POLISH POLAR RESEARCH
vol. 33, no. 3, pp. 225–238, 2012 doi: 10.2478/v10183-012-0016-1

Eight species that rule today's European Arctic fjord benthos

Jan Marcin WĘSŁAWSKI*, Maria WŁODARSKA-KOWALCZUK, Monika KĘDRA, Joanna LEGEŻYŃSKA and Lech KOTWICKI

Instytut Oceanologii Polskiej Akademii Nauk, ul. Powstańców Warszawy 55, 81-712 Sopot, Poland
** corresponding author <weslaw@iopan.gda.pl>*

Abstract: The eight most abundant species (mean density >20 ind. m^{-2}), which occurred at high frequencies (mean >30%) were selected from grab samples in the three Svalbard fjords: Hornsund, van Mijenfjord, and Kongsfjord, in the summer seasons between 1997 and 2007. Six polychaete and two bivalve species comprised more than 47% of the individuals and the biomass in all the samples examined. Four species are cosmopolitan, while the others are widely distributed Arctic-boreal species, and none has Arctic origin. Their density, frequency of occurrence, and biology are very similar across the wide geographical range from boreal to Arctic conditions. As the diversity of benthic fauna in the fjords studied increases (from 172 to 238 species), the dominance of the eight species in the soft bottom community diminishes from 76% to 47%. In times of hydrological regime shift, *i.e.*, the warming of the European Arctic, it is unlikely that the abundancy of these species in the soft bottom fjordic ecosystems will change. The most common soft bottom species are not good indicators of environmental change in the Arctic, and rare, specialized species are better option for indicative purposes.

Key words: Arctic, Svalbard, benthos, Polychaeta, common species.

Introduction

The fjords of Spitsbergen, the largest island in the Svalbard archipelago, are undergoing serious environmental change from local sea warming (ACIA 2006; Walczowski and Piechura 2006), rapid retreat of tidal glaciers, and increased sedimentation (Węsławski *et al.* 2011). Most of the sea bed area below wave action depth is covered by fine, muddy, glacial sediments with little organic matter content (Svendsen *et al.* 2002; Włodarska-Kowalczuk and Pearson 2004). Three fjords have been studied extensively over the last ten years and over 500 benthic macrofauna species have been recorded in quantitative soft bottom grab-samples (Kędra *et al.* 2010; Włodarska-Kowalczuk *et al.* 2012). It is generally believed that in marine ecosystems most species are rare, while common species are few (Heip *et al*. 2009). In the studied area singletons (species represented by single individuals in all collection) were noted to comprise 16 to 20% of all the macrofauna (Włodarska-Kowalczuk *et al.* 2012). In order to assess the effect of environmental change on benthic communities, we focused on the most common and abundant species, since only a few taxa comprise the main bulk of biomass and abundance in the studied basins (*op. cit.*). We selected only those species that had a frequencies of occurrence exceeding 30% and an average density exceeding two specimens per sample (20 ind. m^{-2}), and that were recorded in all, but one of the studied locations.

Since the most abundant and common species are responsible for the majority of the biomass, oxygen consumption, and energy turnover, understanding their patterns of occurrence is important for linking environmental changes with biological responses. Thus, the aim of this study was to investigate if the distribution and density of widespread, eurytopic, opportunistic species that dominate the system in the stressful, extreme environment of Arctic fjords are stable in time and space?

Materials and methods

Study area. — Spitsbergen, the largest island of the Svalbard archipelago, is situated on the western edge of the Barents Sea between 76 and 80° N. Despite its high northern location, the waters of the western coast of Spitsbergen are relatively warm because of the influence of the West Spitsbergen Current, which is an extension of the North Atlantic Current. Cold Arctic waters are transported by the East Spitsbergen Current that flows around the southern tip of the island, and then northward along its west coast (Loeng 1991). Hydrological regimes of the west Spitsbergen fjords are shaped by warm, saline water masses of Atlantic origin that flow from the shelf (T >3°C, S >34.65), and by freshened, cold water masses (T >1°C, S <34) from large meltwater inflows, from tidal glaciers, or glacier-fed rivers located in the inner parts of the fjords. The glacial and glaciofluvial inflows transport large amounts of mineral suspensions and produce steep gradients of water turbidity and mineral sedimentation along the fjord axes. The sediment in Svalbard fjords are composed of glacio-marine deposits dominated by silt and clay. Additionally, the shelf currents influence outer parts of the fjords bringing there a admixture of coarse fraction (Włodarska-Kowalczuk and Pearson 2004). The west Spitsbergen fjordic and shelf waters are well oxygenated (Jørgensen *et al.* 2005). The late spring phytoplankton bloom generates large fluxes of organic matter to the bottom sediments. When the fast ice cover persists for longer periods and water turbidity in the inner basins is significant, then the fluxes of organic matter to the bottom are low (Zajączkowski *et al.* 2007). The particulate organic carbon concentrations in the sediment increase with proximity to fjord mouths (Włodarska-Kowalczuk and Pearson 2004; Winkelman and Knies 2005).

The present study is based on samples collected in three large fjords along the west coast of Spitsbergen: Kongsfjord, van Mijenfjord, and Hornsund. The northernmost of these, Kongsfjord is 20 km in length and there is no still there. Three large tidal glaciers terminate in the fjord waters, including Kongsbreen, which is the most active glacier in the Svalbard archipelago. With increasing proximity to the inner Kongsfjord glaciers, the mineral sedimentation in the surface waters increases from 25 g m^{-2} day^{-1} in the central basin to 800 g m^{-2} day^{-1} in Kongsbreen glacial bay, and the particulate organic carbon content in the sediments decrease from 2 mg g^{-1} to 0.2 mg g^{-1}, respectively (Hop *et al*. 2002). The entrance to van Mijenfjord is nearly closed by a 30 m sill and the long, narrow island (Akseløya). Fresh water and mineral suspensions are transported to the 50 km long fjord by the Kjelleströmelva River and the Paulabreen glacier. The coal dust produced by the Svea coal mine likely contributes to the high sedimentation in the inner part of the fjord (Renaud *et al.* 2007). Hornsund is a wide, open fjord with eight major tidal glaciers located in its central and inner areas. The banks of the inner basin, Brepollen, are almost entirely formed by tidal glacier cliffs. The sediment accumulation rate in Brepollen can reach 35 cm y^{-1}, while in the outer parts of Hornsund it is as low as 0.1 cm y^{-1}.

Sampling. — The samples were collected in all locations along the fjord axes in the inner, central, and outer basins (Fig. 1). Sampling depth ranged from 50 to 300 m, and near-bottom salinity was from 34.5 to 35 PSU. The summer temperature near the bottom in the coldest inner basins dropped below 0°C, while it was 4°C in the warmest, outermost basins. There were no major hydrological differences between the three fjords studied, except for the open, configuration near the shelf (see www.iopan.gda.pl/projects/biodaff, Table 1). The samples were collected with a van Veen grab (0.1m^2), and sieved (mesh size 1 mm in van Mijenfjord, 0.5mm in Hornsund and Kongfsjord) aboard the research vessel. General information regarding the benthos from the reported sampling campaigns was published in Włodarska-Kowalczuk and Pearson (2004), Renaud *et al.* (2007), Kędra *et al.* (2011), Grzelak and Kotwicki (2011). Increasing number of benthic species were noted from Hornsund (172 species) to van Mijenfjord (194 species), and Kongsfjord (238 species; Table 1).

Data analysis. — Frequency of occurrence was calculated as a percentage of the number of samples containing given species in total number of samples. Dominance was calculated as a percentage of number of specimens of given species in the total number of specimens in the samples. Abundance (density of specimens per area unit) was a key factor of choice. The small fragile polychate worms are easily damaged in the process of sieving and sorting, and so, instead of weighting actual individuals in samples, we have calculated the species biomass in samples using the mean individual biomass values for species (own unpublished data IO PAN).

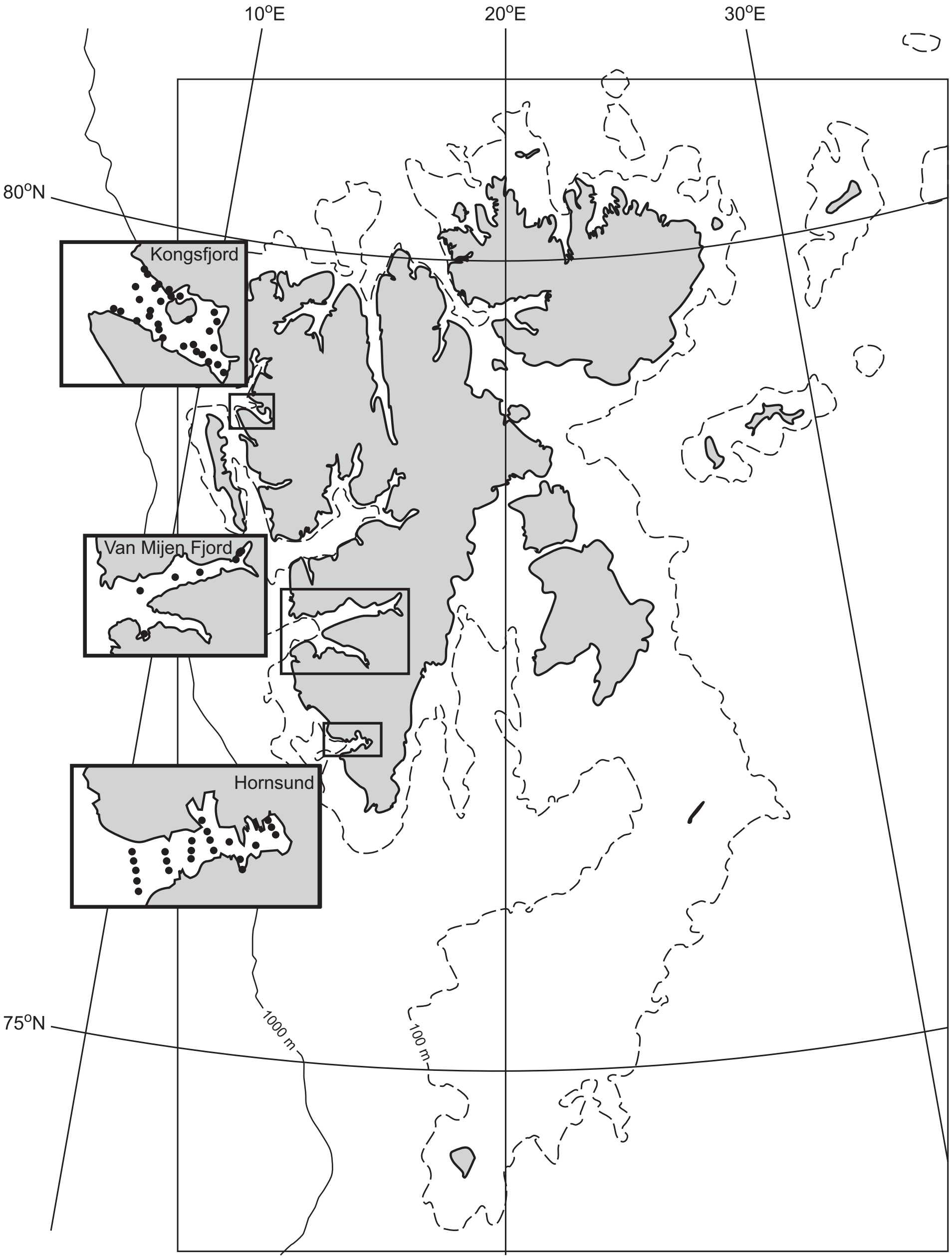

Fig. 1. Study area: Svalbard and three selected fjords. Dots indicate sampling sites.

Estimations of oxygen consumption rates, production to biomass ratios, and relations between biomass and organic carbon were derived using Barents Sea, Svalbard Shelf (Piepenburg *et al*. 1995) and Laptev Sea shelf (Schmidt *et al*. 2006) data as follows:

Table 1

Sampling effort and basic information on samples used in the present study. N_{st} – number of sampling stations, N_s – number of benthic samples taken, N_{sp} – number of species recorded.

	Hornsund	Kongsfjord	van Mijenfjord
Connection to the shelf	wide open, small sill at the entrance	wide open, no sill at the entrance	semi-closed, narrow entrance
Sampling years	2002, 2003, 2005, 2007	1997–2006	2000, 2001
N_{st}	24	30	5
N_s	125	84	59
N_{sp}	172	238	194

Polychaeta P/B = 1.9; Mollusca P/B = 0.1; carbon mineralization to carbon ingestion rate 1.79. The ratio of 1g wet weight of infaunal Polychaete biomass to oxygen consumption (μmol O_2 m^{-2} h^{-1}) is 0.6; the same ratio for infaunal mollusks is 0.3.

Respiration formulas were adapted from Grodziński *et al.* (1975) and Opaliński and Węsławski (1989) at $1cm^3$ O_2 = 0.42 mg C; respiration quotient 0.8; assimilation coefficient 30%. Respiration (R)=0.2 W $^{0.76}$, where W is wet weight.

Primary production was adapted using summer Hornsund values reported by Piwosz *et al.* (2009) as 14–86 mg C m^{-2} h^{-1}. The organic sedimentation reaching the seabed in Hornsund was assessed to be from 7 to 20 mg C m^{-2} d^{-1} (Ronowicz *et al.* 2008).

Results

Only eight species were widely distributed and found in high abundances in all of the three fjords studied, and, in some cases, they reached a frequency of occurrence of 90% (Table 2). These species comprised 76, 53, and 47% of the individuals collected in three localities: Hornsund, van Mijenfjord and Kongsfjord, respectively (Table 2). Two taxa, *Chaetozone* spp. and *Lumbrineris mixochaeta*, were the most widely distributed with a mean frequency of more than 50%. *Chaetozone* spp. dominated by having the highest mean density in all the fjords, followed by *Cossura longocirrata* and *L. mixochaeta* (Table 3).

The density varied from sample to sample, from species to species, fjords, and years with SD equal to or higher than the mean values, nevertheless in all years the eight species were among top abundant taxa in samples (Table 3). The estimated carbon demand of these eight species ranged from 3.9 to 8.8 mg C m^{-2} d^{-1}, and the annual secondary production ranged from 3 to 7 g C m^{-2} y^{-1} (Table 3).

The distribution within the fjords indicated an even distribution of *Chaetozone* spp. and *C. longocirrata* throughout the fjord basins, a lower frequency of *Ennucula*

Table 2

Mean frequency of occurrence and dominance of the taxa in three fjords studied.

Fjord	Hornsund		Kongsfjord		van Mijenfjord	
Taxon	F[%]	D [%]	F [%]	D [%]	F [%]	D [%]
Chaetozone spp.	66	33.2	81	16.4	90	30
Cossura longocirrata Webster *et* Benedict, 1887	49	8.7	89	7	47	1
Ennucula tenuis (Montagu, 1808)	45	8.7	54	1.6	46	5
Heteromastus filiformis (Claparède, 1864)	61	0.6	76	4.3		
Leitoscoloplos mammosus Mackie, 1987	37	5.6	55	5.3	50	5
Lumbrineris mixochaeta Oug, 1998	66	9.3	95	8.8	75	28
Maldane sarsi Malmgren, 1865	50	9.1	51	2.9	41	2
Nuculana pernula (O.F. Müller, 1779)	26	1.2	52	0.9	27	2
Summary dominance in density		76.2		47.2		53

Table 3

Average density (avN, [ind. m^{-2}], average individual biomass (B_i, [mg m^{-2}]), biomass (B, [g WW m^{-2}]), respiration rates (R, [O_2 m^{-2} h^{-1}]), carbon demand [mg C $m^{-2}d^{-1}$] and production [g C $m^{-2}y^{-1}$] estimated for the taxa in three fjords studied.

Fjord		Hornsund				Kongsfjord				van Mijenfjord		
Taxon	B_i	avN	sd	B	R	avN	sd	B	R	avN	B	R
Chaetozone spp.	15	1009	1067	15	9.1	360	520	5	3.24	527	8	4.74
C. longocirrata	3	262	363	1	0.5	270	270	1	0.49	14	0.0	0.03
E. tenuis	9	23	20	0.2	0.1	90	180	1	0.49	95	1	0.52
H. filiformis	12	31	38	0.4	0.2	150	220	2	1.08			
L. mammosus	15	146	112	2	1.3	210	280	3	1.89	122	2	1.10
L. mixochaeta	15	171	87	3	1.5	480	490	7	4.32	138	2	1.24
M. sarsi	58	236	136	14	8.2	120	200	7	4.18	24	1	0.84
N. pernula	10	5	4	0.1	0.02	30	80	0.3	0.09	26	0.3	0.08
total		1883		35	21	1710		26	16	947	14	9
carbon demand					8.8				6.9			3.9
production estimated					7				5			3

tenuis, *Heteromastus filiformis*, *Maldane sarsi*, and *L. mixochaeta* in the innermost areas, and a absence of *Leitoscoloplos mammosus* and *Nuculana pernula* in the inner fjord basins (Fig. 2).

The species characteristics (size, habitat, distribution etc.) was similar as most species belong to small to medium sized (3 to 15 mg wet weight) infauna, except for *M. sarsi*, which was threefold heavier (58 mg) in comparison to other species (Table 3). Geographically, all the species were widespread, cosmopoli-

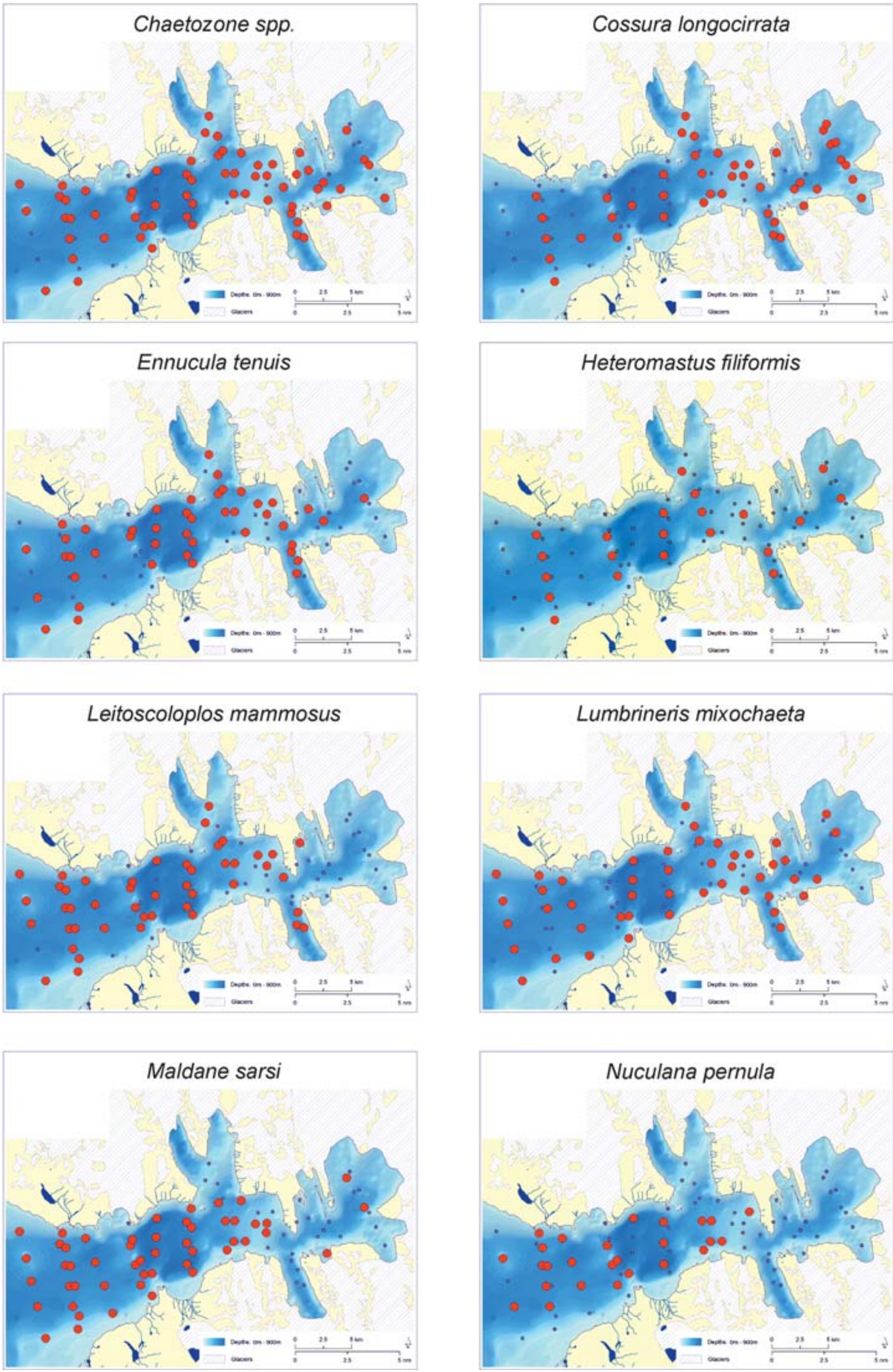

Fig. 2. Distribution of species examined in Hornsund; samples from 2002, 2003, 2005 and 2007. Large dots indicates presence, small absence of species.

Table 4

Species characteristics including: mean and maximal size [mm], mobility, feeding type, reproduction mode and zoogeographic status. P – Polychaeta, M – Mollusca, AB – arctic-boreal, C – cosmopolitan. Data compiled from http://www.iopan.gda.pl/projects/Polychaeta, Fauchald and Jumars (1979), Fetzer and Arntz (2008) and Kędra *et al.* (2010).

Taxon (higher taxon)	Mean/ max size [mm]	Functional group	Reproduction mode	Zoogeography
Chaetozone spp. (P)	15/25	discretely motile, surface deposit feeder, facultative suspension feeder	lecithotrophic	C
C. longocirrata (P)	3/4	motile, non selective subsurface detritus feeder, burrowing	lecithotrophic	AB
E. tenuis (M)	3/5	motile, surface deposit feeder	lecithotrophic	AB
H. filiformis (P)	12/29	discretely motile, head down, subsurface detritus feeder, burrows with mucous	planktotrophic	C
L. mammosus (P)	20/100	discretely motile, non selective surface detritus feeder, burrowing	no data	C
L. mixochaeta (P)	25/100	motile, carnivore, scavenger, omnivore	no data	AB
M. sarsi (P)	58/109	sessile, head down, subsurface detritus feeder, deep burrows	lecithotrophic	C
N. pernula (M)	10/15	motile, subsurface deposit feeder	lecithotrophic	AB

tan, or Arctic-boreal, and none was assigned specifically to the Arctic domain (Fig. 3, Table 4).

Discussion

Are the most abundant species "jacks-of-all-trades" in terms of functional groups? — Knowledge on the biology of the species examined is very limited despite their commonness and abundance. Four of these species are non-selective, subsurface detritus feeders, while three are surface deposit feeders, and only *L. mixochaeta* is reported to be a carnivore/omnivore (http://www.iopan.gda.pl/projects/polychaeta). The analyzed group of species did not include any specialized feeders or species linked to specific micro-habitats. The most common, abundant species has not been identified as prey for local top predators such as seabirds, seals, or walruses, or fjordic fish species such as Cottidae, Lumpenidae, or Gadidae (see prey check lists in Węsławski and Kuliński 1986; Lydersen *et al.* 1989; Węsławski *et al.* 1994, 2000). This might indicate that carnivorous invertebrates and small fish species serve as intermediary links in the local food web between the most common soft bottom benthos and the top predators.

Are they found in more than one specific habitat, zone, or community? — All but two of the species examined occurred throughout the studied area along the

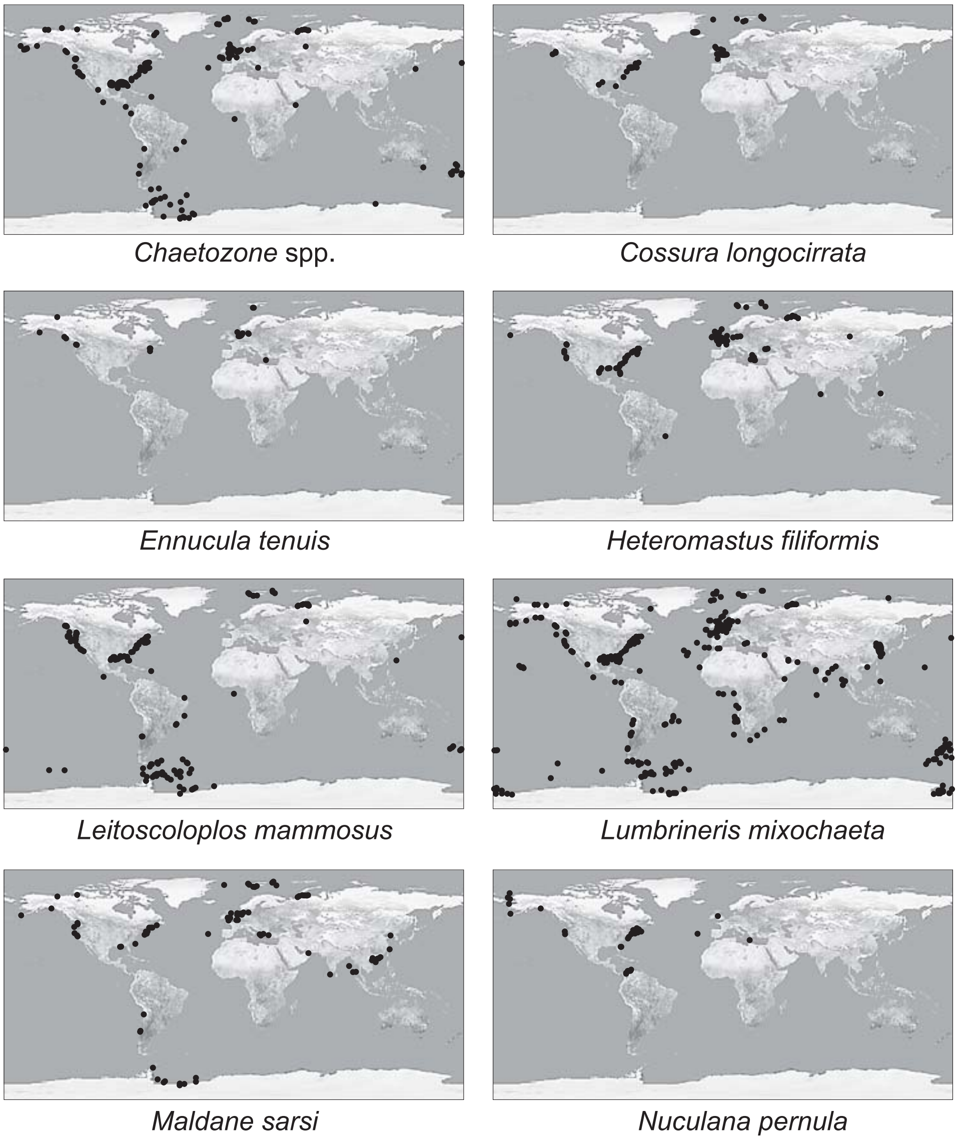

Fig. 3. Global occurrence of species considered in present study based on OBIS database (http://www.iobis.org).

fjord axes from the inner to the outer basins and across the observed gradients of environmental parameters, however, they were least frequent in the innermost basins where faunal impoverishment is known due to the harsh environment (Görlich *et al.* 1987; Włodarska-Kowalczuk and Węsławski 2008). *L. mixochaeta*, *L. mammosus*, and *E. tenuis* were either not numerous or absent from the Arctic shelf, while *H. filiformis* and *M. sarsi* were also fairly abundant outside the fjords (Cochrane *et al.* 2009; Włodarska-Kowalczuk *et al.* 2012).

Do they have similar breeding strategies, life cycles, and dispersion patterns? — Although it is possible that widespread species might have pelagic larvae, almost all of the species examined reproduce through the production of short-living benthic larvae or by direct development with strong seasonality (Fetzer and Arntz 2008). Based on a study conducted in northern Norwegian fjords, Oug (2000) reported almost the same list of dominants (*Chaetozone* spp., *M. sarsi*, *H. filiformis*, *C. longocirrata*, *L. mixochaeta*) as in the present study, but the mean density of soft bottom fauna and species numbers were higher (4000 ind. m^{-2} and 395 species, respectively) compared to the present data. Most of the eight species considered in the present study have also been reported as key species in Franz Josef Land, the Barents Sea, northern Norway, and southwest Greenland (Table 5).

Table 5

Range of density of the species studied from other Arctic localities. Data from: [1] Holte and Gulliksen (1998), [2] Włodarska-Kowalczuk *et al.* (1998), [3] Włodarska-Kowalczuk *et al.* (2007), [4] Schmid and Piepenburg (1993), [5] Cochrane *et al.* (2009).

Fjord	Raud-fjord[1]	van Mijen-fjord [1]	Isfjord[2]	Advent-fjord[3]	Hollands-fjord[1]	Disco fjord[4]	Barents Sea[5]
Area / taxon/ind. m^{-2}	Svalbard	Svalbard	Svalbard	Svalbard	N Norway	SW Greenland	NW Barents Sea
Chaetozone spp.	58–138	3–47	226–1359	70–2200	65–600	70–365	46–68
C. longocirrata			22–622	90–2900			
E. tenuis	10–277	2–110		10–80	3–26		
H. filiformis		2	4–119	10–100	65–659	6	16–142
L. mammosus			33	10–340			
L.michochaeta	33–165	23–177	22–467	10–180	9–395	18–45	18–220
M. sarsi	22–205	2–18	4	10–410	3–530		12–100
N. pernula	5–73	8–12	4				

The geographical distributions of the studied taxa indicate that four are cosmopolitan (*Leitoscoloplos mammosus*, *M. sarsi*, *Chaetozone* spp., *H. filiformis*), while the other four are widely-distributed arctic-boreal forms (*L. mixochaeta, C. longocirrata*, *E. tenuis*, *N. pernula*) (OBIS database; http://www.iobis.org/) (Fig. 3). We are awared the uncertain taxonomic status of most species considered in this paper. The label "cosmopolitan" is often misleading, as in many cases molecular methods reveal series of cryptic species that were traditionally named as one widely distributed form (Bleidron *et al.* 2006; Carrera-Parra 2006; Barroso *et al.* 2010).

Role of the key species in benthic system. — In the area studied, the eight species comprise a minor fraction of the biomass in comparison to their density;

this is also true for the Barents Sea where Wassman *et al.* (2006) considered polychaetes to be numerous but only of secondary importance in terms of biomass.

The estimated carbon demand of the eight species ranged from 3.8 to 8.8 mg C m^{-2} d^{-1} (Table 3), which corresponds to 7 to 19% of the daily sedimentation of organic carbon in Hornsund in summer (7 to 20 mg C m^{-2} d^{-1}; Ronowicz *et al.* 2008), or about 1–2 % of the local primary production of 14 to 86 mg C m^{-2} h^{-1}; Piwosz *et al.* 2010). Wassman *et al.* (2006) estimated the pelagic carbon sink to a depth of 100 m in the Barents Sea to be 40g C m^{-2} y^{-1}. Compared to other Arctic locations, the present data are similar to the East Greenland Young Sound in terms of density and biomass (Rysgaard *et al.* 2007), while the benthos of the Arctic shelf exhibits more even species distribution in sample, with less-pronounced dominants (Schmidt and Piepenburg 1993; Cochrane *et al.* 2009; Włodarska-Kowalczuk *et al.* 2012).

In conclusion, the eight species described in the present study are widely distributed and abundant in the Svalbard fjord benthos, and they are also widespread throughout large areas extending from the boreal to the subarctic. In times of hydrological regime shift, i.e., the warming of the European Arctic, it is unlikely that geographic distribution and abundance of these abundant species will change in the soft bottom fjordic ecosystems. Firstly, they are highly tolerant of and well-adapted to a wide range of temperatures. Secondly, unstable soft sediments and high sedimentation rates are key factors controlling the coastal Svalbard biocenose regardless of temperature change. Hence, the most common soft bottom species are not good indicators of large scale environmental change in the Arctic. They may show differences in density or percent share in benthic community on a small scale (e.g. glacier to fjord mouth transect in Włodarska-Kowalczuk and Pearson 2004). In order to use soft bottom fauna as indicator of large scale climate change, one shall search for rare species that are stenothermic or linked to specific sedimentary conditions, since it is the temperature and sedimentation that will differ substantially, between pre-warmed and post warmed regime.

Acknowledgments. — This paper was partially funded by Ministry of Science grants SPB Hornsund/ ENIBANK, and Polish National Polar Project for 2005–2006 funded by Ministry of Science and Informatics. The authors wish to acknowledge the assistance of Sławomira Gromisz, Barbara Maciejewska, Artur Opanowski, Radomir Jaskuła, and Karolina Ostrowska, who sorted and identified some of the materials examined.

References

ACIA 2006. *Arctic Climate Impact Assessment. Scientific Report*. Cambridge University Press, Cambridge: 1042 pp.

BARROSO R., KLAUTAU M. and SOLE-CAVA A.M. 2010. *Eurythoe complanata* (Polychaeta: Amphinomidae), the "cosmopolitan" fireworm, consists of at least three cryptic species. *Marine Biology* 157: 69–80.

BLEIDORN C., KRUSE I., ALBRECHT S. and BARTOLOMAEUS T. 2006. Mitochondrial sequence data expose the putative cosmopolitan polychaete *Scoloplos armiger* (Annelida, Orbiniidae) as a species complex. *BMC Evolutionary Biology* 6: 47. Published online 2006 June 15. doi: 10.1186/1471-2148-6-47

CARRERA-PARRA L.F. 2006. Revision of *Lumbrineris* de Blainville, 1828 (Polychaeta: Lumbrineridae). *Zootaxa* (1336): 1–64.

COCHRANE S.K.J., DENISENKO S.G., RENAUD P.E., EMBLOW C.S., AMBROSE W.G., ELLINGSEN I.H. and SKARĐHAMAR J. 2009. Benthic macrofauna and productivity regimes in the Barents Sea – ecological implications in a changing Arctic. *Journal of Sea Research* 61: 222–233.

FAUCHALD K. and JUMARS P.A. 1979 The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology. An Annual Review* 17: 193–284.

FETZER I. and ARNTZ W.E. 2008. Reproductive strategies of benthic invertebrates in the Kara Sea (Russian Arctic): adaptation of reproduction modes to cold water. *Marine Ecology Progress Series* 356: 189–202.

GØRLICH K., WĘSŁAWSKI J.M. and ZAJĄCZKOWSKI M. 1987. Suspensions settling effect on macrobenthos biomass distribution in the Hornsund fjord, Spitsbergen. *Polar Research* 5: 175–192.

GRODZIŃSKI W., KLEKOWSKI R.Z. and DUNCAN A. 1975. *Methods for ecological bioenergetics*. Blackwell Scientific Publications. Philadelphia: 367 pp.

GRZELAK K. and KOTWICKI L. 2012. Meiofaunal distribution in Hornsund fjord, Spitsbergen. *Polar Biology* 35: 269–280.

HEIP C., HUMMEL H., VAN AVESAATH P., APPELTANS W., ARVANITIDIS C., ASPDEN R., Austen M., BOERO F., BOUMA T.J., BOXSHALL G., BUCHHOLZ F., CROWE T., DELANEY A., DEPREZ T., EMBLOW C., FERAL J.P., GASOL J.M., GOODAY A., HARDER J., IANORA A., KRABERG A., MACKENZIE B., OJAVEER H., PATERSON D., RUMOHR H., SCHIEDEK D., SOKOLOWSKI A., SOMERFIELD P., SOUSA Pinto I., Vincx M., WĘSŁAWSKI J.M. and NASH R. 2009. *Marine Biodiversity Ecosystem Functioning*. MarBEF: 91 pp.

HOLTE B. and GULLIKSEN B.1998. Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. *Polar Biology* 19: 375–382.

HOP H., PEARSON T., HEGSETH E.N., KOVACS K., WIENCKE C., KWAŚNIEWSKI S., EIANE K., MEHLUM F., GULLIKSEN B., WŁODARSKA-KOWALCZUK M., LYDERSEN C., WĘSŁAWSKI J.M., COCHRANE S., GABRIELSEN G.W., LEAKEY R., LØNNE O.J, ZAJĄCZKOWSKI M., FALK-PETERSEN S., KENDALL M., WÄNGBERG S.A., BISCHOF K., VORONKOV A.Y., KOVALTCHUK N.A., WIKTOR J., POLTERMAN M., DI PRISCO G., PAPUCCI C. and GERLAND S. 2002. The ecosystem of Kongsfjorden, Svalbard. *Polar Research* 21: 167–208.

JØRGENSEN B.B., GLUD R.N. and HOLBY O. 2005. Oxygen distribution and bioirrigation in Arctic fjord sediments (Svalbard, Barents Sea). *Marine Ecology Progress Series* 292: 85–95.

KĘDRA M., GROMISZ S., JASKUŁA R., LEGEŻYŃSKA J., MACIEJEWSKA B., MALEC E., OPANOWSKI A., OSTROWSKA K., WŁODARSKA-KOWALCZUK M. and WĘSŁAWSKI J.M. 2010. Soft bottom fauna of an All Taxa Biodiversity Site – Hornsund (77°N, Svalbard). *Polish Polar Research* 31: 309–326.

LOENG H. 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Research* 10: 5–18.

LYDERSEN C., GJERTZ I. and WĘSŁAWSKI J.M. 1989. Stomach contents of autumn feeding marine invertebrates from Hornsund, Svalbard. *Polar Records* 25: 107–114.

OPALIŃSKI K.W. and WĘSŁAWSKI J.M. 1989. Ecology, metabolic rate and metabolic adaptations in Spitsbergen amphipods. *Polish Archive of Hydrobiology* 36: 333–350.

OUG E. 2000. Soft-bottom macrofauna in the high-latitude ecosystem of Balsfjord, northern Norway: species composition, community structure and temporal variability. *Sarsia* 85: 1–13.

PIEPENBURG D., BLACKBURN T.H., VON DORRIEN C.F., GUTT J., HALL P.O., HULTH S., KENDALL A., OPALIŃSKI K.W., RACHOR E. and SCHMID M.K. 1995. Partitioning of benthic community respiration in the Arctic (northwestern Barents Sea). *Marine Ecology Progress Series* 118: 199–213.

PIWOSZ K., WALKUSZ W., HAPTER R., WIECZOREK P. and WIKTOR J. 2009. Comparison of productivity and phytoplankton in a warm (Kongsfjorden) and a cold (Hornsund) Spitsbergen fjord in mid summer 2002. *Polar Biology* 32: 549–559.

RENAUD P.E., WŁODARSKA-KOWALCZUK M., TRANNUM H., HOLTE B., WĘSŁAWSKI J.M., COCHRANE S., DAHLE S. and GULLIKSEN B. 2007. Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (Van Mijen fjord, Spitsbergen). *Polar Biology* 30: 295–305.

RONOWICZ M., WŁODARSKA-KOWALCZUK M. and KUKLIŃSKI P. 2011. Patterns of hydroid (Cnidaria, Hydrozoa) species richness and distribution in an Arctic glaciated fjord. *Polar Biology* 34: 1437–1445.

RYSGAARD S. and GLUD R.N. 2007. Carbon cycling in Arctic marine ecosystems: Case study Young Sound. *Meddellelser om Grønland, Bioscience*. 58: 1–214.

SCHMID M.K. and PIEPENBURG D. 1993. The benthos zonation of the Disko Fjord, West Greenland. *Meddellelser om Grønland, Bioscience* 37: 1–21.

SCHMID M.K., PIEPENBURG D., GOLIKOV A.A., VON JUTERZENKA K., PETRYASHOV V.V. and SPINDLER M. 2006. Trophic pathways and carbon flux patterns in the Laptev Sea. *Progress in Oceanography* 71: 314–330.

SVENDSEN H, BESZCZYNSKA-MØLLER A., HAGEN J.O., LEFAUCONNIER B., TVERBERG V., GERLAND S., ØERBAK J.B., BISCHOF K., PAPUCCI C., ZAJĄCZKOWSKI M., AZZOLINI R., BRULAND O., WIENCKE C., WINTHER J.G. and DALLMANN W. 2002. Physical Kongsfjord Environment overview paper. *Polar Research* 21: 133–166.

WALCZOWSKI W. and PIECHURA J. 2006. New evidence of warming propagating toward the Arctic ocean. *Geophysical Research Letters* 33: L12601, doi: 10.1029/2006GL025872.

WASSMAN P., REIGSTAD M., HAUG T., RYUDELS B., CARROLL M.L., HOP H., GABRIELSEN G.W., FALK-PETERSEN S., DENISENKO S.G., ARASHKEVIVH E., SLAGSTAD D. and PAVLOVA O. 2006. Food webs and carbon flux in the Barents Sea. *Progress in Oceanography* 71: 232– 287.

WINKELMANN D. and KNIES J. 2005. Recent distribution and accumulation of organic carbon on the continental margin west off Spitsbergen. *Geochemistry, Geophysics, Geosystems* 6: doi:10.1029/2005GC000916

WĘSŁAWSKI J.M. and KULIŃSKI W. 1989. Notes on fishes in Hornsund fjord area (Spitsbergen). *Polish Polar Research* 10: 241–250.

WĘSŁAWSKI J.M., HACQUEBORD L., STEMPNIEWICZ L. and MALINGA M. 2000. Greenland whales and walruses in the Svalbard food web before and after exploitation. *Oceanologia* 42: 37–56.

WĘSŁAWSKI J.M., KENDALL M.A., WŁODARSKA-KOWALCZUK M., IKEN K., KĘDRA M., LEGEŻYŃSKA J. and SEJR M.K. 2011. Climate change effects on Arctic fjord and coastal macrobenthic diversity – observations and predictions. *Marine Biodiversity* 41: 71–85.

WĘSŁAWSKI J.M., RYG M., SMITH T.G. and ORITSLAND N.A. 1994. Food and feeding of the ringed seal in Spitsbergen. *Arctic* 47: 109–114.

WŁODARSKA-KOWALCZUK M. and PEARSON T.H. 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distribution in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biology* 27: 155–167.

WŁODARSKA-KOWALCZUK M. and WĘSŁAWSKI J.M. 2008. Mesoscale spatial structures in soft-bottom macrozoobenthic communities: effects of physical control and impoverishment. *Marine Ecology Progress Series* 356: 215–224.

WŁODARSKA-KOWALCZUK M., PEARSON T.H. and KENDALL M.A. 2005. Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. *Marine Ecology Progress Series* 303: 31–41.

WŁODARSKA-KOWALCZUK M., RENAUD P.E., WĘSŁAWSKI J.M., COCHRANE S. and DENISENKO S.G. 2012. Species diversity, rarity and functional complexity in Arctic fjordic versus open shelf benthic systems. *Marine Ecology Progress Series* 463: 73–87.

WŁODARSKA-KOWALCZUK M., SZYMELFENIG M. and ZAJĄCZKOWSKI M. 2007. Dynamic sedimentary environments of an Arctic glacier-fed river estuary (Adventfjorden, Svalbard). II. Meio- and macrobenthic fauna. *Estuarine, Coastal and Shelf Science* 74: 66–73.

WŁODARSKA-KOWALCZUK M., WĘSŁAWSKI J.M. and KOTWICKI L. 1998. Spitsbergen glacial bays macrobenthos – a comparative study. *Polar Biology* 20: 66–73.

ZAJĄCZKOWSKI M. and WŁODARSKA-KOWALCZUK M. 2007. Dynamic sedimentary environments of an Arctic glacier-fed river estuary (Adventfjorden, Svalbard). I. Flux, deposition and dynamics of the sediment. *Estuarine, Coastal and Shelf Science* 74: 285–296.

Received 13 July 2012
Accepted 20 September 2012