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Abundance and diversity patterns of annelids from intertidal sandy beaches in Iceland

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Abstract

Patterns in composition, abundance and diversity of the annelid fauna (Polychaeta and Oligochaeta) in 22 sandy beaches in Iceland were explored. The effect of exposure on annelid distribution was studied. A total of 5651 annelids were recorded from 160 core samples. Oligochaetes (chiefly Tubificidae) dominated the annelid assemblage whereas polychaetes represented a minor fraction. Polychaetes were relatively more abundant in exposed than in sheltered beaches, contrary to oligochaetes. Meiofaunal polychaete species were also more abundant in exposed than in sheltered beaches. Southwest beaches seemed more diverse in annelid species than northern ones. Annelid diversity did not differ between sheltered and exposed sites, but higher diversity was attained in fine sands at sheltered areas. Cluster analysis revealed large differences between beaches in the annelid community composition. The general patterns found suggest that beach exposure is a major factor conditioning macro- and meiofaunal polychaete and oligochaete distribution along the Icelandic coast.

Introduction

The geographical situation at subarctic latitude, the pattern of oceanic currents, the insularity and the recent volcanic origin of the substrata are important for Icelandic intertidal faunal assemblages (Ólafsson, 1991; Ingólfsson, 1996) The variability in shape of the coastline creates differences in exposure degree and presence of sheltered areas. Rocky shores predominate along the north coast, whereas exposed sandy shores are interspersed with extensive muddy tidal flats along the south coast (Ingólfsson, 1996). Northern and southern coasts differ greatly with regard to factors such as salinity, temperature and productivity (Stefánsson & Ólafsson, 1991). The variation affects the structure of both macro- and meiofaunal communities in sandy beaches along the Icelandic shoreline (Ólafsson, 1991). Distribution of macro- and meiofaunal taxa may also greatly vary among and within sites due to substrate conditions at local and regional levels (Ólafsson, 1991; Ingólfsson, 1996). Species richness and abundance in sandy beaches are related to environmental variables such as sediment type and granulometry, wave energy and bottom topography, and water temperature, salinity and dissolved oxygen (Armonies & Reise, 2000). At a local level, sediment properties, site exposure and temperature are major factors controlling the distribution of the meio- and macrofauna in Icelandic beaches (Ólafsson, 1991; Ingólfsson, 1996). Although infaunal annelids form a key invertebrate group in Iceland soft substrata, at the local scale these communities are relatively simple in terms of species number (Wesenberg-Lund, 1951; Helgason et al., 1990; Ólafsson, 1991).

Here we explore general patterns of distribution, abundance and diversity of polychaetes and oligochaetes from soft substrata along the Iceland coast. Our objective was to study the variation in community composition, diversity and abundance with respect to exposure. We tried to account for the geographical variation in composition and diversity of the annelid assemblages. We have considered both meiofaunal and macrofaunal annelids, groups differing in life strategy and exploiting different scales of environmental grain and substrate types (Wesenberg-Lund, 1951; Westheide, 1990).

Materials and methods

We collected the samples at 22 beaches located along part of the 555 km of the Icelandic sandy shoreline (Ingólfsson, 1975) (Fig. 1, Table 1) in April 2000. We aimed to sample a wide range of localities to cope for variability in annelid assemblages within time and weather constraints (Table 1). The sampling proceeded clockwise around Iceland, from the southwest coast (Sandgerði) northwards. When possible, we fitted our sampling scheme to tidal movements with available tide tables for 2000. The large gap in sampling locations along the sandy south coast was due to time and logistic transportation constraints. Hence, this work is somewhat biased towards the sandy beaches from west-southwest (13 beaches) and north Iceland (7 beaches), with only two sites studied at the southeast sector (Fig. 1).

We defined the relative exposure of the coast by broadly defining two general beach situations: sheltered (inlets such as fjords and embayments) and wave-exposed, open coasts (sheltered vs. exposed areas). Since finer silt deposition is prevented by high-energy tidal streams, beach exposure to strong waves would determine sediment grain, properties and stability. We aimed to discriminate between high- and low energy beaches, and thus between areas with different degrees of sediment instability potentially affecting annelid communities. At each beach, we distinguished between different sediment patches (biogenic or volcanic origin) and subjectively classified sediment types from which annelids were sorted into five major grain diameter classes: Gravel (>2 mm); coarse sand (2–0.5 mm); medium sand (0.5–0.25 mm); fine sand (0.25–0.063 mm); mud (<0.063 mm).

We haphazardly located 1–3 sampling plots at each beach during receding tides. At each plot, five substrate samples were collected by hand drilling into the sediment with a PVC core (45 cm length, 4.5 cm inner diameter, volume = 450 cm^3), to a depth of 20 cm. We located 3 sampling plots (15 samples) at beaches A–E and 1 sampling plot (5 samples) at the remaining ones, with a total of 160 samples (see Table 1 for beach codes). We selected at random a subset of 5 samples from beaches A–E to perform analysis on equivalent sampling effort. The samples were preserved in buffered 10% seawater/formaldehyde and decanted through a 100 μm mesh sieve. Sorted specimens were preserved in 70% ethanol. Sorting and identification was performed at the Sandgerði Marine Centre (Iceland) and at the Benthos Laboratory (University of La Laguna, Tenerife, Canary Islands). Selected specimens were mounted in glycerine jelly and examined using a Leica DMLB microscope equipped with Nomarski interference contrast.

As univariant descriptors of the annelid community, abundance (density, or number of specimens per sediment volume unit) and diversity (Shannon's H) were compared between exposed ($n = 10$ beaches) and sheltered ($n = 12$ beaches) with the Mann-Whitney's U test. Beaches were classified by clustering based on the abundance and composition of species. By using clustering, we aimed to identify homogeneous groups among the sampling beaches, and to maximize differences between the formed groups (van Tongeren, 1987). The dendrogram was constructed using the single linkage method. Similarity distances were expressed as the Bray-Curtis similarity index.

Results

A total of 5651 annelids were collected from the 22 beaches and 160 samples. We found no annelidian fauna in 21 samples. Oligochaetes dominated the annelid faunal component in terms of abundance, with 4789 individuals (84.8%). Polychaetes were a minor proportion with 862 individuals (15.2%). Oligochaetes were present in 151 samples and polychaetes in 95 samples. We recorded six oligochaete and 14 polychaete species belonging respectively to three and 12 families (Table 2). Enchytraeidae and Tubificidae represented 66.3% (3176 individuals) and 33.7% (1613 individuals) of the oligochaetes, respectively. The two *Lumbricillus* species accounted for ca. 50% (2827 individuals) of all annelid individuals. *Thalassodrilus firmus*, with 1554 individuals (27.5% of all individuals) dominated the Tubificidae (Table 2).

Macrofaunal polychaetes dominated the polychaete group with, in order of abundance, *Capitella capitata*, *Pygospio elegans* and *Malacoceros fuliginosus* (Table 2). Quantitatively, meiofaunal polychaetes represent a minor fraction in the communities on Iceland sandy beaches. Typical meiofaunal species like *Nerilla antennata*, *Microphthalmus aberrans*,

Table 1. Location and description of sampling beaches and faunal diversity and abundance on Iceland in April 2000

Station	Code	Geographical coordinates	Exposure	Substrate type	Grain size range (mm)	Fresh water effluence	Annelid diversity (Shannon's H')	No of individuals
Sandgerði 1	A	64° 02′ N; 22° 42′W	Sheltered	Basaltic fine sand	0.062–0.25	+	1.38	345
Sandgerði 2	B	64° 02′ N; 22° 43′ W	Exposed	Shell coarse sand	0.5–2	–	1.56	664
Bessastaðir (Reykjavík)	C	64° 05′ N; 22° 02′ W	Sheltered	Shell coarse sand	0.5–2	–	1.28	159
Grótta (Reykjavík)	D	64° 10′ N; 22° 02′ W	Exposed	Basaltic gravel-very coarse sand	>2	+	1.32	390
Garðhúsavík (Garður lighthouse)	E	64° 05′ N; 22° 42′ W	Exposed	Basaltic fine sand-shell coarse sand	0.062–2	–	1.65	273
Hvalfjörður	F	64° 23′ N; 21° 23′ W	Sheltered	Basaltic coarse sand and gravel	0.5–>2	+	0.56	276
Neðri-Hóll (Snæfellsnes)	G	64° 24′ N; 23° 15′ W	Exposed	Basaltic coarse sand and gravel	0.5–>2	+	0.64	151
Olafsvík (Snæfellsnes)	H	64° 50′ N; 23° 36′ W	Exposed	Basaltic fine sand and gravel	0.062–>2	+	0	1
Búðardalur (north on the road #60)	I	64° 50′ N; 21° 45′ W	Sheltered	Basaltic coarse sand and gravel	0.5–>2	+	0.95	26
Reykhólar	J	65° 29′ N; 22° 8′ W	Sheltered	Basaltic coarse sand and gravel	0.5–>2	–	0.57	309
Hrútafjörður	K	65° 10′ N; 21° 8′ W	Sheltered	Basaltic coarse sand and mud below	<0.062–2	+	0.69	610
Skagaströnd	L	65° 50′ N; 20° 20′ W	Sheltered	Basaltic coarse sand and gravel	0.5–>2	+	0.45	6
Akureyri	M	65° 40′ N; 18° 15′ W	Sheltered	Basaltic coarse sand	0.5–2	–	0.49	802
Húsavík	N	66° 5′ N; 17° 25′ W	Sheltered	Basaltic coarse sand and gravel	0.5–>2	+	0	376
Kópasker	O	66° 15′ N; 16° 30′ W	Exposed	Basaltic fine sand	0.062–0.25	–	0	4
Hraunhafnartangi	P	66° 29′ N; 15° 57′ W	Exposed	Basaltic medium and fine sand	0.062–0.5	–	0	2
Vopnafjörður	Q	65° 45′ N; 14° 50′ W	Sheltered	Basaltic fine sand	0.062–0.25	–	0.65	385
Breiðdalsvík	R	65° 45′ N; 14° 3′ W	Exposed	Basaltic fine sand	0.062–0.25	–	1.04	6
Höfn	S	64° 15′ N; 15° 10′ W	Sheltered	Basaltic fine sand	0.062–0.25	–	1.28	17
Sandvík	T	63° 51′ N; 22° 42′ W	Exposed	Basaltic coarse sand and gravel	0.5–>2	–	0.64	3
Staðarbót	U	63° 49′ N; 22° 27′ W	Sheltered	Basaltic coarse sand	0.5–2	–	0.48	842
Festarfjall	V	63° 50′ N; 22° 25′ W	Exposed	Basaltic medium and coarse sand	0.25–2	–	0	4

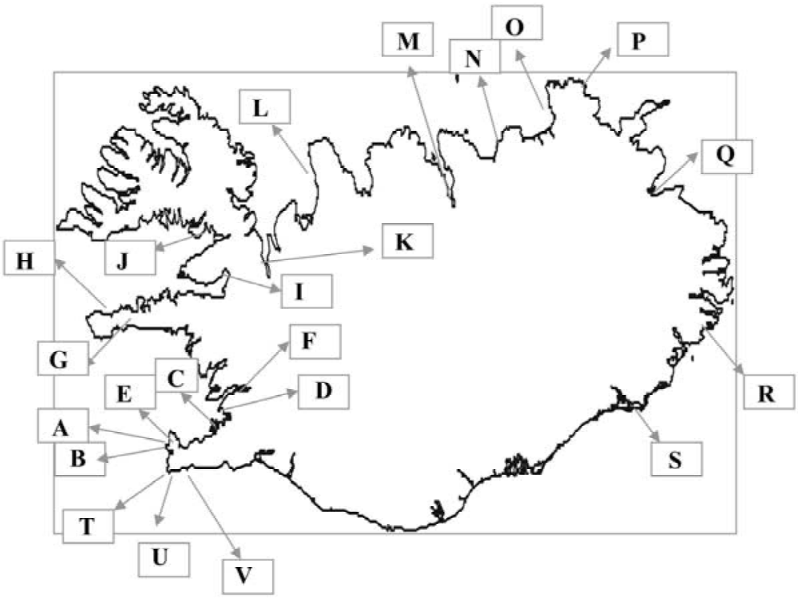

Figure 1. Location map of beaches studied in Iceland.

Table 2. Composition and overall abundance of annelids recorded from the 22 Iceland beaches in April 2000. P = Polychaetes; O = Oligochaetes. Beach letter codes in which a concrete species was collected are given (see Table 1 for codes; letters separated by a hyphen indicate all the range included). * = meiofaunal species; [c] = casual species

Species	Family	No. of individuals	Percent of total	Beaches
Lumbricillus sp.1 (O)	Enchytraeidae	2503	45.25	A–F,I–U
Thalassodrilus firmus * (O)	Tubificidae	1554	28.10	A–C,H–M,Q–S,U,V
Marionina sp. * (O)	Enchytraeidae	349	6.31	A,Q,S
Lumbricillus sp. 2 (O)	Enchytraeidae	324	5.86	C-G
Capitella capitata (P)	Capitellidae	246	4.45	A,B,D,E,G
Microphthalmus aberrans * (P)	Hesionidae	165	2.98	A,B,D,E,G,U
Pygospio elegans (P)	Spionidae	115	2.08	A,B,E,I,M,T,U
*Nerilla antennata** (P)	Nerillidae	74	1.34	C,D
Aktedrilus sp. * (O)	Tubificidae	54	0.98	B,E
Malacoceros fuliginosus (P)	Spionidae	47	0.85	B,E,G,J
*Ophryotrocha bacci** (P)	Dorvilleidae	30	0.54	E
Ophryotrocha gracilis * (P)	Dorvilleidae	25	0.45	C,E
Fabricia sabella[c] (P)	Sabellidae	12	0.22	B,D,S
Hediste diversicolor (P)	Nereididae	12	0.22	A,M
Naineris quadricuspida (P)	Orbiniidae	8	0.14	C,E
Pontodrilus littoralis (O)	Acanthodrilidae	5	0.09	B,E
Spirorbis borealis[c] (P)	Spirorbidae	5	0.09	C
*Protodrilus helgolandicus** (P)	Protodrilidae	1	0.02	E
*Sphaerodorum gracile** (P)	Sphaerodoridae	1	0.02	D
Sphaerosyllis sp. * (P)	Syllidae	1	0.02	B

Note: *Lumbricillus* sp. 1 and sp. 2 were differentiated by the segment number and by chaetal arrangement.

Ophryotrocha bacci and *O. gracilis* did not reach high densities. The most frequent and abundant meiofaunal polychaete was *Microphthalmus aberrans*, followed by*Nerilla antennata* and two *Ophryotrocha* species (Table 2).

Beach exposure seemed important for the relative abundance of oligochaete and polychaete components. Species number and diversity were highly different among sites. Five beaches were represented by only one species, *Lumbricillus* sp.1 (3 beaches) and *Thalassodrilus firmus* (2 beaches) (Table 2). Averaging individual samples per beach, annelid density varied between 0 and 277 individuals per 450 cm^3 of sediment. Mean ($\pm$ 1 SE) annelid abundance (polychaeta plus oligochaeta) was higher in sheltered beaches (31.7 $\pm$ 4.6 individuals per 450 cm^3) than in exposed beaches (8.5 $\pm$ 1.4 individuals 450 cm^3) (Mann–Whitney's U = 6543.5, $p < 0.001$). Mean polychaete abundance was significantly higher in exposed beaches (Mann–Whitney's U = 1194, $p < 0.05$), even though three sheltered inlets (Grótta, Neðri-Hóll and Akureyri) exhibited high abundance (Fig. 2). Oligochaetes seemed to be more abundant at sheltered areas (Mann–Whitney's U = 1221.5, $p < 0.001$) (Figs. 2 and 3). There were not statistically significant differences in abundance between sheltered and exposed beaches for the different polychaete taxa, although they were commonly more abundant at the latter sites (Fig. 3). For oligochaetes, one species of *Lumbricillus* (Mann–Whitney's U = 390.5, $p < 0.001$) and, marginally, *Thalassodrilus firmus* (Mann–Whitney's U = 58, $p = 0.047$), were significantly more abundant in sheltered beaches (Fig. 3). Mean annelid diversity was low and did not differ significantly between sheltered (0.73) and exposed (0.68) beaches (Mann–Whitney's $U = 58$, $p = 0.923$) (Table 1). Only two exposed stations showed diversity values higher than 1.5, and the higher annelid diversity (range of H' = 1.28–1.65) was found in the south-western area (Sandgerði and Reykjavík, Table 1).

Most meiofaunal polychaete species were more abundant in exposed beaches, with the exception of *Nerilla antennata*, recorded at only two sheltered beaches. Typical meiofaunal polychaetes (*Nerilla, Ophryotrocha, Microphthalmus, Protodrilus*) were not recorded from the north coast localities. *Ophryotrocha bacci* was recorded at only one exposed station (Table 2). *Microphthalmus aberrans* and *Ophryotrocha gracilis* were more abundant in exposed than in sheltered beaches.

There were large differences in the distribution of abundance of oligochaete and polychaete taxa among the 22 sites. Cluster analysis revealed three main groups of beaches as a function of annelid composition and diversity (Fig. 4). Most exposed beaches were arranged separately from sheltered ones, showing a grouping at the 23% level of similarity. Group 1 consisted mainly of exposed beaches, whilst clusters 2 and 3 grouped most sheltered ones. Group 2 contained three subsets, the central one with the bulk of sheltered areas from north and southwest Iceland, at a 50% level of similarity (Fig. 4). Southwest beaches were similar in their higher annelidian diversity compared to northern ones. Garðhúsavík was exceptionally classified apart from the remaining beaches, as a result of its higher annelid diversity (by contribution of more polychaete species) and high sediment heterogeneity (Table 1). With the exception of Grótta (annelid diversity, H' = 1.32; gravel: grain size class = $>$ 2 mm), the beaches supporting higher annelid diversity were those formed by fine sand ($H' > 1$; grain size class = 0.063–0.25 mm).

Discussion

Our results show: (a) a low general annelid diversity, (b) that oligochaetes dominate the annelid community in numeric terms at the studied beaches on Iceland, and (c) that polychaetes are relatively more abundant at exposed than at sheltered beaches, while oligochaetes display the opposite pattern. As transition zones (between land or freshwater and marine habitats), sandy beaches support inherently low infaunal diversity, although the ecological value of these communities is high (Levin et al., 2001). Higher abundance and diversity of infaunal annelids were recorded at the west and southwest sandy beaches compared to northern ones in Iceland. In our study, all beaches, but particularly the sheltered ones, were clearly dominated by oligochaetes. This was mostly determined by the high abundance of *Lumbricillus* sp.1 and *Thalassodrilus firmus*, the quantitatively dominant species. Other studies have also shown that oligochaetes and nematodes are dominant groups in subarctic latitudes both in exposed and sheltered beaches (Ingólfsson, 1990; Ólafsson, 1991).

Communities of cohabiting polychaetes and oligochaetes follow global diversity and abundance patterns that may respond to depth and latitudinal gradients. For example, polychaetes have been shown to increase

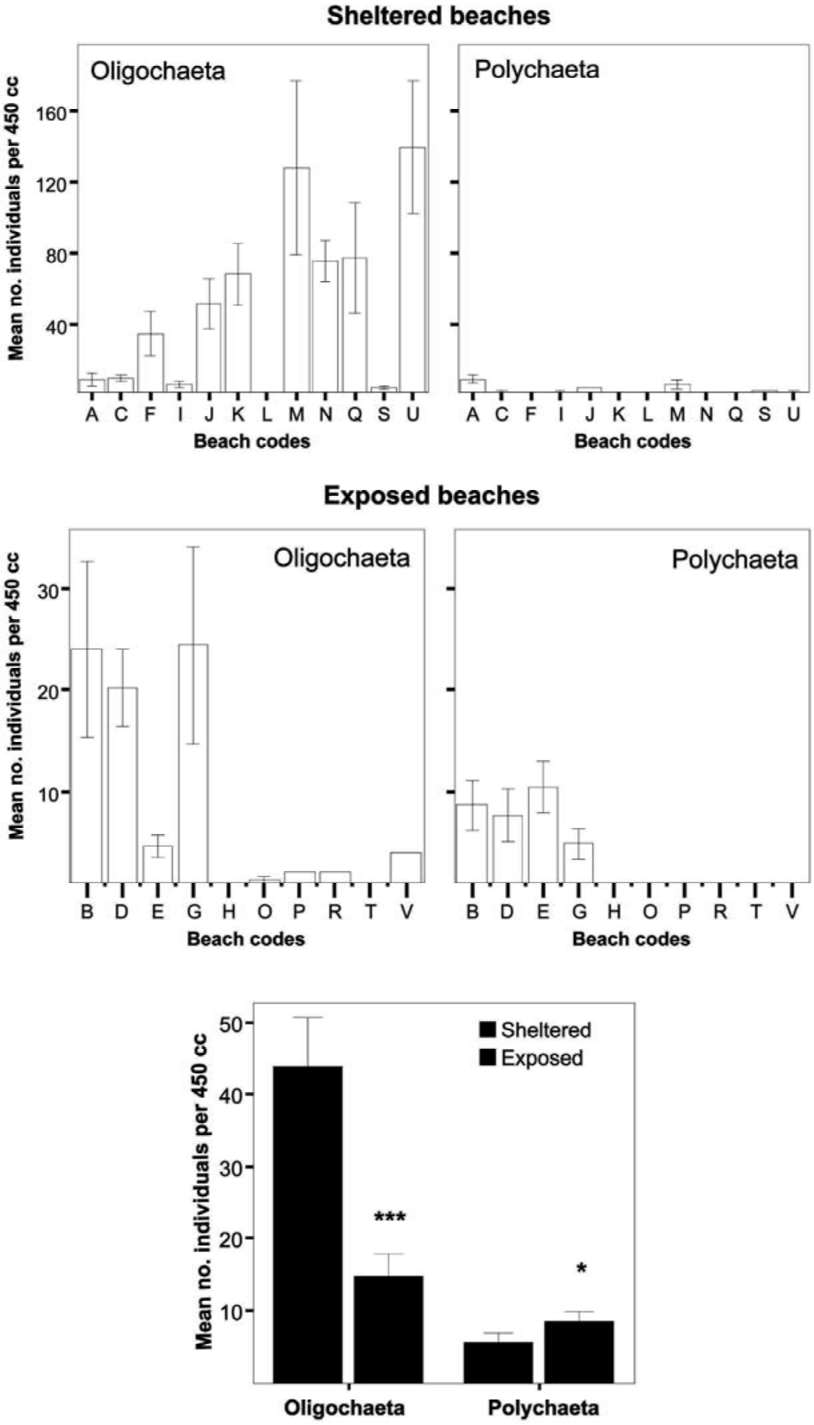

Figure 2. Differences in annelid abundance between sheltered and exposed beaches in Iceland. Bars are means ± 1 SE. Significance levels for paired comparisons (Mann–Whitney's *U* tests: ***: $p < 0.001$; *: $p < 0.05$). Beach codes as in Table 1.

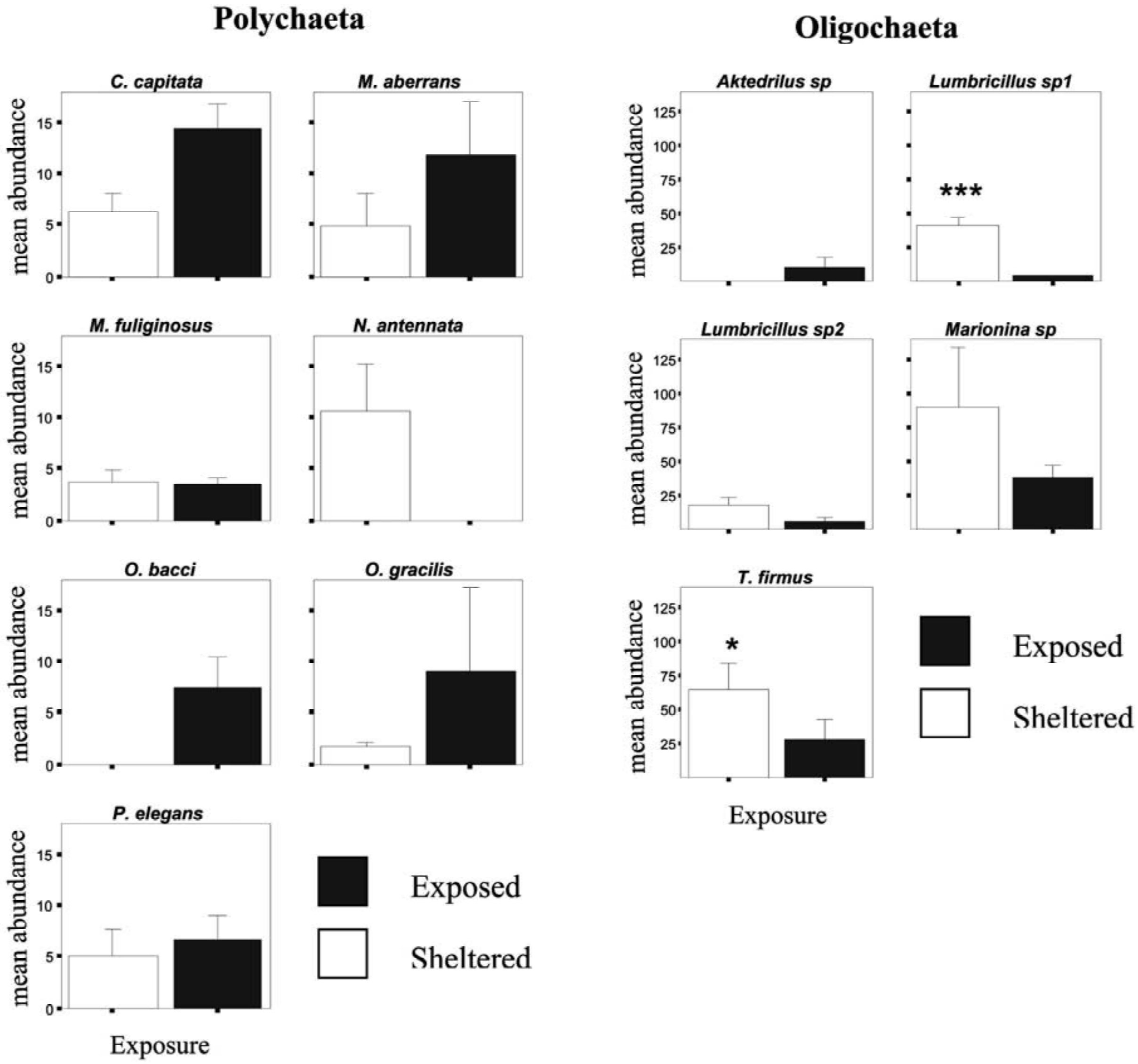

Figure 3. Comparative abundances of major meio- and macrofaunal annelids between sheltered and exposed beaches in Iceland. Bars represent mean no. individuals per 450 cm^3 sample (+ 1 SE), pooled over beaches for each exposure type. Significance levels for *Lumbricillus* sp1 and *Thalassodrilus firmus*: ***: $p < 0.001$; *: $p = 0.047$. Remaining taxa: not significant differences ($p > 0.05$). Tests were not performed for *Nerilla antennata*, *Ophryotrocha bacci* and *Aktedrilus* sp.

in abundance and diversity with increasing depth on Antarctic shores (Bromberg et al., 2000). Our results regarding composition of the annelid fauna contrast with that of beaches at lower latitudes. Polychaetes are commonly the dominant group in sheltered beaches at lower latitudes (Brown & McLachlan, 1990). For instance, basaltic sand beaches on the Canary Islands (Atlantic off the northwest African coast) are highly exposed, and show a clear dominance by polychaetes, oligochaetes making a smaller fraction (Brito, 1999). In our study, the polychaete community was formed mainly by macrofaunal species. Among these, some spionids and *Capitella capitata* were the most frequent in sheltered areas with fine sand or mud rich in organic matter. Estuarine beaches at higher latitudes consisting of mixtures of sand and mud commonly support an infauna mostly dominated by oligochaetes, capitellids and spionids, as occur at upper tide reaches in our study (Connor et al., 1997; Méndez et al., 1997). Oligochaetes are often common in sediments with a

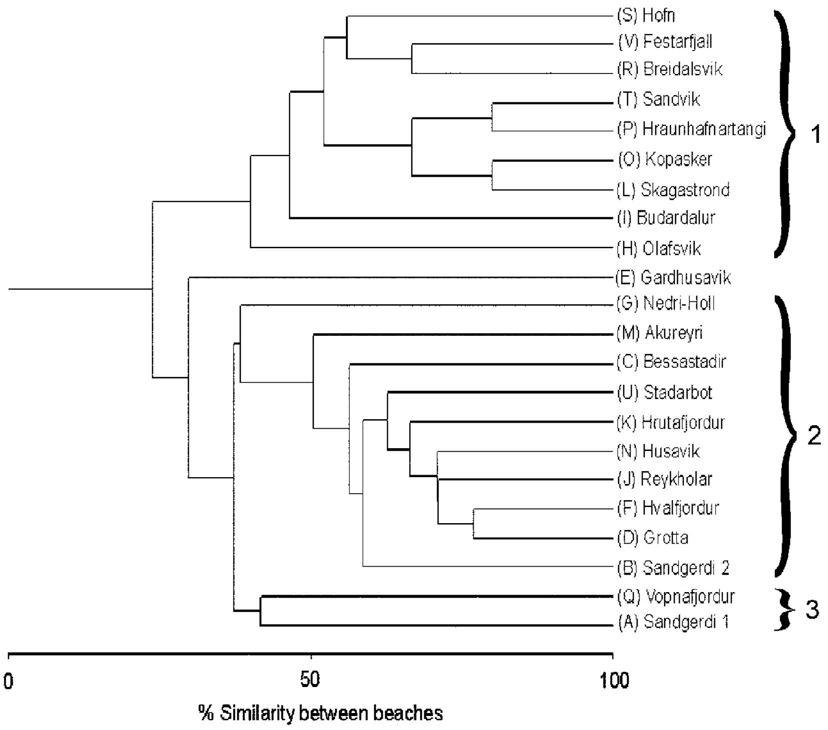

Figure 4. Dendrogram of the 22 sandy beaches sampled on Iceland. Cluster distances were calculated with the Bray–Curtis similarity index (single link) for the composition and diversity of annelid taxa (Oligochaeta and Polychaeta).

freshwater input, and this is frequently associated to an impoverishment of the polychaete fauna (Connor et al., 1997). As infaunal deposit feeders, oligochaetes are favoured at the upper reaches of sandy estuaries and inlet sediments rich in organic matter (Connor et al., 1997). Stations with higher diversity values, such as Sandgerði, Garðhúsavík and Reykjavík in this study, are influenced by fresh water effluents and organic matter from sewage. These factors, along with intrinsic sediment patchiness, could modify the sediment properties and stability. The virtual absence of meiofaunal polychaetes from the northern beaches sampled in our work might be interpreted in terms of gradients in productivity, salinity and temperature (in our case including freezing of the upper reaches), and the dominant currents between different sectors of the Iceland coast (Stefánsson & Ólafsson, 1991).

At the microhabitat scale, the assemblage composition is determined by particular life history traits, behavior and habitat selection patterns, determining capabilities of each species to tolerate different sediment grain, drainage and mobility regimes (Giere, 1975; Allen & Moore, 1987; Pinedo et al., 2000). The exposure degree and thus wave energy affecting the sediment is determinant for the establishment of the macro- and meiofaunal taxa in sandy beaches (Bloom et al., 1972). Low energy beaches have been shown to support higher density and diversity of macrofauna (Allen & Moore, 1987). These patterns may be related to sediment grain size distribution and stability through the degree of compaction (Pinedo et al., 2000). The compaction attainable by fine sediments is higher than that of coarse-grained substrata. Shelter from wave action allow fine sediment to deposite, and sediments are more stable at these areas (Connor et al., 1997). Despite the range of grain sizes of our samples was poorly defined, fine sands of sheltered beaches apparently supported higher annelid diversity and abundance than coarse sands or gravels.

Patterns of annelid community variation on Iceland deserve further study, with a stress on factors conditioning composition and diversity of the oligochaete and polychaete components at the local and regional scales. These groups might serve, considered simultaneously, as indicators for which responses to environmental gradients (e.g. local sediment properties, exposure, latitudinal gradients and current regimes) can be measured.

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