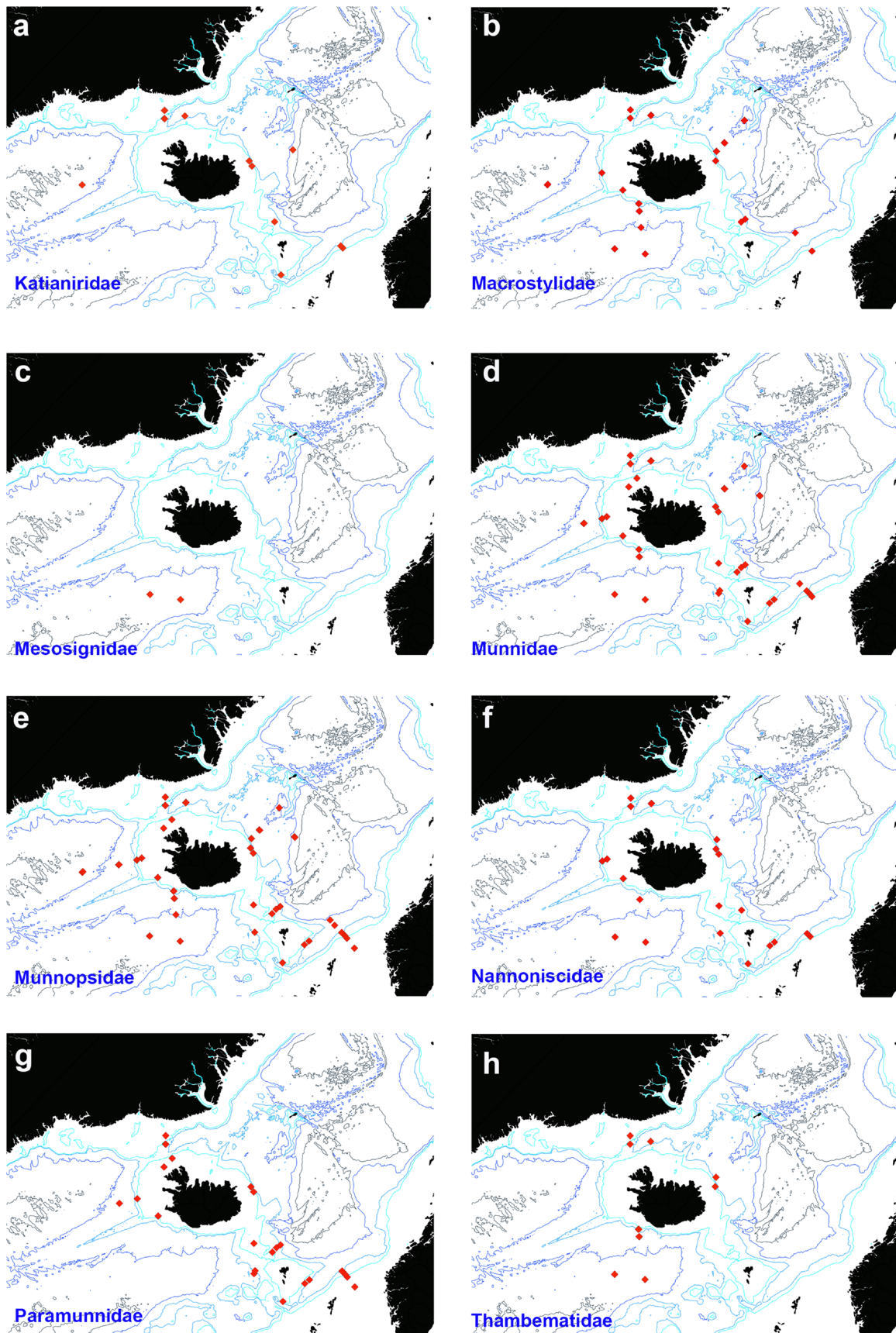
Fig. 5 **a** Katianiridae, **b** Macrostylidae, **c** Mesosignidae, **d** Munnidae, **e** Munnopsidae, **f** Nannoniscidae, **g** Paramunnidae, and **h** Thambematidae
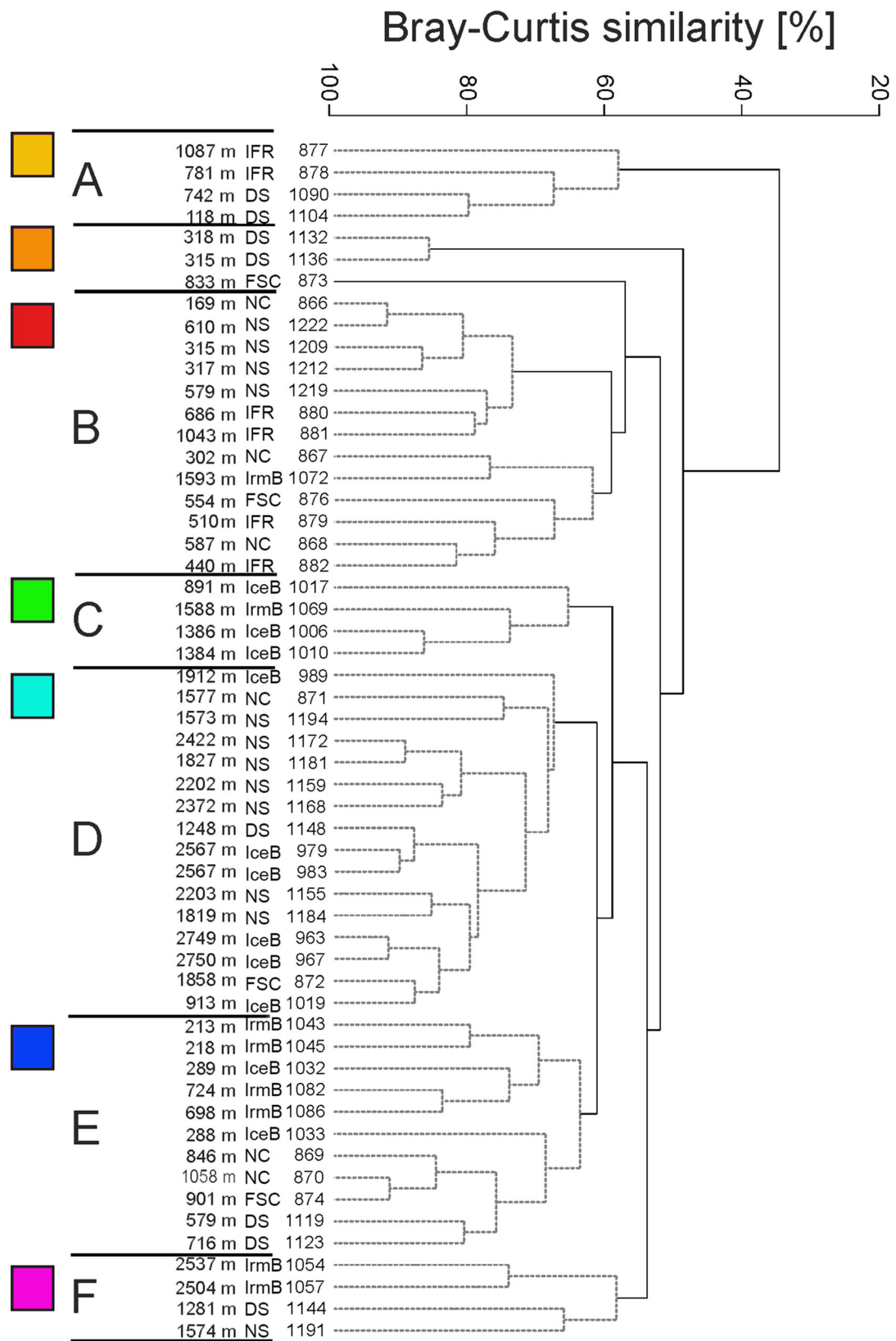
Fig. 6 Dendrogram of samples for the family-level data (Bray–Curtis similarity, group average grouping method, standardized and square root transformed data). NS Norwegian Sea, NC Norwegian Channel, DS Denmark Strait, IceB Iceland Basin, IrmB Irminger Basin, FSC Faeroe–Shetland Channel, IFR Iceland–Faeroe Ridge. (Gray spotted lines indicate the samples that cannot be significantly differentiated)
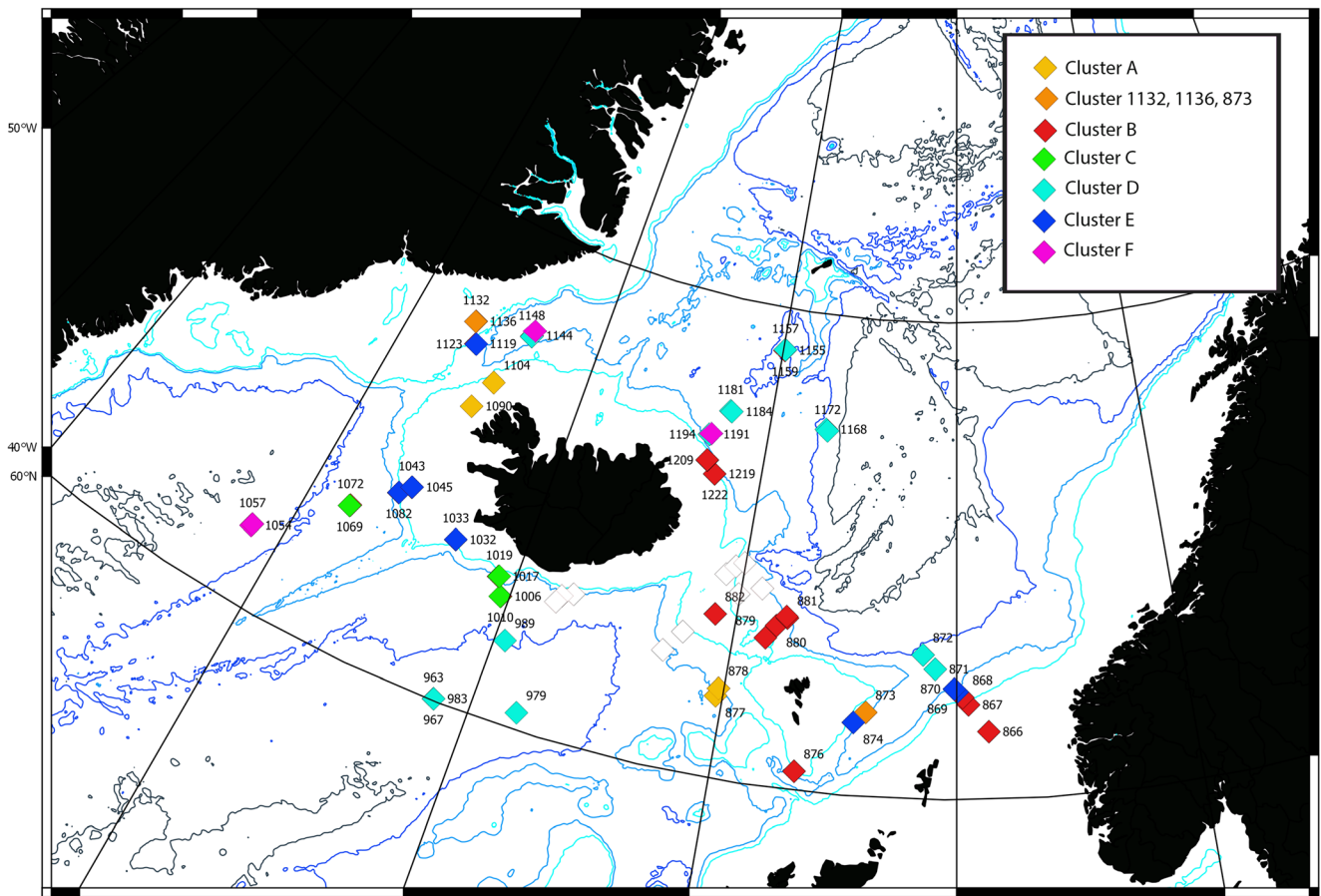
Fig. 7 Color coded map of cluster distribution of Fig. 6
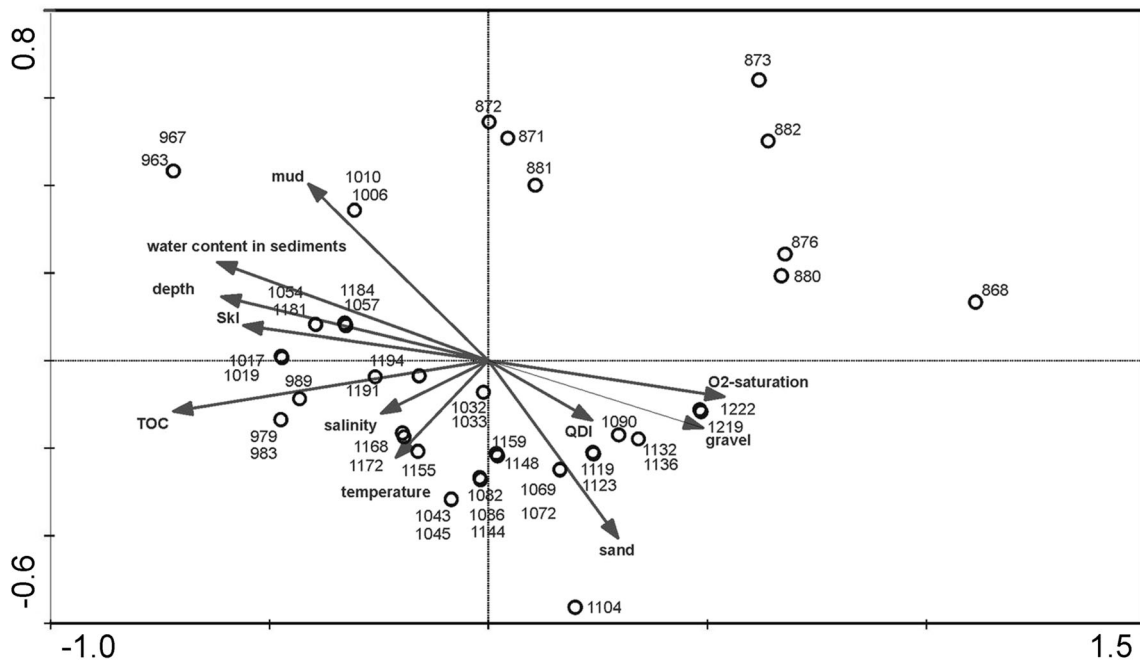
Fig. 8 Results of the redundancy analysis (RDA) for the isopod family-level data
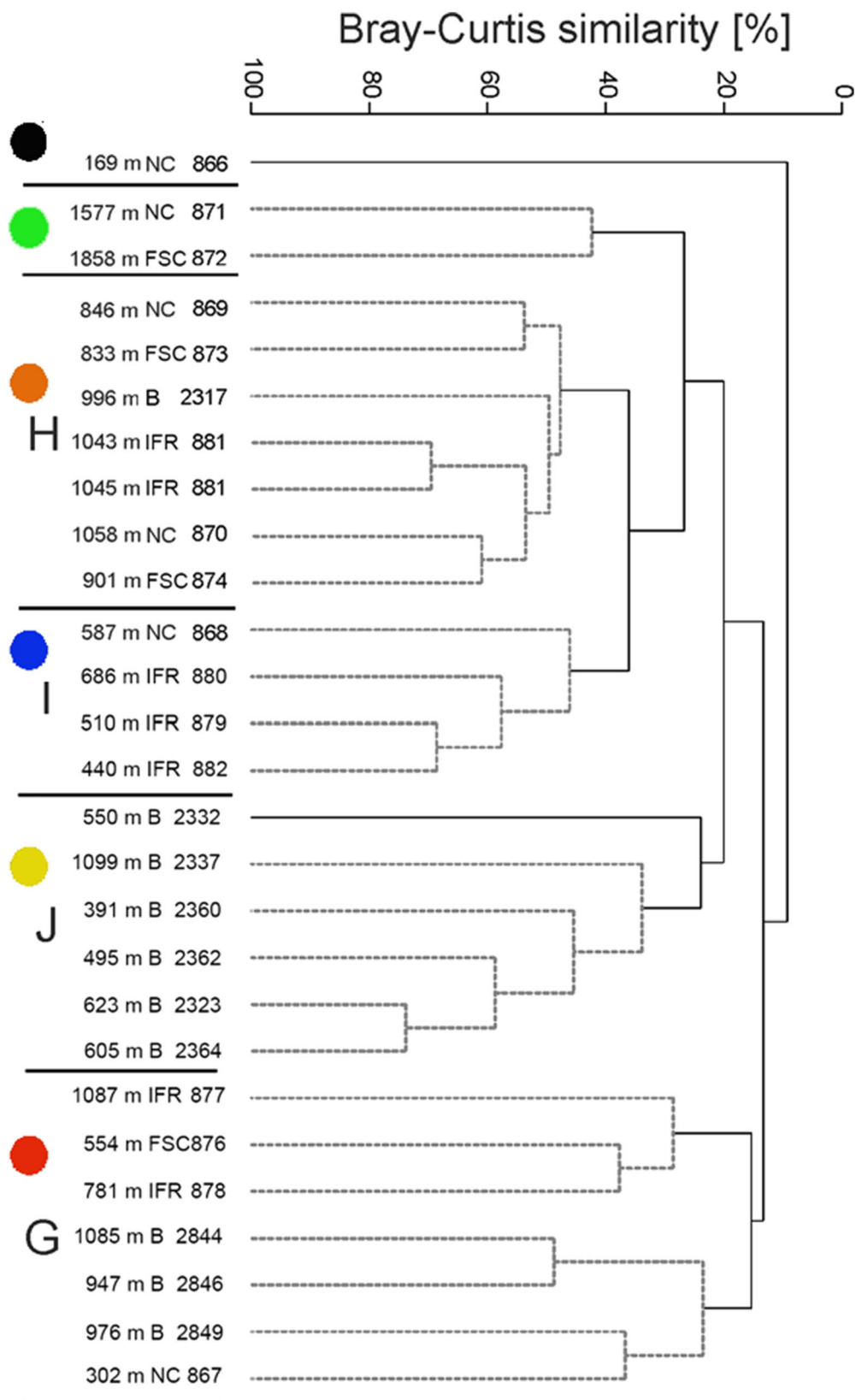
Fig. 9 Dendrogram of samples for the species-level data (Bray–Curtis similarity, group average grouping method, standardized and square root transformed data). NS Norwegian Sea, NC Norwegian Channel, DS Denmark Strait, IceB Iceland Basin, IrmB Irminger Basin, FSC Faeroe–Shetland Channel, IFR Iceland–Faeroe Ridge, B BIOICE samples (gray spotted lines indicate the samples that cannot be significantly differentiated). The colors indicate the clusters plotted in Fig. 10
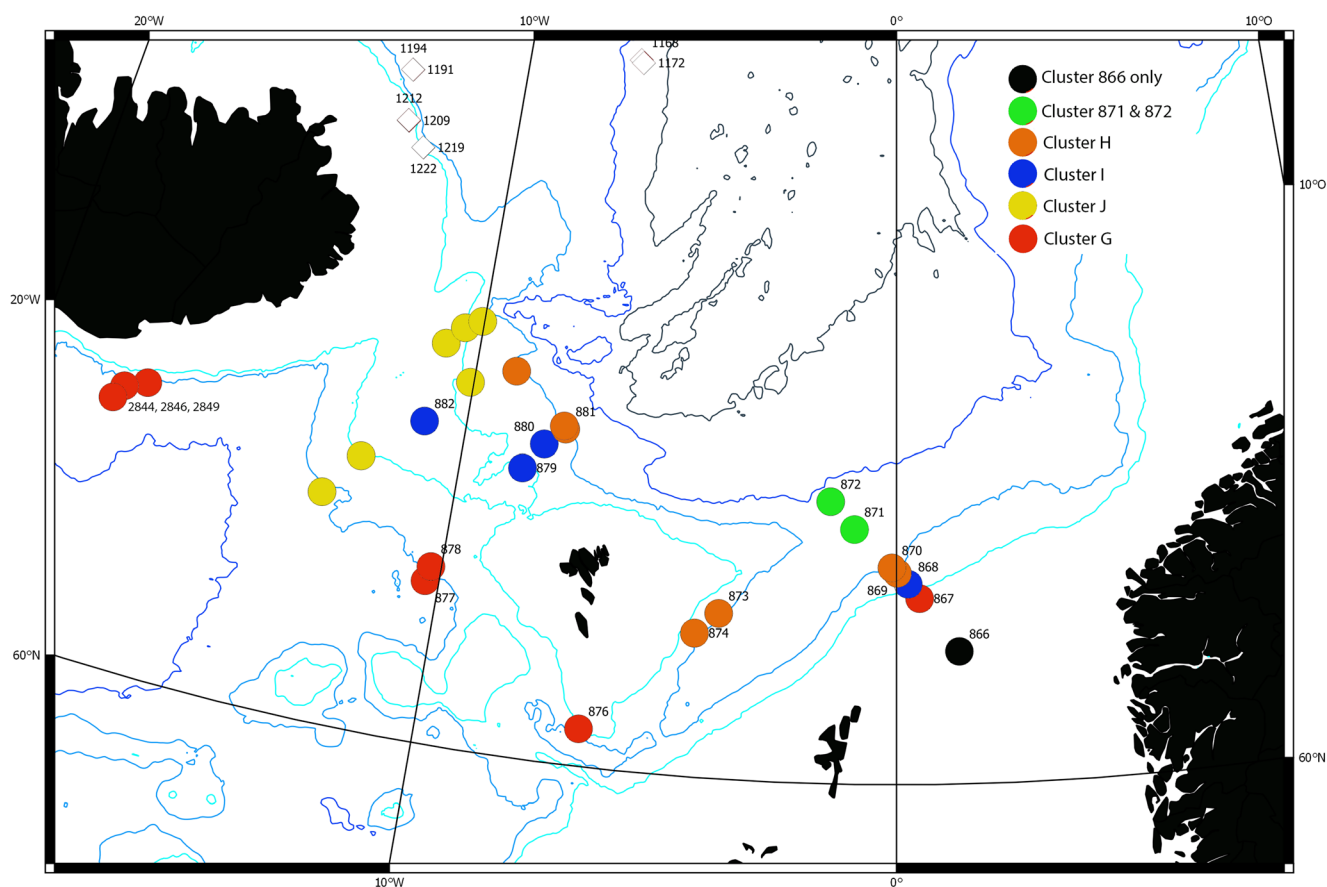
Fig. 10 Color coded map of cluster distribution of Fig. 9

Cluster H had much higher species richness (25.0 ± 5.7; min = 21, max = 37) and was dominated by *Eurycope brevirostris* Hansen, 1916, *E. inermis* Hansen, 1916, *Ilyarachna hirticeps* Sars, 1870 and *Haploniscus bicuspis* (Sars, 1877). Group I was also characterized by high species richness per sample (29.5 ± 9.1; min = 21, max = 42), an even higher species richness than cluster H, although cluster I consisted only of four stations. The most frequent and abundant elements in this assemblage were *Munna acanthifera* Hansen, 1916, *Eurycope producta* Sars, 1866, *Ilyarachna hirticeps*, *Pleurogonium rubicundum* (Sars, 1864), *Echinozone arctica* Hansen, 1916, and *Munna hanseni* Stappers, 1911. The last cluster (group J) was characterized by a low species richness per sample (13.1 ± 3.1; min = 9, max = 17) and was dominated by *Ilyarachna hirticeps*, *I. torleivi* Svavarsson, 1988 and *Calathura brachiata* (Stimpson, 1853).

Discussion

Underwater ocean ridges may be stepping stones and pathways for the dispersal of the slope fauna, but may also act as barriers for the abyssal seafloor fauna (Gebruk et al. 2010). Combined with other hydrographic features, ridges may play

an important role in shaping faunal distributions because they disrupt the continuity of the abyss and potentially impede gene flow among populations (Etter et al. 2011; Bober et al. 2018). Constituting a patchwork of basins and ridges with differing hydrographic regimes and depths, the Icelandic area thus contains sharp distribution limits for many of its inhabitant species (Weisshappel 2001; Brix and Svavarsson 2010; Parapar et al. 2011; Dauvin et al. 2012; Schnurr et al. 2014). The Iceland–Faeroe Ridge formed 57–16 million years ago (Larsen 1983) and since then has provided a bridge for shallow-water organisms between east and west. For deep-sea and especially abyssal fauna, however, it became an obstacle (Svavarsson et al. 1993).

Distribution of isopod families

Many isopod families show a remarkable distribution range (both geographically and across depth) north and south of the GIF Ridge, as well as east and west of the Reykjanes Ridge. They occur across extensive depth ranges and areas under influence of different temperatures and salinities. During our study, some families were collected either only north or only south of the GIF Ridge: Mesosignidae and Haplomunnidae occurred only in the southern samples and at great depths.

Table 2 List of isopod families sorted from all IceAGE EBS samples per station giving the information about numbers of individuals per family per station

Station	866	867	868	869	870	871	872	873	874	876	877	878	879	880	881	882	963	967	979	983	989	1006	1010	1017	1019	1032	1033	1043	1045
Arcturidae	0	3	15	1	0	0	0	47	0	1	1	2	106	16	0	7	0	0	0	0	0	382	295	12	4	1	0	1	1
Antarcturidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthaspididae	0	1	3	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2
Desmosomatidae	3	1	0	49	60	0	10	3	25	0	0	0	4	31	99	85	491	629	74	45	6	112	145	16	317	29	14	30	4
Dendrotionidae	0	57	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	10	5	13	0	108	52	2	0	1	0	0	0
Haploniscidae	0	0	0	64	9	0	1	148	6	0	0	0	14	141	108	0	0	10	7	13	0	0	6	3	24	0	0	0	0
Haplomunnidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	16	0	0	0	0	0	0	0
Ischnomesidae	0	1	0	42	21	0	5	2	5	4	0	10	0	2	34	0	85	98	113	86	0	32	13	1	44	0	2	0	0
Janiridae	0	32	15	1	0	0	0	0	0	6	1	284	2	1	0	4	0	0	0	0	0	1	2	0	0	5	0	0	12
Katianiridae	0	0	1	8	0	0	0	0	0	10	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Munnopsidae	389	103	521	852	454	17	69	139	85	30	0	22	1807	606	987	1474	701	1094	352	293	80	819	1429	46	1075	126	11	97	52
Munnidae	0	25	817	72	48	2	0	23	12	16	0	46	864	178	44	1264	0	0	8	3	0	53	27	0	0	2	14	0	3
Mesosignidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Macrostylidae	0	1	0	0	0	0	1	0	0	1	0	0	0	27	20	0	16	30	13	10	17	26	23	22	56	3	0	13	5
Nannoniscidae	0	0	6	39	5	0	0	23	1	1	0	7	0	27	20	0	1	0	5	5	0	3	0	0	0	1	2	0	0
Paramunnidae	171	21	72	67	5	0	0	32	3	9	1	1	580	864	516	200	0	0	0	0	0	3	0	0	1	12	3	0	0
Thambematidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	0	0
Aegidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Anthuroidea	0	0	42	0	0	0	0	0	0	2	0	6	0	0	0	9	0	16	1	1	0	8	8	0	0	2	2	7	0
Cirolanidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	1	1	0	0

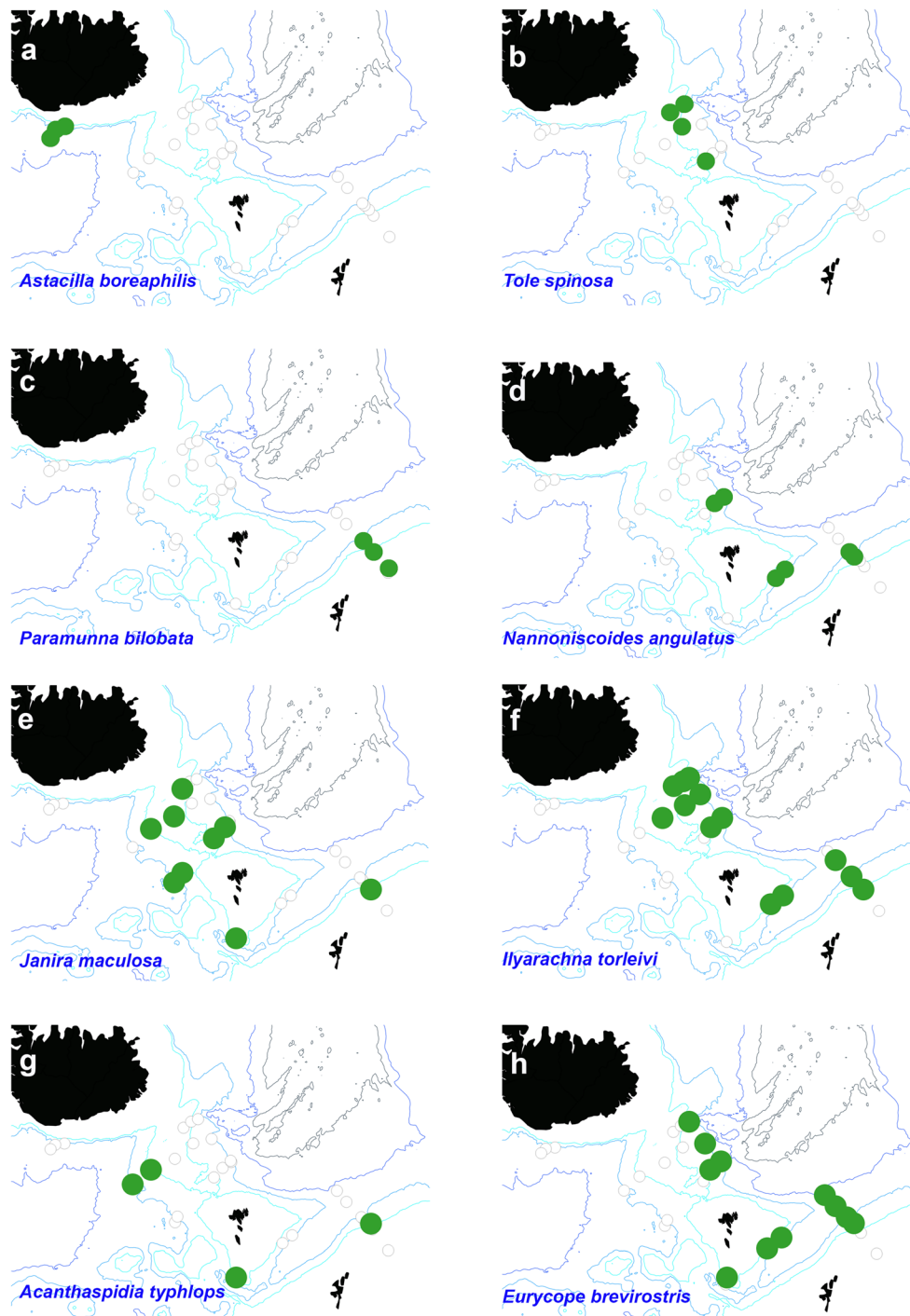| Station	1054	1057	1069	1072	1082	1086	1090	1104	1119	1123	1132	1136	1144	1148	1155	1159	1168	1172	1181	1184	1191	1194	1209	1212	1219	1222	Sum
Arcturidae	0	0	20	21	7	15	0	1	11	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	974
Antarcturidae	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Acanthaspididae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
Desmosomatidae	3	12	0	24	19	29	0	0	67	231	38	10	13	79	6	6	3	53	10	12	37	10	75	33	24	2	3087
Dendrotionidae	2	4	17	128	25	124	0	0	0	0	5	22	11	13	1	12	0	2	1	0	5	1	0	0	2	0	539
Haploniscidae	8	5	0	83	0	0	0	0	29	48	0	0	0	0	0	0	0	30	0	5	3	0	0	2	0	0	827
Haplomunnidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22
Ischnomesidae	16	12	9	3	16	6	15	0	42	0	0	2	12	71	10	24	20	16	9	6	3	0	1	0	0	0	876
Janiridae	9	7	2	16	0	0	0	27	6	1	3	1	0	1	0	0	0	0	0	0	0	4	0	2	0	0	497
Katianiridae	1	0	0	0	2	1	0	27	24	14	141	172	12	1	10	0	1	0	0	0	0	0	0	4	3	0	382
Munnopsidae	89	75	443	253	10	602	9	10	440	229	137	137	10	262	95	519	290	1307	232	3	3	13	471	443	77	21	19,921
Munnidae	0	14	12	40	15	15	9	2	148	109	68	64	4	17	1	48	7	10	2	1	0	0	15	42	9	0	4158
Mesosignidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
Macrostylidae	21	3	0	0	0	58	0	0	1	0	37	55	0	13	27	3	0	4	0	11	3	0	0	6	0	0	363
Nannoniscidae	0	0	0	8	0	22	6	2	33	36	1	0	0	5	0	0	0	0	3	3	0	0	9	2	0	0	376
Paramunnidae	0	0	84	0	0	0	0	0	50	23	0	7	0	2	0	0	0	0	0	0	0	254	0	180	104	12	3295
Thambematidae	0	0	0	0	2	6	0	0	1	0	0	0	0	0	0	0	0	0	0	4	0	0	0	3	0	0	28
Aegidae	0	0	0	2	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	5
Anthuroidea	1	1	0	0	7	1	0	0	13	1	3	5	0	1	0	0	1	0	0	0	0	0	2	11	0	0	136
Cirolanidae	0	0	0	5	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34

35,536 in total

Fig. 11 Species distribution maps for selected species. **a** *Astacilla boreaphilis* occurring at the three west-southern stations on the Icelandic side of the IFR. **b** *Tole spinosa* occurring at the stations between 400 and 800 m depth on top of the IFR in the overflow region. **c** *Paramunna bilobata* occurring in the shallower part of the Norwegian Channel. **d** *Nannoniscoides angulatus* occurring north of the Faeroe Islands. **e** *Janira maculosa* showing distribution along the whole IFR and in the Norwegian Channel. **f** *Ilyarachna torleivi* occurring at all stations north of the IFR. **g** *Acanthaspidia typhlops* found south of the IFR and at one station in the Norwegian Channel. **h** *Eurycope brevirostris* showing a northern distribution limit entering also the Faeroe Channel

While their rarity may indicate that this distribution is an artifact, an abyssal nature of these taxa can be concluded from previous published records and indicates that the observed patterns are real and that these families have never managed to cross the GIF Ridge. These differences in distribution may, accordingly, be caused by both historical (evolutionary) and ecological factors. Among the historical factors may be the origin of the families and their diversification (i.e., in deeper
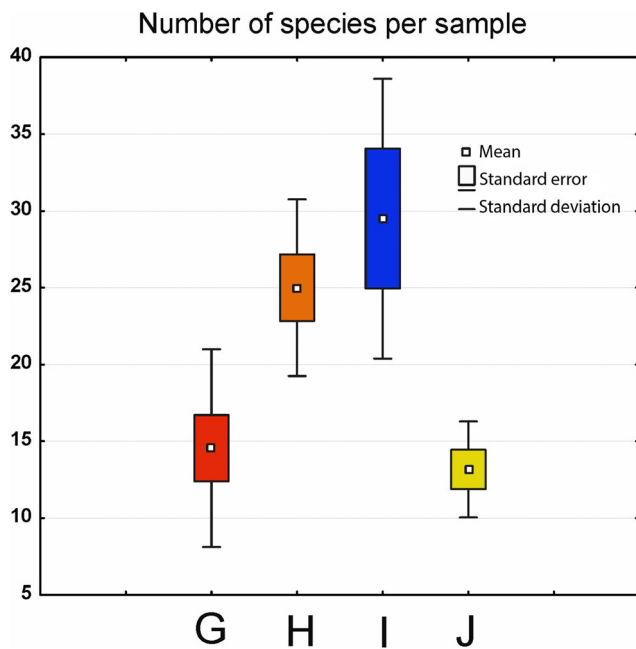
Number of species per sample

Fig. 12 Number of isopod species per sample in four groups obtained in the cluster analysis (for clusters see color coded map in Fig. 10 referring to Fig. 9)

or shallower waters), the influences of the ridge as a physical barrier (Svavarsson et al. 1993), the life history of the species, and even the potential for adapting to environmental extremes, i.e., physiological tolerance to very low temperatures (< 0 °C), and specialization of diets or feeding modes (Somero and Childress 1990; Würzberg et al. 2011). Isopods are brooders, except a few taxa with planktonic larvae in their life history (Wägele 1989) and most isopods live as epifauna or infauna (Hult 1941; Harrison 1987; Hessler and Strömberg 1989), while only a few species are pelagic, like some species of Munnopsidae (Osborn 2007). Therefore, isopods' dispersal abilities are probably poor in comparison with macrofaunal taxa having larvae. Among the ecological factors driving isopod distributions, their feeding preferences, potential specializations in the diet/feeding modes (Somero and Childress 1990), and local habitat condition (bottom structure and sediment type) may be the strongest, as the isopods differ extensively in their use of the habitat.

Little is known concerning the biology and lifestyle of species of the family Acanthaspidiidae (Fig. 3a). The family occurs predominantly in the deep sea at intermediate depths (Wägele 1989; Timm et al. 2013). Their core distribution is the southern hemisphere, with only four species of the genus *Iolanthe* Beddard, 1886 (previously known as *Acanthaspidia*) described from the northern hemisphere. Two of these species have been described from the North Atlantic where they have been recorded from intermediate depths (Hansen 1895; Chardy 1975; Stransky 2007; Timm et al. 2013). During the IceAGE expedition, this family was found on the shelf and in intermediate waters at eight

stations—mainly on the ridge—following the previously described distribution pattern.

The superfamily Anthuroidea (Fig. 3d) belongs to the suborder Cymothoida Wägele, 1989. It comprises only two Arctic species and a small number of species living in the northernmost part of the North Atlantic. These species mainly belong to genera with a wide bathymetric distribution and to species-rich genera in the area (Negoescu and Svavarsson 1997). This pattern is mirrored in the distributions of anthuroids collected during IceAGE (Fig. 3), which shows the occurrence of Anthuroidea from the shelf to the deep sea. Negoescu and Svavarsson (1997) suggested that the GIF Ridge restricts the dispersal of deep-living species into the Arctic Ocean, while a rapid decline of water temperature restricts the dispersal of shallow living species into the Arctic. Nevertheless, individuals were found in the north southeast from Greenland and northeast from Iceland in different depths. The Anthuroidea are compared to other parasitic Isopoda in the last paragraph of the section below (Fig. 3b: Aegidae and Fig. 3f: Cirolanidae).

The family Arcturidae (Fig. 3e; suborder Valvifera Sars, 1883) is one of the dominant isopod groups in northern polar regions (Poore and Bruce 2012) and is a common family in south and southeast of Iceland and southeast of Greenland (Stransky and Svavarsson 2006). Arcturids are widely distributed from the shelf down to the deep sea (Kussakin 1982). During the expeditions from which we report here, the family was collected at several sites on the GIF Ridge (Fig. 2). The arcturids are passively filter-feeding, benthic isopods (Wägele 1987; Poore 2001) with a dorsally flexed body, enabling the filtering legs (pereopods) 2–4 to be held above the substrate for feeding while the posterior legs are used for clinging to the substrate (Poore 2001). Their region of occurrence is known to have very productive surface waters and high total organic carbon content in the sediments was observed, which may explain the high abundances also of other suspension feeding peracarids as found for amphipod crustaceans (Brix et al. 2018). The ridge sites, influenced by currents and thus rich in food supply, likely provides their preferential habitat.

Species of Dendrotionidae (Fig. 3g) were present south and northeast of Iceland, while they were missing in the region between Iceland and Greenland. The Desmosomatidae (Fig. 3h) is a species- and genus-rich family. Svavarsson et al. (1993) reported Nannoniscidae (Fig. 4f) occurring in the deep sea and in shallow waters. These two families are distributed all over the world: in shallow waters at high latitudes and at bathyal and abyssal depths in the Nordic seas, the Arctic Ocean, the Northwest Pacific (e.g., Hansen 1916; Hessler 1970; Just 1980, Kussakin 1999; Golovan 2015). The desmosomatids and the nannoniscids had also wide distribution in the Icelandic region, although the nannoniscids were more restricted to shallow waters than the desmosomatids (Brix and Savavarsson 2010). Desmosomaidae and

Table 3 Species list of all samples in the primer analysis for selected BIOICE and IceAGE2 (EBS only) stations

Station	B 2317	B 2323	B 2332	B 2337	B 2360	B 2362	B 2364	B 2844	B 2846	B 2849	866/7	867/1	868/3	869/3	870/4	871/1	872/4	873/6	874/2	876/5	877/2	878/1	879/5	880/2	881/4	881/5	882/5	Summe
Acanthaspidia typhlops	0	0	10	3	0	0	0	0	3	15	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	35
Acanthomunna hystrix	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arcturus baffini	0	0	0	0	8	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
Aspidarachna clypeata	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Astacilla sp. A	0	0	0	0	0	0	0	0	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Astacilla intermedia	0	2	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	3	0	0	0	0	0	0	0	0	0	14
Astacilla granulata	24	2	0	0	177	0	0	0	0	0	0	0	8	0	0	0	26	0	0	0	0	0	16	2	0	0	0	272
Astacilla boreaphilis	0	0	0	0	0	0	0	1677	47	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1725
Austroniscus norbi	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Austroniscus groenlandicus	0	0	0	0	0	0	0	0	0	0	0	3	5	1	0	0	0	0	0	1	0	0	0	0	0	0	0	10
Baeonectes pygmaea	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Baeonectes muticus	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	42	6	0	1	32	83
Calathura brachiata	0	21	354	0	99	1	38	0	0	0	0	0	43	0	0	0	0	0	0	0	0	0	0	6	0	0	0	608
Chelator insignis	0	0	0	0	0	0	0	127	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	134
Cryodesma agnari	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Dendromunna compsa	0	0	0	216	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	230
Dendrotion spinosum	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Dendrotion setosum	0	0	0	0	0	0	0	7	0	0	0	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Desmosoma lineare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	1	7
Desmosoma strombergi	34	0	0	0	0	1	0	0	0	30	0	0	0	20	10	21	0	0	0	0	0	0	0	0	0	0	0	115
Disconectes furcatus	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Disconectes phalangium	0	0	0	0	0	0	0	169	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	172
Disconectes latirostris	0	0	0	0	0	0	0	0	0	0	288	28	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	319
Echinozone sp. A	0	0	0	0	0	0	0	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34
Echinozone coronata	0	1	0	0	18	0	0	7	0	75	0	22	2	0	0	0	0	0	0	4	0	0	0	0	0	0	0	129
Echinozone arctica	0	0	0	0	99	0	0	0	0	0	0	2	151	102	21	0	8	0	3	0	0	0	235	24	0	5	146	936
Eugerda arctica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Eugerda intermedia	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Eugerda glopiceps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	4	0	0	0	11
Eugerda latipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	5	0	2	0	11
Eugerda tenuimana	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	5	23	0	64
Eugerda reticulata	0	0	0	0	0	0	0	7	0	0	0	0	0	13	24	5	0	15	4	0	0	0	0	1	3	35	12	119
Eugerdella ischnomesoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Eugerdella hessleri	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	2	0	2	12
Eugerdella armata	0	7	0	0	0	9	49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	83
Euryope hanseni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Euryope dahli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	4
Eurycope sandersi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	26	0	0	0	0	0	0	10	0	0	39
Eurycope cornuta	0	0	0	0	0	0	0	0	0	0	0	0	0	193	0	2	15	0	0	0	0	0	0	8	0	0	15	283
Eurycope inermis	46	0	0	0	0	1	0	0	0	0	0	0	0	316	2	0	11	7	0	0	0	0	17	101	6	1	64	722
Eurycope aculeata	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	2	0	0	0	0	470	81	0	0	355	910
Eurycope producta	18	2	0	2	0	33	0	0	0	11	126	20	0	62	32	0	0	2	4	0	0	18	401	142	2	6	298	1219
Eurycope brevirostris	147	0	0	0	0	27	0	0	0	0	0	0	0	86	198	4	98	0	48	0	0	0	0	80	126	554	0	1373
Eurydice pulchra	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Exiliniscus clipeatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Gnathia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Table 3 (continued)

Station	B 2317	B 2323	B 2332	B 2337	B 2360	B 2362	B 2364	B 2844	B 2846	B 2849	866/7	867/1	868/3	869/3	870/4	871/1	872/4	873/6	874/2	876/5	877/2	878/1	879/5	880/2	881/4	881/5	882/5	Summe
Gracilimesus gorbunovi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	4
Haplomesus quadrispinosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	2	2	0	0	0	0	0	22	5	0	36
Haplomesus bicuspis	3	4	0	0	0	0	0	91	5	1	0	0	0	85	9	0	1	146	9	0	0	0	16	133	65	0	0	584
Heteromesus schmidtii	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Heteromesus longiremis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	4
Heteromesus frigidus	0	0	0	0	0	0	0	0	0	0	0	0	0	37	10	0	0	1	2	4	0	8	0	0	1	0	0	63
Ilyarachna bicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Ilyarachna dubia	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	4	43	1	0	57
Ilyarachna denticulata	0	0	0	0	0	0	0	23	0	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65
Ilyarachna bergendahli	86	31	0	0	0	26	36	0	0	0	24	1	0	3	0	3	0	2	17	0	0	1	0	4	24	1	5	264
Ilyarachna longicornis	0	0	0	0	0	0	0	28	0	77	80	3	7	0	3	6	51	0	5	0	0	0	0	41	0	9	9	319
Ilyarachna torleivi	91	315	0	0	8	57	408	0	0	0	0	1	0	11	36	2	0	4	2	0	0	0	0	313	30	22	4	1304
Ilyarachna hirticeps	36	178	1	166	270	152	189	0	0	0	0	34	1	16	64	0	0	2	2	0	0	0	190	63	245	475	57	2139
Ischnomesus profundus	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Ischnomesus norvegicus	4	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Ischnomesus bispinosus	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0	0	0	0	0	0	0	0	0	1	0	0	0	8
Janira maculosa	0	0	58	0	16	0	0	0	1	52	0	32	0	0	0	0	0	0	1	3	0	270	1	1	0	1	0	439
Janiralata pulchra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
Katianira biloba	0	0	0	0	0	0	0	0	0	0	0	0	1	15	0	0	0	0	0	7	0	0	0	5	0	0	0	28
Lipomera curvintestinata	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Macrostylis longipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	0	0	8
Macrostylis subinermis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	23	17	3	0	46
Mirabilicoxa cornuta	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mirabilicoxa gracilipes	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Munna fabricii	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	2	0	0	0	1	0	8
Munna groenlandica	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	10	0	39	2	5	0	0	0	80
Munna kroyeri	0	0	0	0	0	0	0	0	0	0	0	0	30	9	0	0	0	1	1	0	0	1	4	6	0	281	0	322
Munna hanseni	26	0	0	0	0	0	0	0	0	0	0	0	242	9	50	0	0	26	10	9	0	1	121	51	0	72	0	523
Munna acanthifera	77	0	0	0	0	1	0	0	0	0	114	0	323	94	0	2	1	10	0	0	1	0	616	123	26	1131	10	2517
Mumeurycope murrayi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Munnopsis typica	14	5	0	13	186	0	2	0	0	1	0	0	16	0	0	0	0	1	0	0	0	0	149	14	114	0	0	518
Munnopsurus giganteus	0	10	0	0	0	0	5	0	0	0	0	0	2	5	3	0	0	0	0	0	0	0	0	2	0	0	0	43
Nannoniscoides angulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	97	6	0	30	0	1	0	0	1	0	1	0	0	0	136
Nannoniscus plebejus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Nannoniscus oblongus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	6
Oecidiobranchus nanseni	16	0	0	0	0	0	0	0	0	0	0	0	0	26	2	2	9	2	1	0	0	0	0	16	0	2	1	118
Paramunna typica	0	0	0	0	0	0	0	0	0	82	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	83
Paramunna bilobata	0	0	0	0	0	0	0	0	0	0	114	13	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	129
Pleurogonium spinosissimum	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Pleurogonium latinanum	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	1	0	0	0	0	0	0	5
Pleurogonium pulchrum	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	6
Pleurogonium inerme	0	0	0	0	0	0	1	0	0	0	0	13	72	47	1	0	4	1	1	0	0	0	14	0	0	2	0	155
Pleurogonium intermedium	0	1	0	0	0	0	0	0	0	1	0	0	6	9	0	0	0	1	1	0	0	1	0	2	292	33	2	345
Pleurogonium rubicundum	64	0	0	0	3	0	0	0	0	0	0	0	2	82	2	0	33	0	2	0	0	0	612	488	100	285	93	1770
Pleuroprion murdochi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	12	0	0	1	0	1	23	13	0	7	0	59
Pleuroprion hystrix	59	51	35	0	32	17	22	0	0	0	0	0	1	1	0	0	17	0	0	0	0	1	11	6	0	0	0	253
Prochelator lateralis	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4

Table 3 (continued)

Station	B 2317	B 2323	B 2332	B 2337	B 2360	B 2362	B 2364	B 2844	B 2846	B 2849	866/7	867/1	868/3	869/3	870/4	871/1	872/4	873/6	874/2	876/5	877/2	878/1	879/5	880/2	881/4	881/5	882/5	Summe
Rapaniscus crassipes	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Thylakogaster sp. A	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Tole spinosa	0	3	0	25	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	33
Tole laciniata	0	35	0	0	0	0	20	1	31	0	2	17	0	0	0	0	3	3	0	3	0	0	0	0	0	0	0	115
Tjtthocope megalura	0	0	0	0	0	0	1	0	9	0	6	0	0	74	102	0	0	0	0	0	0	0	3	3	0	5	0	199
Whoia angusta	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10

Nannoniscidae both contain bottom-dwelling species (Hult 1941; Hessler and Strömberg 1989). The copulatory males have natatory legs, enter the water column in search of females, and can be dispersed by bottom currents. This sexual dimorphism is more pronounced in Desmosomatidae than in Nannoniscidae which may influence dispersal abilities along the Vema fracture zone crossing the MAR (Mid Atlantic Ridge; Bober et al. 2018).

The Haplomunnidae (Fig. 4a) currently has only 11 known species in five genera, described worldwide (Ahyong et al. 2011). This group is characterized by a "spider-like" appearance with unusually long appendages and in some genera (e.g., *Thylakogaster* Wilson and Hessler, 1974) with a dorsally flexed pleotelson (Wilson and Ahyong 2015). Haplomunnids are supposed to live entirely epibenthic and epizoic lifestyles (Wilson and Hessler 1974; Beaulieu 2001a, b). Though rare, they occur in diverse environments in the deep sea (Cunha and Wilson 2003). Their occurrence has been reported from the Mediterranean, North and South Atlantic, northeastern Pacific, and Japan from bathyal to hadal depths (Gamô 1983; Cunha and Wilson 2003). The northernmost record from the North Atlantic is from off the British Isles (Cunha and Wilson 2003), and our findings are, accordingly, extending the known distribution of this family considerably.

The Haploniscidae (Fig. 4b) and Ischnomesidae (Fig. 4c) are also pronounced deep-sea families, without eyes, occurring in Icelandic waters (Lincoln 1985; Svavarsson et al. 1993). Brökeland and Svavarsson (2017) found most haploniscid species occurring to the south of the ridge. Haploniscidae have a flat, bulldozer-like appearance, which may be an adaptation to shallow digging in soft sediments and is reminiscent of terrestrial oniscids (Hansen 1916). Ischnomesidae are more elongated "stick-like" habitus animals with slender legs. However, approaches to classify both families into in- or epifauna remained inconclusive (Thistle and Wilson 1996). Haploniscids have been found to feed on phytodetritus and soft-walled foraminiferans (Brökeland 2010). Like the ischnomesids, the Haploniscidae lack eyes, which is commonly interpreted as a deep-sea adaptation (Wägele 1989). Generally, haploniscids are conserved morphologically, which makes inference of their phylogenetic position troublesome and also hinders differentiation of genera and species (Wägele 1989; Brökeland 2010; Brix et al. 2011). The family Ischnomesidae is distributed throughout the world's deep oceans and continental slopes (Merrin and Poore 2003). This family also occurs frequently in the Nordic Seas and the North Polar Sea (Svavarsson 1984; Malyutina and Kussakin 1996) covering depths from shallow subtidal to the abyss (Sars 1899; Svavarsson et al. 1993). This family appears to live both above and beneath the water-sediment interface with adaptations for both ambulatory

Table 4 Abundance of isopod families in the studied material (mean abundance per sample with standard deviation—SD). The most abundant families in each cluster are marked in italic

	Total		Cluster A	Cluster B	Cluster C	Cluster D	Cluster E	Cluster F
	Mean ± SD	Max	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Arcturidae	17.7 ± 65.4	382	1.0 ± 0.8	13.0 ± 28.8	177.2 ± 189.5	0.2 ± 1.0	3.6 ± 5.1	0.2 ± 0.5
Antarcturidae	0.03 ± 0.2	2	–	–	–	–	0.1 ± 0.6	–
Acanthaspidiidae	0.2 ± 0.5	3	–	0.6 ± 0.9	0.2 ± 0.5	0.06 ± 0.2	0.1 ± 0.6	–
Aegidae	0.09 ± 0.3	2	–	0.1 ± 0.5	–	–	0.2 ± 0.6	
Anthuroidea	2.4 ± 6.2	42	1.5 ± 3.0	5.0 ± 11.6	4.2 ± 4.3	0.2 ± 0.4	3.0 ± 4.2	0.5 ± 0.5
Cirolanidae	0.6 ± 2.5	16	–	0.1 ± 0.3	–	1.0 ± 4.0	1.4 ± 2.9	–
Desmosomatidae	56.1 ± 114.8	629	–	29.3 ± 35.0	68.2 ± 71.1	*110.0 ± 193.3*	50.6 ± 62.7	16.2 ± 14.5
Dendrotionidae	9.8 ± 28.9	128	–	14.2 ± 37.6	44.7 ± 47.0	1.1 ± 3.1	13.6 ± 37.3	1.5 ± 1.9
Haploniscidae	15.0 ± 32.8	148	–	26.7 ± 49.4	1.0 ± 1.4	7.1 ± 9.4	14.1 ± 22.6	7.2 ± 2.8
Haplomunnidae	0.4 ± 2.2	16	–	–	5.5 ± 7.5	–	–	
Ischnomesidae	15.9 ± 26.7	113	2.5 ± 5.0	3.3 ± 9.2	13.7 ± 13.1	36.6 ± 39.9	12.0 ± 15.9	10.7 ± 5.5
Janiridae	9.0 ± 38.3	284	*81.7 ± 135.2*	6.2 ± 9.4	1.2 ± 0.9	0.1 ± 0.7	5.5 ± 5.7	4.0 ± 4.6
Katianiridae	6.9 ± 29.7	172	–	1.5 ± 2.8	–	0.1 ± 0.3	4.1 ± 8.0	0.2 ± 0.5
Munnopsidae	362.2 ± 436.6	1807	10.2 ± 9.0	*567.0 ± 551.8*	*592.2 ± 662.6*	*402.8 ± 421.4*	*291.0 ± 266.1*	*29.0 ± 40.2*
Munnidae	75.6 ± 227.5	1264	14.5 ± 21.2	*254.9 ± 428.6*	23.0 ± 22.8	6.2 ± 12.1	*39.5 ± 49.7*	1.0 ± 2.0
Mesosignidae	0.03 ± 0.1	1	–	–	–	0.1 ± 0.3	–	–
Macrostylidae	6.6 ± 11.2	56	–	3.7 ± 8.8	17.7 ± 11.9	12.2 ± 15.0	0.4 ± 0.9	10.2 ± 7.8
Nannoniscidae	6.8 ± 13.7	58	1.7 ± 3.5	2.2 ± 2.9	0.7 ± 1.5	1.0 ± 1.9	18.2 ± 19.7	1.0 ± 1.4
Paramunnidae	59.9 ± 158.1	864	2.5 ± 2.3	*235.9 ± 260.6*	–	–	16.8 ± 22.5	
Thambematidae	0.5 ± 1.2	7	–	0.2 ± 0.8	1.0 ± 0.8	0.5 ± 1.0	0.09 ± 0.3	1.0 ± 2.0

and fossorial behavior (Hessler and Strömberg 1989). Their habitus appears long, stalked, and brittle (Sars 1899); however, ischnomesids are flexible and motile. While the first pair of legs (pereopods) are used for grasping and burrowing, all other pereopods are walking legs (Hessler and Strömberg 1989). Most IceAGE stations with an abundance of Haploniscidae and Ischnomesidae were located in deeper waters south of the GIF Ridge, with fewer stations occurring on the shelf. Even though these families occurred at several shallow and deep-water sites, the distribution of the species is biased. As mentioned above, Brökeland and Svavarsson (2017) found most haploniscid species occurring south of the ridge. In this case, the physical presence of the ridge may strongly influence this pattern.

The Janiridae (Fig. 4d) are typically found in shallow waters, although deep-sea species are known (Doti and Wilson 2010). Most stations where this family was present were located on the shelf at depths around 400–500 m.

The Katianiridae (Fig. 5a) were previously found in the Norwegian, Greenland and North Polar Seas and in the North Atlantic Ocean, from sublittoral to the abyss with a wide depth range between 5 and 5779 m. During the IceAGE project, the Katianiridae were mainly found in the Nordic Seas. One individual has also been found in the deep Irminger Basin south of the ridge. They were rather rare in the samples when compared to other families, though, and thus it is difficult to draw a conclusion from the observed pattern.

The Macrostylidae (Fig. 5b) have a conserved morphology which is probably the reason for their monogeneric status (Riehl et al. 2014b). A single observation of living animals (Hessler and Strömberg 1989) as well as sampling evidence suggests that this family is comprised of specialized tube dwellers or burrowers (Hessler and Sanders 1967; Thistle and Wilson 1987, 1996, Wägele 1989). This behavior may be reflected in their typically compact habitus and armament with mostly short, heavily setose, and muscled pereopods (Riehl 2014; Riehl et al. 2014b). Although first described from the relatively shallow waters of the Norwegian coast (Sars 1864), the species of the family occur primarily in the abyss (Riehl and Brandt 2010). Macrostylids occur across all depth zones from near-shore and deeper sublittoral habitats to hadal trenches and thus can be considered among those isopod families with the largest depth range (Riehl 2009). The distribution map based on the IceAGE data supports this pattern. It shows an occurrence of the Macrostylidae at stations at all depths. Despite no apparent adaptations for active natatory behavior, macrostylid species have been shown to achieve gene flow across significant distances and depths (Riehl and Kaiser 2012, Bober et al. 2018).

Table 5 The most abundant isopod species in the studied material (mean abundance per sample with standard deviation—SD and maximum). The most abundant species in each cluster are marked in bold

	Total Mean ± SD	Max	Cluster G Mean ± SD	Max	Cluster H Mean ± SD	Max	Cluster I Mean ± SD	Max	Cluster J Mean ± SD	Max
Astacilla granulata	11.3 ± 36.1	177	0.1 ± 0.4	1	7.1 ± 12.2	26	6.5 ± 7.1	16	32.5 ± 70.9	177
Astacilla boreaphilis	63.8 ± 322.5	1677	**246.4 ± 631.0**	**1677**	–	–	–	–	–	–
Calathura brachiata	25.3 ± 73.6	354	1.5 ± 2.8	7	–	–	13.5 ± 20.3	43	**90.8 ± 133.0**	354
Desmosoma strombergi	4.7 ± 9.9	34	–	0	12.8 ± 13.6	34	6.0 ± 11.3	23	0.1 ± 0.4	1
Echinozone arctica	39.0 ± 66.9	235	0.8 ± 1.3	3	19.8 ± 36.9	102	**139.0 ± 86.8**	**235**	39.3 ± 62.1	137
Eugerda reticulata	4.4 ± 8.5	35	1.0 ± 2.6	7	13.4 ± 12.6	35	3.2 ± 5.8	12	–	0
Eurycope brevirostris	57.2 ± 120.0	554	1.5 ± 1.9	4	**179.5 ± 171.8**	**554**	20.0 ± 40.0	80	4.5 ± 11.0	27
Eurycope inermis	27.7 ± 65.1	316	**10.7 ± 27.4**	**73**	64.4 ± 113.4	316	45.7 ± 45.5	101	0.3 ± 0.5	1
Eurycope producta	45.1 ± 95.7	401	**11.7 ± 7.3**	**20**	18.0 ± 22.3	62	241.7 ± 131.4	401	6.1 ± 13.1	33
Haploniscus bicuspis	21.6 ± 42.4	146	**13.8 ± 34.0**	**91**	**47.4 ± 53.8**	**146**	37.2 ± 64.2	133	0.8 ± 1.6	4
Ilyarachna bergendahli	11.0 ± 19.7	86	0.8 ± 1.1	3	19.5 ± 30.5	86	1.2 ± 1.8	4	15.5 ± 17.2	36
Ilyarachna hirticeps	89.1 ± 120.8	475	5.6 ± 13.8	34	**60.0 ± 85.3**	**245**	182.2 ± 210.4	475	**159.3 ± 87.9**	270
Ilyarachna torleivi	54.3 ± 115.5	408	0.5 ± 0.8	2	25.4 ± 31.9	91	83.7 ± 153.1	313	**131.3 ± 181.9**	408
Janira maculosa	16.2 ± 53.0	270	**51.7 ± 98.2**	**270**	–	–	0.7 ± 0.5	1	12.3 ± 23.2	58
Munna acanthifera	104.8 ± 258.1	1131	2.0 ± 3.5	9	**41.8 ± 33.0**	**94**	548.2 ± 438.0	1131	3.1 ± 5.5	14
Munna groenlandica	3.3 ± 9.2	39	**12.1 ± 16.1**	**39**	–	–	1.7 ± 2.3	5	–	0
Munna hanseni	21.7 ± 55.3	242	–	–	5.2 ± 9.6	26	**121.5 ± 85.5**	**242**	–	0
Munnopsis typica	21.4 ± 50.9	186	–	–	–	–	**72.5 ± 69.6**	149	37.3 ± 73.1	186
Nannoniscoides angulatus	5.6 ± 20.4	97	–	–	19.2 ± 35.9	97	0.2 ± 0.5	1	–	0
Pleurogonium rubicundum	73.7 ± 160.7	612	–	–	**53.7 ± 41.5**	**100**	346.7 ± 266.4	612	1.1 ± 1.4	3
Pleuroprion hystrix	10.5 ± 17.3	59	0.1 ± 0.4	1	11.0 ± 22.07	59	4.5 ± 5.0	11	26.1 ± 17.4	51
Pleuroprion murdochi	2.4 ± 5.7	23	0.5 ± 0.5	1	1.7 ± 4.5	12	11.0 ± 9.3	23	–	–

The Mesosignidae (Fig. 5c) is also a pronounced deep-sea family (Wägele 1989). During IceAGE, this rare taxon, with only 17 known species worldwide (Ahyong et al. 2011), was only found at two stations in deep waters south of Iceland. The family occurs primarily at tropical latitudes in the east Pacific Ocean and the Caribbean Sea (George 2003). It is possible that the Nordic Seas have not been colonized by Mesosignidae as the GIF Ridge with its shallow sills may represent a closed barrier.

The Munnidae (Fig. 5d) is a diverse and speciose family, which occurs predominantly in shallower regions. Yet overall, the family and some individual species have wide depth ranges (Wilson 1980). Reflecting this global pattern of munnid distribution, the individuals found around Iceland belong to several species, occurring at a number of shallow stations near the shelf, and also at some stations in deeper waters. The munnids typically cling to various substrates on the bottom, like hydrozoans or sponges, and hence their occurrence may indicate a diverse substratum.

The Munnopsidae (Fig. 5e) is the most speciose family of the marine asellotes (Ahyong et al. 2011). This is the most common family around Iceland and is additionally the family with the widest distribution. The munnopsids are epibenthic and hyperbenthic and their dispersal depends upon active and passive transport in the water column Brandt (1992, 1993). Comparatively good swimming abilities of most species could explain the wide distribution of this family, because it facilitates colonization of new habitats (Schnurr et al. 2014). The Munnopsidae is the only asellote family that includes fully planktonic species. Some munnopsid species are known to be broadly adapted and tolerant to different environments (e.g., Malyutina and Brandt 2007, 2015; Malyutina et al. 2013). In Icelandic waters, they show no distributional limits caused by submarine ridges (Schnurr et al. 2014). Such wide occurrence of the family may partly be explained by the large number of species within it. This number may even be more enlarged by revealing new species previously known as species complexes like in the case of *Eurycope producta* and *E. inermis* Hansen, 1916 (Schnurr et al. this SI). Here, we treat each complex as a single species.

The Paramunnidae (Fig. 5g) were reported by Just and Wilson (2004, 2007) to occur from the intertidal to abyssal depths, and from the Arctic to the Antarctic. The family today comprises 148 species with a preponderance for cold, shallow waters in the southern hemisphere (Wilson 1980). During IceAGE, Paramunnidae occurred only in samples from the crest or slope on both sides of the GIF Ridge covering a wide range of environmental settings. Abyssal encounters were not

made. Most Paramunnidae were present in the northern transect near to the Icelandic coast.

The Thambematidae (Fig. 5h) are without eyesight (Wägele 1989) and probably tube dwellers or burrowers (Hessler and Sanders 1967). Thambematid species have been described from deep waters (> 1300 m) in the North Atlantic and the North Pacific (Birstein 1961, Harrison 1987). Although Svavarsson et al. (1993) claimed that thambematids do not appear in the Nordic Seas, they were reported here at several stations on the slope. Further encounters were made on the Greenland-Iceland Ridge as well as on the slope and in the abyssal Iceland Basin, both south of Iceland.

Parasitic Isopoda

The parasitic isopod families for which we had sufficient taxonomic expertise were included in the analysis on species level. Distribution maps are shown for all taxa found. One has to take into account that parasitic isopod distribution might depend on hosts, especially fish stocks (see ICES reports). Isopods belonging to the suborder Cymothoida were found north and south of Iceland—Anthuroidea (see above, Fig. 3d) and Gnathiidae—or only southwest of the ridge, i.e., the Aegidae White, 1850 and the Cirolanidae Dana, 1852. Cymothoida are protandric hermaphrodites that live as ectoparasits on fishes. Their food consists of blood, lymph, and tissue (Wägele 1989) and they are therefore excluded from the analyses on species level, since their distribution depends on that of their host. The Aegidae White, 1850 (Fig. 3b) were only found at three stations in the southwest of Iceland near to the shelf and in intermediate waters. These temporary ectoparasites attach themselves to fishes for ingestion but afterwards rest on the ocean floor in lairs (Wägele 1989). Aegidae have been reported from the western and central North Atlantic (Kensley 2004). Most Cirolanidae (Fig. 3f) are known from the littoral of moderate and warm oceans. They live on the seafloor under stones, in corals or digging in the sand. All species are carnivorous but differ in their lifestyles that are adapted to the conditions in their habitats (Wägele 1989). Cirolanidae rely on carrion or diseased fishes and are able to survive a long period of starvation (Wägele 1989). Commonly, Cirolanidae are not found in the deep sea but in shallower areas. In this study, most stations where this family occurred were indeed situated on the shelf or in intermediate depths, but in one instance, they also occurred at abyssal depth in the Iceland Basin.

RDA and cluster analysis for isopod families (Figs. 6, 7, and 8; Tables 2 and 4)

These two analyses (Figs. 6, 7, and 8) do not show the same pattern. While the cluster analysis shows a depth pattern, the RDA finds TOC and mud as the most important factors

shaping species distributions. We may explain this result by noting that the RDA method may be sensitive to imprecisions in our raw data. We have "semi-quantitative" samples, a comparably large sampling area, and family-level data (which are not the smallest taxonomic units and may be the most important factor). As most such data are not precise, the final RDA result is also preliminary and more difficult to interpret, making the cluster analysis more convincing than the RDA. It remains poorly known how varying levels of TOC and mud contents influence the distributions of various families. Many asellotes are detritus feeders or feed on Foraminifera (Wolff 1962; Guðmundsson et al. 2000; Brökeland et al. 2010; Riehl et al. 2016), and the latter may therefore depend upon the nutritional value of the bottom sediments or the presence there of an appropriate food (i.e., foraminifers). This condition may also reflect habitat use, as many species are infaunal (e.g., desmosomatids, haploniscids), while others consist mainly of epibenthic species (e.g., munnopsids). However, the ridge and its local currents themselves may strongly influence the local TOC and mud contents.

Distribution patterns of isopod species (Figs. 9, 10, 11, and 12; Tables 3 and 5)

In the species-level cluster analysis (Figs. 9 and 10), station 866, the shallowest station, located at the southern end of the Norwegian Channel at depths of 169 m, was most the distant to all other stations. The deepest stations (below 1500 m; stations 871 and 872) were closest neighbors of cluster H, but did not form a separate cluster. In both cases, we would expect a more distant isopod fauna as all other stations in the dataset were at depths between 302 and 1099 m. Stations 871 and 872 were the only stations truly positioned in the Norwegian Basin, while all other stations (except 866) were slope stations.

Cluster G consists of two subclusters, one with stations on the IFR and a station at the Faeroe–Scotland Channel (877, 876, and 878) and the other with BIOICE stations southwest of the Iceland–Faeroe Ridge (B2844, B2846, B2849) together with one Norwegian Channel station (867). The stations with strong currents are all located south of the Faeroe Islands in the Faeroe Channel. Here, sampling with towed gear was extremely difficult and the macrofauna in these samples was dominated by ophiuroids in extremely high numbers (> 20,000 individuals per station). Little is known of the ecology of several of the species at these stations. The species shaping group G, i.e., *A. boreaphilis*, is presumably a filter feeder. Interestingly, *A. boreaphilis* occurs only at the southwestern stations on the Icelandic side of the IFR and this is only the eastern edge of the distributional margin of this highly abundant species in BIOICE samples South of Iceland (Stransky and Svavarsson 2006). Although not listed as important for shaping the cluster (Table 5), *Chelator insignis* (Hansen

1916), showing a similar distribution pattern like *A. boreaphilis* (Brix and Svavarsson 2010; Brix et al. 2014), also only occurred at these three stations southwest of the Iceland–Faeroe Ridge, (IFR) having here its distributional limit while occurring in high numbers at many stations along the Reykjanes Ridge area. Both species seem not to be able to cope with the current system and influence of cold water masses in the overflow region of the IFR. The other important species in cluster G are *Eurycope inermis*, *E. producta*, *Haploniscus bicuspis*, *Janira maculosa*, and *Munna groenlandica* Hansen, 1916.

Cluster H (comprised of 25 species) might reflect the habitat variability in the overflow region. The stations in this cluster are mostly northern stations below 800 m depth, which may indicate a more arctic fauna. Most important here are *Eurcope brevirostris*, *E. inermis*, *Haploniscus bicuspis*, *Ilyarachna hirticeps*, *Munna acanthifera*, and *Pleurogonium rubicundum* (Table 4).

In clusters H and I, many of the same species are important. Cluster I is described by a high species richness (mean value of 29 species) found along the continental slopes associated with the thermocline located between 400 and 700 m depth at the Scottish and Norwegian slope (Bett 2001, Høisæter 2010). The shelf edge in the Norwegian Channel is particularly diverse and coincides with a high fluctuation in temperature, where both positive and negative values where observed, indicating a varying thermocline depth. Our isopod data show the same pattern as the amphipod data by Brix et al. (2018), where both results on family and species level for IceAGE amphipods showed that species numbers were highest in the slope edge where cold and warm temperatures (water masses) mix, supporting earlier hypotheses (Høisæter 2010) that the thermocline might play an important role in species diversity and distribution patterns. The number of species per cluster corresponded well to the thermocline-influenced high diversity in cluster I. The diverse group I is characterized by two munnids, one pleurogonid, and three munnopsids. Important species in group I are *Echinozone arctica*, *Eurycope producta*, *Ilyarachna hirticeps*, *I. torleivi*, *Munna acanthifera*, *M. hanseni*, *Munnopsis typica*, and *Pleurogonium rubicundum*.

Cluster J contains mostly northern BIOICE stations between 391 and 1099 m (except station B2317 in cluster H) located on the "Icelandic" side (western side) of the Iceland–Faeroe Ridge with a mean value of 13 species. This is the lowest number of species of the four main clusters. Species important to this cluster are, as in I, *Ilyarachna hirticeps* and *I. torleivi.* Important only in J, but also occurring in G and I is the species *Calathura brachiata*.

We counted 76 species occurring north of the IFR and 53 species south of it, whereas 40 species span the IFR to varying extents. Counting by individuals, we found more specimens at the northern stations than at the southern stations. The cluster analysis does not visualize species restricted to only a certain set of stations. In a detailed view, the three southwestern BIOICE stations (2844, 2946, and 2849) show species distributions differing from all other station in the dataset. The same pattern is observed for some stations in the Norwegian Channel. Singletons (20 species occurring at one station only) are as follows: *Eurycope hanseni* Ohlin, 1901; *Eurydice pulchra* Leach, 1815; *Eugerdella ischnomesoides* Hessler, 1970; *Exiliniscus clipeatus* Siebenaller and Hessler, 1981; *Eugerda globiceps*; *Echinozone arctica*; *Dendromunna compsa* Lincoln and Boxshall, 1983; *Dendrotion spinosum* Sars, 1872; *Cryodesma agnari* Svavarsson, 1988; *Baeonectes pygmaea* (Sars, 1870); *Nannoniscus plebejus* Hansen, 1916; *N. oblongus*; *Munneurycope murrayi* (Walker, 1903); *Mirabilicoxa cornuta* (Hessler, 1970); *Janiralata pulchra* (Hansen, 1916); *Ischnomesus profundus* Hansen, 1916; *Ilyarachna bicornis* Hansen, 1916; *Heteromesus schmidtii* Hansen, 1916; *Whoia angusta* (Sars, 1899); and *Pleurogonium spinosissimum* (Sars, 1866). Of these 20, only four occur in the south and the remaining ones in the north (3 in the Norwegian Channel). Species occurring at two stations numbered 14: *Pleurogonium latimanum* Hansen, 1916; *P. pulchrum* Hansen, 1916; *Eurycope dahli* Svavarsson, 1987b; *E. inermis*; *Prochelator lateralis* (Sars, 1899); *Disconectes furcatus* (Sars 1870); *Rapaniscus crassipes* (Hansen, 1916); *Desmosoma lineare* Sars, 1864; *Chelator insignis*; *Austroniscus norbi* Svavarsson, 1982; *Gracilimesus gorbunovi* (Gurjanova, 1946); *Heteromesus longiremis* Hansen, 1916; *Ischnomesus norvegicus* Svavarsson, 1984; *Mirabilicoxa gracilipes* (Hansen, 1916). Of these, only four species were restricted to the south and ten to the north; four of these ten were occurring in the Norwegian Channel only. Figure 11 shows selected species distribution patterns as examples reflecting important species for the clusters, but also species with restricted distribution like *A. boreaphilis* and species not listed in Table 5, but occurring only in the Norwegian Channel like *Paramunna bilobata* Sars, 1866 as well as abundant species influencing more than one cluster (*Ilyarachna torleivi*, *Eurycope brevirostris*).

Diversity patterns north and south of the Iceland–Faeroe–Ridge—a tiny puzzle piece?

The latitudinal species diversity gradient (LSDG) in the northern hemisphere is a well-established diversity pattern with a poleward decline of diversity (Rex et al. 2000). In particular, several authors have shown lower diversity in the deep sea of the Arctic Ocean than in the deep sea of the North Atlantic Ocean. Svavarsson et al. (1993) showed this pattern for isopods at the suborder level, and Brix and Svavarsson (2010) described this for desmosomatid and nannoniscid isopods. For the amphipod family Eusiridae Stebbing, 1888, Weisshappel (2000) documented the same pattern. In our study, we observed higher species numbers in the North to the border of the Arctic Ocean in a restricted area, the IFR and Norwegian

Channel and in a restricted depth range. Interestingly, Chaudary et al. (2017) reported bimodal peaks in species richness at about 40° latitude with a decline polewards. In a worldwide analysis of biogeographic realms, the shelf always showed unique patterns (Costello et al. 2017). Both papers rely on OBIS data which do not include BIOICE or IceAGE datasets so far. In our small-scale analysis, we might observe the shelf as a pathway from Norway to Iceland and further on to Greenland or vice versa, and at the same time observe specific patterns at the local scale. In the case of different example species (e.g., *Idotea* Fabricius, 1798 as isopod), the shallow water fauna (0 to 100 m depths) around Iceland is much more similar to the fauna of the Northeast Atlantic than to the fauna of the West Atlantic (Wares and Cunningham 2001). Recently, in the case of echinoderms and polychaetes a Pacific–Arctic connection was recognized as well as shared European–American haplotypes (Hardy et al. 2011).

Conclusion

The thermocline seems to affect species numbers both north and south of the IFR, but in north more than in the south. The number of species per cluster was correlated with the high thermocline diversity in cluster I. Cluster G was also clearly explainable as a southern cluster. The cluster 871/872 contained the deepest stations (below 1500 m), which appear to be different from the rest of stations below 1000 m, and also the Nordic Seas station 866 is separate, indicating a specific northern fauna not found at any other station. Possibly, a more "warm water fauna" and a more "cold water/arctic fauna" overlap with varying conditions (fluctuations of the water masses) on the slope edge in the region of the Norwegian Channel in connection with a faunal turnover from shallow to deep-water fauna. Interestingly, the northern slope of the IFR yields a higher number of species (76) than the southern slope (53). Looking at the distribution pattern of single species, we find restrictions not visible in the cluster analysis. We have to take into account that our dataset—although it is comparably large—is relatively a small one (27 stations, 100 species, not complete abiotic data) in a statistical sense on a species level. On the level of isopod families, we are limited by the taxonomic resolution. However, summarizing our family-level data, a depth pattern can be observed for shallow water families like the Paramunnidae and typical deep-sea families, like the Haploniscidae and Ischnomesidae, while most families have high abundances at many different stations and at different depths both north and south of the ridge.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors. Permits and approval of field or observational studies have been obtained by the authors. Museum collection numbers are not provided, but a statement is given: So far all material is planned for the final storage in two museums: Zoological Museum Hamburg and Senckenberg Crustacean Collection in Frankfurt. All IceAGE isopod specimens and the BIOICE munnopsids used in this study are available via DZMB HH numbers and stored in the material archive hosted at the DZMB. All remaining BIOICE isopods determined during this study are hosted at the University of Iceland under the responsibility of Jörundur Svavarsson. We do not describe new species and do not use any genetic data.

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