

Shallow winter and summer macrofauna in a high Arctic fjord (79° N, Spitsbergen)

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Abstract Very little is known about benthic organisms surviving strategies in extreme winter conditions in polar areas. Most of the research conducted in Arctic has been carried out during the summer from depths available to research vessels. Our study is the first one conducted in winter within a high Arctic fjord at shallow depths. The main aim was to examine the patterns of diversity and community structure of shallow macrobenthos along the depth and distance-to-glacier gradients during winter in Kongsfjorden. The results are compared against reference sampling conducted during the summer. Samples were taken at four depth transects located along the shore of the fjord from the Kongsbreen glacier to the Ny-Ålesund settlement, in March 2009, when the fjord was frozen, with ice cover of 47 cm thickness and no signs of a phytoplankton bloom. The overall species abundance and biomass at shallow depths reached up to 11,800 ind. m⁻² at 15 m and 180 gm⁻² with over 120 taxa found in winter and another 26 taxa found in summer. Shallow benthic fauna stayed relatively stable throughout the year with carnivores and opportunistic species increasing in numbers during winter. The need for further studies on overwintering strategies of bottom fauna is stressed.

Keywords Benthos · Arctic · Winter · Sublittoral

Introduction

Polar areas are now facing rapid changes, mainly due to increasing temperatures due to global climate change as well as increases in human activities. Climate change will likely decrease strong seasonal differences, leading to significant changes, especially during winter (ACIA 2005; IPCC 2007). Such changes will affect polar fauna, which is highly adapted to the harsh winter conditions. Knowledge of seasonal changes in species assemblages and diversity is crucial for understanding polar ecosystems. Arctic ecosystems are characterized by seasonal or permanent ice cover, low temperatures, variable salinities nearshore, strong seasonality with a period of no sunlight and variable levels of organic carbon input (Grebmeier and Barry 1991). Winter data are necessary to understand the contemporary adaptations of benthic organisms to extreme Arctic environments, including adaptations to food shortages (Piepenburg 2005). Primary production influences shallow benthos mainly through winter resource limitations; however, shallow benthic responses to seasonal variations in polar regions remain largely unknown (Grebmeier and Barry 1991; Echeverria and Paiva 2006). Most of the prior research conducted in polar areas was carried out during the summer (Echeverria and Paiva 2006; Piepenburg 2005). Studies including year round sampling or even just winter–summer comparisons remain scarce (Echeverria and Paiva 2006; Jażdżewski et al. 2001) and in the Arctic mainly deal with the pelagic system (Berge et al. 2009) or sympagic fauna (Werner and Auel 2005). Also, shallow coastal areas in the Arctic have gained relatively little scientific attention (Beuchel and Gulliksen 2008; Beuchel et al. 2006; Laudien et al. 2007; Urban-Malinga et al. 2009).

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Our study was conducted in Kongsfjorden (79° N), a high Arctic fjord in the Svalbard archipelago. Though its soft-bottom macrobenthic fauna has received much scientific attention in recent years, most research was conducted during the summer at depths available from research vessels (Hop et al. 2002; Włodarska-Kowalczyk 2007; Włodarska-Kowalczyk and Pearson 2004; Włodarska-Kowalczyk et al. 2005). In Kongsfjorden, shallow benthic surveys remain rare and these mainly focused on rocky bottom (Beuchel and Gulliksen 2008; Beuchel et al. 2006) or macroalgae associated fauna (Lippert et al. 2001) with few surveys on soft bottoms (Ambrose and Leinaas 1988; Kaczmarek et al. 2005; Laudien et al. 2007). There have been no benthic surveys conducted on a muddy bottom at shallow depths during the winter in the fjord prior to this study.

The aim of our study was to examine the patterns of diversity and community structure of shallow macrobenthos along the depth and distance-to-glacier gradients during the winter (March 2009). The results are compared against reference sampling conducted during the summer (August 2008).

Material and methods

Study area

Kongsfjorden is an open fjord situated on the north-western coast of Spitsbergen, the main island of the Svalbard archipelago (12° E 79° N; Fig. 1). The fjord is divided into a well-separated inner basin, later in the text referred to as a glacial bay, of 50–60 m depth on average and an outer one, with average depths of 200–300 m. Due to the warm Atlantic waters carried by the West Spitsbergen Current influencing local hydrology, the fjord has a sub-Arctic character despite its high latitude location (Beszczynska-Möller et al. 1997; Loeng 1991; Svendsen et al. 2002). The

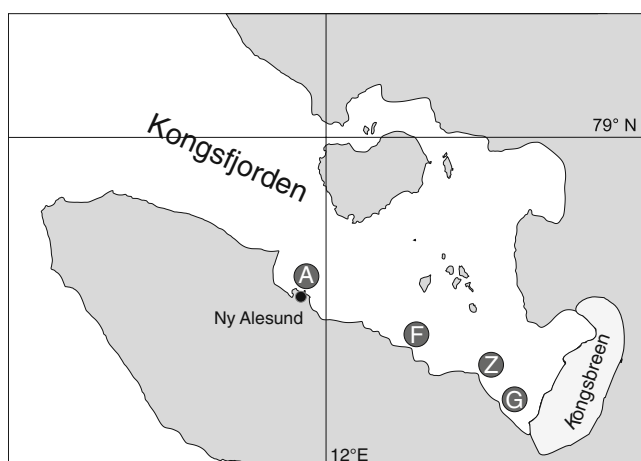


Fig. 1 Location of sampling stations in Kongsfjorden

glacial activity causes environmental gradients in salinity, temperature, sedimentation rates and bottom sediment composition (Lefauconnier et al. 1994), causing gross changes of benthic composition and diversity at depths ranging from 50 to 350 m (Włodarska-Kowalczyk and Pearson 2004; Włodarska-Kowalczyk et al. 2005). Kongsfjorden has been extensively investigated in recent years and the results of the ecological surveys are summarized by Hop et al. (2002, 2006), while physical settings are described by Svendsen et al. (2002).

Sampling was carried out at shallow locations from one of the glaciers, Kongsbreen, toward the Ny-Ålesund settlement (Fig. 1). The hydrological conditions at 5–35 m depth vary seasonally and are strongly influenced by ice-melting and freshwater input (Jørgensen and Gulliksen 2001). Mean sea surface temperature slightly exceeds 0°C, while maximal values may reach 7°C in summer; the mean temperature at the 20 m isobath is 3.6°C (Bluhm et al. 2001). During the winter time (March), sea water temperatures at shallow depths up to 35 m range from -1.5°C to -1.8°C (this study) and sea ice occurs. The salinity may decrease to ca. 30 psu at the surface and 32 psu at the 30 m due to the large freshwater discharge into the middle and inner part of the fjord (Jørgensen and Gulliksen 2001). Semidiurnal tides in the fjord system range between 1.5 and 2 m and only weak currents prevail. Scouring from the sea ice and icebergs also influences the shallow depths (Dowdeswell and Forsberg 1992).

Sampling

Samples were collected during the winter in March 2009. Sampling was conducted while the fjord was frozen with ice cover of 47 cm thickness present through the whole sampling period. Hand drills and sews were used to cut the sea ice. The remaining ice block was cut and removed leaving an open ice hole enabling sampling. Though daylight was already present, no primary production was observed. The end of the winter was chosen for sampling because it should represent the time when food is scarcest.

Samples were taken along four transects from the Kongsbreen glacier to Ny-Ålesund (G, Z—glacial transects; F, A—Ny-Ålesund transects) at 5, 15, 25 and 35 m (Fig. 1, Table 1). Material was collected with a Petit Ponar grab (0.045 m² sampling area), operated by hand directly from the ice with five replicates per station. This resulted in 76 quantitative grab samples. Completely frozen sediment prevented replicate sampling at the 5-m deep station of the transect F. Summer reference stations were located at 15 m at transects G and A (named GS and AS). Ten samples were collected from a rubber boat in August 2008. All samples were sieved on 0.5-mm mesh, fixed in a buffered 4% formaldehyde solution and later transferred to

Table 1 Sampling effort and basic information on samples used in the present study

Date	Transect	Location	Depth (m)	Number of samples taken
21.03.2009	G	78° 52' N; 12° 23' E	5, 15, 25, 35	20
29.03.2009	Z	78° 53' N; 12° 21' E	5, 15, 25, 35	20
30.03.2009	F	78° 54' N; 12° 08' E	5, 15, 25, 35	16
27.03.2009	A	78° 55' N; 11° 55' E	5, 15, 25, 35	20
1.08.2008	GS	78° 52' N; 12° 22' E	15	5
1.08.2008	AS	78° 55' N; 11° 55' E	15	5

a 70% solution of alcohol. Macrofauna was sorted, counted and identified to the lowest possible taxonomic level. All organisms were weighed, molluscs with and without shells, and wet weight values (g m^{-2}) are given for each taxon.

The taxonomy of the family Cirratulidae is presented according to the revision by Woodham and Chambers (1994). Most of cirratulids were identified to the species level (including *Chaetozone setosa*, *Chaetozone christiei*, *Tharyx* spp., *Aphelochaeta marioni*, *Aphelochaeta* spp.). However, identification of cirratulid species is often problematic, with *Ch. setosa* species being complex and at least five undescribed species in European waters (Chambers and Woodham 2003). Consequently, to avoid identification errors and comparison problems, all cirratulids in the text are referred to as Cirratulidae group or cirratulids.

Environmental data

At each station of a transect, samples for granulometry and particulate organic carbon (POC) in the sediment were taken. The coarse grains (>2 mm) were separated by dry sieving. Fine fractions of the sediment (0.02–2000 μm) were analysed using a Malvern instrument Mastersizer 2000 (Syvitski 1991). Organic carbon and nitrogen concentrations were measured with a Flash EA 1112/IRMS Delta V Advantage (Thermo, Germany). Surface water chlorophyll-*a* concentration was measured at the 15-m deep stations of the A and G transects in winter and summer using fluorometry (TUNER DESIGNES; 10-AU-005) with 90% acetone extraction for 24 h in 4°C temperature and full darkness (Evans et al. 1987).

Data analysis

The species accumulation curves with 95% confidence intervals for the number of observed species (*Sobs*) and the *Chao2* estimators were computed using the formulae of Colwell (2009) and plotted as a function of the sampling effort. Non-metric multidimensional scaling (nMDS) of Bray-Curtis similarities, computed after fourth-root transformation of species level abundance data, were conducted for each depth profile. One-way ANOSIM permutation tests of the Bray-Curtis similarity data were performed (Clarke and

Warwick 2001) in order to test for differences in community composition between (1) different depths for each profile during the winter and between (2) summer and winter samples collected at 15 m depth at Ny-Ålesund and glacial stations (A and G transects). Thereafter, a SIMPER test was used to identify characteristic species that contributed the most to the statistical similarity between samples.

Species number and diversity [Hurlbert rarefaction index, $ES(n)$, where $n=50$] were calculated for all samples. Mean values with 95% confidence intervals were calculated for abundance, biomass, species numbers and diversity indices within groups of samples coming from different depths, profile and sampling time. The non-parametric Kruskal-Wallis test and Mann-Whitney *U*-test were used to check for significant differences in abundance, biomass, species richness and diversity. Relationships between values of abundance, biomass, species richness and species diversity and environmental factors (distance to glacier, depth, organic carbon and nitrogen amount, sediment type) were explored using nonparametric Spearman *R* rank correlation. Non-parametric statistics were used since, even after data transformation, the normality of the data distribution could not be assessed.

On the basis of results of a preliminary de-trended correspondence analysis (DCA) based on the length of the main gradient canonical correspondence analysis (CCA) was chosen as the most appropriate for the analysis of species-environmental variable relationships (ter Braak and Smilauer 2002). The forward selection of environmental variables was used to identify and rank the importance in determining the species distribution (ter Braak and Smilauer 2002). A subset of best fitted variables was selected via repeated forward selection analyses and the progressive elimination of variables with non-significant conditional effects until a set of variables with only significant effects was attained. The significance of the ordination axis in CCA, and the effects of environmental variables, was tested employing Monte Carlo permutation tests using 499 unrestricted permutations.

The data analyses were performed using the PRIMER package v. 6 (Clarke and Warwick 2001), the Statsoft software STATISTICA v. 6 and CANOCO 4.5 (ter Braak and Smilauer 2002).

Results

Abiotic factors

Mud and muddy sand dominated in the sediment at all transects and depths, except for the 5-m station in transects G and F, where sand and stones prevailed (Table 2). The amount of organic carbon in the sediment was low, below 0.3% for most of the transects, except for the A transect, close to Ny-Ålesund, where the amount of organic carbon in the sediment at 35 m depth reached 9.48%. The amount of the organic carbon was similar in summer. The amount of chlorophyll-*a* was below 0.2 mg m⁻³ in the surface water layer and the sea ice was free of algae. In March 2009 the fjord was frozen, with an ice cover of 47 cm thickness present. The mean air temperature during winter sampling was -14.5°C with minimum of -22.8°C, while the water temperature above the bottom was -1.8°C. During the summer, the air temperature was 5.7°C and water temperature was 3.9°C close to the Kongsbreen glacier and 4.9°C in the central part of the fjord. Salinity in the winter was between 32.6 and 32.8 psu, while in summer dropped down to 31.6 psu in the surface layer and between 34.2 and 34.7 psu at the bottom.

Macrofauna

A total of 12,422 specimens belonging to 120 taxa were collected in the winter and 4,581 specimens of 89 taxa during the summer. At a reference station close to

Ny-Ålesund (AS), 2,656 specimens (54 taxa) were collected in winter and 3,952 specimens (75 taxa) in summer. At the reference station close to the Kongsbreen glacier (GS), 769 individuals representing 32 taxa were identified in winter compared with 629 specimens of 42 taxa in summer. Zoogeographical taxa composition was comprised of 26% of Arctic, 52% Arctic-boreal, 8% boreal and 12% of cosmopolitan species. A list of all species found is provided in the [Appendix](#).

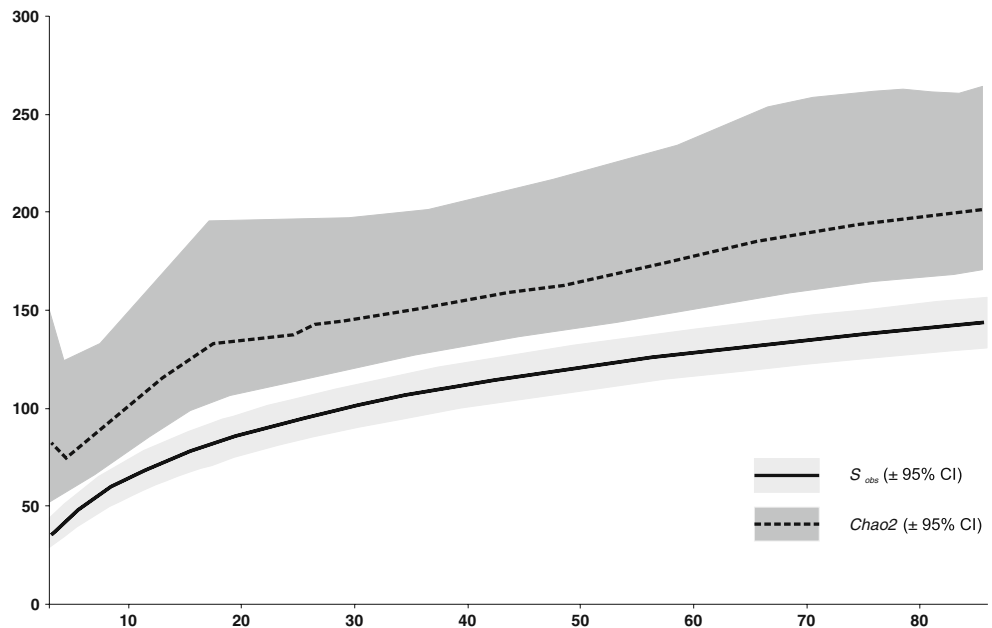
Polychaetes (85%), followed by molluscs (11.5%) and crustaceans (1.5%) dominated the benthic fauna in both seasons. Species-accumulation curves did not reach asymptotic values for the estimated number of species (Fig. 2). *Chao2* gave an estimate of 200 species. Since the total number of species (146 taxa during winter and summer) was below the 0.95 confidence interval of estimated number of species (with 95% confidence intervals from 170 to 264), it is likely that there are still new species to be found in shallow Kongsfjorden areas.

The overall mean winter abundance was 3,680 ind. m⁻² with a minimum of 329 ind. m⁻² at the 5-m station of the G transect, closest to the glacier and a maximum of 11,800 ind. m⁻² noted at 15 m at the A transect adjacent to Ny-Ålesund. In summer, mean abundance (stations GS and AS) reached 2,795 ind. m⁻² and 17,564 ind. m⁻² respectively. The overall mean biomass in winter was 43.00 gm⁻² (biomass with decalcified molluscs: 18.90 gm⁻²), with a minimum of 2.11 gm⁻² (1.36 gm⁻²) at G transect (25 m) and maximum of 180 gm⁻² (79.6 gm⁻²) at F transect

Table 2 Sediment characteristics for all sampling stations

	Transect	Depth (m)	Sediment type	% gravel	% sand	% mud	% clay	% N	% C
Winter	G	5	Sand	0.0	100.0	0.0	0.0		
		15	Sandy mud	0.0	12.4	87.6	0.6	0.04	0.14
		25	Sandy mud	0.0	11.3	88.7	0.7	0.02	0.11
		35	Mud	0.0	9.7	90.3	0.7	0.04	0.13
	Z	5	Sandy mud	0.0	46.3	53.7	0.2	0.02	0.09
		15	Muddy sand	0.0	74.9	25.1	0.2	<0.0	0.11
		25	Sandy mud	0.0	33.9	66.1	0.4	0.03	0.13
		35	Mud	0.0	7.7	92.3	0.9	0.03	0.16
	F	5	Stones						
		15	Sandy mud	0.0	44.9	55.1	0.0	0.04	0.17
		25	Sandy mud	0.0	24.3	75.7	0.0	0.04	0.22
		35	Sandy mud	0.0	37.4	62.6	0.1	0.03	0.19
A	5	Muddy sand	0.0	62.2	37.8	0.0			
	15	Muddy sand	0.0	52.8	47.2	0.0	0.16	6.22	
	25	Sandy mud	0.0	43.5	56.5	0.0	0.12	4.04	
	35	Sandy mud	0.0	35.5	64.5	0.1	0.22	9.48	
Summer	GS	15						0.04	0.46
	AS	15						0.04	0.19

Fig. 2 Species accumulation curves plotted for observed number of species (S_{obs}) and the true number of species estimated using *Chao2*. S_{obs} and *Chao2* are plotted with 95% confidence



(25 m). In summer mean biomass values were 58.7 gm^{-2} at GS station and 69.8 gm^{-2} at AS station (Figs. 3, 4, 5).

Polychaetes were the major contributors to total macrofaunal abundance in winter and summer along all transects.

Apistobranchus tullbergi followed, in rank order, by cirratulids and oligochaetes; cirratulids, *Leitoscoloplos mammosus* and *Scoloplos armiger* dominated at A and F transects in winter. During summer, close to Ny-Ålesund,

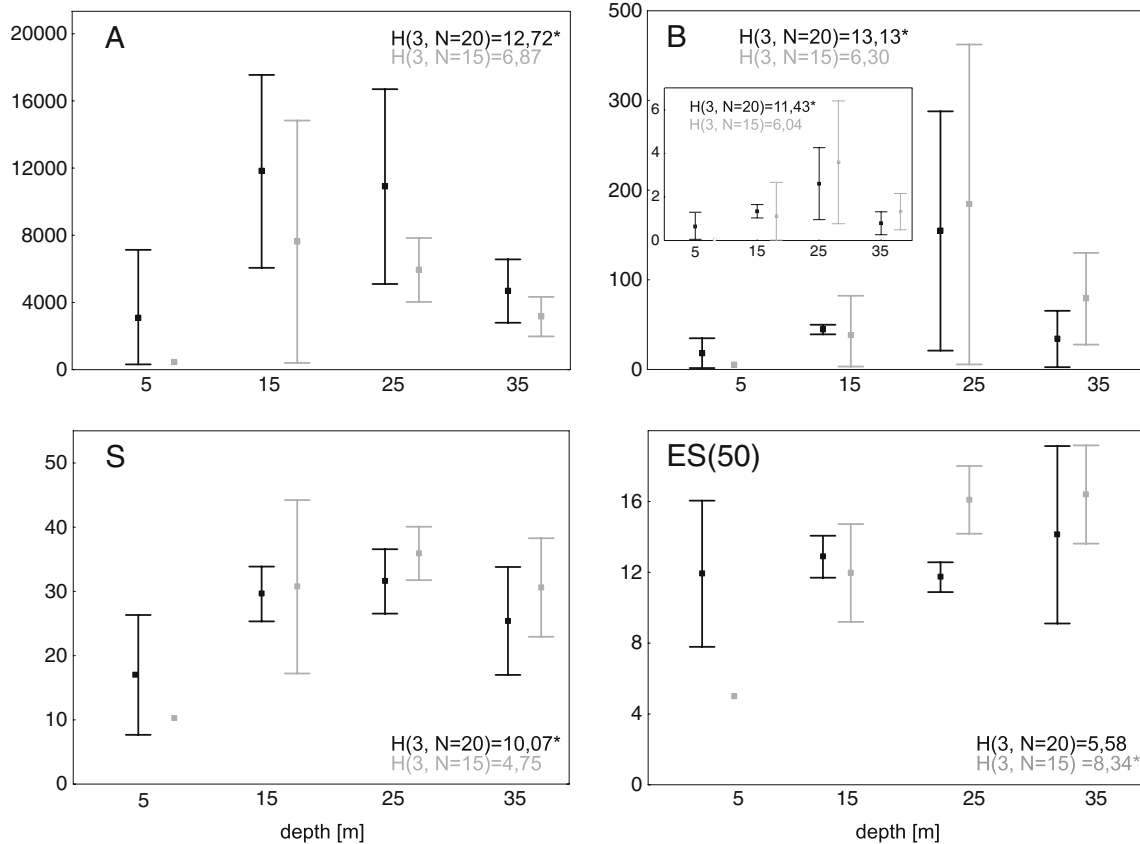


Fig. 3 Mean with 95% confidence intervals for abundance (*A*, number of individuals 0.1 m^{-2}), biomass (*B*) including molluscs with (full panel) and without shells (insert wet weight, $\text{g } 0.1 \text{ m}^{-2}$), species

richness (*S*) and Hurlbert rarefaction index [*ES(50)*] for Ny-Ålesund transects (*A* black, *F* grey) for each depth sampled during the winter. Significant test results are marked with an asterisk

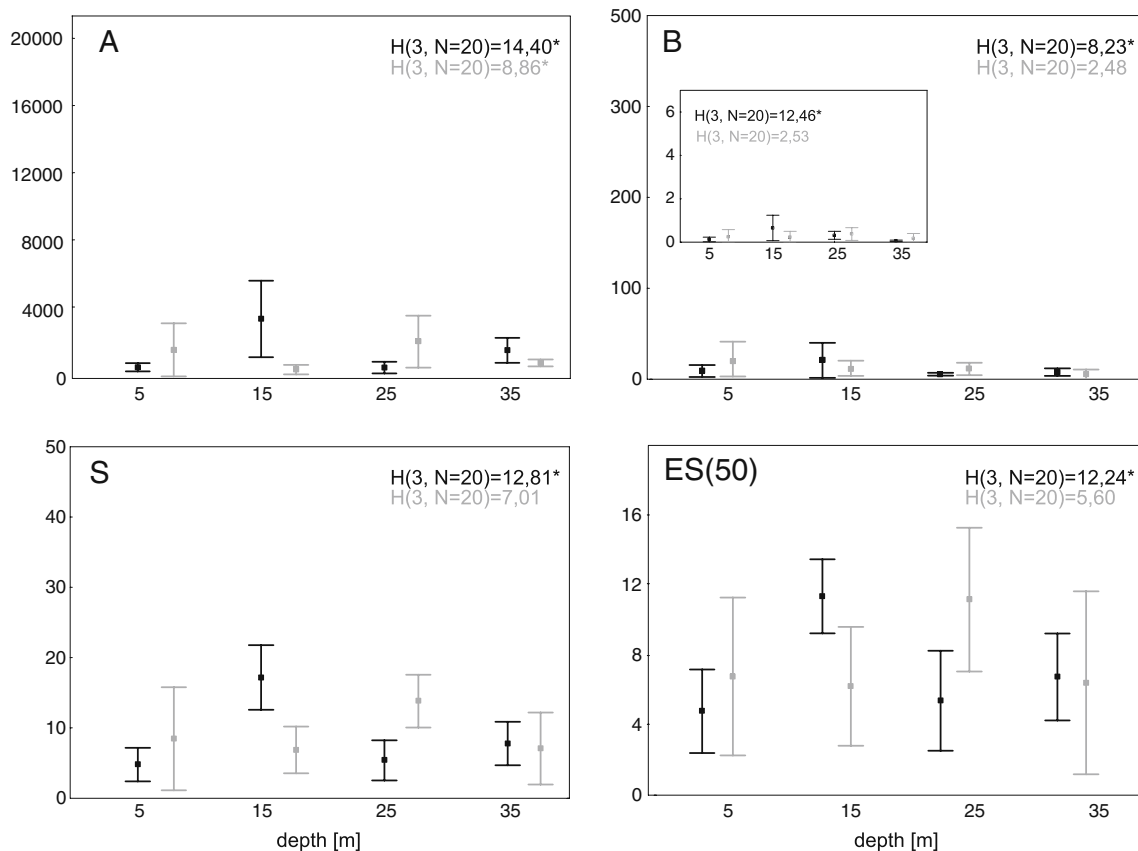


Fig. 4 Mean with 95% confidence intervals for abundance (*A*, number of individuals 0.1 m⁻²), biomass (*B*) including molluscs with (full panel) and without shells (insert wet weight, g 0.1 m⁻²), species

richness (*S*) and Hurlbert rarefaction index [*ES(50)*] for glacial transects (G black, Z grey) for each depth sampled during the winter. Significant test results are marked with an asterisk

the most abundant polychaete was *Paraonella nordica* followed by the same set of dominant species as in winter. At G and Z transects, cirratulids dominated, followed by *Lysippe labiata*, *Cossura longocirrata* and the bivalve *Thyasira dunbari*. In summer, among the most abundant polychaetes at G transect were *Chone cf. paucibranchiata* and *Spio* spp. and the bivalve *Mya truncata*. In terms of biomass, polychaetes (over 80%), followed by molluscs, were the major contributors to the total macrofauna biomass in winter and summer. Only at transect F (25 m and 35 m) and transect G (5 m) was the polychaete contribution lower (75%, 60% and 51%, respectively) than molluscs (Table 3). In winter (A transect, 15 m), polychaetes *A. tullbergi* (41%) and cirratulids (26%) dominated total macrofaunal abundance, while in summer they reached only 10.5 and 14.8%, respectively. Also other species were very abundant, including *P. nordica* (14.2 %) and *L. mammosus* (10.5%) which in winter added only 0.5% and 2.9% to total abundance, respectively. At G transect (15 m), cirratulids (59.8%) and *L. labiata* (14.7%) dominated, while in summer cirratulids were less abundant (27%) and *L. labiata* even increased in numbers (24%). Other taxa gained in

numbers: *Spio* spp. (9.2%) and bivalve *M. truncata* (8.9%) (Table 4).

The SIMPER analysis revealed that cirratulids were characteristic for both glacial and Ny-Ålesund transects (mainly *Chaetozone setosa* and *Aphelochaeta marioni*—15% and 40% of species contribution in winter, and mainly *Ch. setosa* and *Tharyx* spp.—6% and 21% in summer). *A. tullbergi* and *S. armiger* with *L. mammosus* dominated at Ny-Ålesund transects, while *C. longocirrata* and *L. labiata* dominated glacial transects in winter and summer. *Capitella capitata* agg., *M. truncata* and *C. paucibranchiata* were characteristic at the GS station. Species contributions for different depths and seasons are listed in Table 5.

The low stress values on all the two-stage ordination plots indicate the excellent two-dimensional representation of multidimensional space (Fig. 6). The nMDS as well as ANOSIM tests show that there were significant differences among samples collected at different depths at different transects, with an exception of transect Z, where no significant differences were found. The most distinct faunal differences along all transects were in samples collected at 35-m depth (Fig. 6). There were significant differences in

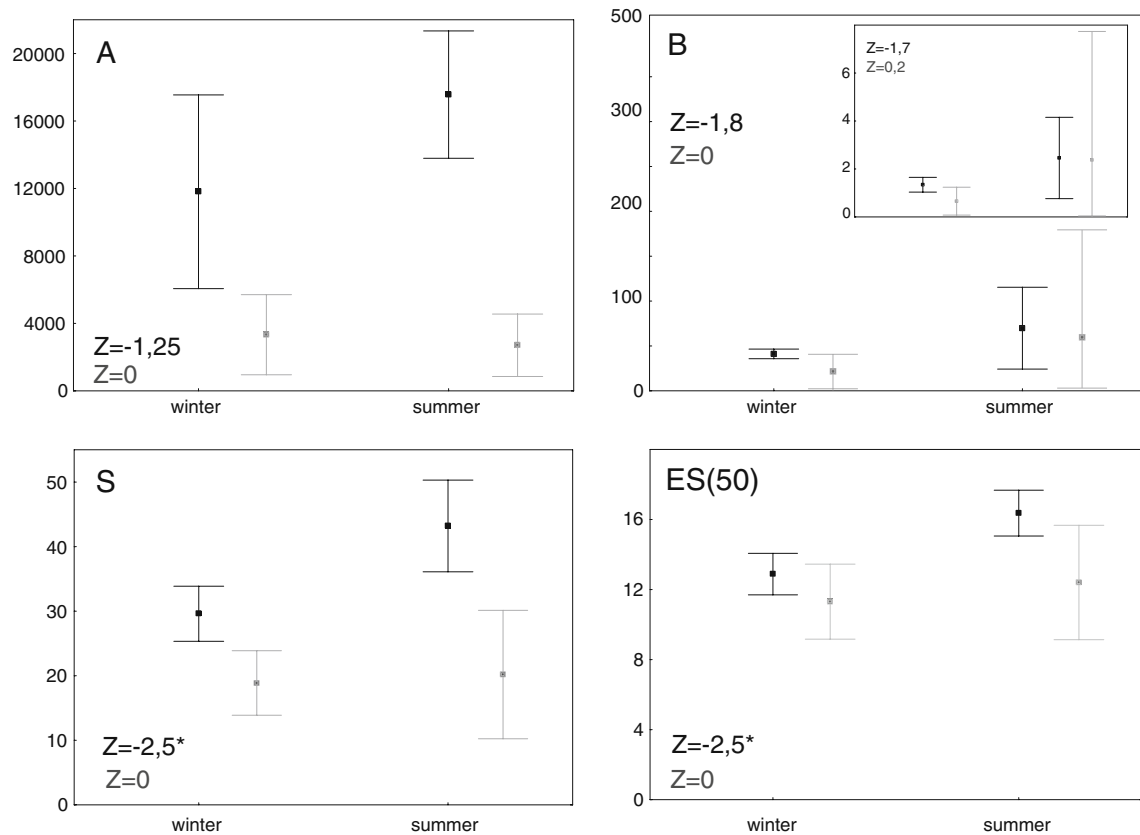


Fig. 5 Mean with 95% confidence intervals for abundance (*A*, number of individuals 0.1 m^{-2}), biomass (*B*) including molluscs with (*full panel*) and without shells (*insert* wet weight, $\text{g } 0.1 \text{ m}^{-2}$), species richness (*S*)

and Hurlbert rarefaction index [*ES(50)*] comparing winter and summer sampling at Ny-Ålesund (*black*) and glacial (*grey*) stations at 15 m depth. Significant test results are marked with an *asterisk*

abundance between 5 and 15 m depths, biomass and species diversity between 5 and 25 m depths at A transect ($p < 0.05$; Dunn's test) while differences between species richness [*ES(50)*] were found for F transect only ($H = 8.34$; $p < 0.05$; Kruskal Wallis test) (Fig. 3). There were significant differences in density between 5- and 15-m depths and 15- and 25-m depths for Z and G transects ($p < 0.05$; Dunn's test), while in biomass significant differences were found for G transect and 15- and 25-m depths only ($p < 0.05$; Dunn's test). There were significant differences between species number and species diversity at G profile between 5- and 15-m depths and 15- and 25-m depths ($p < 0.05$; Dunn's test, Fig. 4).

The nMDS graph showed some separation of samples collected during the summer time (Fig. 6). ANOSIM test revealed significant differences between samples collected at glacial bay and Ny-Ålesund stations during the summer and winter ($R = 0.73$; $p < 0.05$ and $R = 0.91$; $p < 0.05$ respectively). However, significant differences were found only for the number of taxa and taxa diversity [*ES(50)*] along the Ny-Ålesund A transect (15 m) between winter and summer (Mann-Whitney *U*-test; $Z = -2.5$; $p < 0.05$), while no significant differences in the number or diversity of

taxa were found for the glacial station (G transect, 15 m). For neither of the reference stations were significant differences found for abundance or biomass between summer and winter sampling (Mann-Whitney *U*-test; $p > 0.05$; Fig. 5).

Spearman correlation rank showed that density, biomass, taxa richness and diversity were correlated with distance to the glacier ($R = 0.63$; 0.69 ; 0.57 ; 0.6 , respectively) and the percentage of clay in sediment ($R = -0.48$; -0.56 ; -0.56 ; -0.44 , respectively) only ($p < 0.05$). The CCA analysis explained about 19% of the variance of the taxon–environment relationship. The first canonical axis was significant as well as the second one ($p < 0.05$). The occurrence of clay and distance to the glacier were significantly correlated with the first axis (0.83 and -0.81 , respectively). Five variables were selected as significant predictors of taxon distribution by the forward selection analyses: percentage of clay, sand and mud in the sediment, depth and distance to the glacier ($p < 0.05$). Two groups of taxa can be delineated on the CCA diagram: the first group of five taxa (*L. labiata*, *Montacuta spitzbergensis*, *C. longocirrata*, *Arrhis phyllonyx*, Cirratulidae group), whose occurrence was correlated with percentage of clay in the sediment, and a second group consisting of 11

Table 3 List of taxa dominating with *Ab* (abundance) and *Bm* (biomass) at profiles *A*, *F*, *G* and *Z* in winter and *GS* and *AS* in summer. Only taxa with densities exceeding 100 ind. m⁻² or 0.1 gm⁻² wet weight (weight for molluscs without shells *in parentheses*) were included (values for biomass are presented only when higher than 0.09 gm⁻²)

	A		F		G		Z		GS		AS	
	Ab	Bm	Ab	Bm	Ab	Bm	Ab	Bm	Ab	Bm	Ab	Bm
Annelida												
<i>Aglaophamus malmgreni</i>	1.1	0.5			14.4	0.7	1.1	0.2			4.4	13.3
<i>Apistobranchus tullbergi</i>	3292.2	1.5	1312.6	0.4	2.2		48.9				1844.4	0.7
<i>Chone</i> cf. <i>paucibranchiata</i>	3.3				2.2		16.7		168.9	0.1	613.3	0.2
<i>Cirratulidae</i> group	1305.6	2.3	951.1	1.3	808.9	1.7	578.9	0.9	755.6	1.7	2591.1	1.9
<i>Cossura longocirrata</i>	23.3		29.6		102.2		46.7		48.9		66.7	
<i>Eteone flava</i> ; <i>E. longa</i>	120.0	0.4	203.0	0.3	27.8	0.1	53.3	0.3	53.3	0.1	213.3	0.6
<i>Euchone</i> spp.					1.1		7.8		26.7	0.3	177.8	0.4
<i>Exogone naidina</i>	5.6		1.5								128.9	0.1
<i>Harmothoe</i> cf. <i>vridis</i>	1.1								40.0		364.4	0.4
<i>Laphania boeckii</i>	8.9		4.4						8.9		164.4	0.4
<i>Leitoscoloplos mammosus</i>	343.3	1.1	611.9	1.8			38.9	0.1	13.3		1848.9	3.7
<i>Lumbrineris mixochaeta</i>	115.6	0.4	128.9	0.3	12.2		13.3		35.6	0.1	417.8	0.6
<i>Lysippe labiata</i>	213.3	0.7	35.6	0.1	181.1	0.3	42.2	0.1	675.6	1.6	937.8	8.5
<i>Maldane sarsi</i>	30.0	0.2	1.5						4.4		262.2	2.5
<i>Nephtys ciliata</i>	3.3	2.6	7.4	1.3	10.0	0.6	24.4	2.4	13.3	0.8		
<i>Oligochaeta</i> indet.	428.9	0.1	65.2				3.3		8.9		1377.8	0.4
<i>Paraonella nordica</i>	103.3		37.0								2488.9	0.6
<i>Pholoe assimilis</i>	145.6		54.8		46.7	0.3	17.8		57.8		186.7	0.2
<i>Phyllodoce groenlandica</i>			3.0	1.5								
<i>Scoletoma fragilis</i>	22.2	0.9	29.6	2.1	2.2	0.6					31.1	3.0
<i>Scoloplos armiger</i>	360.0	2.4	283.0	1.1			3.3				191.1	0.8
<i>Spio</i> spp.	11.1		25.2						257.8	0.2	31.1	0.1
Mollusca												
<i>Astarte montagui</i>	23.3	27.7 (5.3)	35.6	29.4 (5.0)							35.6	0.1 (-)
<i>Axinopsida orbiculata</i>	185.6	0.5 (0.3)	223.7	0.8 (0.3)	13.3		10.0		8.9		906.7	3.5 (1.3)
<i>Ennucula tenuis</i>			114.1	6.6 (1.9)	1.1		5.6 (-)				48.9	0.6 (-)
<i>Macoma calcarea</i>	122.2	6.8 (1.6)	274.1	5.2 (1.6)	47.8	0.7 (0.1)	20.0	0.1 (-)	93.3	0.2 (0.1)	702.2	4.2 (1.3)
<i>Mya truncata</i>	18.9	2.2 (0.8)	38.5	3.1 (1.0)	37.8	1.9 (0.5)	11.1	1.3 (0.4)	244.4	4.1 (0.9)	84.4	4.2 (3.1)
<i>Serripes groenlandicus</i>	5.6	1.9 (0.4)	7.4	3.6 (0.8)	3.3	1.2 (0.2)	4.4	3.2 (0.8)	40.0	5.2 (1.8)	4.4	0.1
<i>Thyasira dunbari</i>	76.7	0.9 (0.5)	102.2	1.0 (0.7)	2.2		3.3		13.3	0.2 (-)	71.1	1.3 (-)
<i>Thyasira gouldi</i>	28.9	0.5 (0.2)	40.0	0.5 (0.3)							120.0	2.1 (0.1)
<i>Yoldia hyperborea</i>	2.2	1.6 (1.4)	13.3	4.0 (1.7)					4.4			
Others												
<i>Cerianthus lloydi</i>					2.2	0.4			4.4	43.3		
<i>Edwardsidae</i> sp.	3.3	3.3	11.9	10.6								
<i>Nemertea</i> indet.	143.3	0.3	75.6		8.9	0.1	3.3		8.9		13.3	0.6
<i>Tanaidacea</i> indet.	115.6		38.5								26.7	

taxa (*T. dunbari*, *T. gouldi*, *S. armiger*, *L. mammosus*, *Maldane sarsi*, *A. tullbergi*, *P. nordica*, *C. capitata* agg., *Tanaidacea* indet., *A. montagui*, *Nemertea* indet.) whose abundance increased along with increasing distance to the glacier (Fig. 7).

Discussion

Winter, with its low temperature and ice, may be a challenge to survival for shallow benthic macrofauna in polar regions. In March, at the end of winter, Arctic shallow

Table 4 List of species dominating with abundance (ind. m⁻²) and percent composition in winter and summer at 15-m depth at Ny-Ålesund (A transect) and glacial bay (G transect). Feeding method of species is provided: C carnivore, D deposit feeder, F filter feeder

Location	Species	Summer		Winter	
		Abundance	%	Abundance	%
Ny-Ålesund	Polychaeta				
	<i>Apistobranchus tullbergi</i> D	1,844.4	10.5	4,840	41
	<i>Capitella capitata</i> agg. D	884.4	5.0	182.2	1.5
	<i>Chone</i> cf. <i>paucibranchiata</i> F	613.3	3.5	4.4	0.04
	Cirratulidae group D	2,591.1	14.8	3,066.7	26
	<i>Leitoscoloplos mammosus</i> D	1,848.9	10.5	342.2	2.9
	<i>Lysippe labiata</i> D	937.8	5.3	448.9	2.8
	<i>Oligochaeta</i> indet.	1,377.8	7.8	480	4.1
	<i>Paraonella nordica</i> D	2,488.9	14.2	62.2	0.5
	Mollusca				
	<i>Axinopsida orbiculata</i> D	96.7	5.2	342.2	2.9
	<i>Macoma calcarea</i> D	702.2	4.0	128.9	1.1
	<i>Nemertea</i> indet. C	13.3	0.1	351.1	3
Glacial Bay	Polychaeta				
	<i>Aglaophamus malmgreni</i> C	0	0	57.8	1.7
	<i>Capitella capitata</i> agg. D	106.7	3.8	0	0
	<i>Chone</i> cf. <i>paucibranchiata</i> F	168.9	6	8.9	0.3
	Cirratulidae group d	755.5	27	2,044.4	59.8
	<i>Eteone flava</i> ; <i>E. longa</i> C	53.3	1.9	93.3	2.7
	<i>Lysippe labiata</i> D	675.6	24	502.2	14.7
	<i>Pholoe assimilis</i> C	57.8	2.1	115.6	3.4
	<i>Spio</i> spp. D	257.8	9.2	0	0
	Mollusca				
	<i>Macoma calcarea</i> D	93.3	3.3	155.6	4.6
	<i>Mya truncata</i> F	244.4	8.7	97.8	2.9

benthic fauna are likely to be most affected by winter conditions. However, abundance and biomass were at similar levels and the species number was only slightly lower than during the summer.

Presence of ice, including ice scour, is a major structuring force acting on polar benthic communities, depending on the depth and hydrographic conditions (Barnes and Conlan 2007; Gutt 2001; Laudien et al. 2007; Smale and Barnes 2008). In Kongsfjorden, fast ice forms relatively late, between December and February, and the ice cover is usually up to 1-m thick (Gerland and Hall 2006). In 2009, when samples for this study were taken, a 47-cm-thick ice cover was present in March, though in previous years (e.g. 2006 and 2007) the ice cover was not always present. Low temperatures, lack of light and the presence of sea ice are limiting factors for primary production (Hop et al. 2002). Wiktor (1999) reports 19.6–24.4 chlorophyll-*a* mg m⁻² for early spring and 176–260 chlorophyll-*a* mg m⁻² during the spring bloom in the inner part of the fjord. During our study, despite the fact that the sunlight was

already present, the amount of chlorophyll-*a* was below 0.2 mg m⁻³, indicating that the spring bloom had not started and so no fresh supply of organic material was yet available for benthic organisms.

The overall species abundance and biomass at shallow depths during the winter in Kongsfjorden reached up to 11,800 ind. m⁻² at 15 m with over 120 taxa found in the south central part of the fjord. To our knowledge, no other data on Arctic shallow soft-bottom fauna during winter are available for comparison. The only shallow quantitative survey in Kongsfjorden, off Brandal, conducted during the summertime, reports similar densities (6,296 ind. m⁻²) and 63 taxa present (Laudien et al. 2007). The biomass they report (6 and 11 gm⁻²) is similar to our results in glacial bay but much lower than we found close to Ny-Ålesund. At greater depths (40–85 m) in Kongsfjorden, on average 24 species and 4,490 ind. m⁻² with a wet weight of 91 gm⁻² were found during the summer in the glacial area and 44 species, with average abundances of 3,760 ind. m⁻² and wet weight of 149 gm⁻² in central part of the fjord (August,

Table 5 SIMPER results and species contribution (higher than 10% are listed) for different sampling depths at Ny Ålesund and glacial profiles in winter and summer

Time	Profiles	Depth (m)	Taxa	Species contribution (%)
Winter	G, Z	5	<i>Capitella capitata</i> agg.	26.85
			<i>Mya truncata</i>	22.82
			<i>Pholoe assimilis</i>	15.95
			Cirratulidae group	11.97
			<i>Hiatella arctica</i>	10.01
		15	Cirratulidae group	46
			<i>Cossura longocirrata</i>	10.75
		25	Cirratulidae group	33
			<i>Cossura longocirrata</i>	18.13
	35	Cirratulidae group	49.18	
		<i>Cossura longocirrata</i>	24.75	
		<i>Lysippe labiata</i>	12.03	
	A, F	5	Cirratulidae group	23.5
			<i>Scoloplos armiger</i> ; <i>Leitoscoloplos mammosus</i>	22.5
			Oligochaeta indet	14.65
15		Cirratulida group	20	
		<i>Apistobranchus tullbergi</i>	12.24	
25		<i>Apistobranchus tullbergi</i>	10.52	
35	Cirratulidae group	16.2		
Summer	GS	15	Cirratulidae group	21
			<i>Lysippe labiata</i>	15.19
			<i>Capitella capitata</i> agg.	11.37
	AS	15	Cirratulidae group	10
			<i>Scoloplos armiger</i> <i>Leitoscoloplos mammosus</i>	13

2006; Kędra et al. 2010; own data). This corresponds with the much lower values for shallow waters (5–35 m) during the wintertime (Fig. 4), with the exception of average abundance, which was two-times higher close to Ny-Ålesund (Fig. 3). In the Antarctic, in shallow, soft-bottom sublittoral zone of Admiralty Bay, Jazdzewski et al. (1991) estimated the mean summer abundance of macrofauna at 14,400 ind. m⁻² with maximum of over 25,000 ind. m⁻² and biomass from 80 to over 260 gm⁻².

During our study 54 taxa were found close to Ny-Ålesund and 32 taxa in glacial bay in winter. This shows that taxa diversity during the winter is lower compared with the summer reference sampling when 75 and 42 taxa were found, respectively. Ice, as the most important factor structuring benthic species composition, may cause denudation or absence of certain species in winter (Barnes 1999; Barnes and Conlan 2007; Barnes et al. 2006). Antarctic observations suggest that the sharp decreases in benthic abundance that occur during winter are directly related to lowered water temperature and sea ice occurrence (Jazdzewski et al. 2001). Echeverria and Paiva (2006) showed that shifts in benthic communities in Admiralty Bay were mainly related to

the ice impacts and storminess. Along with low temperatures and lack of fresh food supply, sea ice may be the reason for lower species richness found during the winter (120 taxa) than in summer (146 taxa with a smaller sampling effort) in this study. However, abundance and biomass values in the Ny-Ålesund area during winter are high, which indicates that some of the taxa there are able to survive during the winter. Only a limited number of taxa were eliminated from the shallow sublittoral in winter likely by complete mortality at shallow depths. Bowden (2005) showed that in the Antarctic, the period of recruitment did not coincide with the summer pulse of primary production and many shallow species recruited during winter. This may indicate that winter conditions in polar shallow areas are more favourable to the fauna that one might expect. Moreover, shallow areas are relatively rich in detritus and the remains of benthic organisms resulting from ice scour (Richardson and Hedgepeth 1977; Slattery and Oliver 1986; Smale and Barnes 2008). Ice-berg scour depressions become filled with algal debris and the remains of organisms, which attract motile deposit feeders and scavengers (Peck et al. 1999; Conlan and Kvittek 2005). Most of species found in our study were deposit feeders.

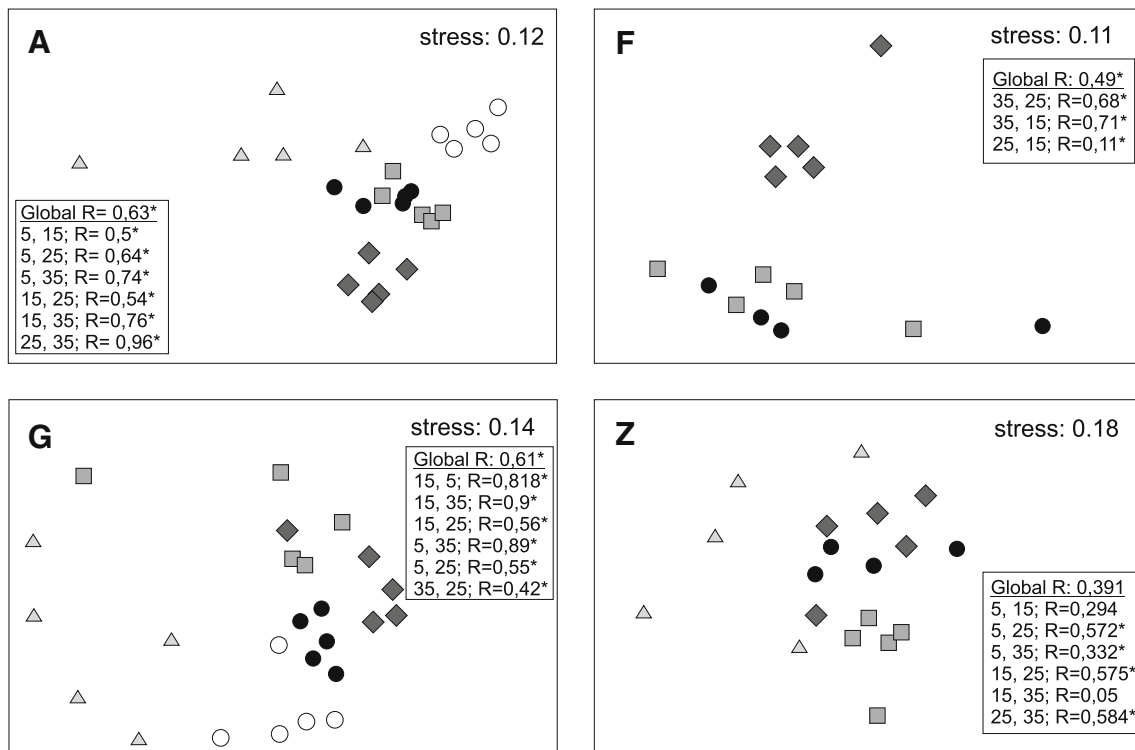


Fig. 6 Non-metric multidimensional scaling (nMDS) of Bray-Curtis similarities of fourth-root transformed data of benthic species densities in Kongsfjorden conducted for each sampling profile (A, F, G, Z) separately. The results of ANOSIM tests differences between depths

(winter sampling only) are also presented on the plot. \blacktriangle 5 m, \bullet 15 m, \blacksquare 25 m, \blacklozenge 35 m; *filled symbols* samples collected during winter sampling; *open symbols* samples collected during summer sampling. Significant test results are marked with an *asterisk*

Carnivorous species (Nephtyidae, *Eteone* spp., Nemertea), along with opportunistic species (cirratulids), increased their abundance in winter. In the Antarctic, cirratulid polychaetes, *Capitella* aggregations and *Leitoscoloplos* are important post-disturbance soft-sediment inhabitants (Lenihan and Oliver 1995).

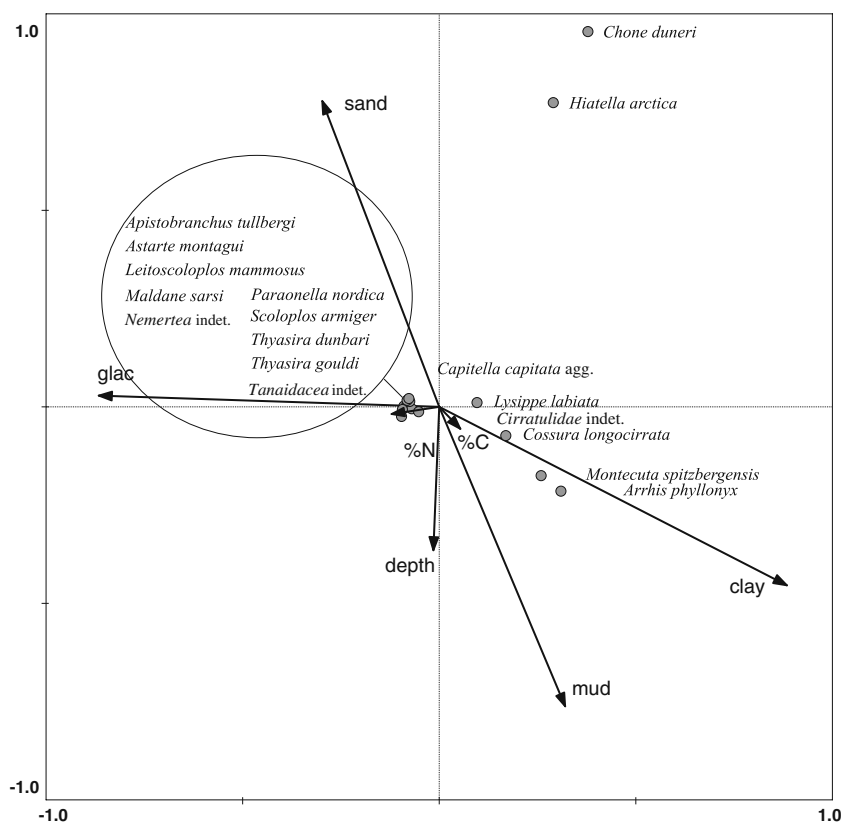
The soft-bottom fauna of Kongsfjorden is well known, but, hitherto, all of the previous benthic studies were conducted during summer and at greater depths. During our study, 120 taxa were identified in winter and another 26 in summer in the shallow sublittoral. The *Chao2* estimator indicated the possible presence of 200 species. Laudien et al. (2007) reported 63 taxa west of Ny-Ålesund from 5 to 30 m and Kaczmarek et al. (2005) presented a list of 169 taxa in the shallow waters around Kongsfjorden (qualitative dredging). Shallow areas, with different sediment characteristics, changing temperature, salinity, ice scour and different levels of food may provide many microhabitats that could be inhabited by a higher number of species than deeper areas. There is clearly a need for further shallow-depth research.

During our study, distance to the glacier was the most important factor structuring species occurrence and diversity in shallow depths. Glacial bay, with limited food availability resulting from lower primary produc-

tivity (Wiktor 1999; Hop et al. 2002) and a low amount of organic material in the sediment (Kędra et al. 2010), is less favourable to the benthic organisms than the less affected outer part of the fjord (Włodarska-Kowalczyk and Pearson 2004; Włodarska-Kowalczyk et al. 2005). Gradients in taxa occurrence and abundance along the fjord shore noted during our study are also likely to be related to glacial activity, as the number of taxa increased toward the fjord mouth in our study, similar to the pattern showed by Włodarska-Kowalczyk et al. (2005) for deeper fauna.

Cirratulids dominated within all transects and depths. They are well-known opportunists and have been recorded with high abundances in physically disturbed and organically polluted sediments (Hily 1987). Cirratulids were reported to dominate in Svalbard waters (Kendall and Aschan 1993; Włodarska-Kowalczyk et al. 1998; 1999) and the Barents Sea (Kendall 1996). In deeper parts of Kongsfjorden, a cirratulid abundance and dominance increase towards the glacier (Kendall et al. 2003; Włodarska-Kowalczyk and Pearson 2004) which confirms their opportunistic character. A similar dominance trend was also observed in shallow waters. Moreover, in winter, compared with summer, cirratulids strongly increased their abundance.

Fig. 7 Ordination diagram based on the canonical correspondence analyses (CCA) of species occurrence with respect to environmental variables at shallow depths in Kongsfjorden. Arrows represent linear variables and circles are species. Only species with minimum 15% fit to the lower axis are plotted



Another polychaete with high dominance in the glacial bay in our study was *Cossura longocirrata*, often reported among dominants in west Spitsbergen glacial bays (Włodarska-Kowalczyk et al. 1998; Włodarska-Kowalczyk and Pearson 2004). It is a mobile, burrowing, detritus-feeder (Fauchald and Jumars 1979) obviously resistant to high sedimentation. However, it does not have an opportunistic mode of dispersal (Włodarska-Kowalczyk et al. 2005), and is probably less adapted to survive repeated environmental disturbance by winter ice scour (Włodarska-Kowalczyk et al. 2007). Consequently, its abundance in winter is considerably lower than those of the cirratulids.

Axinopsida orbiculata, a discretely mobile deposit feeding thyasirid bivalve (Włodarska-Kowalczyk 2007), is reported in high numbers in Kongsfjorden from the outlet of the straits at Blomstrandoya (Włodarska-Kowalczyk and Pearson 2004) as well as at Brandal (Laudien et al. 2007). In our study, it also occurred in high abundance but only at transects close to the Ny-Ålesund station. The subsurface deposit feeder *Capitella capitata* agg. dominated at 5-m depth at glacier transects and was abundant in intertidal waters off Ny-Ålesund (Bick and Arlt 2005) and shallow waters (5–30 m) at soft bottom and in association with kelp in Kongsfjorden (Kaczmarek et al. 2005). *Leitoscoloplos mammosus*, a non-selective, discretely mobile detritus-feeder that burrows in the sediment (Fauchald and Jumars 1979) and the subsurface deposit-feeder *Scoloplos armiger*

dominated Ny-Ålesund transects. *S. armiger* was also mentioned as a dominating species by Bick and Arlt (2005), Kaczmarek et al. (2005) and Laudien et al. (2007) in shallow waters. The above taxa are known for their high reproductive plasticity and adaptability to different habitat conditions, and are likely to overwinter in fjords (Kruse 2003).

Lack of winter data makes assessing the fate of macrofauna in Kongsfjorden difficult. Little is known about the capability of different species to spend the winter in shallow depths under ice cover (Bick and Arlt 2005). Although shallow benthic faunal abundance is relatively stable throughout the year, it is difficult to speculate on the seasonal patterns of macrofauna in deeper waters. We would like to emphasise the need for further studies on overwintering strategies of bottom fauna.

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Appendix

Table 6 List of all species found in this study

Taxa	A & F	G & Z	AS	GS
Annelida	*	*	*	*
<i>Aglaophamus malmgreni</i>	*	*	*	
<i>Ampharete finmarchica</i>	*	*		
<i>Ampharete goesi</i>		*	*	
<i>Ampharete lindstroemi</i>		*		
<i>Anobothrus gracilis</i>	*		*	*
<i>Aphelochaeta</i> spp.	*	*		
<i>Aphelochaeta marioni</i>	*	*		
<i>Apistobranchus tullbergi</i>	*	*	*	
<i>Aricidea (Allia) suecica</i>	*		*	
<i>Artacama proboscidea</i>	*	*		
<i>Brada villosa</i>	*	*		
<i>Capitella capitata</i> agg.	*	*	*	*
<i>Chaetozone</i> spp.	*	*	*	*
<i>Chone duneri</i>		*		
<i>Chone</i> cf. <i>paucibranchiata</i>	*	*	*	*
<i>Circeis armoricana</i> subsp. <i>fragilis</i>			*	
<i>Cirratulus caudatus</i>		*	*	
<i>Clymenura polaris</i>	*		*	
<i>Cossura longocirrata</i>	*	*	*	*
<i>Diplocirrus</i> cf. <i>hirsutus</i>	*			
<i>Dysponetus pygmaeus</i>	*		*	
<i>Eteone flava</i> ; <i>Eteone longa</i>	*	*	*	*
<i>Eteone foliosa</i>			*	
<i>Euchone analis</i>	*	*		
<i>Euchone papillosa</i>		*		
<i>Euchone</i> spp.		*	*	*
Euclymeninae indet.			*	
<i>Exogone naidina</i>	*		*	
<i>Exogone</i> sp.	*			
<i>Fabricia stellaris stellaris</i>			*	
<i>Galathowenia oculata</i>	*			
<i>Glycera lapidum</i>	*			
<i>Harmothoe imbricata</i>			*	
<i>Harmothoe</i> cf. <i>viridis</i>	*		*	*
<i>Heteromastus filiformis</i>		*		
<i>Lanassa nordenskiöldi</i>			*	
<i>Laphania boeckii</i>	*		*	*
<i>Leitoscoloplos mammosus</i>	*	*	*	*
<i>Levinsenia gracilis</i>			*	
<i>Lumbrineris mixochaeta</i>	*	*	*	*
<i>Lumbrineris</i> sp.	*			
<i>Scoletoma fragilis</i>	*			
<i>Lysippe labiata</i>	*	*	*	*
<i>Maldane sarsi</i>	*		*	*
<i>Microphthalmus</i> sp.	*		*	

Table 6 (continued)

Taxa	A & F	G & Z	AS	GS
<i>Myriochele heeri</i>				*
<i>Nephtys ciliata</i>	*	*		*
<i>Nereimyra punctata</i>	*		*	*
<i>Notomastus latericeus</i>	*	*		
<i>Ophelina acuminata</i>	*			
<i>Ophryotrocha</i> sp.	*		*	
<i>Paraonella nordica</i>	*		*	
<i>Paraonida</i> indet.		*		
<i>Parougia</i> sp.	*	*		
<i>Pectinaria (Cistenides) hyperborea</i>	*			
<i>Pholoe assimilis</i>	*	*	*	*
<i>Phyllodoce groenlandica</i>	*			
<i>Polycirrus arcticus</i>	*	*		
<i>Polycirrus medusa</i>			*	
<i>Proclea malmgreni</i>		*		
<i>Rhodine loveni</i>			*	
<i>Sabellides borealis</i>			*	
<i>Scalibregma inflatum</i>	*	*	*	*
<i>Scoletoma fragilis</i>	*	*	*	
<i>Scoloplos armiger</i>	*	*	*	
<i>Sphaerosyllis erinaceus</i>	*		*	
<i>Spio</i> spp.	*		*	*
<i>Syllides</i> cf. <i>longocirrata</i>	*		*	
<i>Syllis (Ehlersia) cornuta</i>	*		*	
<i>Terebellides ströemi</i> agg.	*		*	
<i>Tharyx</i> spp.	*	*	*	*
<i>Travisia forbesii</i>			*	
<i>Trichobranchus roseus</i>	*			
Crustacea	*	*	*	*
<i>Arrhis phyllonyx</i>		*		
<i>Brachydiastylis resima</i>	*			
<i>Caprella septentrionalis</i>			*	
<i>Corophium volutator</i>	*		*	
<i>Diastylis rathkei</i>		*		
<i>Eudorella emarginata</i>	*	*		
<i>Eugerda</i> sp.	*			
<i>Hyas araneus</i>				*
<i>Ischyroceros anguipes</i>		*		
<i>Lamprops fuscata</i>	*	*	*	
<i>Lysianassoidea</i> indet.	*			
<i>Melita formosa</i>				*
<i>Monocolodes borealis</i>	*		*	
<i>Munna</i> sp.			*	
<i>Orchomenella minuta</i>			*	
<i>Pagurus pubescens</i>	*			
<i>Paroediceros lynceus</i>	*		*	
<i>Pleurogonium</i> sp.			*	
<i>Pontoporeia femorata</i>	*			
<i>Protomedeia fasciata</i>	*	*	*	

Table 6 (continued)

Taxa	A & F	G & Z	AS	GS
<i>Sclerocrangon boreas</i>	*			
Tanaidacea indet.	*		*	
Echinodermata		*		*
<i>Ophiocten sericeum</i>		*		
<i>Ophiura</i> juv.				*
Holothuroidea indet.		*		
Mollusca	*	*	*	*
<i>Arctinula groenlandica</i>		*		*
<i>Astarte montagui</i>	*		*	
<i>Axinopsida orbiculata</i>	*	*	*	*
<i>Buccinum undatum</i>	*			
<i>Chaetoderma nitidulum</i>	*	*	*	
<i>Ciliatocardium ciliatum</i>	*	*	*	*
<i>Cylichna alba</i>	*			
<i>Colus sabini</i>	*			
<i>Cuspidaria subtorta</i>				*
<i>Diplodonta torelli</i>	*			
<i>Dipolydora quadrilobata</i>		*		
<i>Ennucula tenuis</i>	*	*	*	
<i>Euspira</i> sp.			*	
<i>Frigidoalvania cruenta</i>	*			
<i>Hiatella arctica</i>	*	*	*	*
<i>Liocyma fluctuosa</i>	*			
<i>Macoma calcarea</i>	*	*	*	*
<i>Margarites halicinus</i>	*			
<i>Montacuta spitzbergensis</i>		*		
<i>Musculus corrugatus</i>	*			
<i>Mya truncata</i>	*	*	*	*
<i>Nuculana pernula</i>	*	*		*
<i>Oenopota</i> spp.			*	
<i>Onoba</i> sp.			*	
<i>Retusa</i> sp.	*			
<i>Serripes groenlandicus</i>	*	*	*	*
<i>Thracia myopsis</i>		*		
<i>Thyasira dunbari</i>	*	*	*	*
<i>Thyasira gouldi</i>	*		*	
<i>Turitellopsis stimpsoni</i>	*		*	
<i>Yoldia hyperborea</i>	*			*
<i>Yoldiella lenticula</i>		*	*	*
<i>Yoldiella lucida</i>	*			
<i>Yoldiella solidula</i>		*		*
Sipuncula	*		*	
<i>Golfingia margaritacea</i>	*		*	
<i>Golfingia vulgaris</i>	*		*	
<i>Nephasoma diaphanes corrugatum</i>	*			
<i>Nephasoma diaphanes diaphanes</i>			*	
Others	*	*		*
<i>Alcyonidium disciforme</i>	*	*		*
Ascidacea indet.			*	

Table 6 (continued)

Taxa	A & F	G & Z	AS	GS
<i>Cerianthus lloydii</i>		*		*
<i>Edwardsiidae</i> sp.	*			
Nemertina indet.	*	*	*	*
<i>Ophiocten sericeum</i>		*		
<i>Ophiura</i> sp.			*	
<i>Priapulius caudatus</i>	*		*	

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