



Predictive models using *randomForest* regression for distribution patterns of meiofauna in Icelandic waters

Alexandra Ostmann¹ · Pedro Martínez Arbizu¹

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Abstract

The exchange of cold polar waters from the north and warm North Atlantic waters from the south is limited by the Greenland-Iceland-Scotland Ridge (GSR) which then may act as a barrier for faunal exchange from the deep Arctic and deep Atlantic basins. We investigated the meiofauna density and distribution patterns from different regions north and south of the GSR at water depths between 307 and 2749 m. A total of 84 multicore samples were examined collected during the IceAGE1 (Icelandic marine Animals: Genetics and Ecology) project in summer 2011. We used a *gradientForest* approach to assess the magnitude of compositional change and the thresholds of remarkable community changes along environmental variables. *randomForest* regression was applied to predict the meiofauna on a spatial contiguous scale with a set of 23 environmental variables. Meiofauna density ranged between 187 and 3185 individuals per 10 cm² with the highest densities observed north of the GSR. Nematoda was the most abundant taxon among the meiofauna community, followed by Copepoda and Nauplii. In the Irminger Basin, Gastrotricha was the third most abundant taxon, while in all other regions, Ostracoda was the third most abundant. Food supply, water depth, bottom water oxygen, and hydrographic activity being the most important variables for community changes explain up to 86% of the variation observed in the meiofauna communities.

Keywords Meiofauna community · Distribution · Iceland · Environmental gradients · *gradientForest* · *randomForest*

Introduction

The sea around Iceland is a perfect natural laboratory for studying the effects of climatic changes to benthic marine communities. It is located at the transition of the Greenland, Iceland, and Norwegian Seas (GIN Seas) to the north (characterized by cold, highly oxygenated and less saline waters) and the northernmost North Atlantic waters to the south (characterized by comparatively warm, less oxygenated and more

saline waters) (Hansen and Østerhus 2000). Although the GIN Seas and the northernmost North Atlantic Ocean are separated by the Greenland-Iceland-Scotland Ridge (GSR), extending from west to east, the exchange of waters is not fully blocked, but there exists an overflow water exchange (e.g., Beaird et al. 2013; Rudels et al. 2002).

Meiofauna organisms are among the most abundant group of the benthic communities (Rex and Etter 2010), even in the deep sea (Wei et al. 2010). Meiofauna organisms are influenced by various environmental variables such as food availability (Danovaro et al. 1996; Hoste et al. 2007; Pfannkuche 1985; Pfannkuche and Thiel 1987; Vanreusel et al. 1995b), sediment granulometry, temperature, and salinity (Kennedy and Jacoby 1999; Soltwedel 2000). Meiofauna densities follow bathymetrical gradients as reported for the Antarctic Ocean (Gutzmann et al. 2004; Herman and Dahms 1992; Vanhove et al. 1995), Pacific Ocean (Kitahashi et al. 2013), North Atlantic Ocean (Pfannkuche 1985; Soetaert et al. 2002; Vanaverbeke et al. 1997a), and Arctic Ocean (Pfannkuche and Thiel 1987; Schewe 2001; Schewe and Soltwedel 1999; Vanaverbeke et al. 1997b; Vanreusel et al. 2000).

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✉ Alexandra Ostmann
alexostmann@googlemail.com

✉ Pedro Martínez Arbizu
pmartinez@senckenberg.de

¹ German Center for Marine Biodiversity Research (DZMB),
Senckenberg am Meer, Südstrand 44,
26382 Wilhelmshaven, Germany

Considering the Icelandic waters, however, research on meiofauna communities and their relationship to environmental variables are rather scarce. Despite some studies related to Harpacticoida Copepoda in an intertidal pool, freshwater Harpacticoida, and Icelandic Ostracoda (Apostolov 2007; Steinarsdóttir et al. 2003; Yasuhara et al. 2014), there are two main research expeditions to the Norwegian Sea (NORBI) and the Faroe Ridge (RV Anton Dohrn) (Dinet 1979; Thiel 1971, 1975), indicating an influence of hydrographic conditions concomitant with changes in food supply to the sea floor.

In the present study, we will investigate the Icelandic meiofauna community in different regions north and south of the GSR along bathymetrical gradients. Further, a *gradientForest* approach will be used to assess community changes along environmental variables, and finally, we will generate predictive models using *randomForest* regression (Breiman 2001; Liaw and Wiener 2002) to predict selected meiobenthic taxa on a contiguous geographic space at regional scale around Iceland.

The following research questions are addressed:

1. Does the meiofauna community differ between the geographical regions?
2. Which are the most important variables causing changes in the community structure and which taxa are most affected by these changes?
3. Do the predictive models reflect observed differences in the study area?

Material and methods

Study site

The study area covers an area of about 750,000 km², including the northernmost North Atlantic and the south-western part of the Greenland, Iceland, and Norwegian Seas (GIN Seas). The Greenland-Scotland Ridge (GSR) extends from west to east, featuring a mean depth of less than 500 m and three deep sills.

West of Iceland, cold and less saline water is transported across the Greenland-Iceland Ridge (GIR) into the Atlantic as Denmark Strait Overflow Water (DSOW), which flows along the Greenlandic coast as the Deep Water Boundary Current (DWBC). The surface East Greenland Current (EGC) transports PW across the ridge. East of Iceland cold water is transported across the Iceland-Faroe Ridge (IFR) as Iceland Scotland Overflow Water (ISOW), which flows along the Reykjanes Ridge into the Irminger Basin (Hansen and Østerhus 2000; Pickart et al. 2005; Logemann et al. 2013; Våge et al. 2011, 2013).

Due to geostrophic forces, there is a warm water inflow from the Atlantic into the Arctic Ocean. Two surface currents, the North Icelandic Irminger Current (NIIC) and the North Atlantic Current (NAC), transport Modified North Atlantic Water (MNAW) into the Arctic Ocean.

Processing of sediment samples

Sediment samples were collected with a multicore (company Oktopus GmbH, MUC, 12 cores, inner area 72.38 cm² per core) during the IceAGE1 cruise (M85/3) from 27 August to 28 September 2011 on board the German RV Meteor at 24 stations. The study area was divided into four regions, Iceland Basin (IceBas, 7 stations), Irminger Basin (IrmBas, 4 stations), Denmark Strait (DenStr, 6 stations), and Norwegian Sea (NorwSea, 7 stations), located north and south of the GSR (Fig. 1, Table 1). Sediment samples were collected along bathymetrical gradients ranging from 307 to 2749 m. At each station, one deployment was conducted. Of each deployment, four cores were used to study density and distribution of metazoan meiofauna. The top 5 cm sediment of each core was fixed in 4% buffered formalin. Due to logistic difficulties with the deployment of the multicore in the Denmark Strait (broken cores and low number of samples), the multicore was deployed twice at each station there. From these deployments, two cores each were chosen for analysis.

Back in the laboratory, the fixed samples were washed through a 40- μ m sieve and centrifuged 3 times at 4000 rpm for 6 min using a colloidal silica polymer (Levasil) as floating medium and kaolin to cover the heavier particles according to McIntyre and Warwick (1984). The supernatant, which contains organic material and organisms, was decanted with tap water after each step and stained with Rose Bengal. Meiofauna was sorted to higher taxon level and counted using a Leica MZ12.5/9 dissecting microscope.

Statistical analyses

Any procedure written in italics refers to analyses performed in R (R Core Team 2016). We tested for differences in meiofauna density between (a) northern and southern samples (of the GSR), (b) 4 regions, and (c) depths classes (upper slope [0–1000 m], lower slope [1000–2000 m], and abyssal [2000–3000 m]) using permutational multivariate analysis of variance (PERMANOVA, *adonis*) (Anderson 2001; Anderson and Walsh 2013; McArdle and Anderson 2001). Post hoc, pairwise comparisons were performed for water depths and regions, with *p* values Bonferroni corrected using the custom function *pairwise.adonis* (<https://github.com/pmartinezarbizu/pairwiseAdonis>). The analyses were performed on fourth root transformed data using a Bray-Curtis dissimilarity matrix (999 permutations).

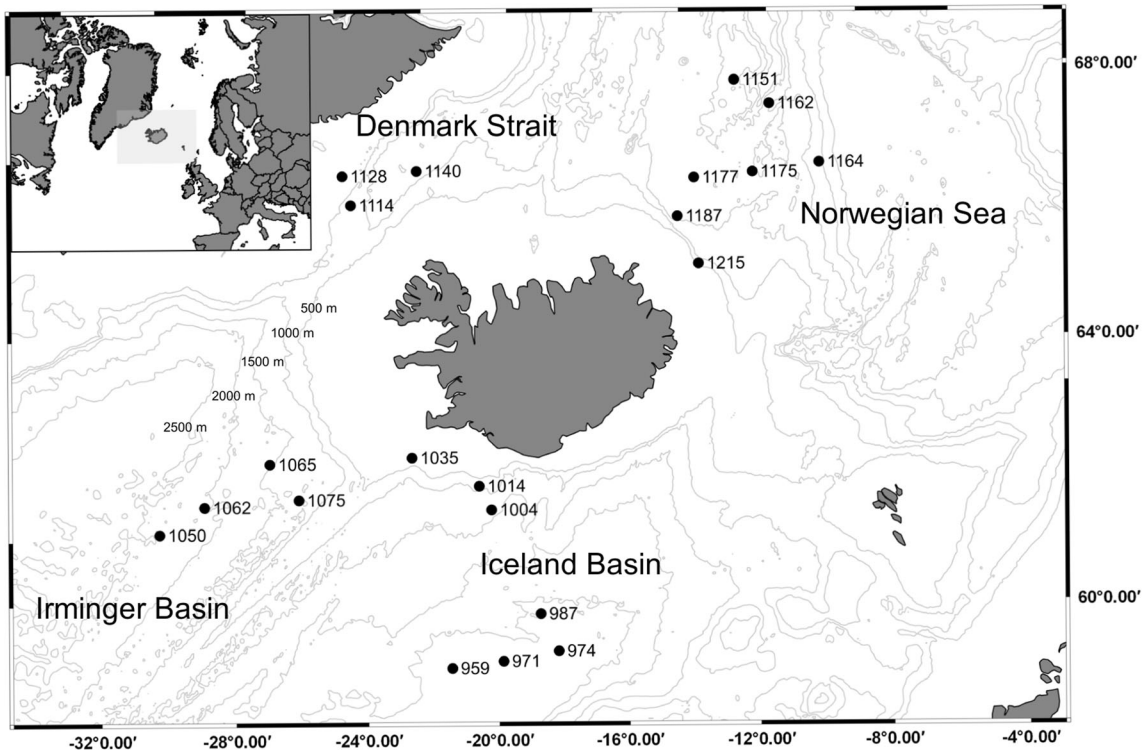


Fig. 1 Sites in the Icelandic waters at which sediments samples were collected with the multicorer. Small numbers at the contours indicate water depth

Table 1 Visited sites during the IceAGE1 cruise. Given are sampling date, respective region, geographical coordinates (decimal degrees), and number of cores (9.6 cm inner diameter)

Station	Date	Region	Longitude	Latitude	Depth [m]	No. of cores
959	28 Aug 2011	IceBas	-21.5	60.05	2749	4
971	29 Aug 2011	IceBas	-19.89	60.18	2670	4
974	30 Aug 2011	IceBas	-18.14	60.34	2563	4
987	31 Aug 2011	IceBas	-18.7	60.93	2493	4
1004	02 Sept 2011	IceBas	-20.35	62.56	1392	4
1014	03 Sept 2011	IceBas	-20.79	62.93	911	4
1035	04 Sept 2011	IceBas	-23.17	63.33	307	4
1050	05 Sept 2011	IrmBas	-31.37	61.62	2528	4
1062	08 Sept 2011	IrmBas	-30.06	62.17	1928	4
1065	08 Sept 2011	IrmBas	-28.08	63	1619	4
1075	09 Sept 2011	IrmBas	-26.93	62.5	1175	4
1114	13 Sept 2011	DenStr	-26.27	67.21	684	4
1128	14 Sept 2011	DenStr	-26.75	67.65	320	4
1140	15 Sept 2011	DenStr	-23.7	67.84	1240	4
1151	17 Sept 2011	NorwSea	-9.93	69.09	2270	4
1162	18 Sept 2011	NorwSea	-8.58	68.64	1962	4
1164	18 Sept 2011	NorwSea	-6.96	67.59	2403	4
1175	20 Sept 2011	NorwSea	-9.74	67.62	1711	4
1177	20 Sept 2011	NorwSea	-12.17	67.65	1820	4
1187	21 Sept 2011	NorwSea	-13.01	67.07	1581	4
1215	22 Sept 2011	NorwSea	-12.37	66.3	733	4

IceBas Iceland Basin, *IrmBas* Irminger Basin, *DenStr* Denmark Strait, *NorwSea* Norwegian Sea

Multivariate statistics were performed using the package *vegan* (Oksanen et al. 2016). We used non-metric Multidimensional Scaling (nMDS, function *metaMDS*) as an unconstrained ordination method (Minchin 1987). The nMDS was based on Bray-Curtis dissimilarity and fourth root transformed data. The function *envfit* was used to fit environmental variables as vectors onto the ordination of the nMDS (999 permutations). This method shows which environmental variable correlates most with the axis of the ordination. The relative length of the vector in comparison to the vector length of other variables is the strength of the variable. Therefore, the direction and length of the respective variable can be related to relative importance for structuring the communities. For image clarity, we display only the 11 most important variables, out of 23.

To explore the nonlinear multispecies response of meiofauna to environmental gradients, we applied the *gradientForest* method (Ellis et al. 2012) as a coherent extension to our *randomForest* regression approach, favoring this method over most popular linear alternatives like CANOCO (ter Braak 1986). *gradientForest* cannot only be used to explore the magnitude of community change along environmental gradients but also to discover threshold values, at which community (or single taxon) changes are most relevant (Pitcher et al. 2012). The R^2 value provides the variance explained weighted over all species. *gradientForest* uses the conditional rather than the marginal importance (by performing conditional permutation of predictors over non-correlated groups of variables) to account for correlated predictors (Strobl et al. 2008; Ellis et al. 2012).

For each predictor, the split values of the regression trees are associated with the model accuracy improvement to produce response functions to community (and taxa) change along predictors. These curves are standardized and normalized to become comparable between species and predictors. For implementing *gradientForest* with our Icelandic dataset, we followed the vignette of the R package *gradientForest* (Pitcher et al. 2011) but growing 1000 rather than 500 trees.

Regression models

The spatial distribution of meiofauna (Nematoda, Copepoda, Nauplii, Ostracoda, Kinorhyncha, Tardigrada, Gastrotricha, Tantulocarida) was predicted using a set of 23 environmental predictor variables. Spatial layers of sediment grain sizes (sand, silt clay) and organic matter (total organic carbon [TOC], total nitrogen [N], C/N ratio, chlorophyll *a*, and pigment derivatives) were taken from Ostmann et al. (2014), who worked on sediment samples from the exact locations and deployments. Hydrographic layers (bottom salinity and temperature including temperature maximum, temperature minimum, and inter-annual temperature range variation) were taken from NISE data (Norwegian Iceland Seas Experiment, 1998–2008, Nilse et al.

2008). Bottom oxygen was based on the dataset provided by Seiter et al. (2005). Further, particulate organic carbon (POC) flux to the bottom and the seasonal variation index (SVI) of POC flux (Lutz et al. 2007), depth (GEBCO_08 layer, 30 arc seconds' resolution from www.gebco.net), sediment thickness (NOAA; Divins 2003), and bottom roughness (NOAA) were used as environmental layers.

The point sampling tool of QGIS (QGIS Development Team 2016, version 2.4.0, Chugiak) was used to extract the values of the 23 prediction layers at the exact position of IceAGE1 stations and for producing the predicting dataset.

randomForest regression is a nonparametric and nonlinear method to predict a quantitative variable using an ensemble of regression trees (Breiman 2001). At each split of the *randomForest* tree, the model is using a random subset of the predictors for the best split. The decision tree is built from 2/3 of the data (in-bag) and the other 1/3 of the dataset is used for prediction error and importance of predictors. The *randomForest* models were generated with the R package *randomForest* (Liaw and Wiener 2002) using 2000 random trees ($n_{tree} = 2000$) and 8 random variables ($m_{try} = 8$). The performance of the model is given as the % of explained variance of the model (R^2). The resulting models were used to predict meiofauna density on a grid of 22,139 points distributed around Iceland.

Maps were generated on a regional scale interpolating the values of this point-grid using the Generic Mapping Tools (Wessel et al. 2013, GMT 5.1.0, SOEST, Hawaii). Interpolation was done with the surface function (continuous curvature surface gridding algorithm) using a gridding space of 0.005 geographic degrees (WGS84) and a tension factor of 0.5.

Results

Meiofauna density (per 10 cm²)

In 84 samples, 680,701 meiofauna individuals out of 25 taxa were counted (total area of all corers covering 0.608 m²). The highest densities (per corer) were observed at stations in the Iceland Basin and Norwegian Sea (2554–3185 ind/10 cm²). Lowest densities (187–486 ind/10 cm²) were found in the Irminger Basin as well as the Iceland Basin (Table 2). In the other samples, density was intermediate varying between 500 and 2000 ind/10 cm². Most taxa, such as Kinorhyncha (max. 19 ind/10 cm²), Ostracoda (max. 28 ind/10 cm²), and Copepoda (max. 109 ind/10 cm²) reached their maximum density in the Norwegian Sea. Tardigrada reached a maximum of 25 ind/10 cm² in the Denmark Strait. The density of Gastrotricha was highest in the Irminger Basin. Significant differences were found between (a) northern and southern sites, (b) between the basins, and (c) different water depths (PERMANOVA, Table 3, Fig. 2). Sites located north of the

Table 2 Meiofauna density in Icelandic waters. Given are individual numbers per 10 cm² at the stations with median, minima, and maxima

	959			971			974			987			1004			1014			1035		
	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median
Halacaroida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Annelida	5	9	6	5	8	6	3	10	5	7	10	8	6	10	9	11	13	13	32	51	45
Bivalvia	0	1	1	0	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	7	4
Coelenterata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copepoda	20	42	27	23	31	29	9	21	10	20	35	26	35	63	42	54	64	58	56	84	71
Nauplii	41	54	45	39	55	49	15	32	19	38	50	45	57	141	80	76	106	94	69	150	79
Crinoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastrotricha	0	1	1	1	1	1	0	1	0	0	1	0	0	1	0	0	1	0	0	3	1
Holothuria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Kinorhyncha	1	2	1	1	4	3	0	1	0	2	3	2	1	3	2	6	10	8	10	11	11
Loricifera	0	2	1	1	5	2	2	3	2	0	2	1	1	2	2	0	2	1	0	2	1
Nematoda	645	892	723	444	764	524	228	371	289	641	977	840	566	1272	824	758	1261	916	1045	2223	1506
Ophiuroidea	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostracoda	5	7	6	3	7	7	2	6	4	2	5	4	3	5	4	4	6	4	9	15	12
Pantopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Priapulida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rotifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sipunculida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solenogastres	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indet	0	3	0	0	1	1	0	1	0	0	2	1	1	4	2	0	2	1	0	7	2
Tanaidacea	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	1
Tantulocarida	0	1	0	0	3	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Tardigrada	0	2	1	2	7	3	0	2	1	3	11	5	3	9	4	9	14	11	2	8	5
Sum	733	1010	809	538	859	630	268	448	328	724	1068	945	687	1512	968	947	1467	1104	1251	2554	1731
Denmark Strait																					
Irminger Basin																					
	733	1010	809	538	859	630	268	448	328	724	1068	945	687	1512	968	947	1467	1104	1251	2554	1731
	1050			1062			1065			1075			1114			1128			1139		
Halacaroida	0	0	0	0	0	0	0	0	0	0	0	0	2	7	4	1	10	6	0	2	1
Amphipoda	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Annelida	3	5	4	6	9	8	3	6	5	8	13	10	11	16	13	19	38	22	8	12	11

Table 2 (continued)

Priapulida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Rotifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sipunculida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Solenogastres	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indet	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	2	0	3
Tanaidacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Tantulocarida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Tardigrada	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Sum	1122	2638	1528	1400	3131	1860	722	1050	974	1479	2072	1687	844	1358	1084	882	1827	1368	2755	3185	3002

GSR exhibit a higher meiofauna density compared to the southern sites (Fig. 2a). Meiofauna density was significantly higher in the Norwegian Sea compared to all other regions, while the lowest densities were observed in the Irminger Basin (Fig. 2b). The overall meiofauna density was significantly higher at the upper slope compared to the abyssal and lower slope (Fig. 2c). The highest taxa richness (18 taxa) was observed at stations in the Iceland Basin, Denmark Strait, and Norwegian Sea, while other stations in the Iceland Basin, Irminger Basin, and Norwegian Sea showed the lowest richness (9 taxa).

Meiofauna community structure

Nematoda were most abundant among the meiofauna community. They dominated with values from 78.38% (Irminger Basin) to 95.71% in the Norwegian Sea with an overall median at 88.13%. Copepoda and their Nauplii followed in dominance (~1.42–5.96 and 1.6–8.82%, respectively), with an overall median of 3.58 and 5.11%, respectively.

Together with Annelida (excluded from further analyses, because fragments were count instead of specimens) and Ostracoda, the mentioned groups were observed in all samples. Kinorhyncha, Tardigrada, Loricifera and Bivalvia (both latter excluded from further analyses), and Gastrotricha were recorded in more than 60 out of 84 samples. Other taxa were found only sporadically (Table 2). In the Irminger Basin, Gastrotricha were the third most abundant taxa, while in the other regions, Ostracoda dominated following Nematoda and Copepoda.

Almost every environmental variable correlated with the ordination of the nMDS (*envfit*, Fig. 2d, Table 4). The vectors of oxygen, chlorophyll *a*, nitrogen, clay, and silt direct to sites in the Norwegian Sea, while POC, bottom roughness, temperature, and sand mostly reflect sites located in the Iceland Basin, Denmark Strait, and Irminger Basin. The C/N value (not shown in the graph) directed to the Irminger Basin, reflecting the second axis of the nMDS. Results indicate an influence of environmental variables on the meiofauna community in the Icelandic waters.

Meiofauna along environmental gradients

Meiofauna density follows bathymetrical gradients in the Norwegian Sea and Iceland Basin, mainly represented by a decline in densities of Nematoda, Copepoda, and their Nauplii. In the Irminger Basin and the Denmark Strait, overall meiofauna density did not decrease with depth (Table 2).

The eight most important variables shaping the overall meiofauna community are in decreasing order POC (particulate organic carbon flux), water depth, TOC (total organic carbon), bottom roughness, oxygen, nitrogen, sediment chlorophyll *a* content, and SVI (seasonal variation index of the

Table 3 Results of the PERMANOVA analysis. Shown are *p* values for meiofauna density

	Df	fm	R^2	Density	
				<i>p</i>	<i>p</i> adj
Location	1	18.595	0.18485	0.001**	
Iceland Basin vs Irminger Basin		20.6923209	0.33006149	0.001	0.006*
Iceland Basin vs Denmark Strait		0.7489722	0.01932883	0.098	0.534
Iceland Basin vs Norwegian Sea		10.3973716	0.16145646	0.001	0.006**
Irminger Basin vs Denmark Strait		19.9515988	0.43418726	0.001	0.006**
Irminger Basin vs Norwegian Sea		39.1409823	0.48238241	0.001	0.006**
Denmark Strait vs Norwegian Sea		4.6918287	0.10989992	0.001	0.042*
North vs south	1	32.95906	0.2867026	0.001	0.001**
Depth classes	1	10.044	0.10912	0.001**	
Abyssal vs lower slope		1.938505	0.03031827	0.146	0.438
Abyssal vs upper slope		13.741667	0.23001814	0.001	0.003**
Upper Slope vs lower slope		5.119085	0.08658937	0.008	0.024*

df degree of freedom, *p* adj Bonferroni-corrected *p* value

Signif. codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' ', 1

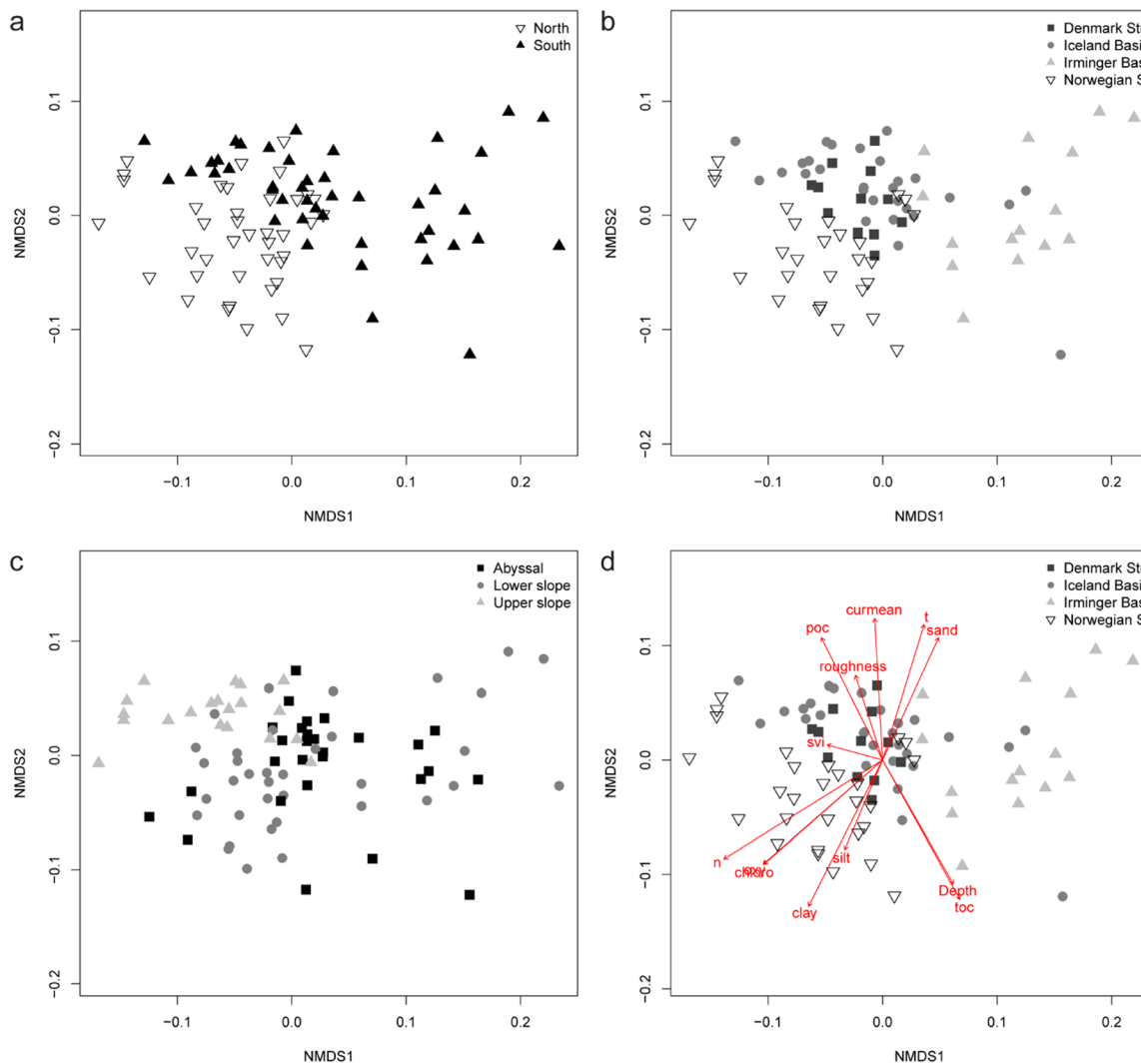


Fig. 2 Non-metrical multidimensional scaling (nMDS, abundance data fourth root transformed) displaying the differences observed between factors (Bray-Curtis dissimilarity, fourth root transformed data. Stress: 0.142), a north-south direction; b regions; c depth classes (upper slope

[0–1000 m], lower slope [1000–2000 m], abyssal [2000–3000 m]); d environmental variables plotted as vectors into the ordination. For significance levels, see Table 4

Table 4 Correlation between environmental variables and nMDS ordination (Bray-Curtis dissimilarity matrix, 999 permutations)

	NMDS1	NMDS2	R^2	Pr (> r)
Depth	0.53574	−0.84438	0.3129	0.001***
Salinity (bottom water)	−0.2064	0.97847	0.0147	0.529
Temperature (bottom water)	0.27358	0.96185	0.3493	0.001***
Oxygen (bottom water)	−0.7058	−0.70842	0.4323	0.001***
Annual minimum temperature	0.27927	0.96021	0.3448	0.001***
Annual maximum temperature	0.23806	0.97125	0.3453	0.001***
Temperature annual difference	−0.10951	0.99399	0.0954	0.016*
Current	−0.11287	0.99361	0.1437	0.003**
Current maximum	−0.1172	0.99311	0.2132	0.001***
Current mean	−0.06371	0.99797	0.33	0.001***
Current minimum	−0.04421	0.99902	0.2458	0.001***
Particulate organic carbon	−0.47167	0.88178	0.3006	0.001***
Seasonal variation index (of POC flux)	−0.99293	0.1187	0.054	0.086
Roughness	−0.37533	0.92689	0.0961	0.021*
Sediment thickness	−0.31717	0.94837	0.0744	0.045*
Sand	0.44689	0.89459	0.2676	0.001***
Silt	−0.45656	−0.88969	0.1258	0.005**
Clay	−0.4362	−0.89985	0.4506	0.001***
TOC	0.49621	−0.86821	0.4206	0.001***
Nitrogen	−0.85453	−0.5194	0.5798	0.001***
C/N	0.99086	−0.13488	0.5403	0.001***
Chlorophyll α	−0.70941	−0.7048	0.4329	0.001***
Pigment derivatives	−0.716	−0.6981	0.426	0.001***

Signif. codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', 0.1 ' ', 1

POC flux) (Fig. 3). The shapes of the cumulative importance curves of the meiofauna to environmental change are nonlinear and some of them show thresholds that produce step changes in community composition (Figs. 4 and 5). The upper panels show the effect on the five most responsive taxa. The cumulative effect on all taxa is displayed in the lower panels (community level response). Meiofauna community changes occurred at around 17 and 27 mg C/m² day (POC flux), with the greatest influence on Kinorhyncha and Copepoda with its Nauplii. Water depth, as second most important factor, influences mostly Copepoda, Kinorhyncha, and Ostracoda with thresholds around 1050 and 650 m which shall correspond with predicted abundance maxima for these taxa at the northern and southern slopes respectively (Fig. 5c, e, f). The largest changes in the meiofauna community occur at 1.7 and 2.1% TOC in the sediments, mainly influencing Nauplii, Copepoda, and Ostracoda. The most abundant taxon, the Nematoda is influenced mostly by bottom water oxygen with a big step at 289 $\mu\text{mol/kg}$, chlorophyll *a* in the sediment with a step at 0.08 $\mu\text{g/g}$, and seasonal variation of POC flux (SVI) with two steps around 1.1 and 1.42 g/m². The amount of nitrogen influences the meiofauna at a threshold of 0.088%, which has effects on Ostracoda.

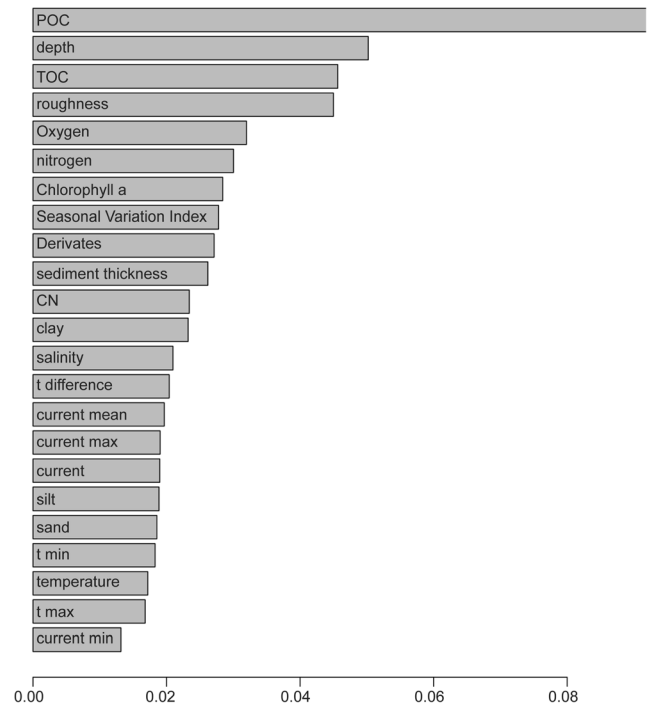


Fig. 3 Predictor importance plot illustrating the mean importance of each variable weighed by species R^2

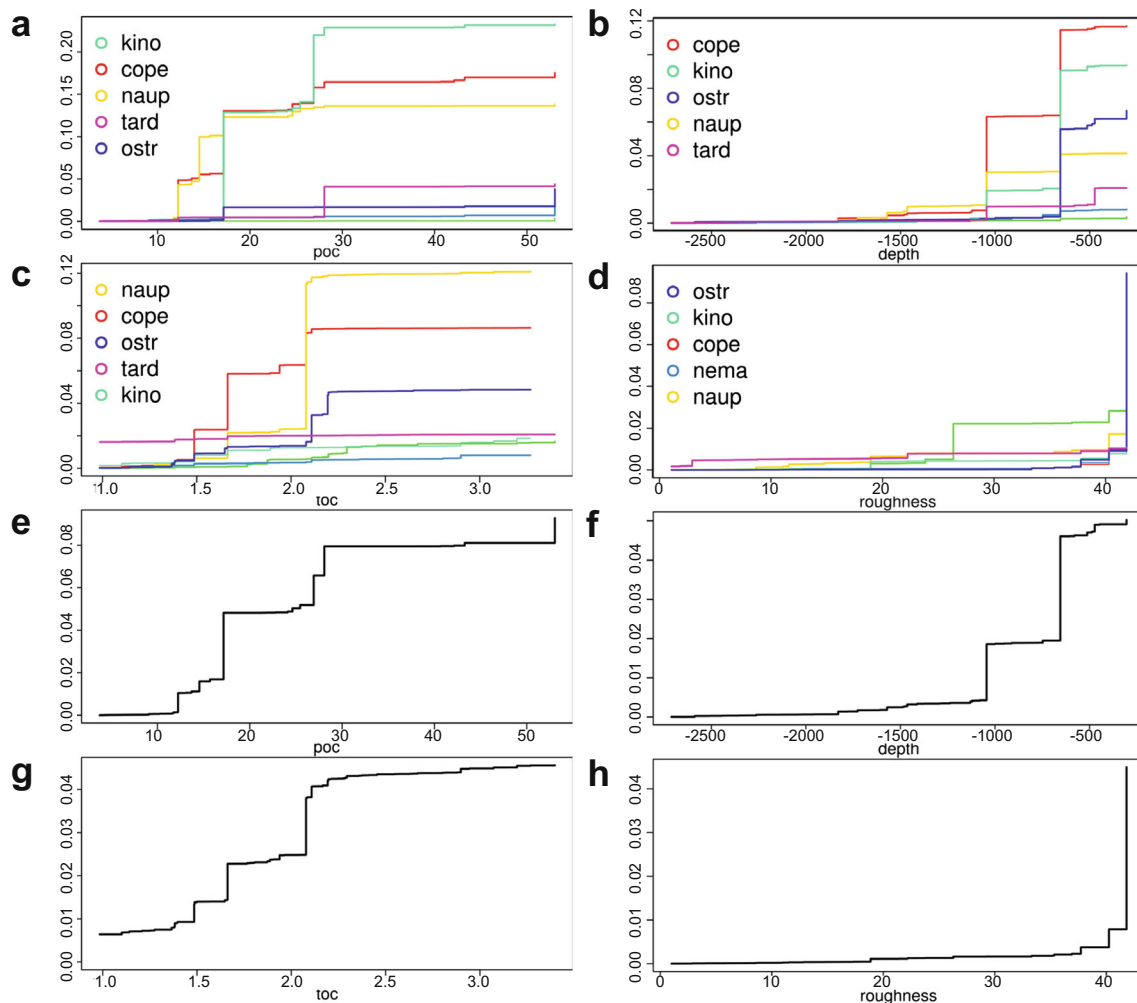


Fig. 4 Cumulative plots. **a–d** Taxa cumulative plots showing the value of the environmental variable at which a split change of respective taxa occurs (in respective color). **e–h** Predictor cumulative plots (particulate organic carbon [POC], water depth, total organic carbon ([TOC],

sediment), bottom roughness) showing the value of the environmental variable which is responsible for the split changes in the overall meiofauna abundance

Regression models

The prediction models were generated with a set of 23 predictors and 84 samples. For each model, a random set of predictors was used. A more intuitive approach to assess model performance was to calculate the Pearson product moment correlation between observed values used for training and predicted values at these sites. The variation of the abundance of the meiofauna taxa could be explained with up to 86% (Table 5). Maps were generated on a regional spatial scale for the overall meiofauna density per 10 cm², the taxa richness, and density of six selected meiofauna taxa (Figs. 6 and 7).

For the six taxa, the explained variation was higher than 65%. Gastrotricha were predicted with a variation of 35.11% and for the Tardigrada, predictor variables could explain 43.62% of the variation. A poor model was performed on Tantulocarida (–19.24% of the variance). High densities of total meiofauna were

predicted along the Greenland-Iceland-Scotland Ridge on the upper slope (1500–2900 ind/10 cm²) and north of the GSR in the Norwegian Sea (Fig. 6a). North-east of Iceland (6–12° W, 68–70° N), the model predicted one spot of high meiofauna densities. Generally, meiofauna density decreased from the upper slope to the abyssal. Nematoda, Copepoda and their nauplii, Ostracoda, and Kinorhyncha densities (Fig. 6b–f) were predicted to be highest at the Icelandic upper slope and along the Greenland-Iceland-Scotland Ridge.

Furthermore, the densities of these groups were predicted slightly higher north than south of the GSR. Tardigrada (Fig. 7a) were predicted to be highest in the Irminger Basin, southwest of Iceland, and south of the Faroe Islands (5–10 ind/10 cm²). High Gastrotricha density (Fig. 7b) was predicted north of the GSR (~2 ind/10 cm²) on the upper Icelandic slope, along the Iceland-Faroe Ridge (2 ind/10 cm²) and at the Reykjanes Ridge south of Iceland (2.4 ind/10 cm²). Lower densities were found in the deep sea north and south of the

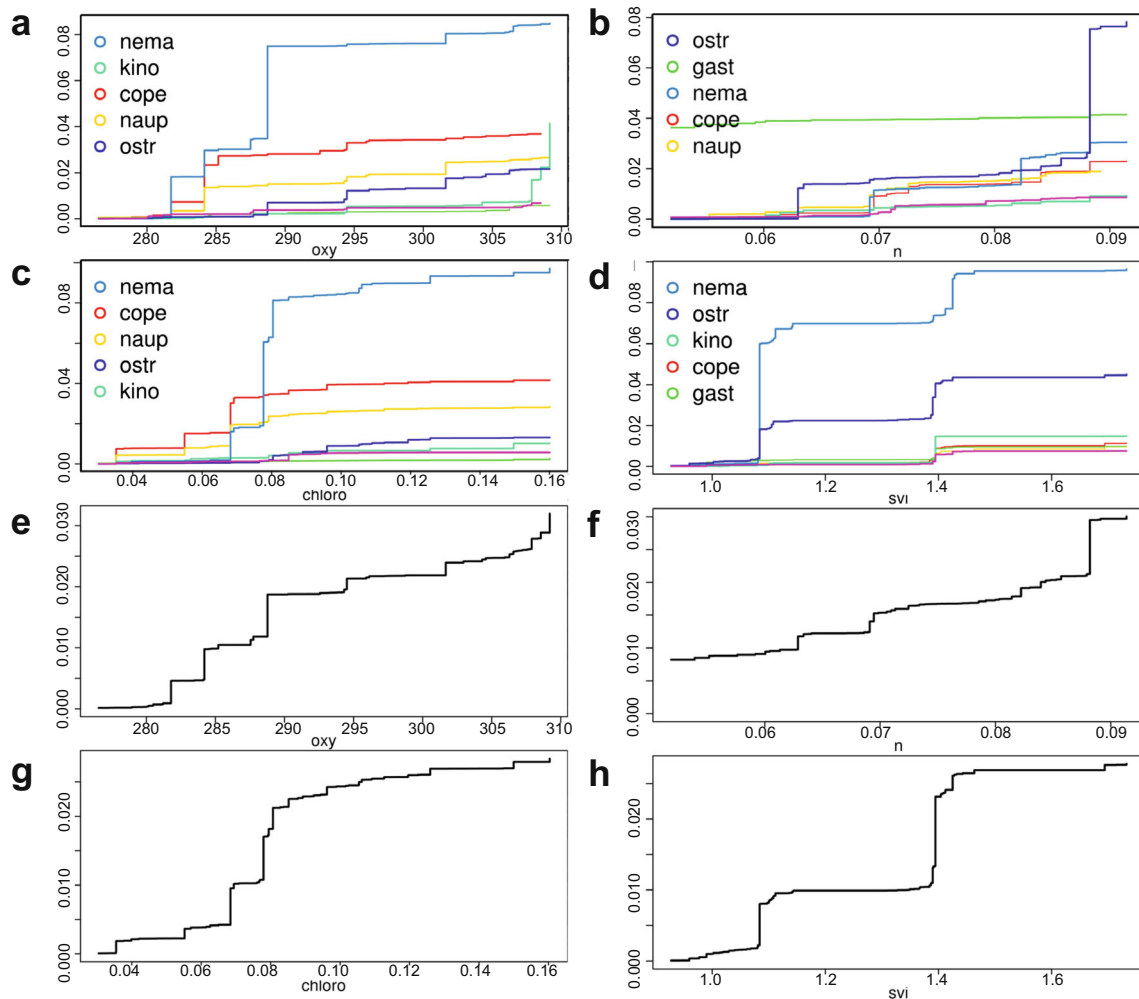


Fig. 5 Cumulative plots. **a–d** Taxa cumulative plots showing the value of the environmental variable at which a split change of respective taxa occurs (in respective color). **(e–h)** Predictor cumulative plots (oxygen,

nitrogen, chlorophyll α , seasonal variation index of the POC flux) showing the value of the environmental variable which is responsible for the split changes in the overall meiofauna abundance

GSR (~0.3 ind/10 cm²). Tantulocarida showed high densities in the deep sea (Fig. 7c), while density was less along the GSR and on the upper slope (0.15 ind/10 cm²). Meiofaunal taxa richness (Fig. 7d) was highest west of Iceland at the Greenland-Iceland Ridge, on the upper slope north of Iceland, and north of the Iceland-Faroe Ridge (15.6–18 taxa).

Discussion

Meiofauna density and community structure

The present study aimed at describing the meiofauna abundance and distribution patterns in Icelandic waters. We

Table 5 Statistics of the *randomForest* prediction model. Given are mean squared residuals (mean R^2), the variation explained in percentages (VE [%]), Pearson’s product moment correlation coefficient

(Pearson), and the adjusted R^2 (AdjRSq) of the linear relationship between predicted and observed data in the training dataset. All correlations are significant at $p < 0.001$

	Sum	Nematoda	Copepoda	Nauplii	Ostracoda	Tardigrada	Kinorhyncha	Tantulocarida	Gastrotricha	Taxa
Mean R^2	126,400	115,577	84.06	318.24	6.65	8.28	2.43	0.24	0.40	0.08
VE [%]	74.55	72.99	81.09	65.32	72.65	43.62	85.65	-19.24	35.11	23.27
Pearson	0.87	0.87	0.90	0.90	0.81	0.87	0.84	0.60	0.64	0.93
AdjRSq	0.76	0.76	0.81	0.81	0.65	0.76	0.71	0.36	0.41	0.87

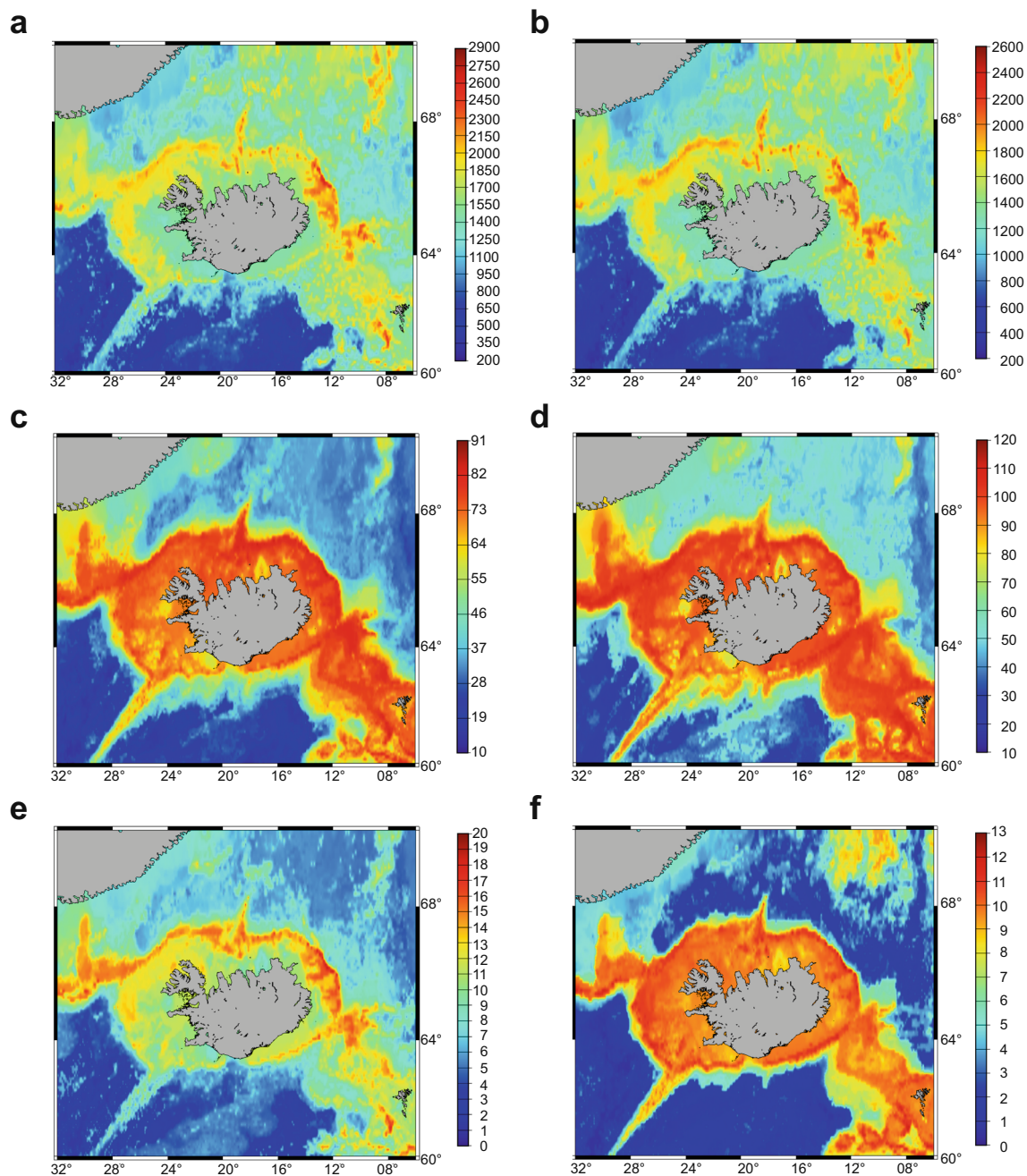


Fig. 6 Distribution of Icelandic meiofauna. The scale indicates the number of individuals per 10 cm². **a** Total meiofaunal density. **b** Nematoda. **c** Copepoda. **d** Nauplii. **e** Ostracoda. **f** Kinorhyncha

identified several environmental variables explaining the regional geographic differences in meiofauna. Based on the knowledge on the complex hydrographic and topographic conditions, collinearity of these environmental variables has to be taken into account. Meiofauna densities in Icelandic waters varied between 187 and 3185 individuals per 10 cm² and fall within the range of meiofauna densities reported from other Arctic and North Atlantic regions. The meiofauna community was dominated by Nematoda, followed by Copepoda, which is similar to other meiofauna studies from the Atlantic

and Arctic Ocean (see Rex and Etter 2010; Soltwedel 2000; and Vincx et al. 1994 for reviews). Meiofauna density and community structure in Icelandic waters differed regionally. The highest densities were present north of the GSR. Thus, meiofauna density shows a latitudinal limit in the vicinity of the GSR. Studies on meiofauna abundance (Thiel 1971; Soltwedel 2000 for a summary) and Amphipoda abundance (Weishappel and Svavarsson 1998) show similar results.

Meiofauna abundances, and furthermore abundances of Amphipoda, are described to differ north and south of the GSR

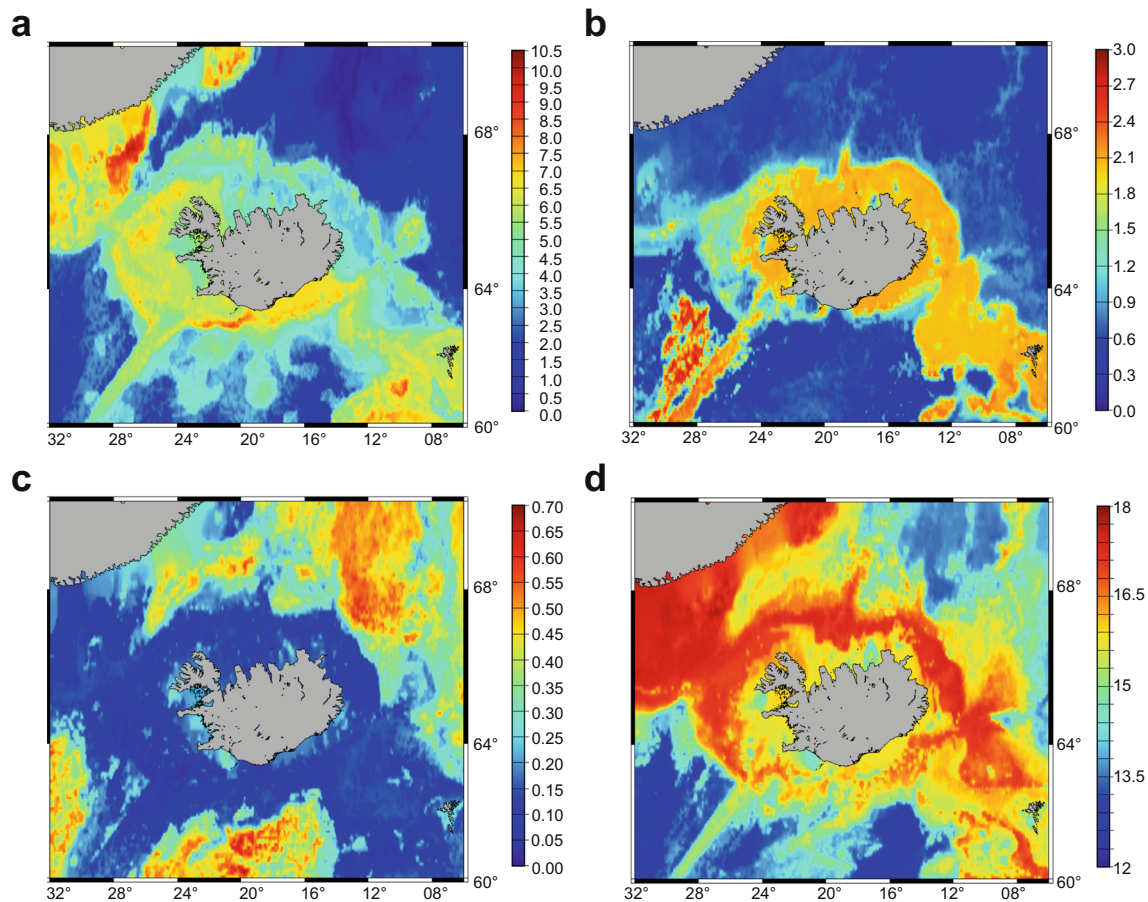


Fig. 7 Distribution of Icelandic meiofauna. The scale indicates the number of individuals per 10 cm². **a** Tardigrada. **b** Gastrotricha. **c** Tantulocarida. **d** Number of meiofauna taxa

(Thiel 1971; Weisshappel and Svavarsson 1998). Regional differences have been explained by the separation of the northern and southern deep-sea basins (topographic barrier), temperature, salinity, hydrographic activity, water depth, as well as food availability (Weisshappel and Svavarsson 1998; Thiel 1971).

Deep-sea ridges and their effect on the distribution and abundance of faunal organisms are to some extent contradictory. In the Atlantic Ocean, studies showed that deep-sea ridges or wide deep-sea areas do not prevent an exchange of meiofauna (Menzel and George 2012; Pointner et al. 2013), while other studies (here on macrofauna diversity) indicated that distribution patterns of macro- and meiofauna are to some extent limited at ridges (e.g., Brix and Svavarsson 2010; Svavarsson et al. 1993; Thiel 1971). Hence, depending on the ridge structure and the studied spatial scale, the answer whether or not ridges limit distributions patterns is varying. Even the faunal groups studied (taxa, genus, species) show different patterns (Brix and Svavarsson 2010; Menzel et al. 2011; Schnurr et al. 2014).

Northern and southern waters differ in temperature, salinity, and oxygen content (Ostmann et al. 2014). There is evidence, that temperature limits the faunal distribution to either warm or cold waters (Brix and Svavarsson 2010) and that the

rapid changes in temperatures along the GSR (outflow of Arctic waters into the North Atlantic and inflow of Atlantic waters into the Arctic Ocean) affect the distribution capacities of Icelandic fauna (Svavarsson 1997). However, in the present study, neither temperature nor salinity could be identified as major factors in structuring meiofauna. Near bottom oxygen content, however, was observed to be correlated with the nMDS axis, particularly pointing towards the Norwegian Sea and furthermore, the *gradientForest* analysis identified two thresholds, at which the meiofauna community changes most. In both regions, Nematoda represent the main part of the meiofauna community. The observed changes and differences north and south are most probably related to changes within this group, although studies showed that Nematoda are less affected by varying oxygen content (e.g., Neira et al. 2001).

The results observed in the Norwegian Sea and the Iceland Basin are congruent with the general trend of decreasing faunal abundance with increasing depth (e.g., Rex et al. 2005, 2006; Smith et al. 2008). Meiofauna density follows similar patterns in different regions, including the Arctic Ocean (Netto et al. 2005), North Atlantic Ocean (e.g.; Pfannkuche 1985; Vanreusel et al. 2000), Gulf of Mexico (Baguley et al. 2006), and the Antarctic waters (Herman and Dahms 1992;

Vanhove et al. 1995; Rose et al. 2015). Although faunal abundances decrease with increasing water depth, depth does not play the dominant role in this pattern (Rex et al. 2005, 2006; Smith et al. 2008). Various environmental variables change with increasing water depth, such as food supply. This was already observed by Thiel (1971) and Dinét (1979) along the Faroe Ridge and the Norwegian Sea, and the present study supports their results.

The proxies for food supply in the present study are POC, TOC, nitrogen, chlorophyll *a*, and SVI. The meiofauna abundance was positively correlated with increasing food supply (Figs. 2, 3, 4, and 5). The ordination of the nMDS was correlated with variables such as POC, TOC, nitrogen, and chlorophyll *a*. The seasonal variation index (SVI) showed a minor correlation to the ordination. Chlorophyll *a* and nitrogen were correlated to the nMDS, pointing to sites located in the Norwegian Sea, while POC was pointing to stations of the Iceland Basin, being indicative of a relationship between the meiofauna and POC in that region. Sites in the Irminger Basin showed an influence of TOC (Fig. 2d).

The nonlinear *gradientForest* analysis supported the observed nMDS results. Food supply was most presumably responsible for the observed meiofauna patterns in Icelandic waters. Greatest changes in the overall community occurred at values of 17 and 27 mg C/m² day (POC), 0.08 µg/g (chlorophyll *a*), 2.1% (TOC), 0.088% (N), and 1.1 and 1.42 g/m² (SVI). Meiofauna taxa were influenced differently by food supply. Chlorophyll *a* and SVI were highly responsible for changes in Nematoda, while Kinorhyncha, Copepoda, and their Nauplii as well as Ostracoda changed with other proxies for food supply (Figs. 4 and 5).

Food-driven changes in meiofauna community structure, standing stocks, and abundance are reported in several studies from Atlantic and Arctic regions (e.g., Pfannkuche 1985; Pfannkuche and Thiel 1987; Soltwedel 2000, Thiel 1983; Vanreusel et al. 1995a). The decrease in abundances and biomasses along depth gradients are often associated with changes in food availability. The deep-sea benthos depends on sea surface production, where no chemoautotrophic systems are present (Rex et al. 2005, 2006; Smith et al. 2008). With increasing depth and distance to the coast, food availability decreases. The uptake of particles in the water column, degradation, and current activity influence the amount of organic material reaching the sea floor. Hence, approximately 1% of the surface production serves benthic communities as food (Rex and Etter 2010 and references therein).

Along the GSR cold, nutrient-rich deep-sea water and warm nutrient-poor surface water mix and provide a perfect habitat for plankton. Regions with high planktonic activity show high detritus production. Thus, the higher production results in higher faunal densities along the GSR. On the upper slope, the organic material is still of more quality and quantity compared to the lower slope and abyssal. Therefore, food

supply explains the densities observed along depth gradients in the Iceland Basin and the Norwegian Sea.

To explain the distribution pattern and abundance of meiofauna in the Irminger Basin and the Denmark Strait, another variable has to be taken into account. When Arctic water crosses the GSR into the Atlantic Ocean, the outflow current can reach velocities of about 1 m/s. We therefore assume a complex system of water depth, food supply, and hydrographic conditions to be the limiting factor for meiofauna densities. The correlation between hydrographic activity and food supply was already described at the Iceland-Faroe Ridge and the Norwegian Sea (Dinét 1979; Thiel 1971). The strong overflow currents west and east of Iceland erode and resuspend small grains and organic material.

West of Iceland, in the Denmark Strait, meiofauna abundance was highly variable, with the highest densities at the deepest station. In this region, we observe an outflow (East Greenland Current) of cold waters across the Greenland-Iceland Ridge (Ostmann et al. 2014), which erodes fine sediments and organic material at the shallower stations. As the deepest station is less affected by the current, food availability is higher, sediments are finer. Consequently, meiofauna abundances are higher.

In the Irminger Basin, meiofauna density was high at the shallow station and at the deepest station. In the Irminger Basin, we observe the outflow of the EGC, represented further as Denmark Strait Overflow Water (DSOW), which sinks down with high velocities into the Irminger Basin (Ostmann et al. 2014). Similar to the study by Thiel (1971), the strong hydrographic activity causes a lower organic matter supply to the Irminger Basin. As a result, meiofauna densities are lower.

Nevertheless, for some taxa the coarse, nutrient-poor sediments show advantages.

Gastrotricha, the third most abundant taxon in that region, was highly diverse in the Irminger Basin and comprises various genera (pers. observation, unpublished). This meiofauna taxon is known to be interstitial (Higgins and Thiel 1988; Leasi and Todaro 2010) and their abundance is lower in muddy sediments (Coull 1988). Gastrotricha seem to be adapted morphologically, through the presence of lateral and terminal adhesive tubes. Besides Gastrotricha, Tardigrada were present in high numbers in one of the most disturbed and sandy areas observed during this study, indicating that both depend on coarse sediments rather than water depth. Hansen et al. (2001) already hypothesized this for Tardigrada from the Faroe Bank.

Regression models

To predict selected meiobenthic taxa on a contiguous geographic space at regional scale around Iceland, we generated predictive models using *randomForest* regression (Breiman 2001; Liaw and Wiener 2002). The *randomForest* approach

is widely used for classification and regression modeling (Breiman 2001; Cutler et al. 2007; Grömping 2009; Evans and Cushman 2009). In marine ecology, these methods begin to establish (Ostmann et al. 2014; Prasad et al. 2006; Reiss et al. 2011; Wei et al. 2010). Compared to other methods, random forests improve the model performance by using many trees and selection of a random number of predictors at each node (Elith et al. 2008).

Our model explained 65–86% of the variance observed in meiofauna densities. This performance is similar the study performed by Wei et al. (2010). Sampling density plays an important role for the prediction performance (Li and Heap 2008). This is congruent with our best performances for taxa observed in more than 75 samples.

Less predictive performance was found for Tardigrada (43%) and Gastrotricha (35%). Tantulocarida were predicted with a negative performance (−19%). This happens when the mean error is larger than the explained variance of the predicted value (see Liaw and Wiener 2002 for the equation of %variance explained). The lack of samples and a patchy distribution in the study area may explain this result (Bučas et al. 2013 and references therein). However, assessing model performance by looking only at *randomForest* own index for explained variance may be misleading. A more intuitive approach to assess model performance was to calculate the Pearson product moment correlation between observed values used for training and predicted values at these sites (Table 5). The correlation values are higher than 0.8, indicating good prediction accuracy, with exception of Tantulocarida (0.6) and Gastrotricha (0.64) displaying moderate accuracy.

Although, the prediction performances were moderate for some taxa, the model could support the results observed in the study area. Moreover, when comparing total meiofauna abundances predicted in our model and with abundance data of Thiel (1971) for the Faroe Ridge or data from Dinert (1979) in the Norwegian Sea, the results are quite comparable. Tantulocarida (having the lowest prediction accuracy) is the only taxon for which the model predicts an increase of abundance with depth. This however corresponds to a natural pattern, as already pointed out by Gutzmann et al. (2004).

Conclusion

1. Does the meiofauna community differ between the geographical regions?

Meiofauna communities differ in abundance between the geographical regions. Meiofauna abundances north of the Greenland-Iceland-Scotland Ridge were higher compared to the south.

2. Which are the most important variables causing changes in the community structure and which taxa are most affected by these changes?

There are several environmental variables causing differences in the meiofauna community. We found that food supply, hydrographic conditions as well as the hydrographic activity influence the meiofauna community, and we assume that all these variables show a collinearity to some extent that, e.g., food availability is regulated by hydrographic activity and sediment grain sizes and that the GSR limits the exchange of northern and southern waters which has an effect on the different temperatures and salinities observed. As a result, primary production at the surface differs north and south. We further observed that some taxa adapted to harsh environmental conditions, e.g., in the Irminger Basin.

3. Do the predictive models reflect observed differences in the study area?

The models used to predict different meiofauna taxa on a contiguous spatial scale are quite comparable to the observed data. The differences in abundance and also the number of taxa were quite well modeled with the *randomForest* approach.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

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