Aquat Ecol (2009) 43:221–233
DOI 10.1007/s10452-008-9200-0

Distribution and abundance of meiofauna in intertidal sand substrata around Iceland

Juan D. Delgado · Rodrigo Riera · Óscar Monterroso · Jorge Núñez

Received: 28 September 2007 / Accepted: 11 June 2008 / Published online: 29 June 2008

Abstract Iceland is situated in an important subarctic transition area where complex oceanographic dynamics occur. The intertidal, subtidal, and deep-sea faunal communities of Iceland are being intensively studied, as a critical resource for continued sustainability of fisheries and the preservation of northern littoral ecosystems. However, the meiofaunal communities and the environmental factors affecting them are still relatively poorly known. The meiobenthic metazoan community was studied with core sampling in 23 sandy beaches along the intertidal zone of the Iceland coast in a campaign developed in September 2003. Small-scale variation in meiofauna composition (major taxa) was explored and related to biotic and abiotic factors at different scales, such as beach exposure, granulometry, and organic matter content. Differences in meiofaunal community structure at a low taxonomic resolution appeared among beaches located within wide biogeographical zones of hydrobiological significance (NE and SW Shelf regions) and exposure degrees. Seventeen major taxa were recorded. In contrast with more local and taxon-focused studies, oligochaetes were the dominant group all around Iceland, followed by nematodes, turbellarians, gastrotrichs, and copepods (mainly harpacticoids). Acari, ascidians, bivalves, cnidarians, collembolans, gastropods, isopods, kinorhynchs, insects, nemerteans, ostracods, and polychaetes were relatively scarce groups, together being less than 1.6% of the meiofauna. There was a large variation in meiofaunal abundance between sites. Maximum abundances (>500 ind. cm^{-2}) were found in Sauđarkrökur, Hraunhafnartangi, and Skálaness, whereas minimum abundances (<40 ind. cm^{-2}) were recorded in Magnavík, Jokülsárlón (glacier beach site), Vikurnúpur, Breidalsvík, and Stokknes. We did not find a clear pattern in overall meiofaunal abundance regarding the degree of exposure of beaches. Oligochaetes, nematodes, and copepods were relatively more abundant in sheltered beaches, whereas turbellarians and gastrotrichs tended to be more abundant in exposed beaches. The best correlates of meiofaunal composition and abundance within beaches were the proportion of gravels and the content of utilizable organic matter in the sediment. We should consider factors operating at wider scales (importantly beach exposure and overall situation in the complex oceanographical context of Iceland) to find a pattern in the local structure of intertidal meiofaunal assemblages.

J. D. Delgado (✉)
Dept. de Sistemas Físicos, Químicos y Naturales, Área de Ecología, Univ. Pablo de Olavide, Ctra. de Utrera, km 1, Sevilla, Spain
e-mail: jddelgar@upo.es

J. D. Delgado
Dept. de Ecología, Fac. Biología, Univ. de La Laguna, Tenerife, Canary Islands, Spain

R. Riera · Ó. Monterroso · J. Núñez
Laboratorio de Bentos, Dept. de Biología Animal, Facultad de Biología, Universidad de La Laguna, 38206 Tenerife, Canary Islands, Spain

Keywords Iceland · Sandy beaches · Meiofauna · Oligochaeta · Nematoda · Granulometry · Shelf region

Introduction

Benthic macroinfauna (i.e., animals living within aquatic sediments and large enough to be seen with the naked eye), especially polychaetes, has been intensively studied in Icelandic intertidal areas (e.g., Wesenberg-Lund 1951; Helgason et al. 1990; Ingólfsson 1996), and is being thoroughly surveyed around the Iceland SW and NE Shelf regions within the Benthic Invertebrates in Icelandic Waters (BIOICE) program, especially regarding deep-sea communities. However, the meiofaunal (i.e., organisms between 53 and 500 μm in length) communities of soft substrata along the Iceland coastline are still poorly known (see, e.g., Helgason et al. 1990; Ólafsson 1991; Delgado et al. 2003). In contrast, meiofaunas of Arctic and polar areas have received greater attention (e.g., Vanreusel et al. 2000). Coastal sand meiofaunal communities are critical for the maintenance and integrity of whole marine ecosystems (Heip et al. 1990). Aside quantitative meiofaunal assessments (Heip et al. 1990; Ólaffson 1991; Vanaverbeke et al. 2000; Kotwicki et al. 2004), studies dealing with spatial dynamics of meiofauna are important to elucidate biogeographical associations at various scales (e.g., Soltwedel 2000; Kotwicki et al. 2005), relationships with environmental factors—most especially nutrients, salinity, and granulometry—(e.g., Herman et al. 2001; Gobin and Warwick 2006), and pollution and sediment disturbance in intertidal flats and sandy shores (e.g., Soetaert et al. 1994).

Subarctic latitudes show a complex confluence of Polar, Arctic, and Atlantic waters, contrasting current and tidal regimes, and varied coastal configurations that may affect meiofaunal as well as macrofaunal resources at the regional and local scales (Urban-Malinga et al. 2004). Oceanographically, the Iceland area is characterized by a confluence of waters, with four main currents, the Irminger, the East Iceland, the East Greenland, and the coastal Icelandic (Stefánsson and Ólafsson 1991; Malmberg and Kristmansson 1992; Guđmundsson 1998). Iceland has a convoluted coast with fjords and estuaries alternating with outlets exposed to high wave energy (Ólafsson 1991; Ingólfsson 1996). Most of Iceland's shoreline is rocky, especially the southwest, west, north, and northeast. There are also wide stretches dominated by wave-exposed sandy beaches along the south coast, and sandy areas interspersed with mudflats along the southwest, west, and north coasts (Ingólfsson 1996). This variation, along with regional oceanographical factors (i.e., main currents), causes contrasting coast morphodynamics and sediment properties that may affect meiofaunal community composition and structure (Ingólfsson 1996; Ólafsson and Elmgren 1997; Ólafsson 2003; Steinarsdóttir et al. 2003). Latitudinal effects on meiofauna are suggested to be driven by distance to the continental shelf or distance to ice edge in the Arctic Ocean (Vanreusel et al. 2000). In addition, the meiofauna is strongly dependent on organic matter fluxes, which couple coastal communities with pelagic processes on large biogeographical scales (Fabiano and Danovaro 1999). Thus, it is relevant to know the structure, composition, and variation factors of the intertidal meiofauna for the understanding of regional patterns in the North Atlantic subarctic systems and their fluctuations. In short, spatial meiofaunal patterns are shaped by a combination of local environmental cues as well as by biogeographical factors operating at larger scales.

The aim of this paper is to characterize the structure and regional variation of meiofaunal communities along the Iceland sandy shoreline. We studied the major metazoan meiofaunal groups, with the following aims: (a) to explore variation in meiofaunal community structure and composition in the context of the major biogeographical divisions along the Iceland shoreline; we specifically asked if distant meiofaunal assemblages differ, since they are influenced by different regional oceanic regimes (i.e., there are different patterns of meiofaunal community structure among defined sections in Iceland beaches); and (b) to assess the relationships among relevant abiotic and biotic factors operating at the local scale (relative beach exposure, sediment granulometry, and organic matter content) and meiofauna.

Study area

We performed sampling at 23 beaches distributed along the Icelandic sandy shoreline (Fig. 1, Table 1) between 17 and 29 September 2003. We sampled as many different localities as possible around the

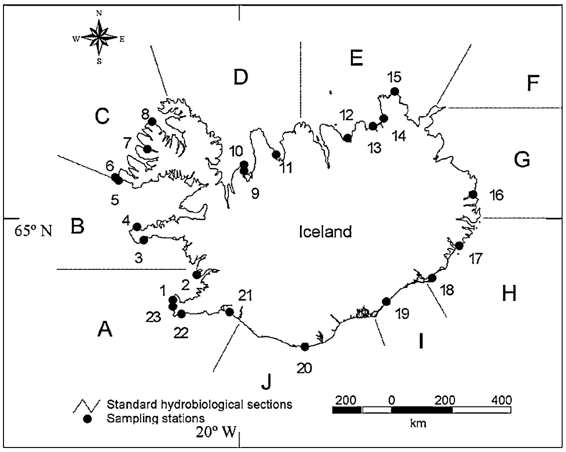


Fig. 1 Map of the beaches sampled in Iceland (station codes in Table 1)

Iceland coast, excluding muddy areas. We accounted for a wide geographical range in beach conditions, and composition and diversity of the meiofauna. The sampling proceeded clockwise around Iceland, from the southwest coast (Sandgerði, Reykjanes Peninsula) northwards, including areas of the West Fjörds peninsula.

Relevant biogeographical divisions were explored in relation to the variation in meiofaunal community structure along coastal sandy areas in Iceland. Such divisions roughly correspond to differences in the average nutrient concentrations, temperature pattern, and stability of oceanographic conditions (i.e., geographical limits in ocean climate) within the Shelf region (Stefánsson and Ólafsson 1991; Guðmundsson 1998) that could affect coastal invertebrate communities (e.g., Ingólfsson 1996).

The oceanic zones affecting our sampling areas are defined as standard hydrobiological sections described in Stefánsson and Ólafsson (1991), Malmberg and Kristmansson (1992), and Ingólfsson (1996). Regional shelf divisions (SWS, Southwest Shelf region; NES, Northeast Shelf region) were adapted from Guðmundsson (1998). The dominant water masses (Atlantic and Arctic) were considered after Jónsson (1992) and Guðmundsson (1998) (Table 1). Sections D–G (beaches 9–16) are comprised within the NES, which is part of the North Icelandic Shelf Region (NISR) (Malmberg and Kristmansson 1992; Guðmundsson 1998). These eight beaches are mostly influenced by Arctic and, eventually, polar waters. Fifteen beaches (numbered 1–8 and 17–23) were included in the SWS, being mostly influenced by Atlantic waters (Fig. 1). Most selected beaches were little affected by anthropogenic disturbance (i.e., potential pollution near ports or cities) or large inland freshwater contributions. However, the beach at Jokülsárlón was probably affected by Vatnajökull, the largest glacier in Europe, and the beach at Sandgerði (Reykjanes peninsula) was next to a fishing harbor.

To define the relative coast exposure to wave energy, we broadly identified two types of beach location: sheltered (inlets such as fjords and embayments, $n = 6$) and wave-exposed, open coast sites ($n = 17$) at the sampling beaches.

Materials and methods

Sampling

We fitted our sampling scheme to tidal movements, and the samples were taken during receding tides in the low water tidal level. Four cylindrical polyvinyl chloride (PVC) tubes (diameter 4.5 cm, area 15.9 cm^2, length 30 cm, volume 450 cm^3) were dug into the sand in each beach station to a depth of 20 cm. Three replicates were used for meiofauna assessment and one for granulometric and total organic matter analysis. Due to the large area covered, at the local scale we could not devote a large effort to look for fine differences and patterns at the microscale (i.e., between and within sediment patches) on each site. However, since we expected such variation to be relevant (see, e.g., Kotwicki et al. 2005; Hack et al. 2007), and its effect on the relationships between meiofauna and the abiotic variables of sediment noticeable, we aimed to reduce bias from large spatial variation in meiofauna among sampling points within beaches. We thus concentrated core samples at random within less than 2 m of each other, and did not encompass the full beach gradient.

We collected 69 faunal samples and 23 granulometric samples from 23 beaches. Each sediment core was stored in a plastic pot, preserved in buffered 10% formaldehyde pending its processing at the laboratory. Meiofaunal samples were processed by decanting through a 52 μm sieve in the laboratory (Sandgerði Marine Centre). Main taxa were oligochaetes, nematodes, turbellarians, gastrotrichs, and copepods. The remaining meiofaunal taxa surveyed are detailed in

Table 1 Beaches sampled for meiofauna in Iceland and relevant descriptors

Station number	Locality name	Latitude N	Longitude W	SHS[a]	Dominant water mass[b]	Shelf region[b]	Exposure	No. individuals (10 cm^{-2}, mean ± 1 SD)
1	Sandgerđi	64° 01′ 49″	22° 42′ 49″	A	Atlantic	SWS	Sheltered	355.56 ± 89.39
2	Akranes	64° 23′ 15″	22° 00′ 32″	A	Atlantic	SWS	Exposed	272.33 ± 74.76
3	Breiđavík (S Snaefellsness)	64° 48′ 15″	23° 29′ 30″	B	Atlantic	SWS	Exposed	186.6 ± 90.8
4	Ólafsvík	64° 53′ 25″	23° 37′ 53″	B	Atlantic	SWS	Exposed	140.04 ± 79.88
5	Rauđisandur	65° 28′ 01″	24° 02′ 30″	C	Atlantic	SWS	Exposed	88.89 ± 7.96
6	Rauđsdalur	65° 29′ 57″	23° 11′ 48″	C	Atlantic	SWS	Exposed	252.41 ± 165
7	Þingeyri	65° 53′ 07″	23° 37′ 56″	C	Atlantic	SWS	Sheltered	170.65 ± 86.87
8	Bolungarvík	66° 09′ 00″	23° 13′ 50″	C	Atlantic	SWS	Exposed	167.51 ± 62.35
9	Ósar	65° 35′ 54″	20° 37′ 59″	D	Arctic	NES	Exposed	237.32 ± 20.33
10	Vikurnúpur (N Ósar)	65° 40′ 27″	20° 38′ 57″	D	Arctic	NES	Sheltered	19.71 ± 15.15
11	Sauđarkrökur	65° 44′ 42″	19° 37′ 41″	D	Arctic	NES	Sheltered	2149.06 ± 916.28
12	Húsavík	66° 05′ 39″	17° 19′ 12″	E	Arctic	NES	Exposed	258.7 ± 112.51
13	Öxarfjördur	66° 07′ 34″	16° 56′ 35″	E	Arctic	NES	Exposed	300 ± 56.36
14	Magnavík (Naustursandur)	66° 14′ 21″	16° 25′ 49″	E	Arctic	NES	Exposed	20.13 ± 11.44
15	Hraunhafnartangi	66° 30′ 02″	15° 57′ 55″	E	Arctic	NES	Exposed	955.35 ± 313.67
16	Skálaness	65° 31′ 29″	22° 29′ 00″	G	Arctic	NES	Sheltered	661.84 ± 444.21
17	Breidalsvík	64° 47′ 00″	14° 02′ 15″	H	Atlantic	SWS	Exposed	35.22 ± 25.37
18	Stokknes	64° 14′ 54″	14° 58′ 12″	H	Atlantic	SWS	Exposed	17.19 ± 3.69
19	Jokülsárlón (Vatnajökull)	64° 02′ 31″	16° 10′ 52″	I	Atlantic	SWS	Exposed	3.56 ± 1.82
20	Dýrholaey (near from Vík)	63° 24′ 14″	19° 08′ 28″	J	Atlantic	SWS	Exposed	183.65 ± 41.38
21	Stokkseyri	63° 49′ 45″	21° 01′ 28″	A	Atlantic	SWS	Sheltered	189.1 ± 77.7
22	Gríndavík	63° 51′ 17″	22° 20′ 57″	A	Atlantic	SWS	Exposed	445.07 ± 76.07
23	Njarđvík	65° 34′ 33″	13° 53′ 08″	A	Atlantic	SWS	Exposed	192.66 ± 177.62

[a] SHS: standard hydrobiological sections, after Stefánsson and Ólafsson (1991), Malmberg and Kristmansson (1992), and Ingólfsson (1996)

[b] Regional shelf divisions and dominant waters (Atlantic and Arctic) from Guđmundsson (1998), as follows: SWS: Southwest Shelf region; NES: Northeast Shelf region

Mean number of individuals averaged from three samples per site

SD, standard deviation

Table 2. The capacity of retention, and thus completeness of the species pool, of a given mesh size depends on several factors, such as density of meiofauna, time of year, and taxa among others (de Bovee et al. 1974). Losses of adult meiofaunal individuals with a 50 μm mesh size are less important than for juveniles (Warwick and Clarke 1996), but even in such case some juveniles may be retained (de Bovee et al. 1974). Moreover, with an upper limit of 1 mm established for meiofauna, an exhaustive fraction of meiofaunal species are expected to be sorted with a mesh size comprised between the standard sizes 42 and 63 μm (see, e.g., Galéron et al. 2001). In general, although under certain conditions up to 30% of the individuals of some species (e.g. for nematodes) may pass through a 50 μm sieve, it has been demonstrated that with mesh sizes between 50 and 100 μm, the meiofauna can be retained to a 90% (de Bovee et al. 1974). In all, the assumed mesh size provides a reliable sampling of the meiofaunal fraction from intertidal samples with the advantage of being less time consuming during the sorting phase.

Table 2 Abundance distribution of major meiofaunal groups from 23 Icelandic beaches

Group	No. individuals	%	No individuals (10 cm$^{-2)}$	
			Mean	*SD*
Oligochaeta	17,193	49.36	156.71	481.81
Nematoda	7615	21.86	69.41	129.29
Turbellaria	6485	18.62	59.11	100.69
Gastrotricha	1812	5.20	16.52	46.62
Copepoda	1184	3.40	11.11	26.70
Acari	247	0.71	2.25	9.28
Insecta (larvae)	78	0.22	0.71	3.60
Bivalvia	76	0.22	0.69	2.35
Polychaeta	58	0.17	0.53	1.89
Ostracoda	43	0.12	0.39	1.75
Collembola	19	0.06	0.17	0.63
Cnidaria	8	0.02	0.07	0.41
Nemertea	8	0.02	0.07	0.53
Isopoda	3	0.01	0.03	0.17
Ascidians	2	0.01	0.02	0.11
Gastropoda	1	0.003	0.01	0.08
Kinorhyncha	1	0.003	0.01	0.08

Sorted specimens were preserved in 70% ethanol. Samples were examined under a stereomicroscope and all the metazoans were separated to higher taxa. When necessary, selected specimens were mounted in glycerine jelly and identified using a Leica DMLB microscope equipped with Nomarski interference contrast. We thus did not use a stain to sort the specimens, and we counted only whole specimens or, when necessary, heads plus anterior segments when fragmented bodies were found for worms such as oligochaetes. Meiofaunal density is given as individuals per 10 cm^2 sediment.

Sediment analysis

Standard methods for analysis of soft sediments were applied following Buchanan (1984). Twenty-three core sediment samples were analyzed for total organic matter (OM, g kg^{-1}), percent carbon content (C), and percent of sediment particles in seven granulometric classes [silt/clay (S/C), very fine sand (VFS), fine sand (FS), medium sand (MS), coarse sand (CS), very coarse sand (VCS) and gravel (G)] (Table 3). Total OM (organic matter) and C were highly correlated (Spearman rank correlation $r = 0.997$, $P < 0.0001$), and thus only OM was included in subsequent analyses. Total organic matter is the utilizable dissolved organic matter, which represents the exchangeable organic carbon immerse in sediment. These parameters were used as correlates of the meiofaunal community structure in multivariate ordination analysis (see below).

Data analysis

The abundance of main meiofaunal taxa was tested for significant differences between different situations (i.e., exposed versus sheltered, SWS versus NES regions) with Mann–Whitney's *U* test (Zar 1996). Student's *t* test was applied to study differences in sediment parameters between these situations (granulometry and organic matter content), as these variables fulfilled the requirements for parametric analyses. The three samples taken at each study site were averaged and the mean was compared between and among situations.

Sampled beaches were classified by hierarchical clustering based on (a) the abundance and composition of major taxa and (b) the sediment properties (granulometry and organic matter). By using clustering, we aimed to identify homogeneous groups among the sampling beaches, and to maximize differences between the formed groups (Jongman et al. 1995). The dendrogram was constructed using the single linkage method. Similarity distances were expressed as the Bray–Curtis similarity index. Cluster analysis was performed with the Primer 5 package for Windows.

Canonical correspondence analysis (CCA) in Canoco 4.5 (ter Braak and Smilauer 1998) was used to explore multivariate relationships between meiofaunal community structure and the sediment microenvironmental predictors (ter Braak and Smilauer 1998). The statistical significance of the associations between predictor variables and meiofaunal community structure was evaluated using Monte Carlo permutation tests with 500 randomizations under a full model (ter Braak and Smilauer 1998). The abundance data (averaged per taxa for the three samples per sampling site) were $\log_{10}(x + 1)$ transformed and a down-weighting factor was applied to cope respectively with skewed abundance distributions and scarce taxa. With rare taxa down-

Table 3 Sediment properties of the beaches sampled in Iceland

Station number	Locality name	% Carbon (C)	Organic matter (g kg^{-1}) (OM)	Gravel (G)	Very coarse sand (VCS)	Coarse sand (CS)	Medium sand (MS)	Fine sand (FS)	Very fine sand (VFS)	Silt/clay (S/C)
1	Sandgerði	0.28	4.84	0.57	0.6	0.99	38.65	52.2	6.85	0.03
2	Akranes	0.08	1.39	1.4	0.98	1.26	25.33	56.1	14.67	0.08
3	Breiðavík	0.07	1.21	0.01	0.84	36.78	61.65	0.56	0.08	0.01
4	Olafsvík	0.04	0.69	14.44	7.99	14.59	45.32	17.11	0.24	0.01
5	Rauðisandur	0.12	2.06	0.29	5.25	41.93	51.48	0.62	0.02	0.03
6	Rauðsdalur	0.09	1.55	2.58	0.36	0.35	43.2	50.86	2.24	0.02
7	Þingeyri	0.07	1.25	68.35	17.27	11.22	1.46	1.23	0.37	0.04
8	Bolungarvík	0.06	1.03	0	0.08	6.28	85.25	7.82	0.18	0.05
9	Ósar	0.09	1.55	1.05	0.71	15.16	78.67	3.39	0.14	0.12
10	Vikurnúpur	0.18	3.12	33.74	25.53	25.69	14.63	0.13	0.05	0.16
11	Sauðarkrökur	0.07	1.22	7.8	10.2	5.22	44.03	31.72	0.69	0.08
12	Húsavík	0.12	2.07	8.13	15.25	20.39	46.69	8.57	0.46	0
13	Öxarfjördur	0.04	0.69	31.21	16.37	15.72	36.38	0.25	0.02	0.02
14	Magnavík	0.02	0.34	0.01	0.02	0.96	94.65	4.13	0.11	0.02
15	Hraunhafnartangi	0.27	4.64	0.251	1.08	8.04	30.75	53.54	6.16	0.1
16	Skálaness	0.28	4.89	30.02	12.34	11.17	12.51	13.78	16.33	3.62
17	Breidalsvík	0.07	1.22	0	0.2	6.14	62	30.3	0.93	0.1
18	Stokknes	0.02	0.34	7.31	28.19	32.76	27.38	4.19	0.04	0.01
19	Jokülsárlón	0.01	0.17	0.34	3.58	44.29	51.23	0.35	0.11	0.02
20	Dýrholaey	0.02	0.34	24.25	12.46	37.03	25.32	0.35	0.04	0.05
21	Stokkseyri	0.15	2.59	2.37	14.25	27.27	37.25	14.45	3.38	0.43
22	Gríndavík	0.16	2.74	20.23	14.03	38.34	26.91	0.19	0.02	0.04
23	Njarðvík	0.01	0.17	18.82	44.91	20.46	12.22	2.93	0.43	0.01

weighted, i.e., with weights assigned proportionally to their abundance, we avoided excessive influence in the ecological gradient length, which takes both taxa composition and their abundance into account (ter Braak and Smilauer 1998). Univariate associations between sediment parameters (granulometry and organic matter content) and abundances of meiofaunal taxa (averaged for the three samples from each sampling site) were evaluated with the Spearman rank correlation coefficient (*r*) (Zar 1996).

Results

General patterns of meiofaunal abundance and distribution

A total of 34,833 individuals from 17 major taxa were recorded (Table 2). Five taxa accounted for 98% of meiofaunal individuals: oligochaetes, nematodes, turbellarians, gastrotrichs, and copepods (abundance >11 individuals/cm^2; Table 2). Oligochaetes were by far the most abundant group (~49% of the individuals) and presented a higher density (~157 ind. cm^{-2}), followed by nematodes (~22% abundance and ~69 ind. cm^{-2}). Cnidarians, nemerteans, gastropods, kinorhynchs, isopods, collembolans, and ascidians were minor groups (abundance <0.10 ind. cm^{-2}; Table 2) and were recorded at only one sampling locality. Polychaetes (both macrofaunal and strictly interstitial species, mostly Spionidae) made a minor fraction (<0.20% of the total, abundance ~0.50 ind. cm^{-2}) (Table 2). Gastropods and kinorhynchs were represented by only one individual (Table 2).

At the island scale, overall meiofauna abundance (all taxa combined) was significantly higher in intertidal sands from the NES region than from the SWS region ($U = 357$, $P = 0.021$) (Fig. 2). This was

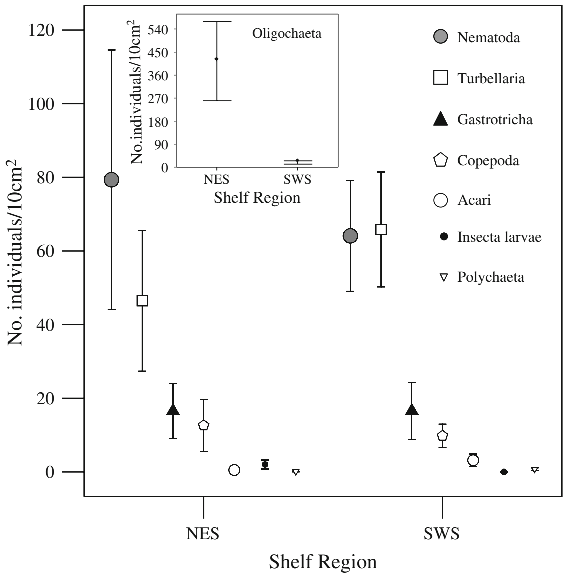


Fig. 2 Mean abundance (no. individuals/10 cm^2; averaged across three samples per site; bars are ± 1 SE) of major meiofaunal taxa from Iceland beaches in NE and SW Shelf regions. For clarity, the overabundant Oligochaeta are shown in the inset

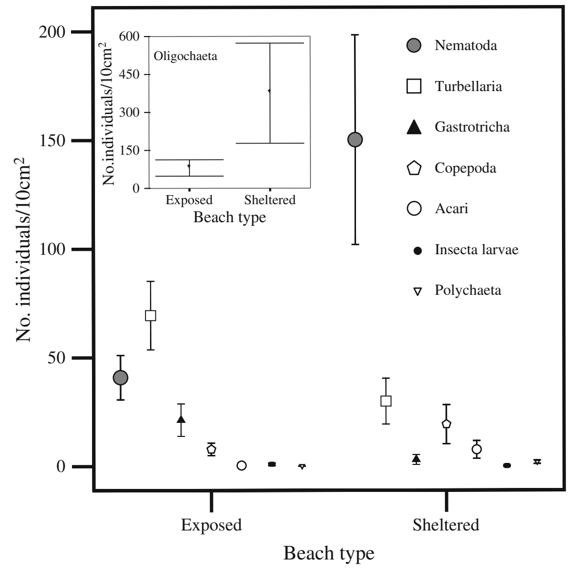


Fig. 3 Mean abundance (no. individuals/10 cm^2; averaged across three samples per site; bars are ± 1 SE) of major meiofaunal taxa from Iceland exposed and sheltered beaches. For clarity, the overabundant Oligochaeta are shown in the inset

related to a significantly higher abundance of the numerically dominant oligochaetes from the NES than from the SWS region ($U = 222$, $P < 0.001$). This pattern was probably due to the overall 14,337 oligochaetes obtained from only two NES beaches (Sauđarkrökur and Hraunhafnartangi). Two dominant oligochaete species accounted for the high dominance of the group, namely *Thalasodrilus firmus* (Tubificidae) and *Lumbricillus* sp. (Enchytraeidae) (see Delgado et al. 2003).

Of the remaining groups with more than 50 individuals, only insect larvae were significantly more abundant in beaches from the NES than from the SWS region ($U = 460$, $P = 0.025$), but they were recorded at only three beaches (Skálaness and Ósar in the NES and Stokkseyri in the SWS). No group was significantly more abundant in beaches of the SWS than of the NES region ($P \geq 0.05$), although Acari and Polychaeta had somewhat higher densities at SWS beaches.

Overall meiofauna abundance did not differ significantly between sheltered and exposed beaches ($U = 36$, $P = 0.294$) (Fig. 3). The major groups were present in both beaches, but only copepods showed significantly higher abundance in sheltered ones ($U = 18$, $P = 0.020$). Oligochaetes and nematodes showed relatively higher abundances in sheltered beaches, whereas turbellarians and gastrotrichs tended to be more abundant in exposed beaches (Fig. 3).

Granulometry and organic matter content

We performed the sampling on sandy beaches, excluding muddy areas, to avoid the large variation between meiofauna of these contrasting sediment types. Most sediments were medium to coarse in size, medium sands representing an average of 41.43% of the sediment composition (±23.66% SD; range 1.46–94.65%; $n = 23$ beaches). Low contents of utilizable organic matter (carbon that is readily utilizable by microorganisms) were common (mean ± SD = 1.74 ± 1.46 g kg^{-1}; range 0.17–4.89 g kg^{-1}) and percentage of total organic carbon was low (0.10 ± 0.08%; range 0.01–0.28%).

The silt and clay fraction was generally low, the highest proportions (3.60%) being found at Skálaness (NES region), which was also the station with the highest organic matter content (4.89 g kg^{-1}) and an important gravel fraction. On the contrary, the Húsavík beach (NES region) presented no silt/clay fraction. No significant differences were found in any of the studied granulometric properties between the NES and the SWS beaches (all t tests, $P > 0.05$).

Beach exposure had a significant influence on certain granulometric traits and organic matter content of the sediment. Percent carbon ($U = 19$, $P = 0.024$), organic matter (g kg^{-1}) ($U = 17.5$, $P = 0.019$), and the fraction of fine sands ($U = 17.5$, $P = 0.018$) were higher in sheltered than in exposed beaches.

Similarity in meiofaunal compositions and sediment properties

Cluster analysis revealed a high variability in both major meiofaunal taxa and sediment traits at the whole-island scale. There was no clear contrast between different exposure degrees or shelf regions in any case. All clusters at about 50% similarity contained both exposed and sheltered beaches, as did beaches of both the SWS and NES regions (Figs. 4, 5).

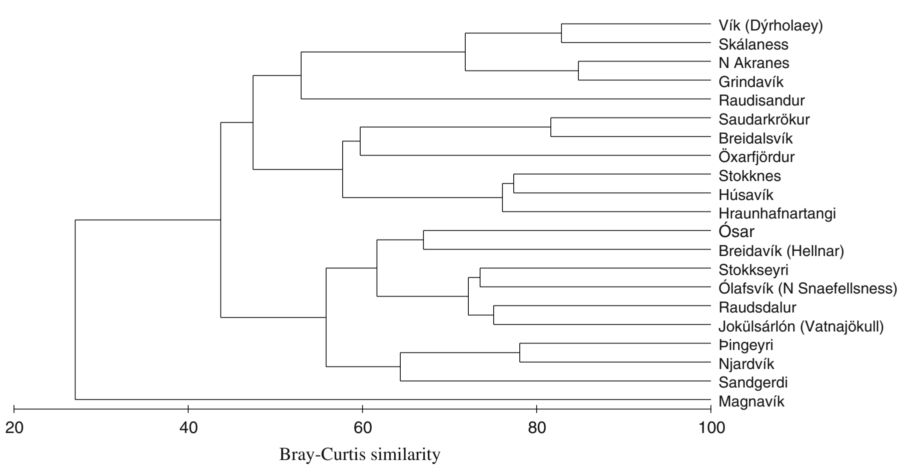
Based on composition and abundance of major taxa, two main beach groups were formed at 30% similarity (Fig. 4). The first group was formed by three beaches with the highest densities of oligochaetes and relatively low densities of nematodes (Hraunhafnartangi, Sauđarkrökur, and Olafsvík). A second large group, at 41% similarity, contained the remaining 20 beaches that showed intermediate to high densities of nematodes, and generally lower oligochaete densities. The third and fourth groups were discriminated at 47% similarity. The third group included sediments dominated by gastrotrichs and was comprised of five beaches (Breiđalsvík, Akranes, Stokknes, Magnavík, and Húsavík). The fourth group included beaches dominated by turbellarians and with low overall meiofaunal abundance. The fourth group also presented two main subgroups at 60% similarity. Vikurnúpur, þingeyri, and Rauđisandur were discriminated as communities with low meiofaunal densities and with some representation of minor groups (Acari, Bivalvia, Cnidaria, Nemertea, and Collembola). Þingeyri was the beach presenting the highest densities of Acari, Bivalvia, and Collembola.

Two main beach groups were discriminated as for their sediment composition at a 44.8% similarity (Fig. 5). One group included sediments formed by medium sand (Húsavík to Ósar in the upper branch of the dendrogram, at 63.56% similarity) and important contribution of fine sands (subgroup at 85% similarity formed by Hraunhafnartangi, Sandgerđi, Rauđsdalur, and Akranes). The other group (at 56.20% similarity, the lower branch of the dendrogram, being comprised of Öxarfjördur to þingeyri) included sediments dominated by the coarser fractions (coarse sand to gravel).

Univariate and multivariate relationships between meiofauna and sediment variables

Spearman rank correlations between abundance and sediment properties were calculated for the principal meiofaunal taxa (those with >100 individuals in all). Oligochaetes were positively correlated with the percentage of very fine sands ($r = 0.463$, $P = 0.026$), where they reached the highest densities. Nematodes were positively correlated with organic matter content ($r = 0.533$, $P = 0.009$), fine sands ($r = 0.450$, $P = 0.031$), and very fine sands ($r = 0.565$, $P = 0.005$). Copepods showed a marginally

Fig. 4 Dendrogram of sampling beaches based on composition of major meiofaunal taxa



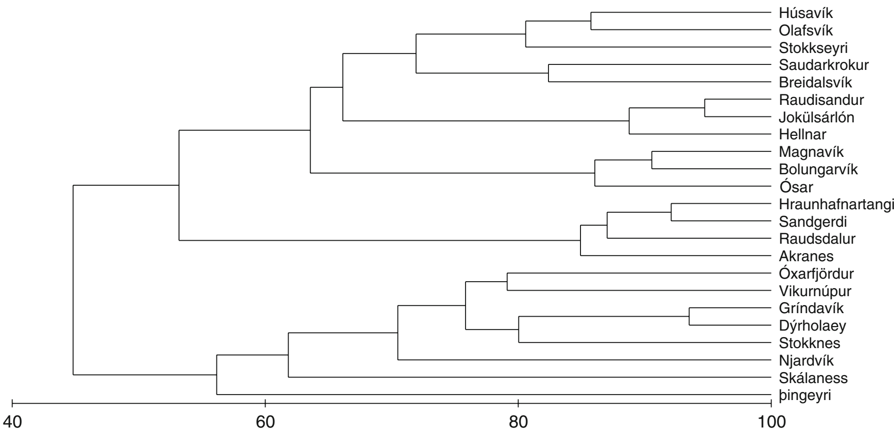


Fig. 5 Dendrogram of sampling beaches based on sediment properties

significant, positive correlation with organic matter content ($r = 0.413$, $P = 0.050$) and the percentage of silt/clay ($r = 0.479$, $P = 0.021$). Turbellarians were negatively correlated with fine sands ($r = -0.537$, $P = 0.008$) and very fine sands ($r = -0.445$, $P = 0.033$), reaching the highest densities in highly exposed beaches characterized by medium to coarse sands and gravels. The abundance of gastrotrichs showed no significant correlations with any of the studied sediment properties ($P > 0.1$).

The CCA yielded four axes that explained 84.4% of the variance in the relationships between meiofaunal community structure and sediment properties (Table 4). Community structure and the CCA axes synthesizing environmental variation were strongly correlated ($R > 0.7$, Table 4). The first two axes alone explained about 52% of the variance in the data (Fig. 6). The Monte Carlo tests selected the gravel fraction (G) and the organic matter content (OM) as the two only significant predictors of meiofaunal community structure (Table 5).

Discussion

A high variability in meiofaunal community structure and sediment properties along the Iceland sandy littoral was found. However, little apparent division of biological significance was revealed between beaches situated in the NES (Arctic influence) and SWS (Atlantic influence) regions, from data of major meiofaunal taxa or sediment traits. Neither sediment granulometric traits nor organic matter content presented a clear contrast between beaches of the NES and SWS regions. Nevertheless, sediment structure and content of utilizable organic matter were important determinants of meiofaunal community structure at a smaller scale, i.e., among beaches.

The meiofaunal distribution patterns observed might be determined in great part by the local abundance of the major groups, Oligochaeta and Nematoda, which jointly formed 71% of the meiofauna. In turn, such patterns seem to be mostly dependent on local determinants of sediment properties and beach configuration. Such groups might respond also to habitat factors operating at local or regional scales that have not been assessed in this work. Amongst potentially influential factors are mean redox potential discontinuity (RPD, see Hack et al. 2007), salinity, fresh water effluence, de-icing, and intrinsic and extrinsic seasonality of meiofauna. However, it seems clear that a great amount of variability on a wide geographical scale along the Iceland coast is mostly due to granulometric

Table 4 Canonical correspondence analysis describing relationships between meiofaunal community structure and sediment properties

CCA axis	1	2	3	4
Eigenvalues	0.116	0.103	0.079	0.058
Correlations between community structure and environmental axis	0.828	0.882	0.768	0.884
Cumulative percentage variance	27.5	51.9	70.7	84.4

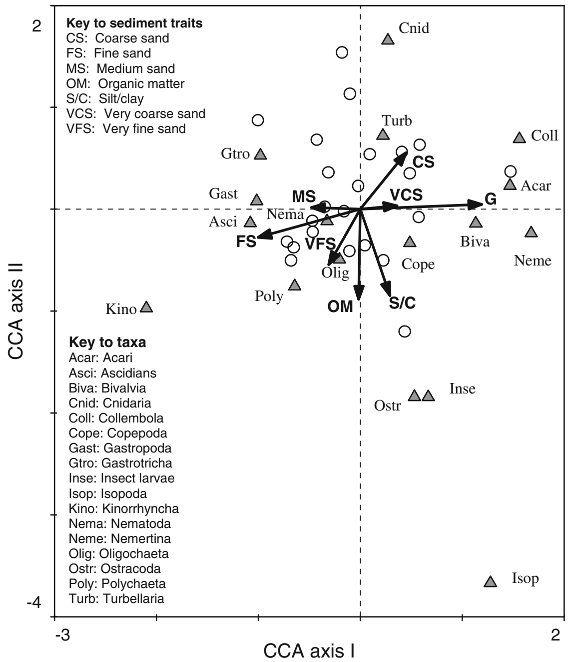


Fig. 6 Biplot of a canonical correspondence analysis (CCA) with sampling sites (open circles), major taxa (filled triangles, lower-case labels), and sediment properties (arrows and upper-case labels)

Table 5 Results of the Monte Carlo permutation tests (500 randomizations)

Variable	*F*	*P*
Gravel (G)	**2.37**	**0.008**
Organic matter (OM)	**2.05**	**0.024**
Coarse sand (CS)	1.63	0.080
Fine sand (FS)	1.45	0.158
Very fine sand (VFS)	1.32	0.216
Medium sand (MS)	1.05	0.374
Very coarse sand (VCS)	0.92	0.512
Silt/clay (S/C)	0.73	0.680

Sediment properties significantly influencing meiofaunal community structure ($P < 0.05$) are shown in bold type

properties and organic matter content of the sediment. A similar conclusion in this sense was attained by Hack et al. (2007) for New Zealand. In addition, we sampled only the upper (first 20 cm) layers of the sand column and next to the low water level (which avoids the lower oxygenation of the upper reaches during low tide, see Dye 1980). We assumed this layer to be a mostly oxygenated section on high-energy beaches, thus giving support to meiofaunal communities.

Oligochaetes were the dominant group in different beaches, with variable sediment conditions and under contrasting wave-exposure regimes. Icelandic beaches were shown to be clearly dominated by oligochaetes in another recent survey (Delgado et al. 2003). Oligochaetes, especially meiofaunal species, are still scarcely known on the Iceland littoral, and little comparison can be made with published studies (see, e.g., Erséus 1976). Oligochaetes have been recorded as the dominant group in eutrophic or polluted sediments in other coasts (Bagheri and McLusky 1982; Connor et al. 1997). Food content of the sediment has been shown to change greatly between years and it changes also over wide geographic areas, affecting the meiofauna (i.e., in transition zones between polar and subpolar areas, Skowronski and Corbisier 2002; Hack et al. 2007).

The result of a high dominance of Oligochaeta contrasts with previous works on Iceland sandy beaches in which oligochaetes represented only a minor meiobenthic fraction (Ólafsson 1991). On the other hand, significantly higher oligochaete abundance was found in beaches of the NES region, which are influenced by cold waters, than of the SWS region, affected by Atlantic waters. Two extremely oligochaete-rich beaches (Hraunhafnartangi and Sauđarkrökur) contributed importantly to this contrast. This result is consistent with those of Delgado et al. (2003) in which a set of beaches of the NES region, surveyed in a different season (April 2000) and different from the ones explored in this study, also presented higher average densities of oligochaetes than SWS beaches. This suggests an asymmetry in distribution of some meiofaunal taxa between NES and SWS meiofaunal communities, difference that may indicate the presence of relevant ecological (perhaps oceanographical) transitions in this subpolar area for meiofauna.

The results of this study confirm those of Delgado et al. (2003) in that sheltered beaches presented higher oligochaete abundance than exposed ones. Moreover, we found in this study a moderate correlation between oligochaete abundance and the proportion of fine sand, which are mostly encountered at sheltered locations such as embayments. Actually, the most exposed beaches had no oligochaetes at all (e.g., Jokülsárlón, Dýrholaey, Stokknes, Rauđisandur, and Hellnar). We found oligochaete abundance from Iceland beaches to be uncorrelated with the coarser fractions of sediments, and positively correlated with the fine sand fraction. Such results contrasts with those of Giere (1993) and Vanaverbeke et al. (2000) who reported higher abundance of this group in coarser sediments.

Interstitial polychaetes were a minor group in this study, being less than 0.20% of the total meiofauna, and were collected in core samples at only six of 23 beaches. This result strongly differs from recent estimates of abundance of meiofaunal polychaetes around Iceland (e.g., 15.2% of the total annelids, Delgado et al. 2003). Other studies have reported relatively low densities of meiofaunal polychaetes, as their abundance fluctuates widely depending on many factors, including seasonality, geographical situation, depth in sediment, and method of collection (Vanaverbeke et al. 2000).

Nematodes are a major invertebrate group in Icelandic shores which show great variation in abundance between and within beaches (Ólafsson 1991). Their abundances are several times higher than those of other representative groups (e.g., Helgason and Svavarsson 1991; Svavarsson and Helgason 2002). These authors gave figures of 853–9,980 nematode individuals per square meter in five Iceland beaches, at depths from 3 to 15 m, and with variable dominance of particle sizes and exposure degrees. Whereas nematodes are commonly the numerically dominant group in the sandy intertidal zone (Ólafsson 1991), coastal shallow areas (Pallo et al. 1998), subtidal sandbanks (Vanaverbeke et al. 2000), and deep-sea sediments (Fabiano and Danovaro 1999; Soltwedel 2000; Vanreusel et al. 2000), oligochaetes dominate along a large part of the Iceland sandy intertidal zone (Delgado et al. 2003; this study). We found no significant difference in nematode abundance between beaches from the NES and SWS regions, or between sheltered and exposed beaches, though nematodes appeared to be more abundant, on average, on sheltered beaches. However, at the local scale, we did find positive relationships between sediment properties (utilizable organic matter, fine sand fractions) and nematode abundance, a result which differ from those of Vanreusel et al. (2000) for deep-sea meiofauna, where no significant relationships were reported. Regarding turbellarians and gastrotrichs, our results coincided with those of Ólafsson (1991) and Giere (1993) in that these groups were differentially abundant in beaches with sediments formed by coarse sand to gravel, and presented higher abundances in exposed beaches.

The variation in meiofauna and granulometry and other sediment structural factors can be attributed to several hierarchical causes. We explored the intertidal soft-sediment meiofauna around Iceland for a diversity of situations, and found a wide variation in both sediment traits and meiofaunal assemblages, although at a low taxonomical resolution. The physical environment of the studied beaches may be subject to seasonality, and thus the general meiofaunal patterns revealed here may not hold for other seasons, especially at the level of species. At a local patch scale within beaches, grain size can be considered a strong factor determining the dominance of some important groups, namely oligochaetes and nematodes in fine sands, and turbellarians and grastrotrichs in more coarse sands. At a wider scale, exposure of beaches to wave energy is a critical factor, since it may shape, vertically and horizontally, sediment grain profiles and hence meiofaunal assemblage composition, perhaps at scales of meters to hundreds of meters. The most evident latitudinal asymmetry (between north and south coastal waters) was found for oligochaetes, which were consistently more abundant in beaches of the NES region. This apparent latitudinal pattern in meiofauna may be conditioned by differences in temperature due to distance to Arctic ice-edge, and to the complex current confluence, in combination with local beach morphodynamics. Biogeographical studies on intertidal meiofauna encompassing wide areas should consider relating data on fine sediment (microhabitat) structure with explanatory factors operating at larger scales.

Acknowledgements We are especially indebted to Guðmundur V. Helgason (Univ. of Iceland), Reynir Sveinsson, Linda Björk Holm, and all the staff of the Fræðasetrið (Large Scale Facility Sandgerði Marine Centre, Sandgerði, Iceland) for their kind support and patience during our stays. This work was economically supported by a Transnational Access to Research Facilities (ARI) under the Improving the Human Potential Programme (IHP) of the European Union. This is manuscript #1 arising from our participation in the ARI-IHP project held by the Sandgerði Marine Centre in September 2003.

References

Bagheri EA, McLusky DS (1982) Population dynamics of oligochaetes and small polychaetes in the polluted Forth

estuary ecosystem. Neth J Sea Res 16:55–66. doi:10.1016/0077-7579(82)90017-5
Buchanan JB (1984) Sediment analysis. In: Holme NA, McIntyre AD (eds) Methods for the study of marine benthos. Blackwell, Oxford, pp 41–65
Connor DW, Brazier DP, Hill TO, Northen KO (1997) Marine Nature Conservation Review: marine biotope classification for Britain and Ireland, vol 1. Littoral biotopes. Version 97.06. [JNCC Report, No. 229.]
de Bovee F, Soyer J, Albert P (1974) The importance of the mesh size for the extraction of the muddy bottom meiofauna. Limnol Oceanogr 19:350–354
Delgado JD, Núñez J, Riera R, Monterosso O (2003) Abundance and diversity patterns of annelids from intertidal sandy beaches in Iceland. Hydrobiologia 496:311–319. doi:10.1023/A:1026121604617
Dye AH (1980) Tidal fluctuations in biological oxygen demand in exposed sandy beaches. Estuar Coast Mar Sci 11:1–8. doi:10.1016/S0302-3524(80)80024-7
Erséus C (1976) Littoral Oligochaeta (Annelida) from Eyjafjördur, North coast of Iceland. Zool Scr 5:5–11. doi:10.1111/j.1463-6409.1976.tb00677.x
Fabiano M, Danovaro R (1999) Meiofauna distribution and mesoscale variability in two sites of the Ross Sea (Antarctica) with contrasting food supply. Polar Biol 22:115–123. doi:10.1007/s003000050398
Galéron J, Sibuet M, Vanreusel A, Mackenzie K, Gooday AJ, Dinet A et al (2001) Temporal patterns among meiofauna and macrofauna taxa related to changes in sediment geochemistry at an abyssal NE Atlantic site. Prog Oceanogr 50:303–324. doi:10.1016/S0079-6611(01)00059-3
Giere O (1993) Meiobenthology: the microscopic fauna in aquatic sediments. Springer Verlag, Berlin
Gobin JF, Warwick RM (2006) Geographical variation in species diversity: a comparison of marine polychaetes and nematodes. J Exp Mar Biol Ecol 330:234–244. doi:10.1016/j.jembe.2005.12.030
Guđmundsson K (1998) Long term variation in phytoplankton productivity during spring in Icelandic waters. ICES J Mar Sci 55:635–643. doi:10.1006/jmsc.1998.0391
Hack LA, Tremblay LA, Wratten SD, Lister A, Keesing V (2007) Benthic meiofauna community composition at polluted and non-polluted sites in New Zealand intertidal environments. Mar Pollut Bull 54:1801–1812. doi:10.1016/j.marpolbul.2007.07.009
Heip C, Huys R, Vincx M, Vanreusel A, Smol N, Herman R et al (1990) Composition, distribution, biomass and production of North Sea meiofauna. Neth J Sea Res 26:333–342. doi:10.1016/0077-7579(90)90095-X
Helgason GV, Svavarsson J (1991) Botndýralíf í Þerneyjarsundi. Fjolrit Liffraedistofnunar 30:1–33 (in Icelandic)
Helgason GV, Gardarsson A, Svavarsson J, Adalsteinsdottir K, Gudmunsson H (1990) Polychaetes new to the Icelandic fauna, with remarks on some previously recorded species. Sarsia 75:203–212
Herman PMJ, Middelburg JJ, Heip CHR (2001) Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. Cont Shelf Res 21:2055–2071. doi:10.1016/S0278-4343(01)00042-5
Ingólfsson A (1996) The distribution of intertidal macrofauna on the coast of Iceland in relation to temperature. Sarsia 81:29–44
Jongman RHG, ter Braak CJF, Van Tongeren OFR (1995) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge
Jónsson S (1992) Sources of fresh water in the Iceland Sea and the mechanisms governing its interannual variability. ICES Mar Sci Symp 195:62–67
Kotwicki L, Szymelfenig M, De Troch M, Zajaczkowski M (2004) Distribution of meiofauna in Kongsfjorden, Spitsbergen. Polar Biol 27:661–669. doi:10.1007/s00300-004-0625-1
Kotwicki L, De Troch M, Urban-Malinga B, Gheskiere T, Weslawski JM (2005) Horizontal and vertical distribution of meiofauna on sandy beaches of the North Sea (The Netherlands, Belgium, France). Helgol Mar Res 59:255–264. doi:10.1007/s10152-005-0001-8
Malmberg S-A, Kristmansson SS (1992) Hydrographic conditions in Icelandic waters, 1980–1989. ICES Mar Sci Symp 195:76–92
Ólafsson E (1991) Intertidal meiofauna of four sandy beaches in Iceland. Ophelia 33:55–65
Ólafsson E (2003) Do macrofauna structure meiofauna assemblages in marine soft-bottoms? A review of experimental studies. Vie Milieu 53:249–265
Ólafsson E, Elmgren R (1997) Seasonal dynamics of sublittoral meiobenthos in relation to phytoplankton sedimentation in the Baltic Sea. Estuar Coast Shelf Sci 45:149–164. doi:10.1006/ecss.1996.0195
Pallo P, Widbom B, Ólafsson E (1998) A quantitative survey of the benthic meiofauna in the Gulf of Riga (Eastern Baltic Sea), with special reference to the structure of nematode assemblages. Ophelia 49:117–139
Skowronski RSP, Corbisier TN (2002) Meiofauna distribution in Martel Inlet, King George Island (Antarctica): sediment features versus food availability. Polar Biol 25:126–134
Soetaert K, Vincx M, Wittoeck J, Tulkens M, Gansbeke DV (1994) Spatial patterns of Westerschelde meiobenthos. Estuar Coast Shelf Sci 39:367–388. doi:10.1006/ecss.1994.1070
Soltwedel T (2000) Metazoan meiobenthos along continental margins: a review. Prog Oceanogr 46:59–84. doi:10.1016/S0079-6611(00)00030-6
Stefánsson U, Ólafsson J (1991) Nutrients and fertility of Icelandic waters. Rit Fiskideildar 12:1–56
Steinarsdóttir MB, Ingólfsson A, Ólafsson E (2003) Seasonality of harpacticoids in a tidal pool, SW-Iceland. Hydrobiologia 503:211–221. doi:10.1023/B:HYDR.0000008489.41581.d7
Svavarsson J, Helgason GV (2002) Botndýralíf við Sundahöfn. Fjolrit Liffraedistofnunar 66:1–35 (in Icelandic)
ter Braak CJF, Smilauer P (1998) CANOCO reference manual and user's guide to Canoco for Windows software for canonical community ordination (version 4). Microcomputer Power, Ithaca, New York
Urban-Malinga B, Kotwicki L, Gheskiere TLA, Jankowska K, Opaliñski K, Malinga M (2004) Composition and distribution of meiofauna, including nematode genera, in two contrasting Arctic beaches. Polar Biol 27:447–457. doi:10.1007/s00300-004-0618-0

Vanaverbeke J, Gheskiere T, Vincx M (2000) The meiobenthos of subtidal sandbanks on the Belgian continental shelf (Southern Bight of the North Sea). Estuar Coast Shelf Sci 51:637–649. doi:10.1006/ecss.2000.0703

Vanreusel A, Clough L, Jacobsen K, Ambrose W, Jivaluk J, Ryheul V et al (2000) Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure. Deep Sea Res 47:1855–1879. doi:10.1016/S0967-0637(00)00007-8

Warwick RM, Clarke KR (1996) Relationships between body-size, species abundance and diversity in marine benthic assemblages: facts or artefacts? J Exp Mar Biol Ecol 202:63–71

Wesenberg-Lund E (1951) Polychaeta. Zool Iceland 2:1–182

Zar JH (1996) Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey