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Annual changes in Arctic fjord environment and modern benthic foraminiferal fauna: Evidence from Kongsfjorden, Svalbard

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ABSTRACT

The relationships between modern Arctic benthic foraminifera and their ecological controls, along with their sensitivity to rapid environmental changes, is still poorly understood. This study examines how modern benthic foraminifera respond to annual environmental changes in the glaciated Arctic fjord Kongsfjorden, western Svalbard. Large environmental gradients due to the inflow of warm and saline Atlantic Water and the influence of tidewater glaciers characterise the fjord hydrography. A transect of six multi-corer stations, from the inner to the outer fjord, was sampled in the late summers of 2005 to 2008 to study the distribution of living (rose Bengal stained) benthic foraminifera. Physical properties of the water masses were measured concurrently. In general, nearly the entire Kongsfjorden region was dominated by ubiquitous *N. labradorica* foraminiferal assemblage that successfully exploited the local food resources and thrived particularly well in the presence of Atlantic-derived Transformed Atlantic Water (TAW). Further, the annual investigation revealed that Kongsfjorden underwent large interannual hydrological changes during the studied years related to variable inflow of warm and saline Atlantic Water. This led to a strong fauna variability particularly at the two marginal sites: the glacially influenced inner fjord and marine influenced shelf region. We also observed significant species shift from the 'cold' to 'warm' years and an expansion of widespread and sub-arctic to boreal species into the fjord.

1. Introduction

Benthic foraminifera are commonly used to deduce paleoceanographic changes in the Arctic, and they have shown to be of great value due to their high abundance and diversity in shelf areas (e.g., Jennings and Helgadóttir, 1994; Polyak et al., 2002; Lloyd, 2006; Wollenburg et al., 2007; Bubenshchikova et al., 2008; Ślubowska-Woldengen et al., 2008; Skirbekk et al., 2010; Rasmussen and Thomsen, 2010; Jernas et al., 2013; Pawłowska et al., 2017). Reconstructing paleoceanographic changes using benthic foraminifera in the Arctic, however, strongly depends on the knowledge about their adaption to changes in biological, chemical, and physical surroundings. Several studies have already demonstrated some of the environmental factors (e.g., sea bottom sediment composition, water masses, oxygen content in the sediments and flux of organic carbon to the sea bed) that control the living benthic foraminifera (e.g., Jorissen et al., 1995; Hald and Korsun, 1997; Rytter et al., 2002; Lloyd, 2006). Still, it is difficult to interpret some palaeofaunal records and to obtain a thorough understanding of the environmental impact on benthic foraminifera. This is either due to the lack of modern faunal analogues or simply the lack of high-resolution paleorecords. Hence, there is a need to improve our knowledge of foraminiferal ecology in order to unravel the full range of past en-

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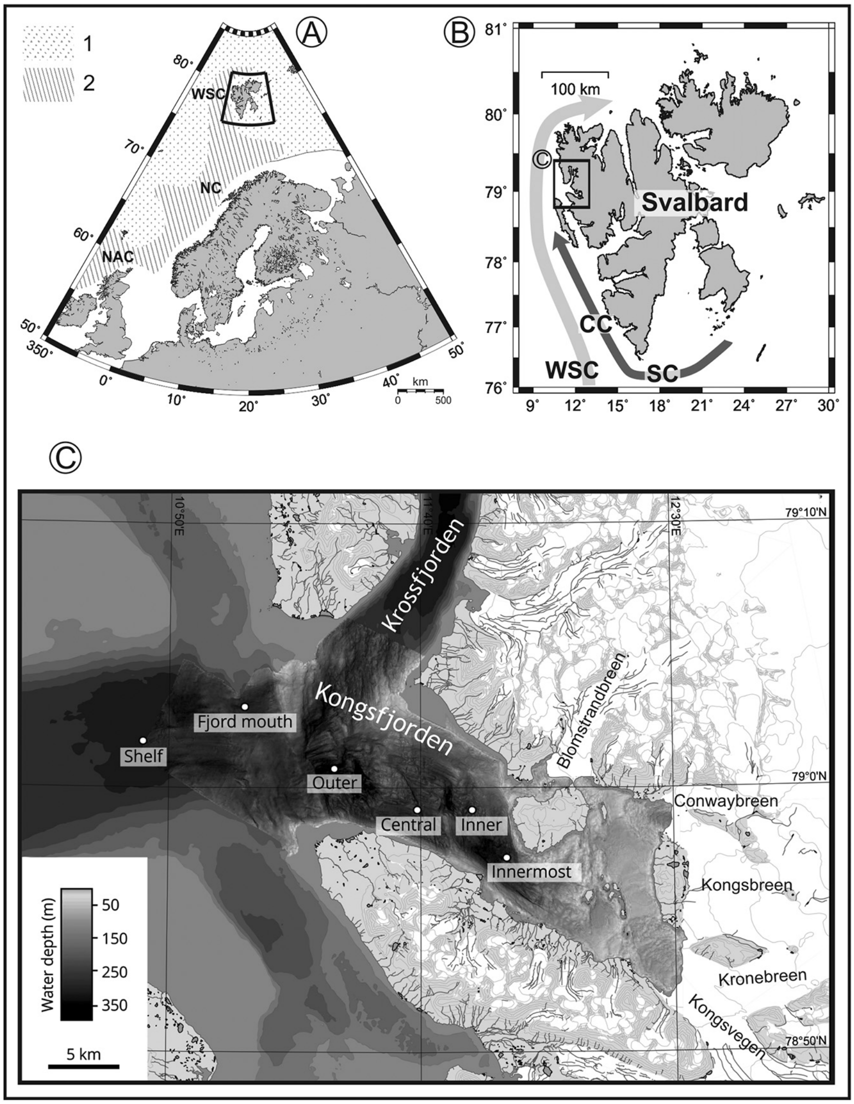


Fig. 1. Study area and regional ocean current system. A) Map of surface waters in the Norwegian Sea and adjacent seas (modified from Hald and Korsun, 1997). The legend refers to water masses shown on inset map A): 1-Arctic water; 2-Atlantic water. Currents: NAC-North Atlantic Current; NC-Norwegian Current; WSC-West Spitsbergen Current. B) Map of the Svalbard archipelago with the location of the Kongsfjorden-Krossfjorden fjord system (black frame). Currents: see above and CC- Coastal Current; SC-Sørkapp Current C) Map of Kongsfjorden and the multicorer/CTD stations from four summer seasons (2005–2008). The high-resolution swath-bathymetry data was provided by the Norwegian Hydrographic Service.

vironmental and climate changes in the Arctic from the time prior to the mid-19th century, when instrumental time series became available.

In this study we focus on Kongsfjorden, an Arctic fjord on the northwestern Svalbard archipelago (Fig. 1). This fjord is characterized by a strong environmental gradient (e.g. temperature, salinity, turbidity/sediment supply) due to marine-terminating glaciers at the fjord head and advection of warm Atlantic water masses from the shelf. The cross-shelf water-mass exchanges are known to affect the physical and biological systems in these Arctic fjords (e.g., Hop et al., 2002; Willis et al., 2008; Hodal et al., 2012; Gluchowska et al., 2016), and hence, make them particularly sensitive to environmental changes.

The main goal of this study is to investigate the Arctic foraminiferal fauna response to rapid environmental shifts by studying living benthic foraminiferal changes on annual time scales (summer season) in the period from 2005 to 2008 along a transect from outer to inner Kongsfjorden, Svalbard.

The knowledge of modern benthic foraminiferal faunas in Kongsfjorden remains sparse and focus mainly on total fauna assemblages (living and dead individuals not distinguished; e.g. Elverhøi et al., 1980; Shetye et al., 2011). Most of these studies are also restricted to certain areas or within shallow water depths in Kongsfjorden. Hald and Korsun (1997) present modern (rose Bengal stained) foraminifera from the neighbouring Krossfjorden while Loubere et al. (2011), and Loubere and Rayray (2016) study the content of living foraminifera using the cell tracker green method at a few stations in Kongsfjorden. In other Svalbard fjords investigations of living foraminifera have been carried out by Hansen and Knudsen (1995), Korsun et al. (1995), Hald and Korsun (1997), Korsun and Hald (2000), Majewski and Zajączkowski (2007), Forwick et al. (2010) and Zajączkowski et al. (2010).

2. Physiographic and environmental settings

The fjord system Kongsfjorden-Krossfjorden is located on northwest Spitsbergen, the largest island of the Svalbard archipelago (Fig. 1 B). Kongsfjorden is 20 km long, 4–10 km wide (Svendsen et al., 2002), and up to 394 m deep (Howe et al., 2003). Kongsfjorden and Krossfjorden merge and continue as a submarine glacial trough, Kongsfjordrenna, out to the shelf edge (Fig. 1 C). Kongsfjorden and Krossfjorden do not possess well-defined sills at their mouths (Howe et al., 2003). At present, five tidewater glaciers drain into the innermost part of the fjord, providing it with fresh water and sediments (Elverhøi et al., 1980, 1983; Svendsen et al., 2002; Streuff et al., 2015). Sediment supply to the fjord occurs also from rivers and sea ice. However, large lateral gradients from the fjord head towards the fjord mouth are found (highest sediment fluxes and generally coarsest composition at fjord head) (e.g., Elverhøi et al., 1980, 1983; Hop et al., 2002; Svendsen et al., 2002; Zajączkowski, 2008). According to Trusel et al. (2010)

Table 1A
Study locations with the individual stations in Kongsfjorden from each cruise in the years from 2005 to 2008. Position and environmental data of various environmental parameters (water depth, granulometry, organic matter, C/N ratio and sediment depth of oxygenated layer).

Station	Station log	Latitude (°N)	Longitude (°E)	Depth (m)	% Clay (< 2 µm) (Dijkstra, 2009)	% Silt (2–63 µm) (Dijkstra, 2009)	% Sand (> 63 µm) (Dijkstra, 2009)	% Corg	% MOC (Kim et al., 2011)	C/N ratio (Kim et al., 2011)	Depth of the oxygenated layer in core (mm) (Loubere et al., 2011)
Shelf	NP05-11-20	79°01.75	10°44.96	319	–	–	–	–	–	–	–
	NP06-16-45			323	–	–	–	1.8	–	–	–
	NP07-13-08			326	20.3	78.7	1.0	2.3	61	8	7 ± 1
	NP08-16-33			328	–	–	–	1.6	–	–	7.5 ± 0.5
Fjord mouth	NP05-11-21	79°03.05	11°05.17	326	–	–	–	2.0	–	–	–
	NP06-16-43			315	–	–	–	1.6	–	–	–
	NP07-13-26			329	19.1	77.2	3.7	1.9	67	8	7.5 ± 0.5
	NP08-16-30			330	–	–	–	2.1	–	–	6 ± 1
Outer	NP05-11-02	79°00.74	11°23.01	375	–	–	–	2.0	–	–	–
	NP06-16-12			377	–	–	–	–	–	–	–
	NP07-13-49			380	19.4	77.6	3.0	1.9	52	8	–
	NP08-16-46			378	–	–	–	1.7	–	–	–
Central	NP06-16-37	78°59.17	11°39.45	287	–	–	–	–	–	–	–
	NP07-13-53			278	22.5	77.5	0.0	1.5	61	8	6.5 ± 0.5
	NP08-16-44			278	–	–	–	1.2	–	–	–
Inner	NP05-11-03	78°59.17	11°50.22	287	–	–	–	1.1	–	–	–
	NP06-16-30			311	–	–	–	0.9	–	–	–
	NP07-13-42			319	20.9	78.1	1.0	1.2	65	8	7.5 ± 0.5
	NP08-16-40			319	–	–	–	0.7	–	–	8 ± 1
Inner-most	NP05-11-05	78°57.37	11°57.14	336	–	–	–	0.9	–	–	–
	NP06-16-31			338	–	–	–	0.7	–	–	–
	NP07-13-40			342	20.6	78.9	0.5	1.0	61	8	9.5 ± 0.5
	NP08-16-37			342	–	–	–	0.5	–	–	8 ± 2

recent sediment accumulation rates at the immediate fronts of Kongsvegen and Kronebreen are > 1 m a^{-1}.

2.1. Oceanographic and sea ice conditions in Kongsfjorden

The hydrography in Kongsfjorden is a result of internal water masses that are influenced by external intrusions, resulting in water masses arising from mixing of these (Svendsen et al., 2002;Cottier et al., 2005). Properties of the different water masses in Kongsfjorden are shown in Table 1B. The presence of both external Atlantic Water (AW) and Arctic Water (ArW) inside the fjord is due to exchange of water masses across the shelf. However, the mechanisms for the exchange are debated. In winter time exchange may be driven by ice production in the fjord (Nilsen et al., 2008) and atmospheric forcing (Nilsen et al., 2016), while in the summer season physical conditions along the front between AW on the slope and ArW on the shelf may be more important

Table 1B
Percentage of main water masses in the water column from 2005 to 2008 in Kongsfjorden (definition after Cottier et al., 2005).

Station	Station log	External	Internal		Mixed	
		Atlantic water	Local water	Surface water	Transformed Atlantic water	Intermediate water
		T (°C) > 3.0	− 0.5 to 1.0	> 1.0	1.0 to 3.0	> 1.0
		S > 34.65	34.30 to 34.85	< 34.65	> 34.65	34.00 to 34.65
Shelf	NP05-11-20	57%	0%	8%	26%	10%
	NP06-16-45	59%	0%	6%	32%	2%
	NP07-13-08	48%	0%	0%	42%	10%
	NP08-16-33	28%	4%	0%	56%	12%
Fjord mouth	NP05-11-21	28%	1%	10%	42%	19%
	NP06-16-43	57%	0%	10%	28%	5%
	NP07-13-26	56%	0%	0%	37%	7%
	NP08-16-30	32%	0%	0%	56%	11%
Outer	NP05-11-02	0%	1%	10%	54%	22%
	NP06-16-12	53%	0%	10%	34%	3%
	NP07-13-49	62%	0%	5%	28%	5%
	NP08-16-46	17%	0%	2%	67%	14%
Central	NP06-16-37	54%	0%	10%	30%	6%
	NP07-13-53	54%	0%	5%	34%	7%
	NP08-16-44	22%	0%	8%	65%	4%
Inner	NP05-11-03	0%	19%	10%	58%	13%
	NP06-16-30	47%	0%	9%	35%	8%
	NP07-13-42	57%	0%	5%	32%	6%
	NP08-16-40	22%	0%	7%	61%	10%
Inner-most	NP05-11-05	0%	18%	10%	61%	11%
	NP06-16-31	51%	0%	9%	34%	7%
	NP07-13-40	55%	0%	4%	34%	7%
	NP08-16-37	22%	0%	5%	59%	14%

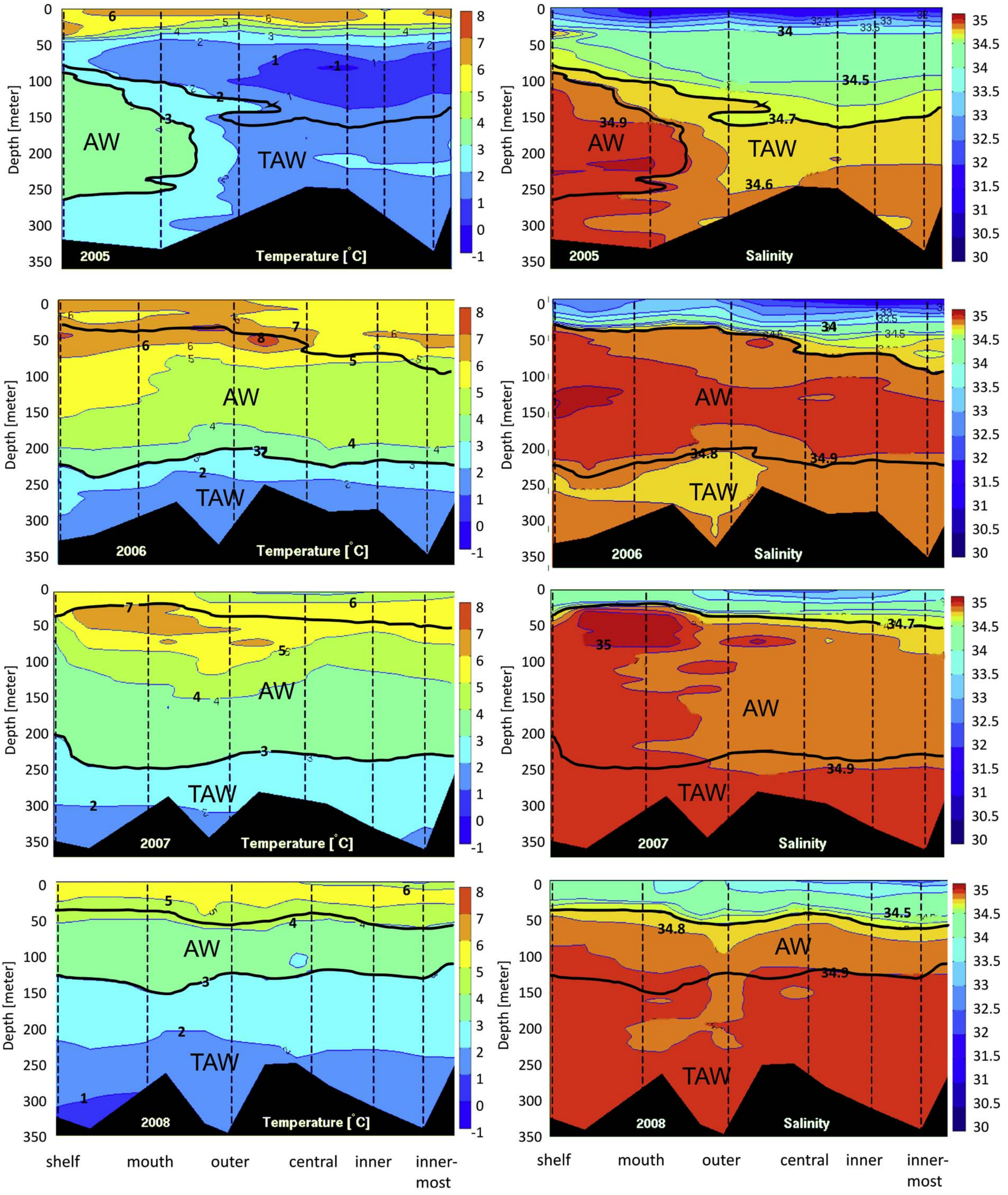


Fig. 2. Temperature (left column) and salinity (right column) transects from August/September 2005–2008. The CTD surveys cover a dense grid from Kongsfjordrenna into Kongsfjorden. The corresponding multicorer/CTD stations are marked as vertical dashed lines. Isolines are drawn at − 1 °C to 7 °C in 1 °C steps for the temperature survey, and at 30 to 35 in 0.1 steps for salinity. Range of the dominant water masses (Atlantic and Transformed Atlantic Water) are indicated with black line.

than plain estuarine circulation (Tverberg and Nøst, 2009).

Atlantic Water is present in the core of the West Spitsbergen Current (WSC) (Figs. 1 A and B) all year round. It is characterized by temperatures above 3 °C and salinities of > 34.65 (Svendsen et al., 2002). Atlantic Water enters the fjord every summer season where it remains present for a few months (Svendsen et al., 2002). The front along the shelf between AW and fresher and colder ArW (− 1.5 to 1 °C; > 34.3) carried by Coastal Current (Fig. 1 B) normally prevents any cross-shelf transport during the winter season. However, unusual and extensive intrusions of AW into the fjords of West Spitsbergen have also recently been recorded in wintertime (Cottier et al., 2007; Willis et al., 2008; Tverberg and Nøst, 2009). In addition, the mixing processes in the fjord lead to formation of Transformed Atlantic Water (TAW), consisting of AW chilled by interaction with ArW and internal water masses (Table 1B).

During the winter season, December/January, fast ice forms in the inner fjord (0.7 m in thickness; Gerland et al., 1999). The extent of sea ice and the sea ice edge position vary from year to year but generally only the innermost part of the fjord is sea-ice covered (Svendsen et al., 2002; Gerland and Renner, 2007).

3. Material and methods

3.1. Sampling

Surface sediment samples were collected along a transect consisting of six stations in Kongsfjorden with *R/V Lance* from 2005 to 2008 (Fig. 1C, Table 1). The samples were collected from similar water depths, ranging from 250 to 375 m, to reduce the influence of bathymetric variability on the fauna. Sampling of surface sediments at the six stations was repeated each year in late summer (August/September) except at the central station in 2005. The surface sediment samples were retrieved with a multicorer (MC) loaded with 6 transparent barrels, each 80 cm long and with an inner diameter of 10.4 cm. After retrieving the multicorer visual inspection of the surface of the cores was performed to evaluate the quality of the samples, i.e., detect and avoid any disturbances. One core from each station with an intact surface, indicated by a fluffy surface layer and delicate epifauna, was used for further processing. The sediment cores were subsampled onboard for the uppermost 0–2 cm of the sediments column. Immediately after subsampling, the samples were stained with a solution of ethanol and rose Bengal (1 g/1 L ethanol) to identify the living (stained) fauna. Stained samples were subsequently stored in a cold room for at least six weeks before further laboratory processing.

3.2. Environmental variables

Samples for analysing environmental parameters were collected simultaneously with the foraminiferal samples. Grain-size analysis of the uppermost 1 cm of the surface sediments were carried out on samples from 2007 and 2008 (Dijkstra, 2009) following the methods described by Konert and Vandenberghe (1997) (Table 1A). The samples (c. 1–2 g bulk sediment) were pre-treated with H_2O_2, HCl and NaOH to remove organic matter, carbonates and opal, respectively. All measurements were performed on a Fritsch Analysette 22 laser particle sizer at the Vrije Universiteit resulting in a grain-size distribution with 56 size classes in the size range 0.15–1600 μm (Dijkstra, 2009).

The content of organic carbon in the surface sediment samples from 2005, 2006 and 2008 were measured with a Leco CS-200 induction furnace at the University of Tromsø (Table 1A). The inorganic carbon was removed from the bulk sediment with HCl (10%) at room temperature prior to the measurements (Espitalié et al., 1977). In addition we used the C_{org}, C/N ratio and marine organic matter (% MOC) of the same sample set from 2007 that were conducted and published previously (Peterse et al., 2009; Kim et al., 2011) (Table 1A). Sediment slices of 1 cm intervals retrieved from a multicore core followed by immediately freezing at $-20\,^{\circ}C$ were used for C_{org} and C/N ratio analyses. Elemental and stable isotope analyses of sediment samples are described in Peterse et al. (2009) and Kim et al. (2011). Oxygen profiles were measured during the cruises in 2007 and 2008 in the surface sediments immediately after sampling the multicores (Loubere et al., 2011) (Table 1A).

Prior to multicorer sampling, physical oceanographic properties were measured with a CTD (Seabird SBE 9111 plus) providing temperature, salinity and pressure in the water column. In each year, a dense grid of CTD stations was measured to obtain oceanographic properties. The results of the oceanographic measurements are presented as water column temperature and salinity transects (Fig. 2), bottom water temperature and salinity (Fig. 3) and the percentage of main water masses in the water column (Table 1B). The percentages of different water masses (Table 1B) are calculated from the CTD profiles taken at the coring sites.

3.3. Laboratory analyses

3.3.1. Foraminiferal sample processing

In the laboratory the samples were wet sieved and wet analysed for living (stained) fauna in > 106 μm fraction. Both calcareous and agglutinated foraminifera were quantified and identified down to species level in each subsample. The calcareous species were identified as living if most of the chambers were completely filled and evenly colored. The agglutinated foraminifera were in addition examined for coloration of the aperture; whereas *Hyperammina subnodosa* tests were crushed to examine the inner content. All live specimens were counted in each sample, ranging from 61 to 1171 specimens per sample. Identification of the species is mainly based on Höglund (1947), Loeblich and Loeblich and Tappan (1953), Feyling-Hanssen (1964), Feyling-Hanssen et al. (1971). After examination, all specimens were stained again with a mixture of ethanol and rose Bengal and stored in a cold room (4 °C) at the Norwegian Polar Institute in Tromsø.

3.4. Data analysis

The absolute abundance of stained individuals was standardized to 100 cc (Fig. 4). Species richness, defined as the number of taxa in a sample (S), species diversity measured with the Shannon-Wiener diversity $\log_e$ based index (H), and evenness of distribution of individuals among taxa expressed by the Pielou index (J), were calculated for all foraminiferal samples. The relative abundances of stained taxa of > 2% at the given sites are presented in Fig. 5A and B, the absolute and relative abundances of the most dominant taxa are presented in Fig. 6A and B.

The foraminiferal assemblages (FAs) were defined with orthogonal rotated (Varimax) Principal Component Analysis (PCA; Malmgren and Haq, 1982; Mackensen et al., 1990). The calculated Principal Component (PC) scores (Table 2) show the contribution of the each foraminiferal species to each FAs whereas PC loadings (Table 3) show importance of particular FAs at particular sites. The patterns of foraminiferal composition was further investigated and illustrated with CAP ordination (constrained ordination) using Bray-Curtis similarities (Fig. 7). This was done in order to visualize the variability along the best discriminated groups of samples defined by fjord site (spatial variability) and sampling year (temporal variability). In order to improve the visualization of the plots both site and year plots were doubled: right figures give the information about samples (Fig. 7A and C); left figures about the vectors indicating the taxa (Fig.7B and D).

Relationships between environmental variables and foraminiferal indices were investigated using Pearson correlations (Table 4). However, due to the lack of granulometry measurements for the years 2005, 2006 and 2008, and the lack of TOC measurements for some of the stations, those two parameters were excluded. The significance level for the statistical test used was $p < 0.05$. All statistical analyses were performed on the untransformed data of living foraminiferal species with relative abundances constituting > 2% of the total assemblages in at least one sample. The statistical analyses were carried out using PRIMER 6, PERMANOVA + (Clarke and Warwick, 2001; Anderson et al., 2008), PAST 3 (Hammer et al., 2001) and SYSTAT 11.

4. Results

4.1. Environmental conditions in Kongsfjorden during the sampling period (2005–2008)

4.1.1. Oceanography

The oceanographic changes (salinity and temperature) in Kongsfjorden in the summers from 2005 to 2008 are shown in Figs. 2, 3 and Table 1B.

Overall, the percentage of Atlantic Water increased in Kongsfjorden in 2006–2008 compared to 2005 (Table 1B). Transformed Atlantic Water is inferred as the prevailing water mass at the bottom during the entire sampling period (Fig. 2). Overall, bottom temperature varied from 1.6 °C to 2 °C between the summers of 2005–2007, exceeding the range at the two outermost stations of 2005 (up to 2.7 °C, Figs. 2 and 3).

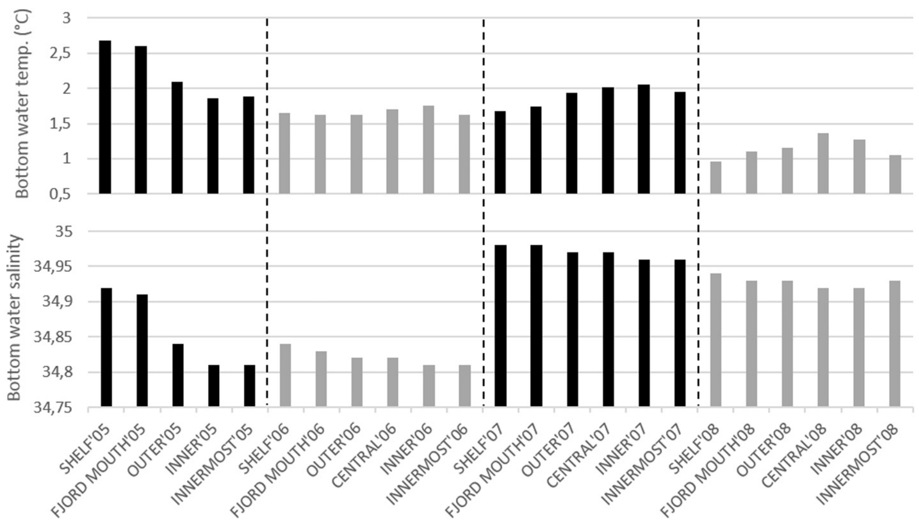


Fig. 3. Bottom water properties: temperature and salinity, in each year (2005–2008) along the Kongsfjorden sampling transect.

The bottom water temperature of 2008 was the lowest measured during the studied period (from 0.9 °C to 1.3 °C). Although the variations of bottom water salinity were generally low (from 34.81 at the two innermost stations in 2005 and 2006; to 34.98 at 'shelf' and 'mouth' in 2007), the summers 2007 and 2008 were characterized by the highest salinities.

4.1.2. Sedimentological properties

The locations of the stations, water depths, granulometric and geochemical parameters of the fjord sediments are presented in Table 1A.

Overall, the grain size distribution was similar at all stations showing high content of silt (2–63 μm) at all stations (approx. 78%), and a clay (< 2 μm) content of approximately 20%. Sand contents (> 63 μm) were slightly higher at the deepest stations (> 3%) and lower or absent (0–1%) at the shallower central and inner stations as well as on the shelf.

4.1.3. Organic carbon

The organic carbon content (C_{org}) varied between 0.5 and 2.4% (% dry weight) along the transect (Table 1A). The content of organic carbon (C_{org}) generally declined from the outer part (around 2%) towards the inner part (around 1–0.5%) of the fjord. The overall gradual decrease of organic carbon from the 'shelf' to the 'innermost' station is comparable between years although the absolute values vary at each station between years (Table 1A). The C/N ratio was stable and relatively low (8) (Table 1A), and most of the organic carbon in Kongsfjorden originated from marine production (MOC ≥ 52%) (Table 1A).

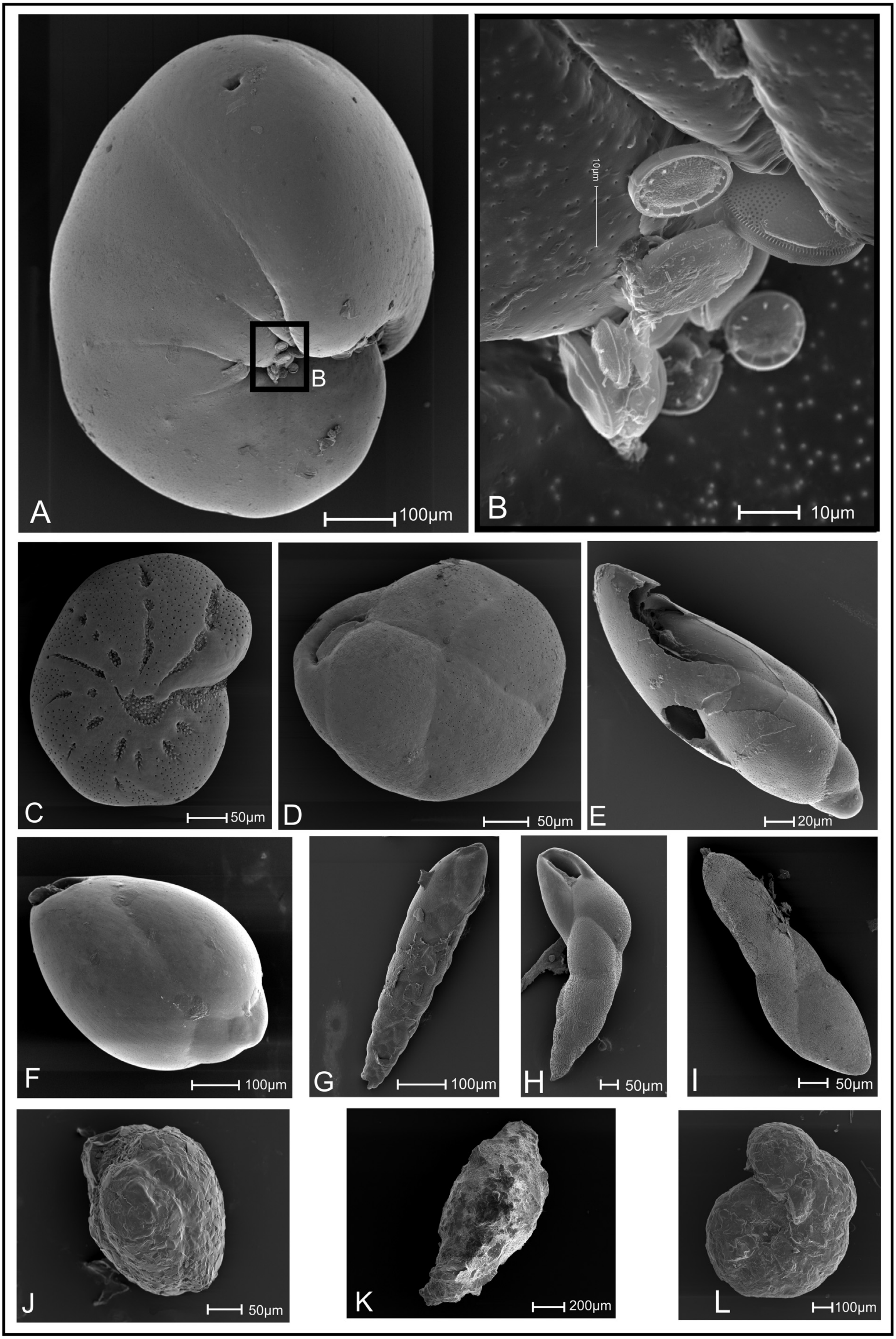
4.2. Foraminifera

In the analysed surface samples, 78 benthic foraminiferal species (Appendix A) were identified among 10.049 counted stained individuals. Some of the most abundant species are shown in Plate 1 (SEM) and Plate 2 (digital image). In this study, the species *Stainforthia loeblichi* and *Stainforthia concava* were grouped together into *Stainforthia loeblichi/concava* due to the morphological resemblance.

Our study shows the highest foraminiferal absolute abundance in 2006 while year 2007 shows the lowest (Fig. 4). The 'shelf' station and the 'innermost' station were characterized by low absolute abundance as well as low diversity in 2006 and 2007 compared to higher values in years 2005 and 2008 (Fig. 4). The highest species evenness and contribution of agglutinated foraminiferal taxa were characterized for 2007 (Fig. 4).

Relative abundance of all living benthic foraminiferal species with > 2% in at least one sample at the given sites are presented in Fig. 5A and B. Prominently, *Nonionellina labradorica* dominates the benthic foraminiferal fauna in Kongsfjorden. Foraminiferal fauna occurrence at the 'shelf' site in 2005 clearly differed from the following years 2006–2008 when great numbers of species became absent. On the contrary, species like *Adercotryma glomeratum*, *Reophax scorpiurus* and *Bolivina pseudopunctata* were more abundant after 2005. *Stainforthia feylingi* appeared only in 2006 and 2008 with occurrences of 25% while *Cassidulina reniforme* were particularly abundant (19%) in 2008. The 'fjord mouth' site was strongly dominated by *N. labradorica* (above 50%) except in 2007. Abundant were also *A. glomeratum* (in 2007) and *C. reniforme* (in 2008). At the 'outer fjord' *N. labradorica* was accompanied by *Alveolophragmium crassimargo* (2006 and 2007), *Reophax subfusiformis* (in 2007), *R. scorpiurus* (2008) and *Silicosigmoilina groenlandica* (in 2008). In the summers of 2006 and 2007 *N. labradorica* occurrence dropped below 20% at the 'central' site. The 'inner fjord' was dominated by *N. labradorica* with *C. reniforme* (2005), *Stainforthia loeblichi/concava* (2005), *Elphidium excavatum* f. *clavatum* (2006) and *Globobulimina auricula* (2007, 2008). After 2005, lower abundances of *N. labradorica* were observed at the 'innermost' site, whereas higher abundances of *S. loeblichi/concava* (2007) and *Reophax subfusiformis* (2007, 2008) occurred.

Absolute and relative abundances of selected, most abundant species are presented in Fig. 6. Some species demonstrated clear patterns in temporal variability. In 2005, *B. pseudopunctata* absolute abundance and occurrence were very low to absent, but increased in the following years. A. *glomeratum* was least abundant in 2006. In the summers 2006 and 2007, *A. crassimargo* became more abundant in the fjord synchronously with decrease of *C. reniforme.* Relative abundances of *N. labradorica* were similar for 2005, 2006 and 2008 (average values of 41%, 37% and 39%, respectively), whereas they were particularly low in 2007 with a minimum value of 4% at the outer fjord. The decrease was also reflected in the absolute abundance. Contrary, *R. subfusiformis* was abundant almost exclusively in 2007. A general increase of *G. auricula* was observed in the summers 2007 and 2008 reaching a highest absolute abundance in the 2008, whereas the abundance of *E. excavatum* f. *clavatum* dropped to a minimum (< 5%). The spatial distribution pattern indicated higher relative and absolute abundances of *S. loeblichi/concava* and *R. subfusiformis* in the inner part of Kongsfjorden. *B. pseudopunctata* was abundant at the two marginal locations ('innermost' and 'shelf'), whereas the middle fjord locations were characterized by increased importance of i.e. *A. crassimargo*, particularly in 2006 and 2007. Other species, like *A. glomeratum,* when abundant (except summer 2006), decreased gradually towards the inner fjord.



(caption on next page)

Plate 1. SEM images of the most abundant species: A-*Nonionellina labradorica* (Dawson, 1860); B-magnification of *Nonionellina labradorica* aperture, filled with diatoms, from Plate 1 A; C-*Elphidium excavatum* f. *clavatum* Cushman, 1930; D-*Cassidulina reniforme* Nørvang, 1945; E-*Stainforthia feylingi* Knudsen & Seidenkrantz, 1994; F-*Globobulimina auriculata* (Bailey, 1894); G-*Bolivina pseudopunctata* Höglund, 1947; H-*Stainforthia loeblichi* (Feyling-Hanssen, 1954); I-*Stainforthia concava* (Höglund, 1947); J-*Adercotryma glomeratum* (Brady, 1878); K-*Reophax subfusiformis* Earland, 1933; L-*Alveolophragmium crassimargo* (Norman, 1892).

4.3. Statistical analysis

The PCA resulted in three-PC model (referred further as three foraminiferal assemblages) that explained 81.31% of the total variance of the dataset (Table 2). Foraminiferal assemblages (FAs) determined for Kongsfjorden are named after the taxon of the highest PC scores. The most important *N. labradorica* FA explained 66.24% of total variance, with accessory species *I. helenae*, *S. loeblichi/concava*, *S. groenlandica* and *G. auricula*. The second *R. subfusiformis* FA explained 8.86% of total variance with *S. loeblichi/concava A. gloemratum*, *A. crassimargo* and *C. involvens.* Less important was the *S. feylingi* FA (6.21% of total variance of the dataset) with *R. scorpiurus*, *C. reniforme*, *B. pseudopunctata*, *C. involvens, A. glomeratum* and *S. loeblichi/concava* showing high PC scores.

The distributions of sites with high PC loadings for each FA is shown in Table 3. The *N. labradorica* FA dominated most sites in Kongsfjorden over the four years survey except in 2007 when it only occurred at the two outermost stations and at the 'inner' site. The *R. subfusiformis* FA was prominent only in 2007 and 2008 in the 'innermost' site and additionally in 2008 at the 'outer fjord' location. The *S. feylingi* FA co-occurred with *N. labradorica* FA at the 'shelf' and 'innermost' site in 2006. It dominated the 'shelf' site in 2008.

In general, points representing samples in both CAP plots, site and year (Fig. 7) were dispersed, indicating that both spatial and temporal variations in fauna composition are important. Groups of samples collected at the 'shelf' (except collected in 2005) and 'innermost' fjord region were clearly separated on the site/year type CAP plot, which indicate spatial variability (Fig. 7A and B). The vectors in the CAP ordination discriminated the species that best defined the fauna in the region. The vectors indicated that *B. pseudopunctata*, *S. feylingi*, *Reophax gracilis*, *R. scorpiurus* and *A. glomeratum* were best correlated with the 'shelf' sites, whereas *Elphidium excavatum* f. *clavatum*, *R. subfusiformis* and *S. loeblichi/concava* with inner fjord region.

Groups of samples collected in 2005 and 2006 were distinguishable on the year/site CAP plot (temporal variability; Fig. 7C and D) while some overlapping was observed between samples collected in 2007 and 2008. A taxonomic composition of foraminifera showed shifts in the taxa composition over the four years. *Cibicides lobatulus*, *C. reniforme* and *Nonionella auricula* were indicated as the best correlated with variability in year 2005, whereas *Reophax* spp. and *Robertinoides arctica* with 2006.

A correlation matrix (Pearson) was calculated for abiotic variables (bottom temperature and salinity, depth) and foraminiferal indices (abundance, diversity, % of calcareous fauna, relative abundance and FAs). Correlation coefficients (r) are given in Table 4. Moderate (> 0.4) positive correlation to the bottom water salinity was found with *A. glomeratum* ($r = 0.55$) and *R. subfusiformis* ($r = 0.46$) and negative correlation with *R. arctica* ($r = -0.57$). Bottom temperature changes correlated with abundance of *C. lobatulus* ($r = 0.46$); *Islandiella islandica* ($r = 0.44$); *Quinqueloculina seminulum* ($r = 0.41$) and anticorrelated with *R. scorpiurus* ($r = -0.42$). There was no significant correlation between environmental variables and any of the determined foraminiferal assemblages (FAs).

5. Discussion

5.1. Methods — sampling bias

Benthic foraminifera are known to show high seasonal variability as well as patchy distributions, both vertically (sediment depth) and horizontally (spatial distribution), (e.g. Gustafsson and Nordberg, 2000; Swallow, 2000; Buzas et al., 2002; Loubere et al., 2011). In this study, it seems that patchiness was of minor importance compared to the influence from the environmental changes in Kongsfjorden as the distribution pattern, at least among the abundant taxa, was fairly consistent. Possible patchiness beyond spatial scales larger than the multicorer tube, i.e., larger than c. 10 cm can, however, not be entirely ruled out. However, no sample replicates were available in this study. Thus, random signals, particularly from species of low abundances, have to be interpreted with caution. Within the multicore tube we know that the foraminifera may be dispersed unevenly due to their microhabitat preferences (Loubere et al., 2011). Higher density of macrofauna may also affect foraminifera population growth due to enhanced bioturbation activity (Włodarska-Kowalczuk et al., 2013). In this study, however, we focus on a fjord setting as a macro-habitat to gain more insight in the general environmental changes affecting the modern benthic foraminiferal distribution patterns.

5.2. Annual environmental changes in Kongsfjorden

5.2.1. Inflow of Atlantic Water and bottom water variability

In February-March 2006 the continental shelf west of Svalbard, as well as Kongsfjorden, was flushed with Atlantic Water (AW; Cottier et al., 2007), an event that increased the yearly temperature and salinity in Kongsfjorden for several years. The presence of AW was already large in the early summer of 2006, and increased throughout the season due to continued inflow of AW. Consequently, there was a large difference between the summer water masses in Kongsfjorden in the 'cold' year in 2005 and of the 'warmer' years in 2006–2007.

Nevertheless, the bottom waters did not reflect directly this major oceanographic change in the fjord. The bottom water mass constituted of Transformed Atlantic Water (TAW) except the 'shelf' station in 2008 that was dominated by cold Local Water. Overall, the differences between the lowest and highest summer bottom temperatures and salinities over the four summer seasons were rather low: maximum 1.7 °C and 0.17 [psu], respectively. In 2005, the three outermost stations were influenced by the recent AW inflow, while in later years the bottom water contained mainly remnants of the winter/spring production of cooled AW. In 2008 the difference was mainly in colder temperatures indicating that the winter production reservoir must have contained a large percentage of cooled AW from previous years. The large-scale oceanographic changes in the fjord influenced the bottom environment only to some degree, most likely due to the water stratification in the summer season.

5.2.2. Primary productivity, bottom C_{org} reservoir and bottom oxygen concentration

Organic carbon (C_{org}), measured on surface sediments shows a general declining trend towards the inner part of the fjord. This is most likely due to the high amounts of sediment load during the melting season and dilution of the concentration of organic matter in the proximity of tidewater glaciers (Włodarska-Kowalczuk and Pearson, 2004). Sampling of primary producers (in this case mainly diatoms and *Phaeocystis*) in Kongsfjorden show a low in biomass and a late bloom in spring 2007 compared to spring 2006 (Hegseth and Tverberg, 2013). In 2007, additional smaller blooms were also registered later during spring and summer. The reason for these changes was attributed to strong inflow of AW into Kongsfjorden (Hodal et al., 2012; Hegseth and Tverberg, 2013). From this study it is clear that the content of organic carbon (C_{org}) in the sediments was not easily reconciled with discrete

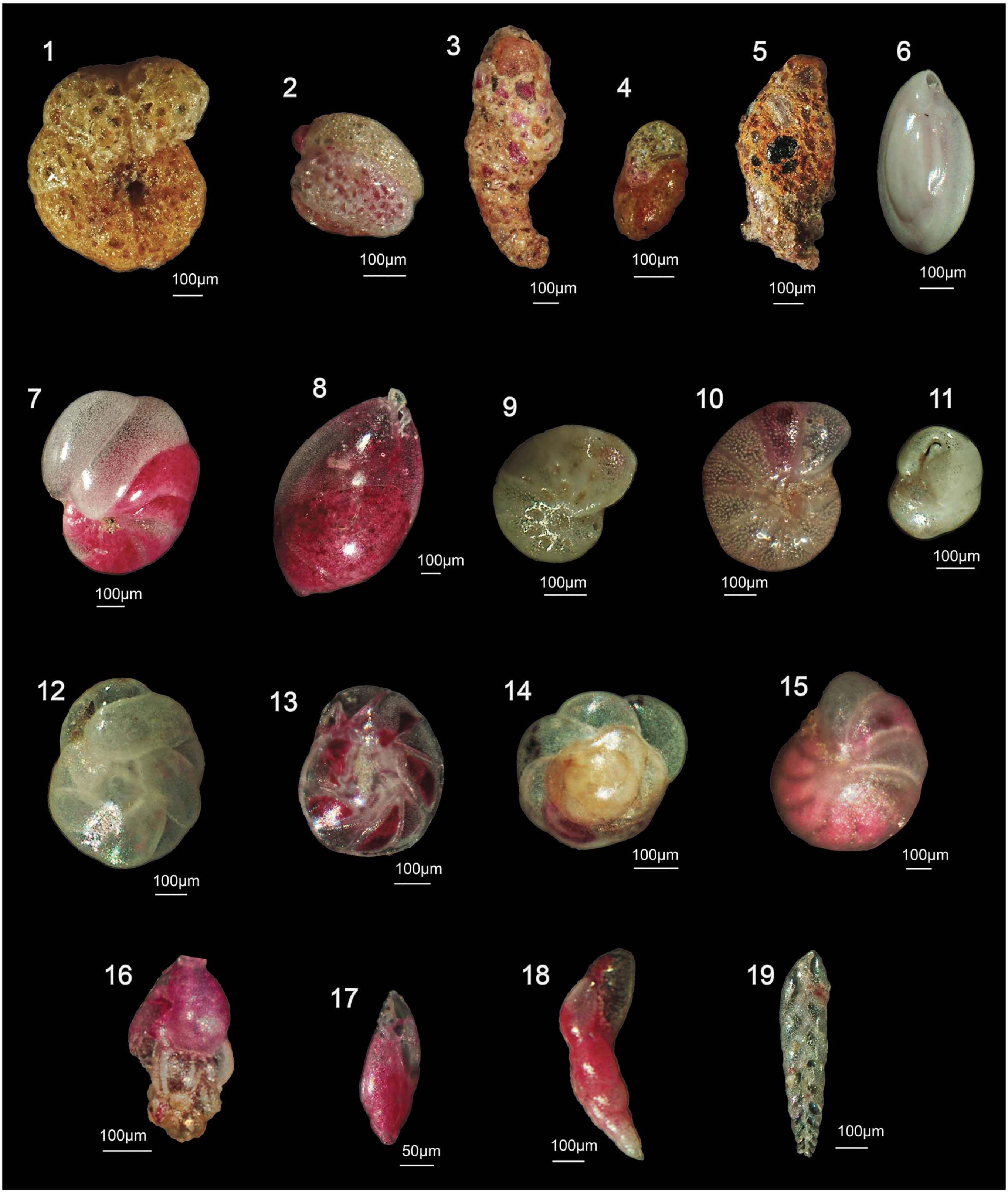


Plate 2. Digital images of the most abundant species: 1-*Alveolophragmium crassimargo* (Norman, 1892); 2-*Adercotryma glomeratum* (Brady, 1878); 3-*Ammotium cassis* (Parker, 1870); 4-*Recurvoides turbinatus* (Brady, 1881); 5-*Reophax subfusiformis* Earland, 1933; 6-*Silicosigmoilina groenlandica* (Cushman, 1933); 7-*Nonionellina labradorica* (Dawson, 1860); 8-*Globobulimina auriculata* (Bailey, 1894); 9-*Elphidium excavatum* f. *clavatum* Cushman, 1930; 10-*Melonis barleeanum* (Williamson, 1858); 11-*Cassidulina reniforme* Nørvang, 1945; 12-*Islandiella helenae* Feyling-Hanssen & Buzas, 1976; 13-*Islandiella norcrossi* (Cushman, 1933); 14-*Buccella frigida* (Cushman, 1922); 15-*Cibicides lobatulus* (Walker & Jacob, 1798); 16-*Trifarina fluens* (Todd, 1947); 17-*Stainforthia feylingi* Knudsen & Seidenkrantz, 1994; 18-*Stainforthia loeblichi* (Feyling-Hanssen, 1954); 19-*Bolivina pseudopunctata* Höglund, 1947;

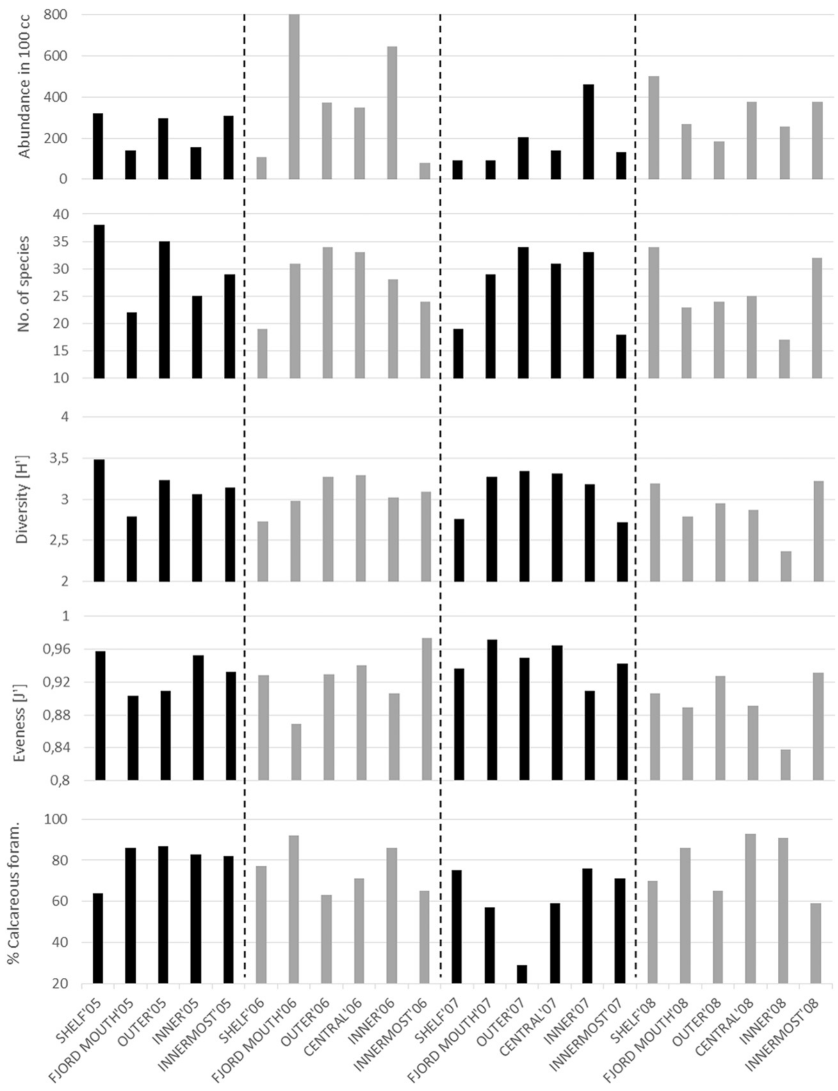


Fig. 4. Living fauna characteristics in each year along the Kongsfjorden sampling transect (from top to bottom panel): abundance (individuals/100 cc of sediment); number of species; diversity (H′); evenness (J′); percentage of calcareous foraminifera.

measurements of primary productivity (Hodal et al., 2012; Hegseth and Tverberg, 2013). In 2007, the observed decrease in primary productivity was not reflected in the C_{org} values as they were comparable or even higher than in other years. Hence, C_{org} measurements reflect an integrated signal covering the average of several years/seasons of productivity (Rathburn et al., 2001) and they include a complex mixture of sources and variable preservation e.g. due to bioturbation.

The available data of bottom oxygen concentrations for the years 2007 and 2008 (Table 1) indicated that the anoxic boundary was located between 0.6 and 0.95 cm sediment depth, i.e. that likely no anoxic conditions occurred at the sediment surface. In the study from Kongsfjorden, Loubere et al. (2011) identified foraminifera occurrence at sediment depths deeper than the pore-water anoxic boundary and substantial numbers of living specimen even down to 3 cm below the sediment surface. The authors indicate that benthic foraminfera can take advantage of partially ventilated sediments associated with macro- and meio-fauna activity allowing them to survive below the average anoxic boundary depth. Based on these observations and the relatively good water exchange between the Kongsfjorden and the shelf environment (Cottier et al., 2005), we consider that the benthic fauna was likely not restricted by the bottom oxygen concentration, at least regarding the years 2007 and 2008 during which oxygen concertation measurements were performed.

5.3. *Foraminiferal fauna*

5.3.1. *General fauna characteristics in a changing fjord environment*

To the best of our knowledge, the present study is the first report of annual variability of living benthic foraminifera from the Arctic region. Our study reveals the annual variability in foraminiferal concentrations in surface sediments from an Arctic fjord, in both temporal and spatial perspectives. The annual observations revealed a high benthic foraminiferal abundance in Kongsfjorden (summer of 2006) which could be related to the reported relatively high primary productivity (Hegseth and Tverberg, 2013; see also Section 5.2.2), as well as an assumed high supply of phytodetritus to the seabed. Contrary in the following years (2007 and 2008), primary production is inferred to be lower due to retention of AW throughout the spring, thus perturbing the spring bloom (Hegseth and Tverberg, 2013). This seems to be as well reflected by benthic foraminifera in observed minimum absolute abundance (2007). The higher foraminiferal concentration in 2008 can be explained by distinctly delayed phytoplankton bloom, albeit low (late spring 2008; Hegseth and Tverberg, 2013) giving foraminifera the opportunity to graze and then flourish later in the summer (conditions we captured during sampling). It is noticeable that the decrease in benthic foraminiferal abundance in 2007 can be directly related to the significant decline of the overall dominant *N. lababradorica.* Hence, the species can greatly influence the total foraminiferal abundance in Kongsfjorden (correlation to fauna abundance; Table 4). Apparently,

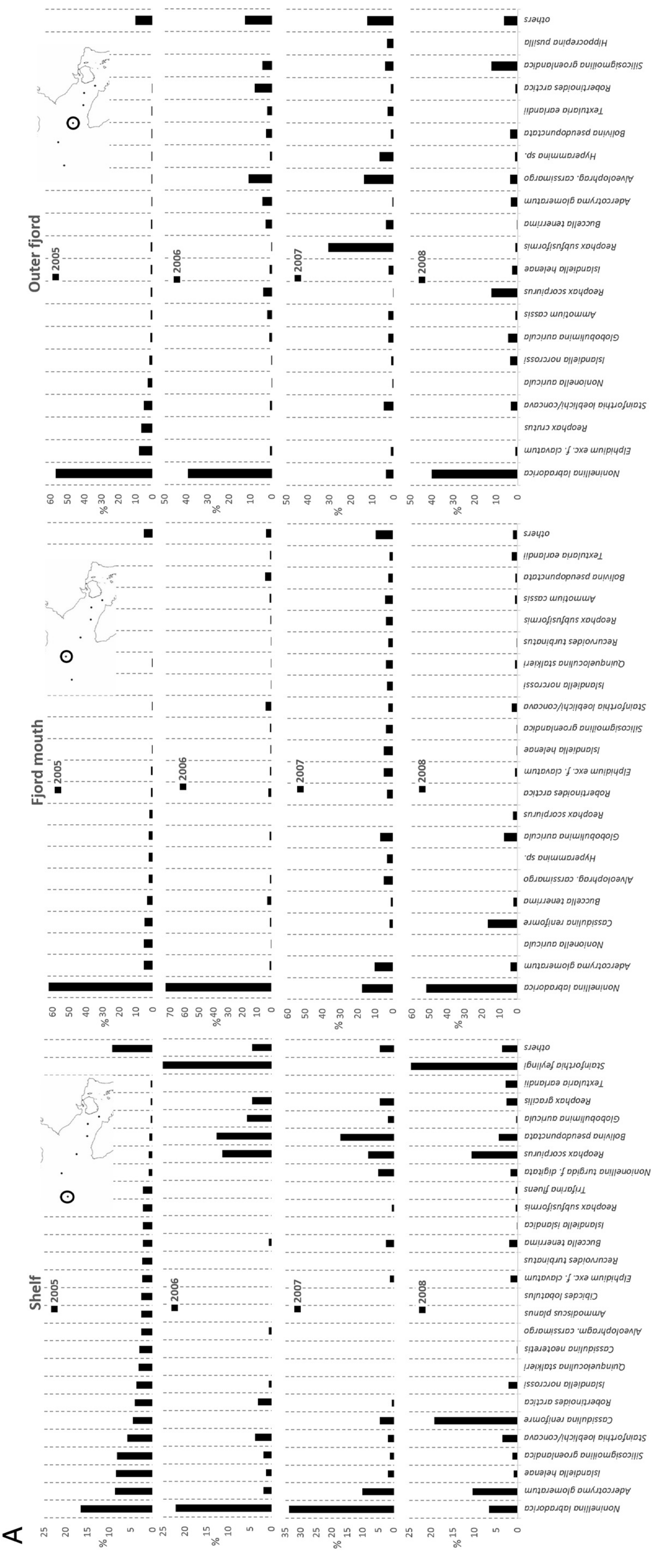


Fig. 5. A and B. Relative abundance (%) of all live benthic foraminifera with > 2% in at least one sample at the given site, at six stations in Kongsfjorden between 2005 and 2008 years.

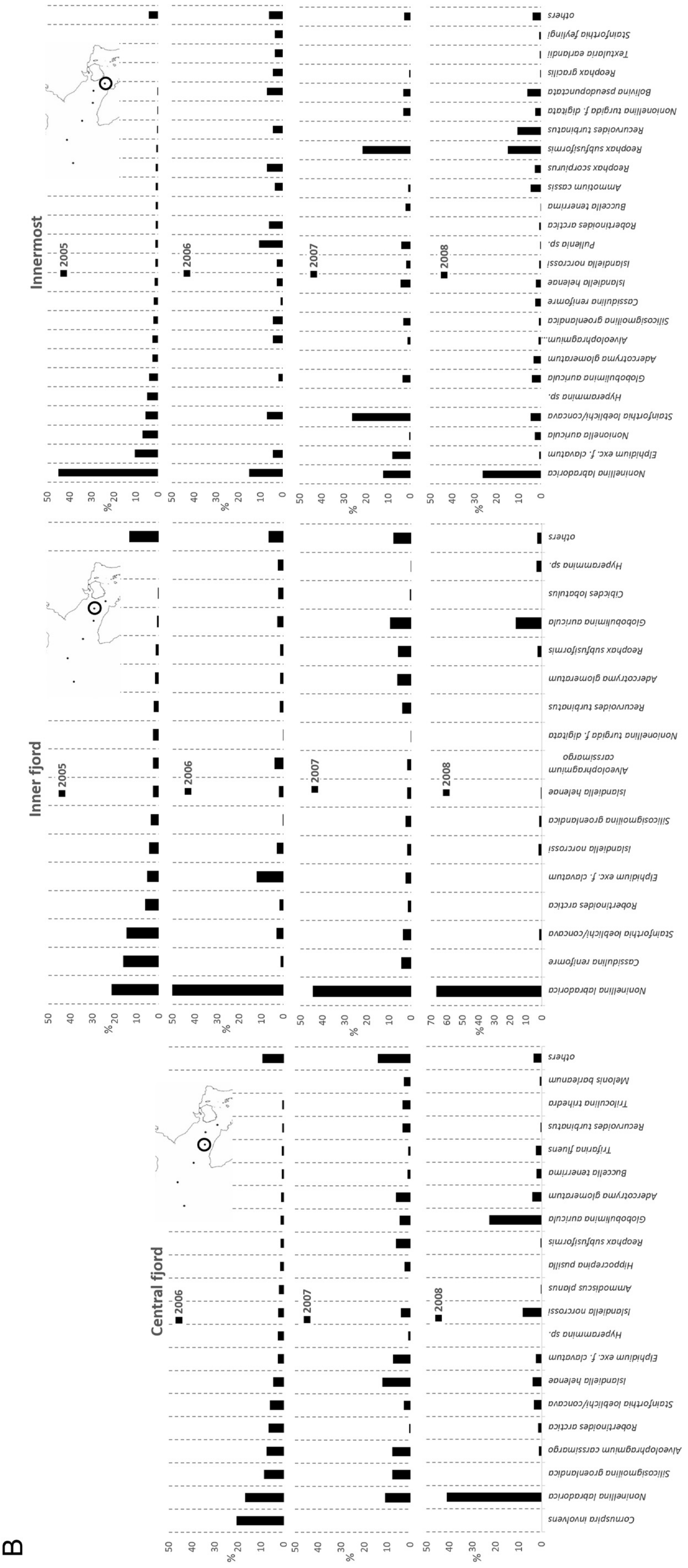


Fig. 5. (continued)

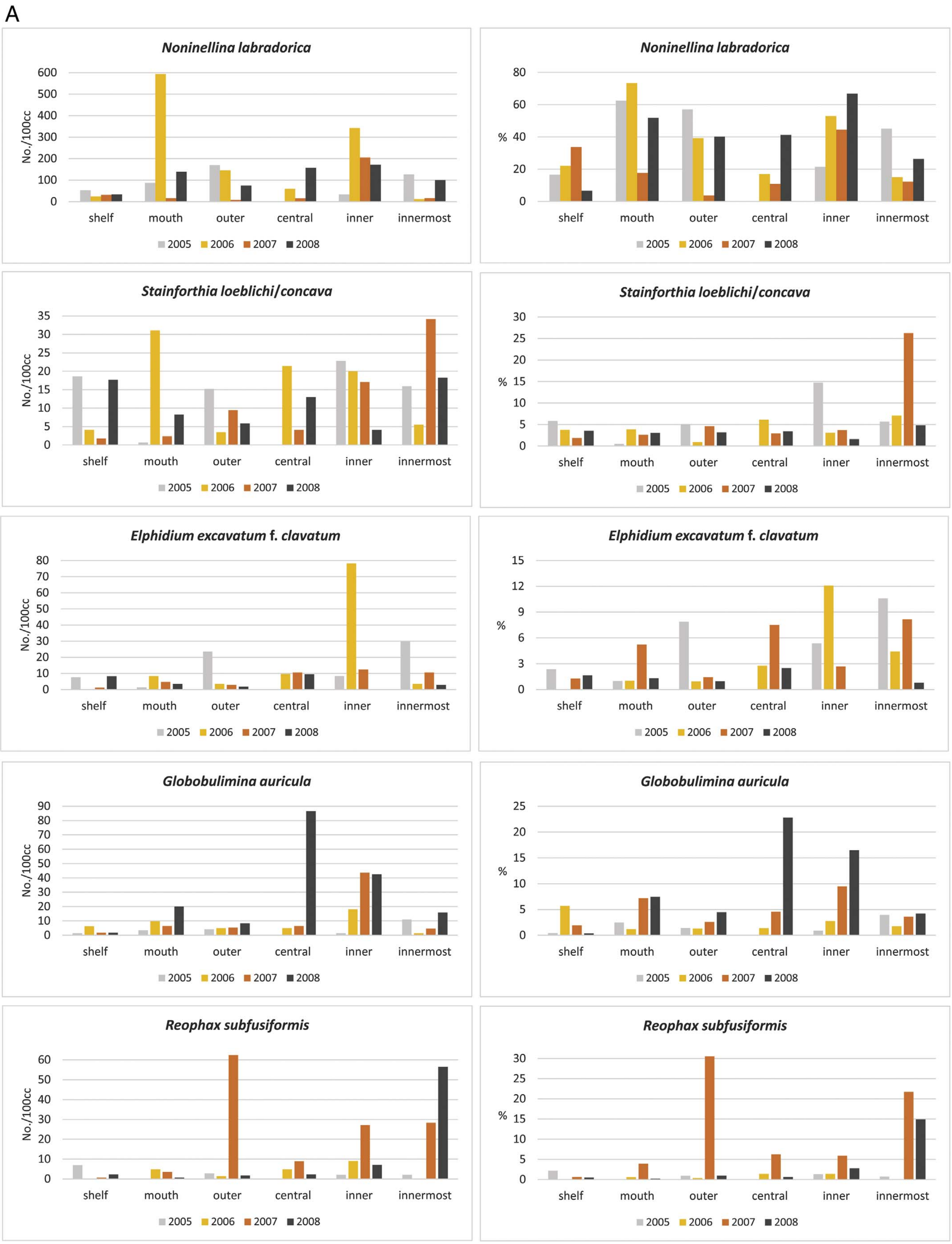


Fig. 6. A and B. Absolute (no. specimens/100 cc) and relative abundance (%) of the most dominant living benthic foraminifera species in Kongsfjorden between 2005 and 2008 years. Note different values on y-axis.

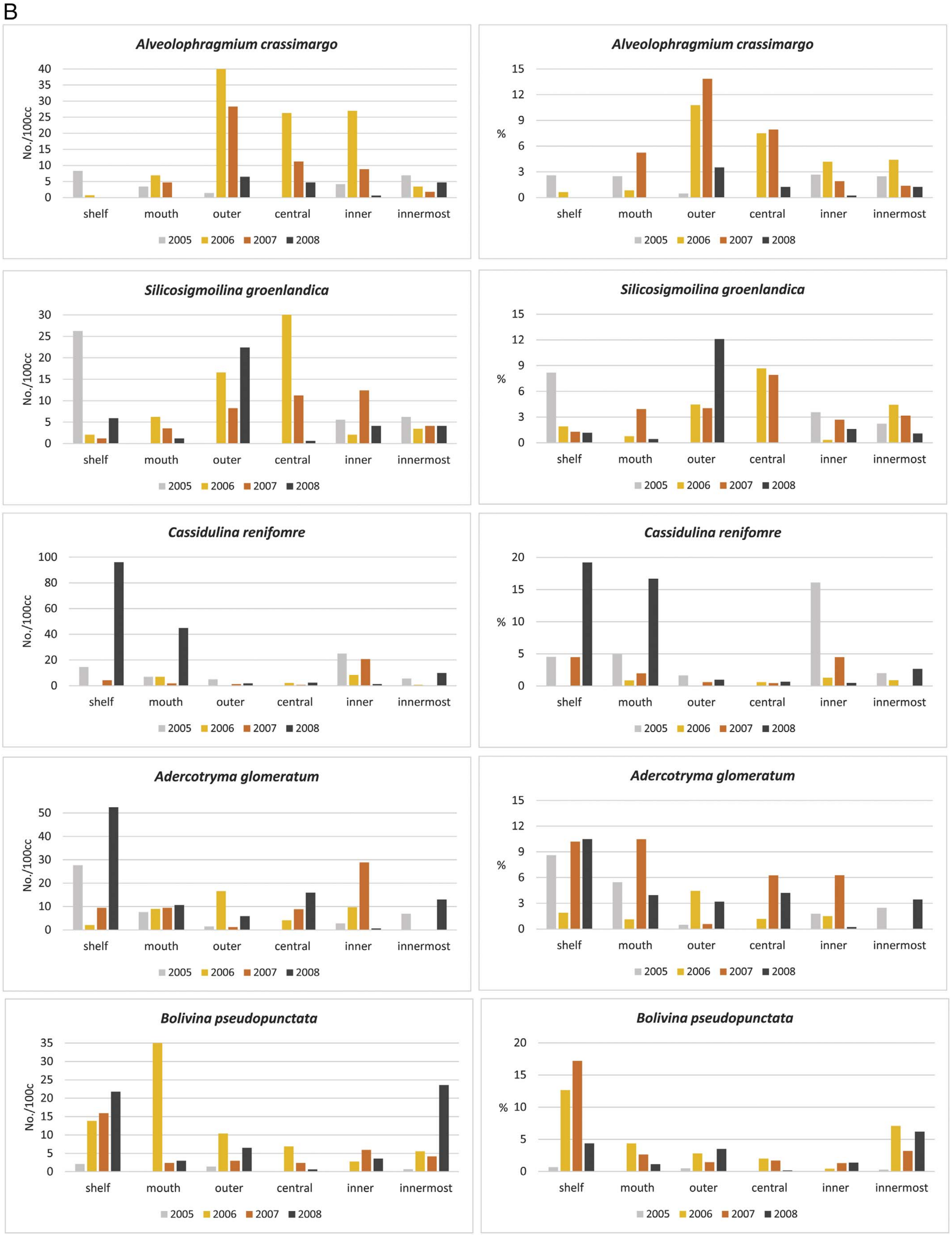


Fig. 6. (*continued*)

Table 2
Foraminiferal PC scores. Significant taxa scores (> 0.7 or < − 0.7) for particular FAs are in bold.

Percent of total variance explained	*N. labradorica FA*	*R. subfusiformis FA*	*S. feylingi FA*
	66.24	8.86	6.21
Noninellina labradorica	**5.86**	0.29	0.57
Adercotryma glomeratum	− 0.39	**− 0.83**	**1.08**
Islandiella helenae	**− 0.91**	− 0.21	− 0.12
Silicosigmoilina groenlandica	**− 0.80**	− 0.30	− 0.06
Stainforthia loeblichi/ concava	**− 0.85**	**2.37**	**0.71**
Cassidulina renifomre	− 0.61	− 0.40	**2.04**
Robertinoides arctica	− 0.30	− 0.50	− 0.03
Islandiella norcrossi	− 0.29	− 0.33	− 0.13
Quinqueloculina stalkieri	− 0.09	− 0.50	− 0.49
Cassidulina neoteretis	− 0.08	− 0.50	− 0.46
Alveolophragmium carssimargo	− 0.42	**0.77**	− 0.50
Ammodiscus planus	− 0.07	− 0.38	− 0.57
Cibicdes lobatulus	− 0.02	− 0.35	− 0.54
Elphidium excavatum f. *clavatum*	− 0.29	0.27	− 0.23
Recurvoides turbinatus	− 0.03	0.25	− 0.18
Buccella tenerrima	0.01	0.03	− 0.27
Islandiella islandica	− 0.06	− 0.45	− 0.47
Reophax subfusiformis	− 0.28	**5.29**	− 0.41
Trifarina fluens	− 0.08	− 0.41	− 0.48
Hyperam subnodosa	0.06	0.11	− 0.70
Quinqueloculina seminulum	− 0.07	− 0.41	− 0.47
Ammotium cassis	− 0.07	0.14	− 0.08
Nonionellina turgida f. *digitata*	0.00	0.12	− 0.20
Reophax scorpiurus	0.01	− 0.27	**2.12**
Bolivina pseudopunctata	0.20	0.31	**1.60**
Globobulimina auricula	**0.78**	0.16	− 0.27
Nonionella auricula	0.28	− 0.13	− 0.57
Reophax gracilis	− 0.02	− 0.16	0.44
Spiroplectammina biformis	0.03	− 0.34	− 0.35
Textularia earlandii	− 0.15	− 0.14	− 0.05
Triloculina trihedra	− 0.15	− 0.35	− 0.51
Cornuspira involvens	− 0.45	**− 0.74**	**− 1.15**
Hippocrepina pusilla	− 0.13	− 0.10	− 0.57
Lagena distoma	− 0.07	− 0.40	− 0.50
Melonis barleeanum	− 0.08	− 0.39	− 0.52
Pyrgo williamsoni	− 0.01	− 0.35	− 0.54
Reophax arctica	0.02	− 0.20	− 0.52
Reophax crutus	0.08	− 0.37	− 0.58
Reophax spp.	0.01	− 0.34	− 0.37
Stainforthia feylingi	− 0.58	− 0.25	**4.33**

the foraminiferal diversity was not affected by the diminished food supply in 2007, mainly because the decrease in calcareous fauna was countered by the increase of agglutinated taxa (Figs. 4 and 5). The arenaceous fauna in Kongsfjorden, represented mainly by *R. subfusiformis*, *A. glomeratum* and *R. scorpiurus*, seems to be less sensitive or more tolerant to the lower quality and/or quantity of food, than the calcareous fauna. This agrees well with observations by Jennings and Weiner (1996), Koho et al. (2008) in addition to laboratory experiments by Alve (2010) where agglutinated species appear to be less influenced by the input of labile organic matter.

The shifting environmental conditions during the four years sampling period affected the two marginal stations, i.e. the 'shelf' station and the more glacier-proximal 'innermost' station, more pronounce than the other stations. Both sites were characterized by low benthic foraminifera absolute abundance as well as low diversity in warmer years (2006 and 2007; Fig. 4). The 'innermost' station normally experiences higher sediment accumulation rates up to 20,000 g m^{-2} yr^{-1} (Svendsen et al., 2002), as a consequence of deposition from suspended matter deriving from runoff from tidewater glaciers. This is often considered as unfavourable conditions to benthic fauna due to potential burial effects. The colder years (2005 and 2008) would presumably provide less glacial suspended matter. This is advantageous to species normally not tolerating higher sediment accumulation rates. Environmental conditions affecting the low abundances and diversity at the 'shelf' station may be related to the larger variations of bottom water temperature recorded here and not elsewhere in the transect (Fig. 3). This could indicate that the outer marginal habitats of Kongsfjorden are more prone to large hydrological changes e.g. cross shelf - fjord water exchange.

5.3.2. *Common foraminiferal assemblages in Kongsfjorden*

The most prominent finding in the study of the foraminiferal fauna was the distinct dominance of one calcareous species *N. labradorica*. Furthermore, the *N. labradorica* FA was the most important assemblage among the three distinguished in the fjord (Tables 2 and 3). The assemblage consists of species *N. labradorica, G. auricula* and *S. loeblichi/ concava*, i.e. species associated with organic-rich sediments in Nordic Seas (e.g. Korsun et al., 1995; Polyak and Mikhailov, 1996; Polyak et al., 2002; Lloyd, 2006). Studies by Bernhard and Bowser (1999) and Cedhagen (1991) have found that *N. labradorica* prefers diatoms as a food source. This is also indicated by the SEM images of *N. labradorica* in Kongsfjorden having several diatoms located along the aperture (Plate 1). Secondary, *I. helenae*, a typical Arctic shelf species, is also known to reflect a high food supply associated with the sea ice margin in seasonally ice-free seas, e.g. the Kara and Barents Seas (Hald and Steinsund, 1996; Husum et al., 2015). Nevertheless. Kongsfjorden is considered to be much less productive than e.g. the colder Hornsund (SW Spitsbergen) due to the lower proportion of diatoms replaced by flagellates and smaller algae (Piwosz et al., 2008). However, a recent study from western Svalbard indicates that benthos can also feed on macroalgal detritus transported down-slope even at depths over 400m (Renaud et al., 2015). Macroalgal detritus can thus contribute significantly to Arctic fjord food webs as additional carbon pool. Indeed, the importance of macroalgal detritus in the warmer and less frequently ice covered Kongsfjorden is higher than in the colder Hornsund (Zaborska et al., 2016). Furthermore, Zaborska et al. (2016) describe the Kongsfjorden ecosystem as mature, characterized by effective food webs and overall better quality food sources compares to Hornsund. This could explain why *N. labradorica* FA in Hornsund (Łącka and Zajączkowski, 2016) as well as several others Svalbard fjords is not as

Table 3
Foraminiferal PC loadings. Statistically important FAs (> 0.4) for particular sites are in bold.

Site	*N. labradorica FA*	*R. subfusiformis FA*	*S. feylingi FA*
SHELF'05	**0.52**	0.07	0.14
FJORD MOUTH'05	**0.94**	0.03	0.12
OUTER'05	**0.93**	0.09	0.10
INNER'05	**0.51**	0.20	0.29
INNERMOST'05	**0.90**	0.11	0.08
SHELF'06	**0.51**	0.03	**0.76**
FJORD MOUTH'06	**0.94**	0.07	0.11
OUTER'06	**0.87**	0.05	0.12
CENTRAL'06	0.39	0.04	− 0.11
INNER'06	**0.91**	0.10	0.08
INNERMOST'06	**0.57**	0.15	**0.42**
SHELF'07	**0.80**	0.04	0.35
FJORD MOUTH'07	**0.65**	0.17	0.13
OUTER'07	− 0.01	**0.89**	− 0.11
CENTRAL'07	0.28	0.29	− 0.03
INNER'07	**0.91**	0.17	0.13
INNERMOST'07	0.17	**0.84**	0.07
SHELF'08	0.02	− 0.07	**0.93**
FJORD MOUTH'08	**0.88**	0.04	0.22
OUTER'08	**0.84**	0.06	0.21
CENTRAL'08	**0.86**	0.07	0.07
INNER'08	**0.95**	0.09	0.08
INNERMOST'08	**0.75**	**0.51**	0.17

Table 4
Pearson's correlation coefficients (r) between abiotic and biotic variables. Statistically relevant correlations ($p < 0.05$) between species and environmental variables are highlighted in bold, strong correlations are highlighted in bold and with gray box.

	Salinity b.w.	Temp. b. w.	Depth (m)	Div.[H']	Ind./100 cc	% calc.	*N. labradorica* FA	*R. subfusiformis* FA	*S. feylingi* FA
Temp. b. w.	-0,05								
Depth (m)	0,05	-0,07							
Div.[H']	-0,07	0,29	0,11						
Ind./100cc	-0,30	-0,19	-0,12	0,17					
% calc.	-0,39	-0,07	-0,41	**-0,58**	0,34				
N. labradorica FA	-0,28	-0,03	0,04	-0,33	0,26	**0,64**			
R. subfusiformis FA	0,36	0,13	0,27	0,12	-0,23	**-0,59**	**-0,52**		
S. feylingi FA	-0,05	-0,37	0,03	-0,19	-0,07	0,11	-0,21	-0,38	
Noninellina labradorica	-0,27	-0,03	0,04	**-0,48**	**0,44**	**0,74**	**0,88**	**-0,44**	-0,22
Adercotryma glomeratum	**0,55**	0,05	-0,15	0,26	-0,08	-0,17	-0,08	-0,34	0,32
Islandiella helenae	0,32	0,36	-0,42	0,45	-0,26	-0,39	**-0,42**	0,21	-0,31
Silicosigmoilina groenlandica	0,08	0,11	0,06	0,40	-0,28	-0,51	-0,32	0,06	-0,21
Stainforthia loeblichi/concava	-0,04	0,15	-0,04	-0,08	-0,21	-0,03	**-0,43**	**0,58**	-0,06
Cassidulina renifomre	0,09	-0,25	-0,17	0,00	0,05	0,17	-0,18	-0,26	**0,51**
Robertinoides arctica	**-0,57**	0,16	-0,09	0,37	-0,06	-0,17	-0,06	-0,19	-0,02
Islandiella norcrossi	0,05	-0,03	**-0,50**	0,14	-0,03	0,09	-0,11	-0,06	-0,15
Quinqueloculina stalkieri	0,26	0,30	0,07	**0,43**	-0,12	-0,32	-0,02	-0,07	-0,20
Cassidulina neoteretis	0,14	0,24	0,14	0,27	-0,02	-0,19	-0,04	-0,15	0,02
Alveolophragmium carssimargo	-0,03	0,22	0,23	**0,55**	-0,13	**-0,72**	-0,39	0,40	**-0,46**
Ammodiscus planus	-0,26	0,40	-0,12	**0,51**	0,18	-0,19	-0,16	-0,02	-0,35
Cibicdes lobatulus	-0,01	**0,46**	-0,16	**0,52**	0,22	-0,13	0,10	0,04	-0,40
Elphidium excavatum f. *clavatum*	-0,28	0,30	-0,13	0,22	0,05	0,12	-0,02	0,17	-0,27
Recurvoides turbinatus	0,10	-0,10	-0,05	0,40	0,02	-0,35	-0,01	0,30	-0,08
Buccella tenerrima	0,31	0,27	0,14	0,05	0,02	-0,19	-0,22	0,21	-0,14
Islandiella islandica	0,10	**0,44**	-0,07	0,37	0,06	-0,14	-0,15	-0,12	0,03
Reophax subfusiformis	**0,46**	0,09	0,32	0,16	-0,15	**-0,66**	**-0,56**	**0,97**	-0,35
Trifarina fluens	0,14	0,30	**-0,42**	**0,44**	0,06	-0,10	-0,12	-0,04	-0,28
*Pullenia*sp.	-0,27	0,08	0,05	-0,04	-0,36	-0,06	-0,18	0,14	0,24
Hyperam subnodosa	0,03	0,25	0,22	0,18	-0,08	-0,37	-0,12	0,28	**-0,48**
Quinqueloculina seminulum	0,01	**0,41**	-0,11	**0,44**	-0,01	-0,32	-0,24	-0,03	-0,09
Ammotium cassis	0,03	-0,15	0,28	**0,42**	-0,25	**-0,57**	-0,18	0,38	0,00
Nonionellina turgida f. digitata	0,30	-0,06	0,02	-0,14	-0,22	-0,07	-0,24	0,31	0,16
Reophax scorpiurus	-0,01	**-0,42**	0,32	-0,18	-0,25	-0,11	-0,12	-0,33	**0,79**
Bolivina pseudopunctata	0,12	-0,25	0,09	-0,27	-0,26	-0,11	-0,08	-0,09	**0,54**
Globobulimina auricula	0,29	-0,30	-0,32	**-0,47**	-0,02	0,34	0,31	-0,07	-0,16
Nonionella auricula	-0,22	0,37	0,08	0,02	-0,05	0,23	0,34	-0,02	-0,15
Reophax gracilis	-0,03	-0,16	0,15	-0,11	-0,27	-0,22	-0,24	-0,11	**0,66**
Spiroplectammina biformis	-0,24	-0,05	0,35	0,24	-0,01	-0,26	-0,03	-0,17	0,28
Textularia earlandii	-0,03	-0,27	0,17	0,40	0,02	**-0,46**	-0,41	0,08	0,13
Triloculina trihedra	0,32	0,21	-0,31	0,37	-0,18	**-0,42**	-0,39	0,17	-0,30
Cornuspira involvens	-0,25	0,00	-0,28	0,22	0,07	-0,06	-0,21	-0,10	-0,27
Hippocrepina pusilla	0,29	0,18	-0,04	**0,42**	-0,19	**-0,67**	**-0,59**	**0,50**	**-0,43**
Lagena distoma	0,04	0,13	-0,39	0,37	-0,19	-0,30	-0,27	-0,01	-0,23
Melonis barleanum	0,29	0,09	**-0,47**	0,18	-0,11	-0,11	-0,22	0,06	-0,20
Pyrgo williamsoni	-0,09	-0,13	-0,07	0,07	-0,15	-0,17	-0,02	-0,01	-0,31
Reophax arctica	0,29	0,19	0,06	-0,19	-0,08	-0,01	-0,23	**0,54**	-0,12
Reophax crutus	-0,11	0,24	0,26	0,21	0,00	0,16	0,17	-0,06	-0,12
*Reophax*spp	-0,34	-0,05	0,06	-0,05	-0,31	-0,10	-0,09	-0,07	0,38
Stainforthia feylingi	-0,07	-0,30	0,00	-0,09	0,00	-0,01	-0,40	-0,25	**0,88**

important as in Kongsfjorden (Hald and Korsun, 1997). The assemblage occurs usually only in the outer to central part of the Svalbard fjords, whereas in the Kongsfjorden-Krossfjorden system it dominated nearly the entire region (this study; Hald and Korsun, 1997). Hence, the frequent occurrence of the *N. labradorica* FA indicates that the assemblage can successfully exploit the food resources from the local biological productivity and thrives particularly well in the presence of near bottom Atlantic-derived TAW.

The second assemblage, the *R. subfusiformis* FA, appears to be related to poorer food conditions when *N. labradorica* becomes reduced (summer 2007). Sampling of primary producers in 2007 in Kongsfjorden reveals a low biomass dominated by *Phaeocystis* algae over diatoms (Hegseth and Tverberg, 2013) which could explain the pronounced decrease of *N. labradorica* in absolute and relative abundances (Fig. 6). The *R. subfusiformis* FA consists of both agglutinated species as *R. subfusiformis, A. glomeratum* and *A. crassimargo*, in addition to the calcareous species *S. loeblichi/concava*, which in turn has been associated with high seasonal productivity (Polyak et al., 2002). However, in Kongsfjorden *S. loeblichi/concava* seems to not be hampered by annual alternation of food conditions neither exhibits any significant annual changes in abundance in general. Consequently, it contributed to all three foraminiferal assemblages.

The random and sparse occurrences of the *S. feylingi* FA is difficult to explain. The recent distribution of *S. feylingi* is poorly understood due to the morphological resemblance and confusion with other *Stainforthia* and *Fursenkoina* species. It has been described an opportunist, generally found in arctic to cold boreal environments (e.g. Lloyd et al., 2007). Moreover, the fossil deposits of the species are related to transitional

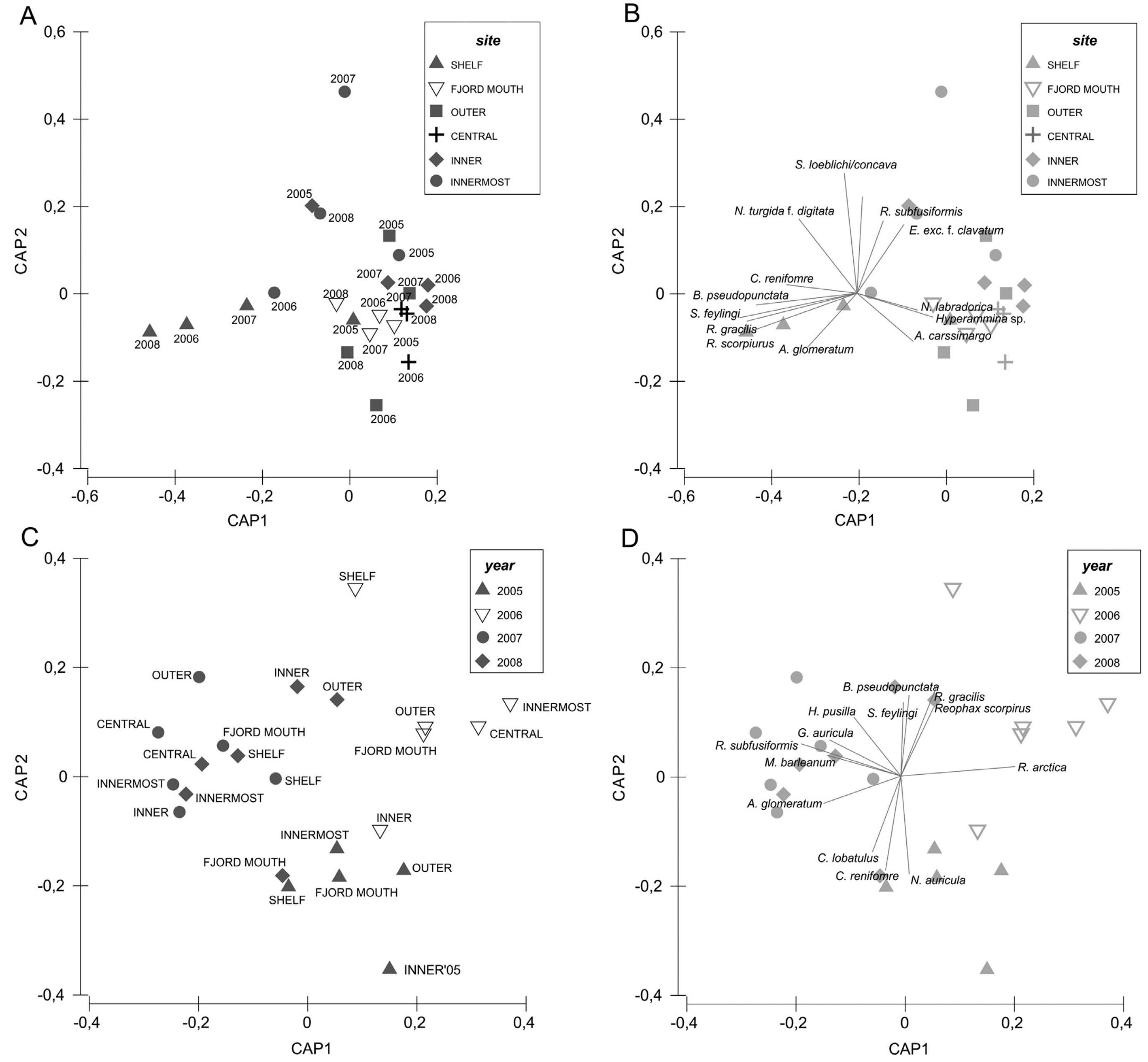


Fig. 7. Plots of CAP ordinations best discriminating groups of samples based on Bray-Curtis similarities of foraminifera relative abundances. Upper panel (a, b) show CAP plots defined by spatial (site) distribution, and lower panel (c, d) show CAP plots defined by temporal distribution (year). Vectors indicate the taxa best correlated with the ordination coordinates ($r > 0.4$); vector length corresponds to the correlation values.

environments between arctic and boreal conditions that require high tolerance of unstable conditions (Knudsen and Siedenkrantz, 1994 and references therein). The accessory species *R. scorpiurus* also tolerates a wider range of salinities and temperatures ranging from sub-tropical to arctic (Williamson et al., 1984), and it has a rather patchy distribution in Svalbard fjords (Hald and Korsun, 1997). It is possible that the occurrence of the species at the 'shelf' location could be related to the random transport of the propagules from the outer shelf or slope (Alve and Goldstein, 2003, 2010). Nevertheless, they found favourable condition to grow whenever the alteration of bottom temperature occurred (2005/2006 and 2007/2008; Fig. 3), which is particularly emphasised at the 'shelf' station. The other accessory species *C. reniforme* can be likely linked to the presence of cold LW (originating from strong cooling of TAW and/or AW) that occupied the outer part of Kongsfjorden in 2008. This suggests that *C. reniforme* prefers cool and saline waters. This concurs with previous studies of *C. reniforme*, where is has been related to cold water environments (Sejrup et al., 1980; Mackensen et al., 1985). *C. reniforme* also commonly replaces *E. excavatum* f. *clavatum* as the dominant species when the fjord environment changes from glacier proximal to distal glaciomarine conditions (Hald and Korsun, 1997). The last accessory species, *B. pseudopunctata*, has been shown to have a significant relation to a high supply of organic material (e.g. Gustafsson and Nordberg, 2001), which explains its occurrence on the shelf with a high content of organic matter. Although these species have been assigned to one foraminiferal assemblage, it does not necessarily mean that they are equally sensitive to the same environmental parameters. Since the ecological niche is a combination of various factors, the species may respond to them selectively.

Table 5
Biogeography of living benthic foraminifera in Kongsfjorden over four summer seasons (from 2005 to 2008) following the biogeographical distribution in NW European fjords by Murray and Alve (2016). For each year, the shading shows contribution (relative abundance) of the species to the total live foraminifera in the fjord. The species abundances are defined as M = minor (< 10%), pale blue = subsidiary (≥ 10% but not dominant), dark blue = dominant (> 10% and the most frequent species).

	2005	2006	2007	2008
WIDESPREAD SPECIES				
Cassidulina renifomre	▨		M	▨
Globobulimina auricula	M	M	M	▨
Adercotryma glomeratum	M	M	▨	▨
Noninellina labradorica	■	■	■	■
SPECIES WITH NORTHERN BOUNDARIES				
Cornuspira involvens		▨		
Bolivina pseudopunctata		▨	▨	M
Reophax scorpiurus	M	▨	M	▨
Reophax subfusiformis	M		▨	▨
SPECIES WITH SOUTHERN BOUNDARIES				
Nonionellina auricula	M	M	M	M
Elphidium excavatum f. *clavatum*	▨	▨	M	M
Stainforthia loeblichi	▨	M	▨	M
Alveolophragmium carssimargo	M	▨	▨	M
Islandiella norcrossi	M	M	M	M
Recurvoides turbinatus	M	M	M	▨

5.3.3. *Spatial and temporal variability of the benthic foraminifera species*

This study clearly shows the significance of the temporal and spatial variability of benthic foraminiferal fauna in Kongsfjorden as indicated by the larger dispersion of the samples on the CAP ordination plotted along the strongest gradients produced by both sites and years (Fig.7).

5.3.3.1. Spatial variability. The foraminiferal fauna distribution along the fjord transect showed overall the strongest variability at the two marginal stations: the glacially influenced inner fjord and marine influenced shelf region. The sites from the middle fjord region, representing probably the most stable conditions, showed much lower benthic foraminiferal variability.

The inner region of the fjord was represented by the typical glaciomarine species *E. excavatum* f. *clavatum* (Figs. 5, 6 and 7A and B). This supports previous observations of *E. excavatum* f. *clavatum* showing the ability to adapt to harsh environments such as near tidewater-glacier fronts and riverine estuaries (e.g., Korsun and Polyak, 1989; Hald et al., 1994; Hald and Korsun, 1997; Korsun and Hald, 1998, 2000; Forwick et al., 2010). *S. loeblichi/concava* and *R. subfusiformis* also thrive in the hostile settings with high turbidity and sediment depositions (Svendsen et al., 2002). *S. loeblichi/concava* is found within sea-ice covered areas in cold waters ~0 °C (Steinsund, 1994) and may, thus, take advantage of the seasonal sea-ice cover restricted to the inner Kongsfjorden (Gerland et al., 1999). In the Kara Sea, *S. loeblichi* was found within a narrow salinity range in the intermediate zone between river-proximal and river-distal areas (< 34) (Polyak et al., 2002). Our study show that *S. loeblichi/concava* can cope also with higher salinities (from 34.8 to 35).

During this study, we observed overall lower occurrence of *N. labradorica* at the two marginal sites what suggest that the open marine - fjord boundary environment as well as the glacial influence in the head of the fjord are not optimal for this species. Similar association with the more stable middle fjord environment was shown by *Hyperammina subnodosa* and *A. crassimargo* (Fig. 7A and B).

It is interesting that the 'shelf 2005' site also fell within this middle shelf group (Fig. 7A and B). The foraminiferal fauna at the 'shelf' in 2005 differed much from 'shelf' site in the following years when many of the species presented in 2005 vanished while others became more abundant (Fig. 5). Most of the species that disappeared or lowered their abundance at the shelf represents typical arctic fauna, e.g. *I. norcrossi*, *E. excavatum* f. *clavatum*, *Q. stalkieri*, *A. crassimargo*, *R. turbinatus* and *Trifarina fluens* (Rytter et al., 2002; Majewski et al., 2009; Murray and Alve, 2016). Although the year 2005 is generally considered as a cold year, the 'shelf' site experienced strong local influence of AW (highest bottom water temperatures) which could also explain the appearance of *Cassidulina neoterestis* and *R. subfusiformis* (Jennings et al., 2004). We speculate that the intrusion of AW onto the shelf site in 2005 had a negative influence on the arctic foraminiferal fauna. Although the arctic species were still present in 2005 we were not able to evaluate their condition. It might be likely that the species remained in the study area but were not able to thrive and reproduce in the following years since the AW inflow into Kongsfjorden continued. Some species, e.g. *C. reniforme*, *R. gracilis*, and *A. glomeratum*, remained on the Kongsfjorden shelf whereas others, *R. scorpiurus*, *B. pseudopunctata* and *S. feylingi*, even flourished after year 2005 suggesting some affinity to more open marine environment.

5.3.3.2. Temporal variability. The temporal variability reveals significant species shift from the 'cold' year 2005 to the 'warm' year 2006 and the following years 2007 and 2008 (Fig. 7C and D). The colder conditions in Kongsfjorden are best represented by *C. reniforme*, *N. auricular* and *C. loabatulus*, whereas *R. arcitca* is more abundant with the enhanced inflow of AW in the summer 2006. We also observe an increase of *A. crassimargo* and *B. pseudopunctata* during the years where AW/TAW has the strongest influence in the fjord. The rapid increases in *G. auriculata* coincide with the low primary productivity in 2007 and 2008 (Hegseth and Tverberg, 2013) indicating that the species is able to exploit periods of low food availability. This is supported by the results from laboratory experiments and samples from natural environments showing that *G. auriculata* is able to feed on stored organic carbon of low quality in the deeper sediment sub-surface (Alve, 2010; Loubere et al., 2011).

It should also be noted that the overall increase of *G. auriculata* coincides with the generally highest values of bottom salinities along the transect. Hence, the more frequent occurrences of *G. auriculata* may also be governed by the increasing bottom water salinities characterising the prevailing TAW. A study on modern benthic foraminifera from the Nova Scotia continental margin also relates *G. auriculata* with high salinity (Williamson et al., 1984). The agglutinated *A. glomeratum* and *R. subfusiformis* which bloomed in 2007 and 2008 may have similar strategies exploiting the situation of increased salinity and/or low food quantity/quality during these years. Indeed, both species show positive correlation to the bottom salinity (Table 4). This is in accordance with previous studies connecting *R. subfusiformis* to areas with relatively high and stable salinities (Höglund, 1947; Thiede et al., 1981) and relating *A. glomeratum* to Atlantic-sourced waters at high latitude shelf areas (Vilks, 1980; Jennings and Helgadóttir, 1994; Hald and Korsun, 1997).

E. excavatum f. *clavatum* has previously been found in water masses with relatively low salinities in Svalbard fjords, e.g. Local Water, Intermediate and Winter-cooled Water (Hald and Korsun, 1997; Forwick et al., 2010; Łącka and Zajączkowski, 2016). The formation and subsequent influence of water masses of low salinities in Kongsfjorden (intermediate, local water and surface waters, Table 2) have been hampered by the enhanced inflow of AW and TAW after 2006. Hence, the increased bottom salinity in Kongsfjorden from 2007 to 2008 probably caused *E. excavatum* f. *clavatum* to decrease in 2008.

Apart from *G. auriculata*, none of the species representing the key foraminiferal assemblage (*N. labradorica* FA) appeared among the fauna characterized by significant temporal variability (Fig. 7C and D). Hence, the *N. labradorica* FA was annually very persistent albeit a minor decrease in 2007 due to reduced primary productivity.

5.4. Biogeographical range of the Kongsfjorden foraminiferal fauna

The modern benthic foraminiferal fauna in Kongsfjorden differs clearly from the fauna reported from other fjords of Svalbard. The main characteristic feature of the Kongsfjorden fauna is the dominance of one single foraminiferal assemblage, ruled by the ubiquitous *N. labradorica*. Hald and Korsun (1997) observed similar fauna association only in the adjacent Krossfjorden. Krossfjorden is part of the same fjord system as Kongsfjorden, thus most probably sharing similar environmental settings. An assemblage dominated by *N. labradorica* together with *S. loeblichi* has been observed in fjords in western and northern Svalbard (Hald and Korsun, 1997). However, in none of these fjords *N. labradorica* was as frequent as in as in Kongsfjorden. The presence of *N. labradorica* in the deeper outer and middle parts of the fjords in western and northern Svalbard has been suggested to reflect the inflow of TAW (Hald and Korsun, 1997). *N. labradorica* is also linked to Atlantic-sourced water and its elevated nutrient level in Disko Bugt, West Greenland (Lloyd, 2006) and on the shelf off northern Iceland (Jennings et al., 2004). In the Barents Sea, the distribution of *N. labradorica* along the Polar front also suggest the affinity with pulses of elevated food concentrations at the seafloor (Steinsund, 1994). We suggest that Kongsfjorden provides a unique habitat with exceptional conditions for *N. labradorica* colonization and growth. The specific conditions are, however, not favourable for the common glaciomarine species *E. excavatum* f. *clavatum* that is abundant in the other fjords of Svalbard (Korsun and Polyak, 1989; Hald et al., 1994; Hald and Korsun, 1997; Korsun and Hald, 1998, 2000; Polyak et al., 2002). Unlike other west Spitsbergen fjords, Kongsfjorden has rather unique deep-water connection between its outer basin and the shelf that promotes water mass exchange and inflow of AW to the fjord (Svendsen et al., 2002). Consequently, the arctic fjord develops sub-arctic like conditions, which most likely explain observed fauna differences.

Following the benthic foraminiferal biogeographical distribution classification for the NW European fjords by Murray and Alve (2016), this study shows that Kongsfjorden is dominated by species with widespread distribution (Table 5). Species, which according to that classification are limited by their northern distribution boundaries i.e. commonly decrease towards higher latitudes, became more frequent after the AW advection into Kongsfjorden in 2006. The species restricted by their southern limit show an overall decrease and they become minor (Table 5). We can thus assume that annual variability of benthic foraminifera fauna in Kongsfjorden is mostly attributed to the influence of AW, unveiled in rapid expansion of widespread and subarctic to boreal species into the fjord, where they successfully competed with arctic fauna.

6. Conclusions

This study presents the first multi-year observations of living benthic foraminiferal fauna variability in an Arctic fjord that was influenced by large variations in seasonal advection of warm and saline Atlantic Water during the study period between 2005 and 2008. Three major fauna assemblages (FA) reflecting specific environmental conditions were distinguished. The *N. labradorica* FA is the most abundant assemblage of the three Kongsfjorden FA. The *N. labradorica* FA exploited the food resources from the local biological productivity and thrived particularly well within Transformed Atlantic Water. It only experienced a minor decrease once in relation to a reduction in primary productivity. The second FA, the *R. subfusiformis* FA, consisted mostly of agglutinated taxa and was more tolerant with regard to a lower quality and/or quantity of available food. The third FA, the *Stainforthia feylingi* FA, had a rather random and sparse occurrence. The *Stainforthia feylingi* FA was associated with alteration of bottom temperature, particularly at the shelf region.

The study reveals significant temporal and spatial variabilities of benthic foraminiferal fauna. Overall, the strongest variability was observed at the two marginal stations: the glacially influenced inner fjord and the marine influenced shelf region. Both stations experienced unstable conditions that affected absolute abundance, diversity and species composition. Furthermore, the temporal fauna variability revealed significant species shift from the 'cold' (2005) to 'warm' and more saline years (2006–2008). The shift is shown as a rapid expansion of sub-arctic to boreal species into the fjord, where they successfully competed with the existing arctic fauna. Our study has revealed that the current Arctic fjord system is a spatially and temporally dynamic system with regard to the hydrography and benthic foraminiferal occurrence.

Acknowledgements

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Appendix A

List of foraminifera taxa identified in Kongsfjorden.

Agglutinated species
Adercotryma glomeratum (Brady, 1878)
Alveolophragmium crassimargo (Norman, 1892)
Ammodiscus planus Höglund, 1947
Ammotium cassis (Parker, 1870)
Eggerella advena (Cushman, 1922)
Hippocrepina indivisa Parker, 1870
Hippocrepina pusilla Heron-Allen & Earland, 1930
Hyperammina subnodosa Brady, 1884
Miliammina fusca (Brady, 1870)
Silicosigmoilina groenlandica (Cushman) emend Loeblich & Tappan, 1953
Spiroplectammina biformis (Parker & Jones, 1865)
Textularia earlandi Loeblich & Tappan, 1957
Trochammina atlantica (Parker, 1952)
Trochammina inflata (Montagu, 1808)
Trochammina squamata Jones & Parker, 1860
Recurvoides turbinata (Brady, 1881)
Reophax arctica Brady, 1881
Reophax curtus Cushman, 1920
Reophax gracilis Earland, 1933
Reophax pilulifera Brady, 1884
Reophax scorpiurus de Montfort, 1808
Reophax nana Rhumbler, 1913
Reophax gracilis Earland, 1933
Reophax subfusiformis Earland, 1933
Quinqueloculina agglutinata Cushman, 1917
Quinqueloculina stalkeri Loeblich & Tappan, 1953

Calcareous species
Astrononion gallowayi Loeblich and Tappan, 1953
Buccella frigida (Cushman, 1921)
Buccella tenerrima (Bandy, 1950)
Bulimina marginata d'Orbigny, 1826
Bolivina pseudopunctata Höglund, 1947
Cassidulina neoteretis Seidenkrantz, 1995
Cassidulina reniforme Nørvangi, 1945
Cibicides lobatulus (Walker & Jacob, 1798)
Cornuspira foliacea (Philippi, 1844)
Cornuspira involvens (Reuss, 1850)
Dentalina baggi Galloway & Wissler, 1927
Dentalina pauperata (d'Orbigny, 1846)
Elphidiella arctica (Parker & Jones, 1864)
Elphidium albiumbilicatum (Weiss, 1954)
Elphidium asklundi Brotzen, 1943
Elphidium bartletti Cushman, 1933
Elphidium excavatum f. *clavatum* Cushman, 1930
Elphidium excavatum (Terquem, 1875)
Elphidium incertum (Williamson, 1858)
Elphidium subarcticum Cushman, 1944
Fissurina marginata (Montagu, 1803)
Fissurina laevigata Reuss, 1850
Fissurina serrata (Schlumberger, 1894)
Glandulina laevigata (d'Orbigny, 1839)
Globobulimina auriculata (Bailey, 1894)
Islandiella helenae Feyling-Hanssen & Buzas, 1976
Islandiella islandica (Nørvang, 1945)
Islandiella norcrossi (Cushman, 1933)
Lagena distoma Buchner, 1940
Lagena parri Loeblich and Tappan, 1953
Lagena laevis (Montagu, 1803)
Lagena mollis Cushman, 1944
Lagena striata (d'Orbigny, 1839)

Melonis barleeanus (Williamson, 1858)
Nonionellina labradorica (Dawson, 1860)
Nonionella turgida f. *digitata* Nørvang, 1945
Nonionella turgida (Williamson, 1858)
Nonionella auricula Heron-Allen & Earland, 1930
Nonionella iridea Heron-Allen & Earland, 1932
Oolina lineata (Williamson, 1848)
Oolina costata (Williamson, 1858)
Patellina corrugata Williamson, 1858
Protelphidium anglicum Murray, 1965
Pyrgo williamsoni (Silvestri, 1923)
Robertina arctica d'Orbigny, 1846
Quinqueloculina seminulum (Linnaeus, 1758)
Stainforthia concava (Höglund, 1947)
Stainforthia loeblichi Feyling-Hanssen, 1954
Stainforthia feylingi Knudsen & Seidenkrantz, 1994
Triloculina trihedra Loeblich and Tappan, 1953
Triloculina trigonula (Lamarck, 1804)
Trifarina fluens (Todd, 1948)
Virgulina loeblichi Feyling-Hanssen, 1954

References

Alve, E., 2010. Benthic foraminiferal responses to absence of fresh phytodetritus: a two-year experiment. Mar. Micropaleontol. 76, 67–75.

Alve, E., Goldstein, S.T., 2003. Propagule transport as a key method of dispersal in benthic foraminifera. Limnol. Oceanogr. 48, 2163–2170.

Alve, E., Goldstein, S.T., 2010. Dispersal, survival and delayed growth of benthic foraminiferal propagules. J. Sea Res. 63 (1), 36–51.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods. Primer-E Ltd, Plymouth, pp. 214.

Bernhard, J.M., Bowser, S.M., 1999. Benthic foraminifera of dysoxic sediments: chloroplast sequestration and functional morphology. Earth-Sci. Rev. 46, 149–165.

Bubenshchikova, N., Nurnberg, D., Lembkejene, L., Pavlova, G., 2008. Living benthic foraminifera of the Okhotsk Sea: faunal composition, standing stocks and microhabitats. Mar. Micropaleontol. 69 (3–4), 314–333.

Buzas, M.A., Hayek, L.C., Reed, S.A., Jett, J.A., 2002. Foraminiferal densities over five years in the Indian River lagoon, Florida: a model of pulsating patches. J. Foraminifer. Res. 32, 68–93.

Cedhagen, T., 1991. Retention of chloroplasts and bathymetric distribution in the sublittoral foraminiferan *Nonionellina labradorica*. Ophelia 33, 17–30.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. PRIMER-E, Plymouth.

Cottier, F., Tverberg, V., Inall, M., Svendsen, H., Nilsen, F., Griffiths, C., 2005. Water mass modification in an Arctic fjord through cross-shelf exchange: the seasonal hydrography of Kongsfjorden, Svalbard. J. Geophys. Res. 110, 1–18.

Cottier, F.R., Nilsen, F., Inall, M.E., Gerland, S., Tverberg, V., Svendsen, H., 2007. Wintertime warming of Arctic shelves in response to large-scale atmospheric circulation. Geophys. Res. Lett. 34, L10607.

Dijkstra, N., 2009. The Holocene Deglaciation History of Two (Sub-) Arctic Fjord Systems—A Comparison of Modern and Holocene Sedimentation Processes in Kongsfjorden (NW Svalbard) and Disko Bay (W Greenland). Master Thesis. VU University Amsterdam, Netherlands, pp. 90.

Elverhøi, A., Liestøl, O., Nagy, J., 1980. Glacial erosion, sedimentation and microfauna in the inner part of Kongsfjorden, Spitsbergen. Norwegian Polar Institute, Skr. 172, 33–61.

Elverhøi, A., Lonns, O., Seland, R., 1983. Glaciomarine sedimentation in a modern fiord environment. Spistbergen. Polar Res. 1, 127–149.

Espitalié, J., Laporte, J.L., Madec, M., Marquis, F., Leplat, P., Paulet, J., Boutefeu, A., 1977. Méthode rapide de caractérisation des roches méres de leur potentiel pétrolier et de leur degree d'évolution. Revue de l'Institut Francais du Pétrole 32, 23–42.

Feyling-Hanssen, R.W., 1964. Foraminifera in late quaternary deposits in the Oslofjord area. Nor. Geol. Unders. 383.

Feyling-Hanssen, R.W., Joergensen, J.A., Knudsen, K.L., Anderson, A.L., 1971. Late quaternary foraminifera from Vendsyssel, Denmark and Sandnes, Norway. Bull. Geol. Soc. Den. 21, 67–317.

Forwick, M., Vorren, T.O., Hald, M., Korsun, S., Roh, Y., Vogt, C., Yoo, K.-C., 2010. Spatial and temporal influence of glaciers and rivers on the sedimentary environment in Sassenfjorden and Tempelfjorden, Spitsbergen. In: Howe, J.A., Austin, W.E.N., Forwick, M., Paetzel, M. (Eds.), Fjord Systems and Archives. 344. Geological Society of London, Special Publications, London, pp. 289–304.

Gerland, S., Renner, A.H.H., 2007. Sea ice mass balance monitoring in an Arctic fjord. Ann. Glaciol. 46, 435–442.

Gerland, S., Winther, J.-G., Ørbæk, J.B., Ivanov, B., 1999. Physical properties, spectral reflectance and thickness development of first year fast-ice in Kongsfjorden, Svalbard. Polar Res. 18 (2), 275–282.

Gluchowska, M., Kwasniewski, S., Prominska, A., Olszewska, A., Goszczko, I., Falk-Petersen, S., Hop, H., Weslawski, J.M., 2016. Zooplankton in Svalbard fjords on the Atlantic-Arctic boundary. Polar Biol. 39 (10), 1785–1802.

Gustafsson, M., Nordberg, K., 2000. Living (stained) benthic foraminifera and their response to the seasonal hydrographic cycle, periodic hypoxia and to primary production in Havstens Fjord on the Swedish west coast. Estuar. Coast. Shelf Sci. 51, 743–761.

Gustafsson, M., Nordberg, K., 2001. Living (stained) benthic foraminiferal response to primary production and hydrography in the deepest part of the Gullmar Fjord, Swedish west coast, with comparisons to Höglund's 1927 material. J. Foraminifer. Res. 31, 2–11.

Hald, M., Korsun, S., 1997. Distribution of modern benthic foraminifera from fjords of Svalbard, European Arctic. J. Foraminifer. Res. 27 (2), 101–122.

Hald, M., Steinsund, P.I., 1996. Benthic foraminifera and carbonate dissolution in the surface sediments of the Barents and Kara Seas. Berichte zur. Polarforschung 212, 285–307.

Hald, M., Steinsund, P.I., Dokken, T., Korsun, S., Polyak, L., Aspeli, R., 1994. Recent and Late Quaternary Distribution of *Elphidium excavatum* f. *clavatum* in Arctic Seas. 32. Cushman Foundation Special Publication, pp. 141–153.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1–9.

Hansen, A., Knudsen, K.L., 1995. Recent foraminiferal distribution in Freemansundet and Early Holocene stratigraphy on Edgeøya, Svalbard. Polar Res. 14, 215–238.

Hegseth, E.N., Tverberg, V., 2013. Effect of Atlantic water inflow on timing of the phytoplankton spring bloom in a high Arctic fjord (Kongsfjorden, Svalbard). J. Mar. Syst. 113, 94–105.

Hodal, H., Falk-Petersen, S., Hop, H., Kristiansen, S., Reigstad, M., 2012. Spring bloom dynamics in Kongsfjorden, Svalbard: nutrients, phytoplankton, protozoans and primary production. Polar Biol. 35 (2), 191–203.

Höglund, H., 1947. Foraminifera in the Gullmar Fjord and the Skagerak. Zoologiska bidrag från Uppsala 26, 328.

Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwasniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Wlodarska-Kowalzuk, M., Lydersen, C., Weslawski, J.M., Cochrane, S., Gabrielsen, G.W., Leakey, R.J.G., Lønne, O.J., Zajączkowski, M., Falk-Petersen, S., Kendall, M., Wangberg, S.Å., Bischof, K., Voronkov, A.Y., Kovaltchouk, N.A., Wiktor, J., Poltermann, M., di Prisco, G., Papucci, C., Gerland, S., 2002. The marine ecosystem of Kongsfjorden, Svalbard. Polar Res. 21, 167–208.

Howe, J.A., Moreton, S.G., Morri, C., Morris, P., 2003. Multibeam bathymetry and the depositional environments of Kongsfjorden and Krossfjorden, Western Spitsbergen, Svalbard. Polar Res. 22, 301–316.

Husum, K., Hald, M., Stein, R., Weißschnur, M., 2015. Recent benthic foraminifera in the Arctic Ocean and Kara Sea continental margin. Ark. Dent. 1 (5).

Jennings, A.E., Helgadóttir, G., 1994. Foraminiferal assemblages from the fjords and shelf of Eastern Greenland. J. Foraminifer. Res. 24, 123–144.

Jennings, A.E., Weiner, N.J., 1996. Environmental changes in eastern Greenland during the last 1300 years: evidence from foraminifera and lithofacies changes in Nansen Fjord, 68°N. The Holocene 6 (2), 179–191.

Jennings, A.E., Weiner, N.J., Helgadottir, G., Andrews, J.T., 2004. Modern foraminiferal faunas of the southwestern to northern Iceland shelf: oceanographic and environmental controls. J. Foraminifer. Res. 34 (3), 180–207.

Jernas, P., Klitgaard Kristensen, D., Husum, K., Wilson, L., Koç, N., 2013. Paleoenvironmental changes of the last two millennia on the Western and Northern Svalbard shelf. Boreas 42, 236–255.

Jorissen, F.J., De Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. Mar. Micropaleontol. 26, 3–15.

Kim, J.-H., Peterse, F., Willmott, V., Klitgaard Kristensen, D., Baas, M., Schouten, S., Sinninghe Damsté, J.S., 2011. Large ancient organic carbon contributions to Arctic marine sediments (Svalbard). Limnol. Oceanogr. 56, 1463–1474.

Knudsen, K.L., Siedenkrantz, M.S., 1994. *Stainforthia feylingi* new species from arctic to subarctic environments, previously recorded as *Stainforthia schreibersiana* (Czjzek). In: Sejrup, H.P., Knudsen, K.L. (Eds.), Late Cenozoic Benthic Foraminifera: Taxonomy, Ecology and Stratigraphy. 32. Cushman Foundation for Foraminiferal

Research Special Publication, pp. 5–13.

Koho, K.A., Langezaal, A.M., van Lith, Y.A., Duijnstee, I.A.P., van der Zwaan, G.J., 2008. The influence of a simulated diatom bloom on deep sea benthic foraminifera and the activity of bacteria: a mesocosm study. Deep-Sea Res. 55, 696–719.

Konert, M., Vandenberghe, J., 1997. Comparison of laser grain size analysis with pipette and sieve analysis: a solution for the underestimation of the clay fraction. Sedimentology 44, 523–535.

Korsun, S.A., Hald, M., 1998. Modern benthic foraminifera off Novaya Zemlya tidewater glaciers, Russian Arctic. Arct. Alp. Res. 30 (1), 61–77.

Korsun, S., Hald, M., 2000. Seasonal dynamics of benthic foraminifera in a glacially fed fjord of Svalbard, European Arctic. J. Foraminifer. Res. 30 (4), 251–271.

Korsun, S.A., Polyak, L.V., 1989. Distribution of benthic foraminiferal morphogroups in the Barents Sea. Oceanology 29, 838–844 (USSR).

Korsun, S.A., Pogodina, I.A., Forman, S.L., Lubinski, D.J., 1995. Benthic foraminifera in glaciomarine sediments from three arctic fjords of Novaya Zemlya and Svalbard. Polar Res. 14 (1), 15–31.

Łącka, M., Zajączkowski, M., 2016. Does the recent pool of benthic foraminiferal tests in fjordic surface sediments reflect interannual environmental changes? The resolution limit of the foraminiferal record. Ann. Soc. Geol. Pol. 86, 59–71.

Lloyd, J.M., 2006. Modern distribution of benthic foraminifera from Disko Bugt, West Greenland. J. Foraminifer. Res. 36 (4), 315–331.

Lloyd, J.M., Kuijpers, A., Long, A., Moros, M., Park, L.A., 2007. Foraminiferal reconstruction of mid- to late-Holocene ocean circulation and climate variability in Disko Bugt, West Greenland. The Holocene 17 (8), 1079–1091.

Loeblich Jr., A.R., Tappan, H., 1953. Studies of Arctic Foraminifera. Smithsonian Miscellaneous Collections. 121, 1–150.

Loubere, P., Rayray, S., 2016. Benthic foraminiferal assemblage formation: theory and observation for the European Arctic margin. Deep-Sea Res. I Oceanogr. Res. Pap. 113, 107–118.

Loubere, P., Jacobson, B., Kritgaard-Kristensen, D., Husum, K., Jernas, P., Richaud, M., 2011. The structure of benthic environments and the paleochemical record of foraminifera. Deep Sea Research I: Oceanographic Research Papers 58 (5), 535–545.

Mackensen, A., Sejrup, H.P., Jansen, E., 1985. The distribution of living benthic foraminifera on the continental slope and rise off southwest Norway. Marine Micropalaeontology 9, 275–306.

Mackensen, A., Grobe, H., Kuhn, G., Futterer, D.K., 1990. Benthic foraminiferal assemblages from the eastern Weddell Sea between 68 and 73°S: distribution, ecology and fossilization potential. Mar. Micropaleontol. 16, 241–283.

Majewski, W., Zajączkowski, M., 2007. Benthic foraminifera in Adventfjorden, Svalbard: last 50 years of local hydrographic changes. J. Foraminifer. Res. 37, 107–124.

Majewski, W., Szczuciński, W., Zajaczkowski, M., 2009. Interactions of Arctic and Atlantic water-masses and associated environmental changes during the last millennium, Hornsund (SW Svalbard). Boreas 38, 529–544.

Malmgren, B.A., Haq, B.U., 1982. Assessment of quantitative techniques in paleobiogeography. Mar. Micropaleontol. 7 (3), 213–236.

Murray, J.W., Alve, E., 2016. Benthic foraminiferal biogeography in NW European fjords: a baseline for assessing future change. Estuar. Coast. Shelf Sci. 181, 218–230.

Nilsen, F., Cottier, F., Skogseth, R., Mattsson, S., 2008. Fjord–shelf exchanges controlled by ice and brine production: the interannual variation of Atlantic water in Isfjorden, Svalbard. Cont. Shelf Res. 28 (14), 1838–1853.

Nilsen, F., Skogseth, R., Vaardal-Lunde, J., Inall, M., 2016. A simple shelf circulation model: intrusion of Atlantic water on the West Spitsbergen shelf. J. Phys. Oceanogr. 46, 1209–1230.

Pawłowska, J., Zajączkowski, M., Szczuciński, W., Zaborska, A., Kucharska, M., Jernas, P.E., Forwick, M., 2017. The influence of Coriolis force driven water circulation on the palaeoenvironment of Hornsund (S Spitsbergen) over the last century. Boreas 46, 737–749.

Peterse, F., Kim, J.-H., Schouten, S., Klitgaard Kristensen, D., Koç, N., Sinninghe Damsté, J.S., 2009. Constraints on the application of the MBT/CBT paleothermometer at high latitude environments (Svalbard, Norway). Org. Geochem. 40, 692–699.

Piwosz, K., Walkusz, W., Hapter, R., Wieczorek, P., Hop, H., Wiktor, J., 2008. Comparison of productivity and phytoplankton in a warm (Kongsfjorden) and cold (Hornsund) Spitsbergen fjord in mid- summer 2002. Polar Biol. 32, 549–559.

Polyak, L., Mikhailov, V., 1996. Post-Glacial Environments of the Southeastern Barents Sea: Foraminiferal Evidence. In: Late Quaternary Paleoceanography of the North Atlantic Margins. 111. Geological Society Special Publications, pp. 323–337.

Polyak, L., Korsun, S., Febo, L.A., Stanovoy, V., Khusid, T., Hald, M., Paulsen, B.E., Lubinski, D.A., 2002. Benthic foraminiferal assemblages from the southern Kara Sea, a river-influenced arctic marine environment. Modern Foraminifera 32, 252–273.

Rasmussen, T.L., Thomsen, E., 2010. Holocene temperature and salinity variability of the Atlantic water inflow to the Nordic seas. The Holocene 20 (8), 1223–1234.

Rathburn, A.E., Perez, M.E., Lange, C.B., 2001. Benthic-pelagic coupling in the Southern California bight: relationships between sinking organic material, diatoms and benthic foraminifera. Mar. Micropaleontol. 43, 261–271.

Renaud, P.E., Løkken, T.S., Jørgensen, L.L., Berge, J., Johnson, B.B., 2015. Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Front. Mar. Sci. 2, 31.

Rytter, F., Knudsen, K.L., Seidenkrantz, M.-S., Eiríksson, J., 2002. Modern distribution of benthic foraminifera on the North Icelandic shelf and slope. J. Foraminifer. Res. 32, 217–244.

Sejrup, H.-P., Holtedahl, H., Norvik, O., Miljeteig, I., 1980. Benthonic foraminifera as indicators of the paleoposition of the subarctic convergence in the Norwegian-Greenland Sea. Boreas 9, 203–207.

Shetye, S., Mohan, R., Shukla, S.K., Maruthadu, S., Ravindra, R., 2011. Variability of *Nonionellina labradorica* Dawson in surface sediments from Kongsfjorden, West Spitsbergen. Acta Geologica Sinica - English Edition 85, 549–558.

Skirbekk, K., Klitgaard Kristensen, D., Rasmussen, T.L., Koç, N., Forwick, M., 2010. Holocene climate variations at the entrance to a warm Arctic fjord: evidence from Kongsfjorden trough, Svalbard. In: Howe, J.A., Austin, W.E.N., Forwick, M., Paetzel, M. (Eds.), Fjord Systems and Archives. 344. Geological Society of London, Special Publications, London, pp. 289–304.

Ślubowska-Woldengen, M., Koç, N., Rasmussen, T.L., Klitgaard-Kristensen, D., Hald, M., Jennings, A.E., 2008. Time-slice reconstructions of ocean circulation changes at the continental margins of the Nordic and Barents seas during the last 16,000 cal yr BP. Quat. Sci. Rev. 27, 1476–1492.

Steinsund, P.I., 1994. Benthic Foraminifera in Surface Sediments of the Barents and Kara Seas: Modern and Late Quaternary Applications. University of Tromsø, Tromsø, pp. 111.

Streuff, K., Forwick, M., Szczuciński, W., Andreassen, K., Ó Cofaigh, C., 2015. Submarine landform assemblages and sedimentary processes related to glacier surging in Kongsfjorden, Svalbard. Ark. Dent. 1 (14).

Svendsen, H., Beszczynska-Moller, A., Hagen, J.O., Lefauconnier, B., Tverberg, V., Gerland, S., Orbaek, J.B., Bischof, K., Papucci, C., Zajączkowski, M., Azzolini, R., Bruland, O., Wiencke, C., Winther, J., Dallman, W., 2002. The physical environment of Kongsfjorden-Krossfjorden, and Arctic fjord system in Svalbard. Polar Res. 21, 133–166.

Swallow, J.E., 2000. Intra-annual variability and patchiness in living assemblages of salt-marsh foraminifera from Mill Rythe Creek, Chichester Harbour, England. J. Micropalaeontol. 19, 9–22.

Thiede, J., Ovale, G., Skarbø, O., Strand, J.E., 1981. Benthonic Foraminiferal Distributions in a Southern Norwegian Fjord System: A Re-evaluation of Oslo Fjord Data. 5. Special Publications of the International Association of Sedimentologists, pp. 469–495.

Trusel, L., Powell, R., Cumpston, R., Brigham-Grette, J., 2010. Modern glacimarine processes and potential future behaviour of Kronebreen and Kongsvegen polythermal tidewater glaciers, Kongsfjorden, Svalbard. In: Howe, J.A., Austin, W.E.N., Forwick, M., Paetzel, M. (Eds.), Fjord Systems and Archives. 344. Geological Society of London, Special Publications, London, pp. 89–102.

Tverberg, V., Nøst, O.A., 2009. Eddy overturning across a shelf edge front: Kongsfjorden, west Spitsbergen. J. Geophys. Res. 114, C04024.

Vilks, G., 1980. Postglacial basin sedimentation on the Labrador shelf. Geological Society of Canada 78, 1–28.

Williamson, M.A., Keen, C.E., Mudie, P.J., 1984. Foraminiferal distribution on the continental margin off Nova Scotia. Mar. Micropaleontol. 9, 219–239.

Willis, K.J., Cottier, F.R., Kwasniewski, S., 2008. The impact of warm water advection on the winter zooplankton community in an Arctic fjord. Polar Biol. 31 (4), 475–481.

Włodarska-Kowalczuk, M., Pearson, T.H., 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). Polar Biol. 27 (3), 155–167.

Włodarska-Kowalczuk, M., Pawłowska, J., Zajączkowski, M., 2013. Do foraminifera mirror diversity and distribution patterns of macrobenthic fauna in an Arctic glacial fjord? Mar. Micropaleontol. 103, 30–39.

Wollenburg, J.E., Mackensen, A., Kuhnt, W., 2007. Benthic foraminiferal biodiversity response to a changing Arctic palaeoclimate in the last 24,000 years. Palaeogeogr. Palaeoclimatol. Palaeoecol. 255 (3–4), 195–222.

Zaborska, A., Włodarska-Kowalczuk, M., Legeżyńska, J., Jankowska, E., Winogradow, A., Deja, K., 2016. Sedimentary organic matter sources, benthic consumption and burial in west Spitsbergen fjords — signs of maturing of Arctic fjordic systems? Journal of Marine Systems, (ISSN 0924-7963).

Zajączkowski, M., 2008. Sediment supply and fluxes in glacial and outwash fjords: Kongsfjorden and Adventfjorden, Svalbard. Polish Polar Res. 29 (1), 59–72.

Zajączkowski, M., Szczuciński, W., Plessen, B., Jernas, P., 2010. Benthic foraminifera in Hornsund, Svalbard: implications for paleoenvironmental reconstructions. Polish Polar Res. 31 (4), 349–375.