



ORIGINAL RESEARCH ARTICLE

# Zooplankton structure in high latitude fjords with contrasting oceanography (Hornsund and Kongsfjorden, Spitsbergen)

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**Summary** Zooplankton inhabiting the Hornsund and Kongsfjorden fjords on Spitsbergen (Svalbard) were investigated in summer 2013. The goal of the study was to determine how the zooplankton communities vary in environments functioning under different oceanographic regimes. Sampling was conducted with nets of different mesh size and selectivity (56  $\mu\text{m}$  WP-2, 180  $\mu\text{m}$  MultiNet, and 1000  $\mu\text{m}$  Tucker Trawl), which permitted comparing a wide size spectrum of zooplankton components. Species composition did not differ substantially between the fjords, but the zooplankton in Hornsund was almost two times less numerous, and it had lower biomass per unit volume. The highest abundance at both sites was in the smallest zooplankton size fraction found only in samples taken with 56  $\mu\text{m}$  mesh WP-2 net. These comprised as much as 71% and 58% of the total zooplankton abundance in Hornsund and Kongsfjorden, respectively. The communities in both fjords had comparable contributions of Arctic and boreo-Arctic species biomass in the year of the study. However, the comparison of zooplankton characteristics over several years showed changes in abundance and biogeographic structure that corresponded with variations in the physical environments of the fjords. The results of the study permit predicting the possible effects of the increasing influence of Atlantic waters on zooplankton communities inhabiting Arctic marine pelagic ecosystems.

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## 1. Introduction

The west coast of Spitsbergen is a region of complex oceanography where different parts function under more Arctic or more Atlantic influences (Cottier et al., 2010; Nilsen et al., 2008; Svendsen et al., 2002). This results in coexisting of marine biota of Atlantic and Arctic affinity, representing the Atlantic Subarctic Province and the Boreal Polar Province according to Longhurst (2007) (Gluchowska et al., 2016; Hop et al., 2006). The marine environments of the fjords are considered to be a balance between Atlantic, Arctic, brine and freshwater inputs, and are potentially sensitive indicators of environmental change (Cottier et al., 2005, 2010; Nilsen et al., 2008). Because of this, they also provide pseudo-mesocosm experimental setups that facilitate investigations of, for example, responses of biota to environmental variations, including those induced by climate change.

In recent years, the Atlantic water (AW) range in the eastern Fram Strait has been observed to shift northward and with it there have been pronounced increases in water temperature and salinity (Walczowski and Piechura, 2011; Walczowski et al., 2012). Consequently, the advection of AW and associated zooplankton into Kongsfjorden (Willis et al., 2006, 2008), the appearance of the blue mussel in Isfjorden (Berge et al., 2006), or decreasing sea ice cover north of Spitsbergen have all been observed (Walczowski et al., 2012). The growing influence of the AW in Fram Strait and the Arctic Ocean are recognized as symptoms of “Atlantification” (Árthun et al., 2012; Polyakov et al., 2010) and the most consequential results of this include the extension of the ice-free water period in the Arctic shelf seas, decreases in the extent and thickness of perennial sea ice, and the warming and mixing of the Arctic Ocean surface layer (ACIA, 2005; IPCC, 2007; Rodrigues, 2009). In pelagic systems, earlier studies on the West Spitsbergen Shelf (WSS) found influence of Atlantic water on plankton communities with respect to species composition, age structure, and biomass (Gluchowska et al., 2016; Kwasniewski et al., 2013; Rokkan Iversen and Seuthe, 2011; Trudnowska et al., 2014), with studies focusing mainly on mesozooplankton. It is anticipated, however, that the northern expansion of Atlantic boreal species will entail a shift toward a smaller size spectrum of zooplankton in Arctic regions (Beaugrand et al., 2002; Grebmeier, 2012; Hop et al., 2006). Zooplankton of small size are important link between microbial and classical (phytoplankton based) trophic levels (Calbet et al., 2000; Roff et al., 1995; Wickham, 1995). At present, the role of small zooplankton in Spitsbergen fjords and its possible modifications as a result of Atlantic influence are still not well known. Given the observed speed of environmental change, the acquisition of the missing knowledge seems necessary.

The aim of this study was to describe the differences between zooplankton communities from Hornsund and Kongsfjorden, two fjords on the WSS that are influenced by different oceanographic regimes. The novelty of the study is that evaluating of the zooplankton composition and structure took into account broad zooplankton size spectrum, based on data from parallel sampling with different nets, performed in the two fjords in the same year and season. Additionally, holo-mesozooplankton was assessed according to trophic preferences and biogeographic affiliations of the

species comprising the community for both, the year of the study and interannually. The leading hypothesis was that the zooplankton in Kongsfjorden, the fjord strongly influenced by AW, would support higher concentrations of smaller/boreal taxa, in comparison to Hornsund.

## 2. Material and methods

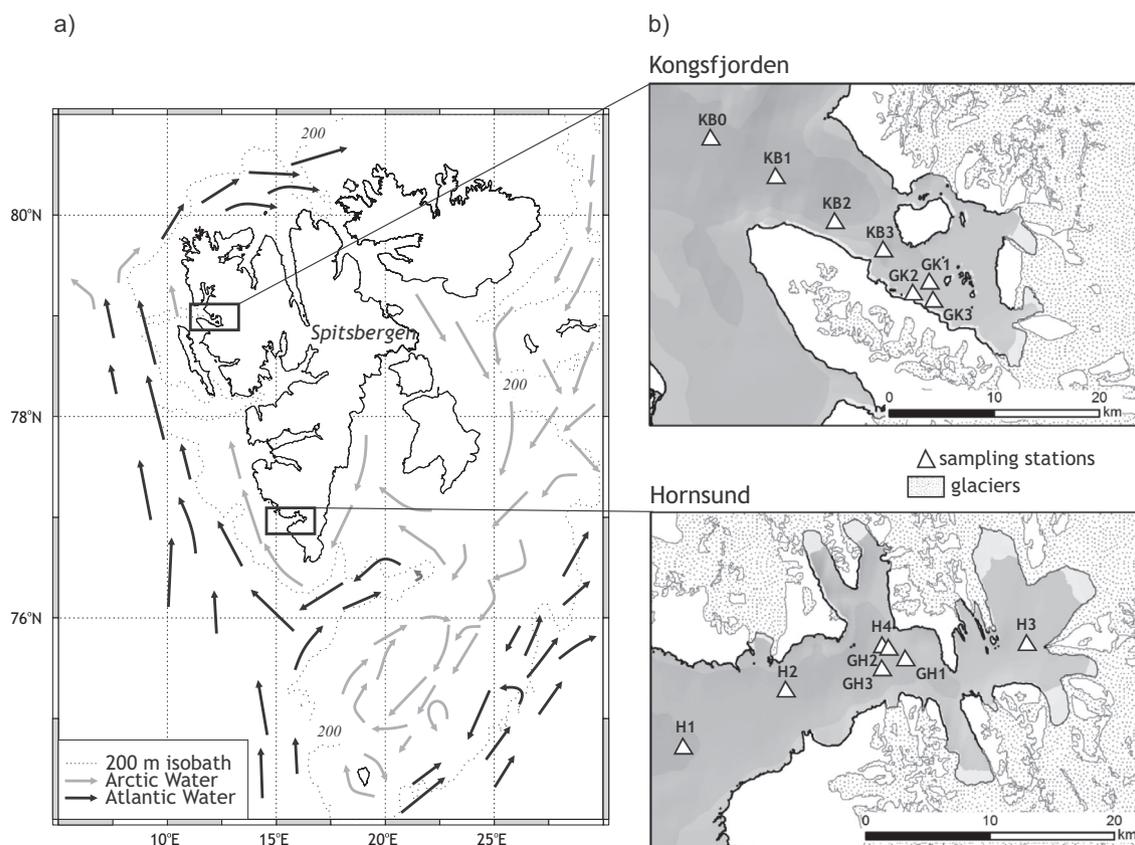
### 2.1. Sampling area

Hornsund and Kongsfjorden are glacial fjords on the west coast of Spitsbergen, separated by a distance of about 250 km (Fig. 1) in a south-north direction. Both fjords have complex bottom topographies with depressions and coastlines with numerous bays. They also have well-marked inner parts, but neither of the fjords has a sill at its entrance. The depressions reach 150–250 m in Hornsund and 250–350 m in Kongsfjorden, and the inner areas are about 90–120 m deep (Prominska et al., 2017a). The number of surging glaciers varies between the fjords: there are 13 glaciers entering Hornsund (Swerpel, 1985) and four entering Kongsfjorden (Svendsen et al., 2002). The fjords are occupied by water masses of local origin and two remote water masses—Atlantic water (AW) carried by the West Spitsbergen Current (WSC) and Arctic-type waters (ArW) of the Sørkapp Current (SC), which fill the fjords in varied proportions (Cottier et al., 2005; Svendsen et al., 2002; Swerpel, 1985). The physical properties and biota of the remote water masses undergo transformations before or while entering the fjord, and the degree of the transformations depends on, among others, the distance from the source region and the complexity of the hydrographic processes the water masses encounter as they move (Cottier et al., 2005, 2010; Nilsen et al., 2008). As a result, the fjords receive different amounts of remote input, and they function under more Arctic-type (Hornsund) or more Atlantic-type (Kongsfjorden) regimes (Piwosz et al., 2009).

### 2.2. Field methods and samples processing

Zooplankton was sampled from *r/v Oceania* in 2013 at stations situated along the main axes of the fjords (Fig. 1, Table 1) with three different zooplankton nets: WP-2 net (Tranter, 1968) with 0.25 m<sup>2</sup> opening area and 0.056 mm mesh; MPS MultiNet Type *Midi* (HYDRO-BIOS Apparategebau GmbH) with 0.25 m<sup>2</sup> opening area and 0.180 mm mesh; Tucker Trawl net (Clarke, 1969) with 1 m<sup>2</sup> opening area and 1.0 mm mesh. The nets were towed vertically from near the bottom to the surface. After collection, the zooplankton were immediately preserved in a 4% formaldehyde solution in sea water buffered with borax. Water temperature and salinity were measured in vertical profiles at all zooplankton stations prior to net sampling with a Sea-Bird SBE 49 FastCAT conductivity-temperature-depth probe.

In the laboratory, the zooplankton samples were analyzed qualitatively and quantitatively following standard procedures described in Postel et al. (2000) and Kwasniewski et al. (2010). For the purposes of biomass estimations based on length-mass relationships, measurements of total length or another appropriate dimension were taken of randomly selected animals for which there was no information on size



**Figure 1** Map of the Spitsbergen region with surface current patterns (after Sakshaug et al. (2009), simplified) (a), and sampling station locations (b).

in literature (at least ten specimens per sample, except in cases when fewer specimens were available). With taxa for which there are no length-mass relationships published (*Pagurus pubescens* zoëa and megalopa, *Hyas* sp. zoëa, and fish larvae), a known number of specimens was collected from a sample, dried for 48 h at 50°C, weighed, and the mean dry mass of an individual, considered as nominal, was calculated.

### 2.3. Data analysis

The characteristics of the zooplankton communities compared were calculated for estimated abundances of zooplankton in a standard water volume unit [ $\text{ind m}^{-3}$ ]. This was done to focus the comparison between the fjords more on the qualitative characteristics of zooplankton community, rather than on the quantitative ones. The basic information on the zooplankton

**Table 1** Zooplankton sampling metadata in the studied fjords in summer 2013.

Fjord	Station	Date	Latitude [N]	Longitude [E]	Depth [m]	Gear type
Hornsund	H1	27.07.2013	76°56.313'	15°22.577'	150	MPS
Hornsund	H2	27.07.2013	76°58.767'	15°42.300'	140	MPS; TT
Hornsund	H3	27.07.2013	77°0.586'	16°28.935'	125	MPS; TT
Hornsund	H4	27.07.2013	77°0.617'	16°1.059'	95	MPS; TT
Hornsund	GH1	29.07.2013	77°0.021'	16°5.439'	70	WP-2; MPS; TT
Hornsund	GH2	29.07.2013	77°0.497'	16°2.233'	95	WP-2; MPS; TT
Hornsund	GH3	29.07.2013	76°59.624'	16°0.930'	100	WP-2; MPS; TT
Kongsfjorden	KB0	05.08.2013	79°2.543'	11°7.842'	310	MPS
Kongsfjorden	KB1	05.08.2013	79°0.788'	11°25.969'	340	MPS
Kongsfjorden	KB2	05.08.2013	78°58.684'	11°42.365'	300	MPS; TT
Kongsfjorden	KB3	06.08.2013	78°57.362'	11°55.688	350	MPS; TT
Kongsfjorden	GK1	07.08.2013	78°55.851'	12°8.367'	95	WP-2; MPS; TT
Kongsfjorden	GK2	08.08.2013	78°55.237'	12°4.131'	115	WP-2; MPS; TT
Kongsfjorden	GK3	08.08.2013	78°54.932'	12°9.652	85	WP-2; MPS; TT

characteristics calculated for the total zooplankton stock was summarized additionally in Section 3.3.1.

### 2.3.1. Size fraction division

In order to better estimate the quantitative characteristics of a zooplankton community considered for its wide size range, it was decided to use the abundance estimates of species and taxa representing particular size fractions based on data from samples collected with different nets. This method for calculating abundance took into account the limitations of zooplankton net sampling (Tranter, 1968) that are related to the differences in the sizes of zooplankton organisms and the different selectivity of the plankton nets used. Every organism identified was initially assigned to one of three operational size categories: 1 – small zooplankton (SZ); 2 – medium zooplankton (MZ); 3 – large zooplankton (LZ).

*Small zooplankton (SZ).* This size fraction included, first of all, metazoans with nominal body sizes <0.2 mm, caught with the WP2/0.056 net. Additionally, a few other organisms with larger nominal sizes were classified to this size fraction. These organisms had small widths or diameters, which precluded them from being efficiently retained on the 0.180 mm mesh of the MPS net. The abundance of emblematic SZ representative *Microsetella norvegica* was evaluated based only on WP2/0.056 net catches since this species was found exclusively in samples from this net. The abundances of other SZ species/taxa were calculated by subtracting from the abundances estimated based on the WP2/0.056 net catches, the abundances based on the MPS/0.180 catches. This was done for the following species/taxa: *Triconia borealis*, *Oncaea* spp., Cyclopoida, Harpacticoida, copepod nauplii, *Limacina helicina* veligers, gastropod larvae, bivalve larvae, polychaete larvae, *Fritillaria borealis*, and *Oikopleura* spp. Consequently, it was assumed that the SZ fraction included individuals of, for example, *T. borealis* and *Oncaea* spp., or bivalve veligers, comprising only younger copepodid stages or smaller specimens of taxa that were not caught by the coarser MPS/0.180 net.

*Medium zooplankton (MZ).* This size fraction comprised organisms with nominal body sizes in the range of 0.2–10.0 mm, predominantly all those caught with the MPS/0.180 net, including copepods and copepod nauplii (except those of smaller sizes included in SZ), ostracods, isopods; larval cirripedes, gastropods, echinoderms and bryozoans; polychaetes and their larvae; hydrozoans, chaetognaths, and appendicularians <10 mm length; as well as hyperiid amphipods, plus euphausiid and decapod larvae with body sizes <5 mm. The hyperiid amphipods and larval euphausiids and decapods with body sizes 5–10 mm were caught in higher abundances in the TT/1.0 net samples most probably because of their mobility, which increased their chances of escaping the net with a smaller opening area that was towed vertically. Therefore, these zooplankters were considered as contributions to the LZ and not the MZ size fraction.

*Large zooplankton (LZ).* The LZ size fraction comprised hyperiid amphipods, euphausiids, and decapods, mysids, hydrozoans, appendicularians, chaetognaths and fish larvae with nominal body sizes >10 mm, and hyperiid amphipods, larval euphausiids, and decapods with body sizes of 5–

10 mm. The abundances of the representatives of this size fraction were calculated based on TT/1.0 net catches, except for the abundances of chaetognaths with body sizes of 10–20 mm, which were based on MPS/0.180 net catches. These were usually higher most probably because 10–20 mm chaetognaths were narrow in cross section, and that allowed them to escape effectively through the width of the coarse mesh on the TT net (Tranter, 1968).

The results of the abundance estimates for the three size fractions were summed to determine the values of total zooplankton community abundance.

### 2.3.2. Biomass estimation

Stage, species, or taxon-specific biomasses used in this study were either obtained earlier (for details see Kwasniewski et al., 2010) or were calculated using the length-mass relationships published in Böer et al. (2005), Gannefors et al. (2005), Lundberg et al. (2006), and Pérez-Camacho et al. (1994) and nominal mean lengths for species determined from our own measurements. The nominal mean lengths used in the formulas were the geometrical mean values calculated from measurements of particular taxa or developmental stages. The way the animals were measured reflected the requirements of the relationships used. Zooplankton biomass (dry mass) was calculated based on the zooplankton abundances per cubic meter and is expressed as mg DM m<sup>-3</sup>.

### 2.3.3. Interannual comparison of zooplankton

The interannual comparison of zooplankton from the fjords focused on the taxonomic community structure, considered in terms of abundance and biomass, and also on the biogeographic and trophic community structures, considered in terms of biomass. The comparisons were done for the summer seasons of 2002, 2007, 2012, and 2013 using published (Gluchowska et al., 2016; Trudnowska et al., 2012; Walkusz et al., 2003) and unpublished (IO PAN, Marine Ecology Department) data. The community biogeographic and trophic structures were assessed by calculating the contributions to the biomass of species representing affinity in their main distribution for particular geographic ranges or trophic groups to the total community biomass. The evaluations were done for a subset of holozooplankton species and for the biomass estimates calculated based on MPS/0.180 net samples, which were the only samples available for the years compared other than 2013. The biogeographic affinity of the species followed that in Gluchowska et al. (2016), and the classification of species according to dietary preferences (herbivorous, omnivorous, carnivorous) was based on data from Blachowiak-Samolyk et al. (2008).

### 2.4. Statistical analyses

To compare the hydrography and the zooplankton characteristics between Hornsund and Kongsfjorden, a number of univariate and multivariate characteristics was used. To test for differences in zooplankton community taxonomic structure, one-way ANOSIM with two a priori sets of samples, each representing one of the studied fjords, was performed. The SIMPER (similarity percentages) procedure was used to determine the contribution of species to group similarities (Clarke and Warwick, 2001). The resemblance between the fjords of the zooplankton structure for each size category was

measured using the Bray–Curtis similarity index that was calculated based on the relative abundance or biomass of species and taxa. The differences between the fjords in univariate characteristics, including water temperature and salinity, and zooplankton abundance and biomass of each of the three size categories, as well as of the dominant species, were tested with the non-parametric Mann–Whitney  $U$ -test. The  $\chi^2$  test for independence was used to compare the proportions of *Calanus finmarchicus* and *Calanus glacialis* copepodid stages and the zooplankton size fraction proportions in the total zooplankton abundance and biomass. The interannual variability in holozooplankton abundance and biomass were compared using the Kruskal–Wallis test. All specified statistical analyses were performed using PRIMER 6 (Clarke and Warwick, 2001) and STATISTICA 10 (StatSoft Inc.). The significance level for all of the statistical tests was 0.05.

### 3. Results

#### 3.1. Hydrography

In 2013, the mean water column salinity was lower in Hornsund (34.09; range: 33.72–34.59) than in Kongsfjorden (34.59; range: 34.28–34.84; Mann–Whitney  $U$ -test:  $Z_{7,7} = 2.30$ ,  $p = 0.021$ ), while the mean water column temperature was in the same range in both fjords (Hornsund: 1.12–3.72°C, Kongsfjorden: 2.69–3.78°C;  $Z_{7,7} = 0.76$ ,  $p = 0.443$ ). With regard to the occurrence of water masses in the years compared (2002, 2007, 2012 and 2013), Hornsund was regularly filled with intermediate water and surface water, with varying amounts of winter cooled water found in the inner basin and both Atlantic transformed water and AW in the front part of the fjord (Prominska et al., 2017a). In contrast, Kongsfjorden was typically occupied by transformed Atlantic water along with varying admixtures of AW, intermediate water, and local water. Characteristic AW occurred in Hornsund in the largest amounts in 2013, but it was not observed at all in 2007 and 2012. However, AW was present in Kongsfjorden in the largest amounts in 2013 and 2007, but it was not found at all in 2012.

#### 3.2. Zooplankton composition

During the present study, a total of 69 taxa were recorded in Hornsund and Kongsfjorden, including 50 species and genera and 19 taxa identified to higher levels in Hornsund and 45 and 24, respectively, in Kongsfjorden. Among the taxa recorded, 52 occurred in both fjords, eight were identified only in Hornsund (including species and genera such as *Bougainvillia superciliaris*, *Dimophyes arctica*, *Halitholus cirratus*, *Hyas araneus*, *Hyperia galba*, *Myrianida* sp., *Sarsia* sp., *Velutina* sp.), and nine only in Kongsfjorden (*Boreomysis arctica*, *Erythroops erythropthalma*, *Meganctiphanes norvegica*, *Mesaiokeras spitsbergensis*, *Neoscolecithrix farrani*, *Pelagobia* sp. and *Cyanea capillata*, plus *Protomedea grandimana*, and larval Appendicularia).

#### 3.3. Zooplankton abundance and biomass

The zooplankton community was almost two times less numerous and had nearly two times lower biomass per unit

volume [ $\text{m}^3$ ] in Hornsund than in Kongsfjorden. The mean abundance in Hornsund and Kongsfjorden was as follows, respectively: 5840 ind  $\text{m}^{-3}$  (range:  $\sim 3800$ –8500 ind  $\text{m}^{-3}$ ) and 9832 ind  $\text{m}^{-3}$  (range:  $\sim 4900$ –14,100 ind  $\text{m}^{-3}$ ); the mean biomass was: 59 mg DM  $\text{m}^{-3}$  (range:  $\sim 42$ –93 mg DM  $\text{m}^{-3}$ ) and 121 mg DM  $\text{m}^{-3}$  (range:  $\sim 65$ –188 mg DM  $\text{m}^{-3}$ ). The contribution of particular size fractions to overall community abundance and biomass also differed between the fjords ( $\chi^2 = 551.3$ ,  $p < 0.05$  and  $\chi^2 = 15.150$ ,  $p < 0.05$  for abundance and biomass, respectively). The majority of community abundance (Table 2) consisted of SZ in both Hornsund (71%) and Kongsfjorden (58%), while MZ comprised less of the abundance in Hornsund than in Kongsfjorden (29% versus 42%). The contribution of LZ to overall community abundance was of much less importance (<1% in both fjords).

The bulk of the zooplankton biomass (Table 3) was composed of MZ, with 72% and 65% shares in Hornsund and Kongsfjorden, respectively. This was followed by LZ (26% in Hornsund and 32% in Kongsfjorden), while the SZ contribution to total zooplankton biomass was negligible (2% and 3%, respectively). When comparing the amounts of zooplankton in the particular size fractions, there was no difference between the fjords in SZ abundance, but there was a difference in its biomass (Mann–Whitney  $U$  test:  $Z_{3,3} = 0.873$ ,  $p = 0.383$ ;  $Z_{3,3} = 1.746$ ,  $p = 0.031$ ). There were significant differences in MZ abundance and biomass between Hornsund and Kongsfjorden, with higher values for both in the latter fjord ( $Z_{7,7} = 2.811$ ,  $p = 0.005$  and  $Z_{7,7} = 2.900$ ,  $p = 0.009$ ). No significant differences in LZ abundance or biomass were noted between the fjords ( $Z_{5,6} = 0.639$ ,  $p = 0.523$ ;  $Z_{5,6} = 0.274$ ,  $p = 0.784$ ), but the values showed high variability, particularly with regard to biomass.

##### 3.3.1. Zooplankton stock size

The zooplankton stock size in terms of numbers per  $\text{m}^2$  was, on average, 524,878 ind  $\text{m}^{-2}$  (range:  $\sim 428,700$ –596,600 ind  $\text{m}^{-2}$ ) and 1,340,252 ind  $\text{m}^{-2}$  (range:  $\sim 657,900$ –1,981,100 ind  $\text{m}^{-2}$ ) in Hornsund and Kongsfjorden, respectively. The main components were copepods nauplii (42% and 38% in Hornsund and Kongsfjorden, respectively), *Oithona similis* (12% and 28%), and bivalve veligers (27% and 11%). A high share (10%) of *Pseudocalanus* spp. was recorded in Hornsund, while in Kongsfjorden *F. borealis* and *L. helicina* veligers contributed considerably to the stock size (both 5%). *Calanus finmarchicus* comprised 3% and 4% in Hornsund and Kongsfjorden, respectively. The contribution of *C. glacialis* to the total mean zooplankton abundance in the water column was 1% in each fjord.

The zooplankton stock biomass was 5.17 g DM  $\text{m}^{-2}$  (range:  $\sim 0.94$ –8.04 g DM  $\text{m}^{-2}$ ) in Hornsund and 23.37 g DM  $\text{m}^{-2}$  (range:  $\sim 7.72$ –44.82 g DM  $\text{m}^{-2}$ ) in Kongsfjorden. The main contributors to zooplankton biomass in both fjords were *C. glacialis* (31% and 29% in Hornsund and Kongsfjorden, respectively) and *C. finmarchicus* (21% and 23%). Other species that contributed substantially to zooplankton biomass in Hornsund were *Parasagitta elegans* (9%), *Calanus hyperboreus* (6%), *Eukrohnia hamata* (6%), *Metridia longa* (5%), and *Pseudocalanus* spp. (3%), while in Kongsfjorden they were *C. hyperboreus* (13%), *Thysanoessa inermis* (5%), *L. helicina* veligers (5%), and *O. similis* (4%).

**Table 2** Most abundant zooplankton species [ind m<sup>-3</sup>] in different size fractions.

	Small Zooplankton (SZ)		Medium Zooplankton (MZ)		Large Zooplankton (LZ)	
	Hornsund	Kongsfjorden	Hornsund	Kongsfjorden	Hornsund	Kongsfjorden
N samples	3	3	7	7	6	5
Total mean zooplankton [ind m <sup>-3</sup> ]	4164	5688	1671	4131	5	13
Min.–max. [ind m <sup>-3</sup> ]	2735–5614	3039–7066	1108–2886	1894–7016	4–7	3–23
<i>Microsetella norvegica</i>	7–9	3–19				
<i>Triconia borealis</i>	0–23	46–49	7–62	15–80		
Copepoda nauplii	2259–2996	2462–6524	47–204	21–121		
<i>Limacina helicina</i> veligers	1–4	17–352	<1–5	37–275		
Bivalvia veligers	427–2975	213–400	<1–20	106–810		
<i>Fritillaria borealis</i>	0–8	0–229	<1–27	54–490		
<i>Calanus finmarchicus</i>			113–311	152–322		
<i>Calanus glacialis</i>			28–74	30–105		
<i>Calanus hyperboreus</i>			3–14	1–46		
<i>Microcalanus</i> spp.			8–62	32–194		
<i>Pseudocalanus</i> spp.			220–934	97–560		
<i>Metridia longa</i>			8–28	<1–20		
<i>Acartia longiremis</i>			8–43	<1–7		
<i>Oithona similis</i>			340–1249	945–4621		
<i>Themisto abyssorum</i>			0–1	<1–1	0–1	0–11
<i>Themisto libellula</i>			0 to <1	0–0	<1	>1
<i>Meganyctiphanes norvegica</i>						0 to <1
<i>Thysanoessa inermis</i>					<1–1	<1–6
<i>Thysanoessa longicaudata</i>					0 to <1	<1
<i>Thysanoessa raschii</i>					0 to <1	<1–1
<i>Eukrohnia hamata</i>			0–4	0–4	<1–3	0 to <1
<i>Parasagitta elegans</i>			1–11	<1–3	2–4	2–10

### 3.4. Zooplankton community structure

The zooplankton community structure, considered in terms of abundance, differed between Hornsund and Kongsfjorden within each of the size fractions: SZ (ANOSIM test:  $R = 0.519$ ;  $p = 0.050$ ), MZ (ANOSIM test:  $R = 0.978$ ;  $p = 0.001$ ), and LZ (ANOSIM test:  $R = 0.448$ ;  $p = 0.015$ ). The overall comparison of the Bray–Curtis index showed that the zooplankton community differed the least between the fjords in the SZ fraction and the most for LZ, while the differences in MZ were intermediate based on this metric (Kruskal–Wallis test  $H_{2,72} = 17.04$ ;  $p < 0.001$ ). The results of SIMPER analysis indicated that the Hornsund and Kongsfjorden communities differed in the contributions to total abundance of, for example, bivalve veligers and copepod nauplii in the SZ fraction, *O. similis* and *Pseudocalanus* spp. in that of MZ, and *Themisto abyssorum*, *T. libellula*, and *E. hamata* in the LZ fraction (Table 2, Fig. 2).

The zooplankton community structure in terms of biomass also differed between Hornsund and Kongsfjorden within the size fractions: SZ (ANOSIM test:  $R = 0.378$ ;  $p = 0.051$ ), MZ (ANOSIM test:  $R = 0.561$ ;  $p = 0.020$ ), and LZ (ANOSIM test:  $R = 0.704$ ;  $p = 0.020$ ). SIMPER analysis results indicated that the main species responsible for differences in the community biomass structure were, among others, *L. helicina* and bivalve veligers in the SZ fraction, *C. finmarchicus* CV, *C. glacialis* CV, and *M. longa* (all stages) in MZ, and *T. libellula*, *T. inermis*, and *E. hamata* in the LZ size fraction (Table 3, Fig. 2).

#### 3.4.1. Small zooplankton (SZ)

The main components of SZ (Fig. 2a) in both fjords were copepod nauplii (57% of SZ abundance in Hornsund and 88% in Kongsfjorden) and bivalve veligers (42% and 5%, respectively). A notable component of SZ in Kongsfjorden was also small *L. helicina* veligers (3%), which were two orders of magnitude more abundant than they were in Hornsund. The highest contribution to the SZ biomass (Fig. 2a) was made by bivalve veligers (64% and 33% in Hornsund and Kongsfjorden, respectively) followed by copepod nauplii (21% and 18%). The contribution of *L. helicina* was also substantial in Kongsfjorden. The contribution of copepods to SZ biomass in both fjords was very small (approximately 3%) in the present study (Table 3).

#### 3.4.2. Medium zooplankton (MZ)

MZ (Fig. 2b) was dominated by copepods, among which the prevailing taxa were *O. similis*, *Pseudocalanus* spp., and *C. finmarchicus* at 39%, 32%, and 9% of MZ abundance in Hornsund and 55%, 7%, and 6% in Kongsfjorden, respectively. The copepods *C. glacialis* (3% and 2%), *Microcalanus* spp. (2% in both fjords), *C. hyperboreus* (<1% and 1%), *M. longa* (1% and <1%), and *Acartia longiremis* (1% and <1%) were less numerous but still important. Populations of *C. finmarchicus* had a different copepodid structure in Hornsund than in Kongsfjorden ( $\chi^2 = 46.119$ ,  $p < 0.001$ ), with higher contributions of younger copepodids in the former fjord. Populations of *C. glacialis* did not differ significantly between the fjords in this respect, ( $\chi^2 = 6.153$ ,  $p = 0.292$ ). Notable MZ components

**Table 3** Main zooplankton biomass species [mg DM m<sup>-3</sup>] in different size fraction.

	Small Zooplankton (SZ)		Medium Zooplankton (MZ)		Large Zooplankton (LZ)	
	Hornsund	Kongsfjorden	Hornsund	Kongsfjorden	Hornsund	Kongsfjorden
N samples	3	3	7	7	6	5
Total mean zooplankton [mg DM m <sup>-3</sup> ]	1.482	3.597	42.671	78.289	15.199	39.172
Min.–max. [mg DM m <sup>-3</sup> ]	1.042–2.035	2.378–5.421	32.536–66.218	58.022–98.717	8.889–24.249	4.358–83.885
<i>Microsetella norvegica</i>	0.007–0.009	0.003–0.020				
<i>Triconia borealis</i>	0.000–0.046	0.095–0.099	0.015–0.126	0.031–0.163		
Copepoda nauplii	0.294–0.338	0.320–0.848	0.211–0.909	0.093–0.540		
<i>Limacina helicina</i> veligers	0.008–0.024	0.145–2.972	0.003–0.073	0.537–4.023		
Bivalvia veligers	0.233–1.606	0.823–1.545	0.002–0.077	0.409–3.124		
<i>Calanus finmarchicus</i>			7.435–16.367	15.224–35.900		
<i>Calanus glacialis</i>			10.965–31.057	13.482–47.508		
<i>Calanus hyperboreus</i>			1.412–6.587	0.432–19.573		
<i>Microcalanus</i> spp.			0.057–0.433	0.226–1.355		
<i>Pseudocalanus</i> spp.			0.815–3.339	0.571–2.356		
<i>Metridia longa</i>			1.662–4.251	0.004–1.582		
<i>Acartia longiremis</i>			0.081–0.426	0.001–0.074		
<i>Oithona similis</i>			0.842–3.097	2.345–11.461		
<i>Fritillaria borealis</i>			0.001–0.039	0.077–0.701		
<i>Themisto abyssorum</i>			0.000–0.016	0.068–0.375	0.000–0.928	0.000–16.107
<i>Themisto libellula</i>			0.000–0.012		0.115–1.408	0.035–1.736
<i>Meganyctiphanes norvegica</i>						0.000–14.701
<i>Thysanoessa inermis</i>					0.000–3.889	0.341–27.248
<i>Thysanoessa longicaudata</i>					0.000–0.052	0.008–0.185
<i>Thysanoessa raschii</i>					0.000–0.247	0.220–24.431
<i>Eukrohnia hamata</i>			0.006–0.074	0.000–0.383	2.685–15.151	0.000–0.631
<i>Parasagitta elegans</i>			0.042–0.249	0.005–0.054	2.012–8.275	0.674–13.543

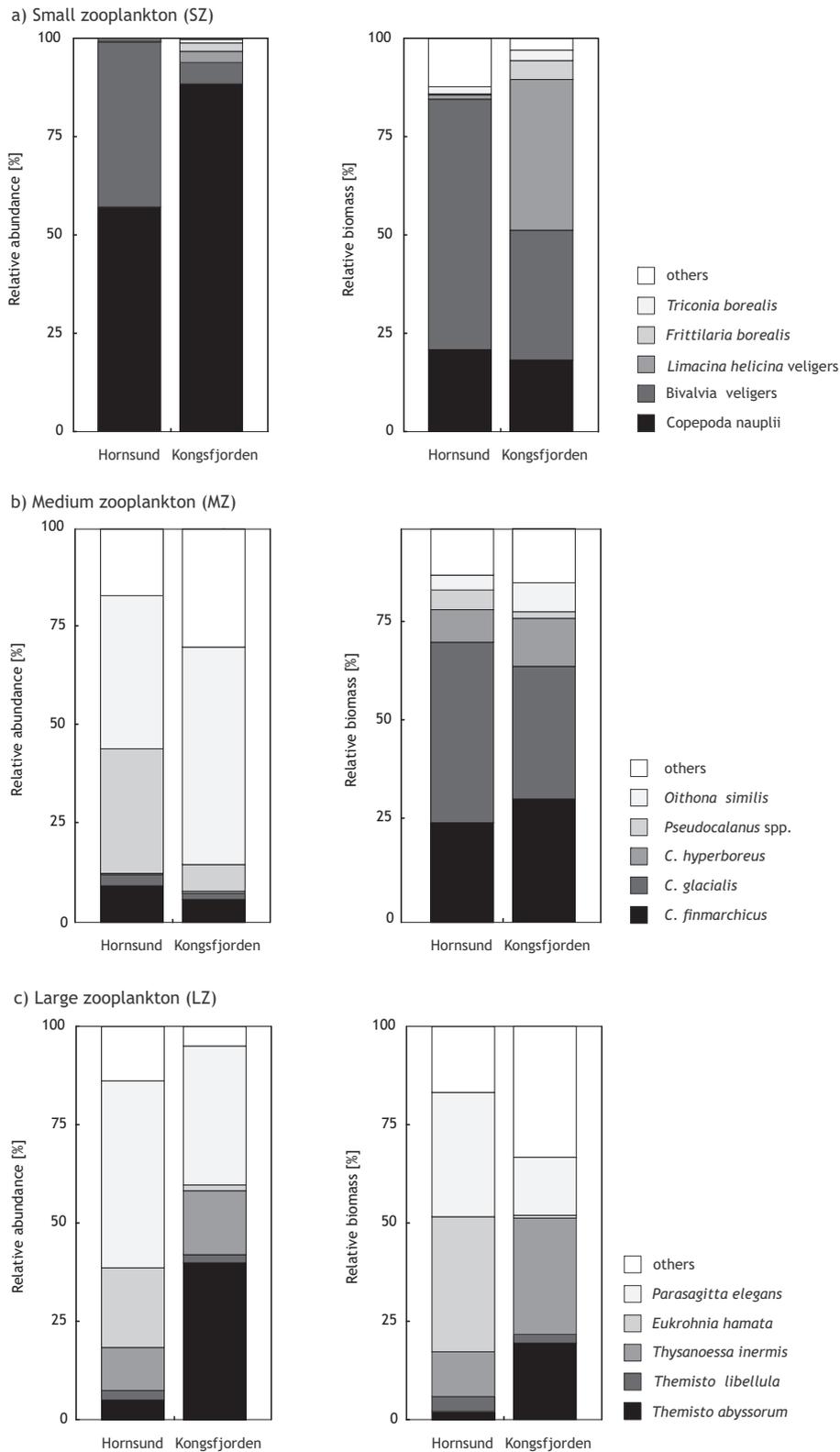
in both fjords also included appendicularians, first of all, *F. borealis* (1% and 5% of MZ abundance), bivalve veligers (1% and 11%), and chaetognaths <10 mm (<1% in both fjords). Some taxa contributed notably to the MZ fraction only in one fjord, for example, cirripede larvae in Hornsund (1% share) and echinoderm larvae in Kongsfjorden (1%). Copepods comprised 97% and 90% of the MZ biomass in Hornsund and Kongsfjorden, respectively. *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* contributed the highest proportions to the biomass in both Hornsund (25%, 46%, 8%), and in Kongsfjorden (31%, 34%, 13%). The remaining portions of the MZ biomass were of *O. similis* (4% and 7%), *Pseudocalanus* spp. (5% and 2%), *M. longa* (6% and 1%), *Microcalanus* spp. (<1% and 1%), and *A. longiremis* (1% and <1%), in Hornsund and Kongsfjorden, respectively. Except for the copepods, a significant portion of the MZ biomass in Kongsfjorden was of *L. helicina* veligers and juveniles (7%), and bivalve veligers (2%). In absolute values, *C. finmarchicus*, *C. hyperboreus*, *Microcalanus* spp., and *O. similis* biomass was higher in Kongsfjorden, whereas that of *Pseudocalanus* spp., *M. longa*, and *A. longiremis* was higher in Hornsund (Table 3). *Calanus glacialis* biomass was, however, comparable in the two fjords (Mann–Whitney *U* test:  $Z_{7,7} = 0.767$ ,  $p = 0.443$ ). Two Hydrozoa species also contributed markedly to the MZ biomass – *B. superciliaris* in Hornsund and *Aglantha digitale* in Kongsfjorden.

### 3.4.3. Large zooplankton (LZ)

Numerically, LZ (Table 2) made a very small contribution to total zooplankton abundance, which is why the taxonomic

structure of this fraction is presented more specifically only for the biomass of LZ (Table 3).

The main biomass components among LZ (Fig. 2c) were chaetognaths (66% in Hornsund and 16% in Kongsfjorden), euphausiids (17% and 61%), amphipods (6% and 27%), and larval fishes (3% and 6%). Moreover, decapods (4% of LZ) and hydrozoans (7%) were the remarkable biomass components in Hornsund. Two species of chaetognaths – *E. hamata* and *P. elegans* – were found in both fjords; in Hornsund their shares of the biomass of chaetognaths were similar (52% and 48% for *E. hamata* and *P. elegans*, respectively), whereas in Kongsfjorden the latter was clearly more important than the former (9% and 91%). Among euphausiids, the most important species was *T. inermis*, which was 79% of the euphausiid biomass in Hornsund and 48% in Kongsfjorden. The second euphausiid present in both fjords was *Thysanoessa raschii* (9% and 23% of the euphausiid biomass in Hornsund and Kongsfjorden, respectively), while *M. norvegica* was noted only in Kongsfjorden, where it constituted 24% of the euphausiid biomass. Two important species of hyperiid amphipods were noted – *T. abyssorum*, which constituted 40% and 91% of the hyperiid biomass in Hornsund and Kongsfjorden, and *T. libellula* (60% and 9%). In Hornsund decapods were represented first by *P. pubescens* (53% of the decapods biomass) followed by *Sabinea septemcarinata* (21%) and *Pandalus borealis* (15%), while in Kongsfjorden the same species constituted 24%, 67%, and 9%, respectively, of the decapod biomass. *Clione limacina* (2%) was also a notable LZ biomass component in Hornsund.



**Figure 2** Relative water column mean abundance [ $\text{ind m}^{-3}$ ] and biomass [ $\text{mg DM m}^{-3}$ ] of zooplankton in Hornsund and Kongsfjorden in each size category: Small Zooplankton, SZ (a), Medium Zooplankton, MZ (b), and Large Zooplankton, LZ (c).

The large zooplankton Hydrozoa were remarkable only in Hornsund, and they were predominantly represented by *H. cirratus* (93%).

### 3.5. Zooplankton interannual variability

The comparison of interannual (2002, 2007, 2012, 2013) changes in holozooplankton abundance and biomass showed clear variability. The differences were not statistically significant among the years compared in Hornsund, while the differences in abundance and biomass among the years in Kongsfjorden were statistically significant (Fig. 3).

When zooplankton composition was assessed for holozooplankton species biogeographic affinity and biomass, Arctic and boreo-Arctic species together comprised nearly the same portion of the biomass in both regions in the year of the study (Fig. 4). The comparison among years showed that in 2002, 2007, and 2012 the biomass of Arctic species was higher in Hornsund than in Kongsfjorden. Even in 2012, when there was a biomass peak in Kongsfjorden caused by the very high biomass of Arctic *C. glacialis*, the contribution of Arctic species to biomass was still higher in Hornsund (Fig. 3b). In turn, the absolute biomass of Arctic species was higher in Hornsund in comparison to Kongsfjorden in 2002 and 2007 (48 vs. 25 mg DM m<sup>-3</sup> in 2002, and 66 vs. 36 mg DM m<sup>-3</sup> in

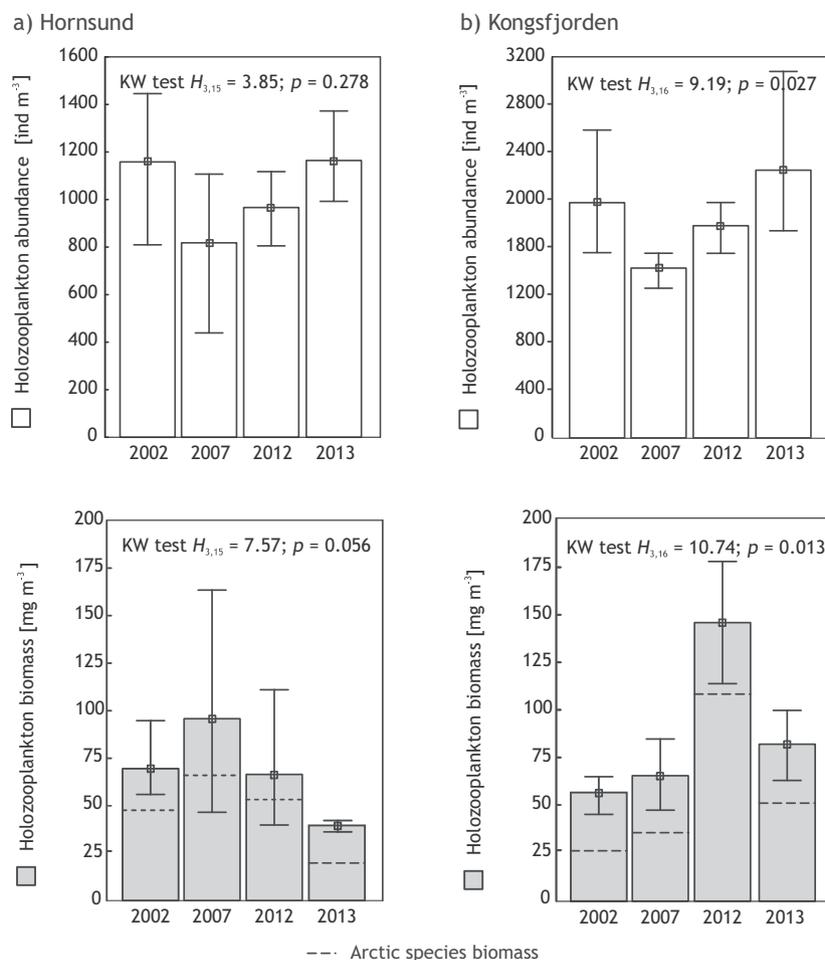
2007), while in 2012 and in 2013 the opposite was observed (53 vs. 109 mg DM m<sup>-3</sup>, and 20 vs. 52 mg DM m<sup>-3</sup>) (Fig. 3b). A comparable pattern was observed in total holozooplankton biomass changes, which were higher in Hornsund in 2002 and 2007 and lower in 2012 and 2013. The biomass in Hornsund in 2013 was the lowest in our records (Fig. 3b).

The zooplankton biomass composition assessment of holozooplankton species for trophic affinity indicated that the predominant trophic group in both fjords was the pelagic herbivores comprised mainly of *Calanus* spp. regardless of year (Fig. 5). The percentage of carnivorous zooplankton was higher in Hornsund compared to Kongsfjorden in 2002, 2007, and 2012. In 2013, the contributions of the different trophic categories to the total holozooplankton biomass were more similar between the fjords.

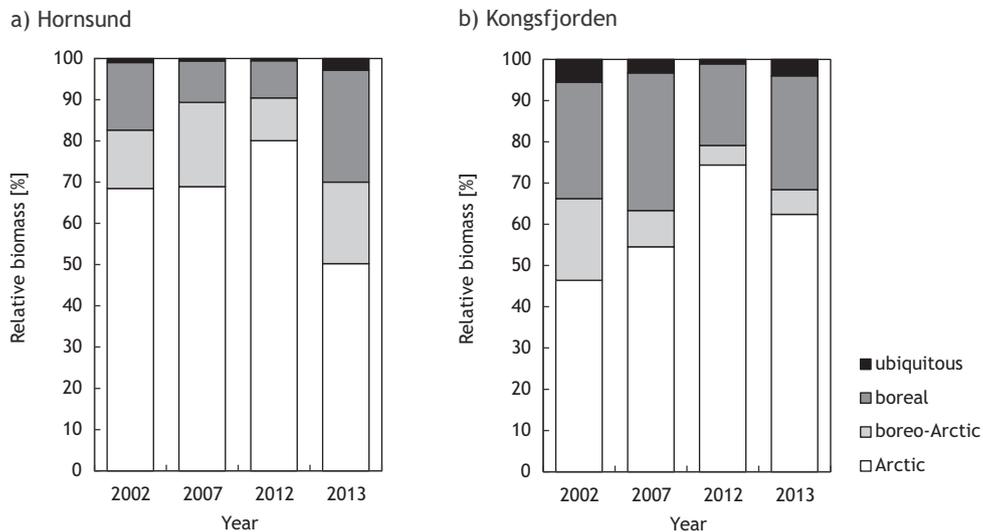
## 4. Discussion

### 4.1. Hydrography

The comparison of the interannual data on temperature, salinity, and water masses distribution in Hornsund and Kongsfjorden showed considerable interannual variability in fjord hydrography (Prominska et al., 2017a,b). Recently, it was suggested that the impact of AW on these environments



**Figure 3** Interannual variability in abundance [ind m<sup>-3</sup>] and biomass [mg DM m<sup>-3</sup>] of holozooplankton in Hornsund (a) and Kongsfjorden (b). Calculations are for zooplankton collected with an MPS/0.180 net. Bars denote ranges between min. and max.



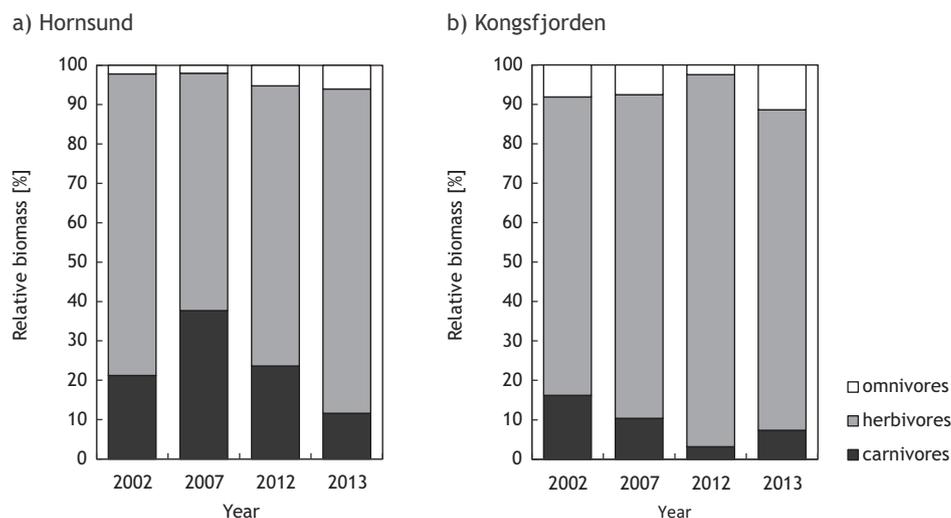
**Figure 4** Biogeographic composition of holozooplankton in Hornsund (a) and Kongsfjorden (b). Calculations are for zooplankton biomass collected with an MPS/0.180 net.

is stronger in Kongsfjorden than in Hornsund. This concurs with earlier observations based on less intense, more loosely coordinated investigations (Piwoż et al., 2009; Swerpel, 1985; Wesławski et al., 1991). However, in 2013, when this study was conducted, the influence of AW in Hornsund was stronger than in previous years, and the highest water temperature since 2001 was measured there (Prominska et al., 2017b). This explains the results of the comparison of fjord hydrography done for this study which indicated that in summer 2013 there was no difference in the mean sea water temperature in the fjords, while, simultaneously, the mean salinity was still, as expected, lower in Hornsund.

#### 4.2. Zooplankton communities in Hornsund and Kongsfjorden

Despite the lack of pronounced differences in hydrography, the 2013 zooplankton community in Hornsund can still be

considered to be more of a cold-water, Arctic character, while that in Kongsfjorden was of a mixed Arctic-Atlantic character. Earlier research suggests a similar plankton diversity pattern on the West Spitsbergen Shelf and in fjords (Gluchowska et al., 2016; Kwasniewski et al., 2010; Piwoż et al., 2009; Trudnowska et al., 2014; Weydmann and Kwasniewski, 2008). This study, however, was the first that attempted to evaluate fjord zooplankton diversity using parallel sampling with different nets done in the same year and season. Based on this unique study material, a wider size spectrum of zooplankton community components was compared for the first time in the two fjords. All of the zooplankton species and taxa recorded during this study had been observed previously in the area (Gluchowska et al., 2016; Hop et al., 2006; Koszteyn and Kwasniewski, 1989; Wesławski et al., 1991), and most of them had been noted in both locations, with a few only observed in one fjord. This agrees with earlier reports that the zooplankton communities



**Figure 5** Trophic composition of holozooplankton in Hornsund (a) and Kongsfjorden (b). Calculations are for zooplankton biomass collected with an MPS/0.180 net.

from different Spitsbergen fjords and shelf waters do not vary as much in faunal composition as they do in community structure (Gluchowska et al., 2016; Kwasniewski et al., 2010; Trudnowska et al., 2015). The differences in the presence of taxa suggest that the occurrence in Hornsund of the hydromedusae *H. cirratus* and *B. superciliaris*, which are considered common in the Arctic (Kramp, 1959; Manko, 2015), confirm the assumption that the environment of this fjord is of a more Arctic character. The presence of the boreal Atlantic euphausiid *M. norvegica* in Kongsfjorden indicates the stronger influence of AW (Buchholz et al., 2012), which could be facilitated by the narrower shelf and deeper trench there (Prominska et al., 2017a; Svendsen et al., 2002). On the other hand, a reason for the differences observed in zooplankton composition could be the imbalanced sampling of all the specific microhabitats in the fjords, such as glacier embayments or near-bottom waters where rare species, such as the benthopelagic copepods *M. spitsbergensis* and *N. farrani*, are typically found (Schulz and Kwasniewski, 2004).

The quantitative assessment of the zooplankton communities revealed that zooplankton was less numerous and its biomass was lower per m<sup>3</sup> and in the overall standing stock (m<sup>2</sup>) in Hornsund. This agrees with findings of other studies, for example Gluchowska et al. (2016), Kwasniewski et al. (2010), Piwosz et al. (2009), and Weslawski et al. (1991), even if the comparison of results is not always straightforward. Possible explanations for the lower zooplankton concentration in Hornsund than in Kongsfjorden could be either better living conditions in a more hydrographically diverse environment, which is the situation in the frontal zones that are typically considered to favor higher plankton productivity (Munk et al., 2003; Skarøhamar et al., 2007), or the more intense influx of AW into Kongsfjorden that transports biota in from the more productive adjacent shelf (Willis et al., 2006, 2008), or both.

Zooplankton is composed of a wide spectrum of organism types and sizes (Lenz, 2000), and every net used to collect it is selective (Sameoto et al., 2000; Skjoldal et al., 2013; Tranter, 1968). Studies show that a significant zooplankton part is omitted in surveys using standard mesozooplankton nets because of the limited retention of small-sized organisms (Gallienne and Robins, 2001; Pasternak et al., 2008; Turner, 2004). Choosing to use three net types in the present study was based on the experience of earlier zooplankton research in the region and on general methodological recommendations (Sameoto et al., 2000; Skjoldal et al., 2013; Tranter, 1968). This approach increased the chances of catching a wider spectrum of plankton organisms and allowed for a more complete description of the communities studied. In terms of abundance, the most numerous metazoan zooplankton components in the studied fjords were those in the SZ size fraction. These comprised as much as 71% and 58% of the total zooplankton abundance in Hornsund and Kongsfjorden, respectively. MZ organisms were generally two times less numerous, although occasionally some of them reached abundances as high as those of SZ, whereas LZ was two orders of magnitude less abundant. In terms of biomass, the main community components were MZ (53–86%) with a marked contribution of LZ (11–45%) and a minor one of SZ (3%). The comparisons of the relative contribution of different size classes to zooplankton communities in other studies showed comparable results (Arashkevich et al., 2002; Hirche et al.,

1994) and concurred with the inherent pattern of organism size distribution in pelagic environments (Platt and Denman, 1977; Sheldon et al., 1972; Zhou and Huntley, 1997).

In Hornsund, the SZ size fraction consisted mainly of small (<0.2 mm in nominal size) copepod nauplii and small bivalve veligers, whereas in Kongsfjorden this size fraction included predominantly small copepod nauplii. Presumably, most of these were *Oithona* spp. nauplii measuring from 132 μm to 218 μm (Castellani et al., 2007), and the high concentrations of small copepod nauplii in Kongsfjorden corresponded with higher concentrations of *O. similis* in this fjord. This was observed during the present study and previously (Gluchowska et al., 2016; Lischka and Hagen, 2005; Piwosz et al., 2009). The higher abundances of bivalve veligers in Hornsund in comparison to those in Kongsfjorden were, however, a new finding. Gluchowska et al. (2016) found higher concentrations of bivalve veligers in Kongsfjorden, but this was based on data from a 0.180 mm mesh net. The present study showed that in addition to the bivalve veligers sampled with the MPS/0.180 net, there was a numerous group of smaller-sized veligers (0.146 mm mean total length) that were found predominantly in Hornsund. Bivalve veligers appear to be the most abundant meroplankton in Svalbard fjords during summer (this study, Gluchowska et al., 2016; Koszteyn and Kwasniewski, 1989; Stübner et al., 2016), but this group is not homogenous in its size structure, or, most probably, in taxonomy. Additionally, *L. helicina* veligers were important SZ organisms in Kongsfjorden. The occurrence of this holoplankton component in large amounts in summer was reported in earlier studies from this fjord (Hop et al., 2006; Weslawski et al., 2000), and it corresponds with the life cycle of this species (Gannefors et al., 2005). Presumably, the differences in the contribution of predominating small zooplankton taxa between Hornsund and Kongsfjorden could have resulted from differences in the seasonal development of zooplankton in these fjords (Gluchowska et al., 2016), but it could also be a consequence of the different impacts AW has on the fjord's marine environment, for example, by influencing the species composition of the fjord biota.

The MZ size fraction distinguished in this study can be considered the equivalent of mesozooplankton, which is probably the most studied category of zooplankton in Svalbard marine ecosystems (Gluchowska et al., 2016; Hop et al., 2002; Kwasniewski, 1990; Lischka and Hagen, 2005; Piwosz et al., 2009; Trudnowska et al., 2014; Walkusz et al., 2009) and elsewhere. The present results correspond with earlier findings (Gluchowska et al., 2016; Kwasniewski et al., 2003; Trudnowska et al., 2014; Walkusz et al., 2009; Weydmann et al., 2014), with respect to both taxonomic composition and the quantity characteristics of this zooplankton size fraction from the fjords studied. The most important mesozooplankton taxa in Hornsund and Kongsfjorden were the copepods *O. similis*, *Pseudocalanus* spp., *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*. Based on this study, it was also estimated that, overall, MZ constituted 29–50% of the total zooplankton abundance, and 53–86% of the total zooplankton biomass. This indicated that, in a simplified approach, mesozooplankton represent the main part of the zooplankton component of the Svalbard marine ecosystem. In Hornsund, which is considered to be a more Arctic system, *Pseudocalanus* spp. was more numerous and its contribution to total MZ abundance was higher, while in Kongsfjorden,

which is influenced more by AW, the most important species was *O. similis*, which corresponds with earlier findings (Gluchowska et al., 2016; Walkusz et al., 2009; Weslawski et al., 1991). The main factors responsible for the species distribution patterns observed in the two fjords with differing environments are not fully explained by this single study. However, the suggestion that *O. similis* benefits from higher concentrations of organic particles, which are its food source (González and Smetacek, 1994; Walkusz et al., 2009) and also that it probably takes advantage of the higher water temperatures found in Kongsfjorden seem plausible. This is also in agreement with the scenarios of pelagic food web modification from increasing temperature, which suggests that smaller boreal species will have increasingly important roles in the higher latitudes (Beaugrand et al., 2002, 2010; Hays et al., 2005; Wassmann et al., 2011). The abundances of other important medium-sized copepods did not differ significantly between the studied fjords; however, the slightly higher abundances of *T. borealis*, *Microcalanus* spp., and *C. hyperboreus* observed in Kongsfjorden were probably related, first of all, to the greater depths in this fjord. Characteristically, these species avoid the upper layers of the water column (Darnis and Fortier, 2014; Østvedt, 1955). In addition to copepods, taxa that made a marked contribution to the MZ fraction, but only in Kongsfjorden, were *F. borealis* and medium-sized bivalve veligers. Differences in the number of veligers could have resulted from the different seasonality in the ecosystem functioning of the two fjords; however, the higher number of *F. borealis* probably fits in with the proposed scenario of the increasing role of small particles in pelagic ecosystems experiencing warming (e.g., Beaugrand et al., 2002; Morán et al., 2010). *Oithona similis* and *Pseudocalanus* spp. were the most numerous copepods, but they were of minor importance to MZ biomass, the majority of which was comprised of three *Calanus* species: *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*. The biomass per cubic meter of these three copepods was 79% and 78% of the total MZ biomass in Hornsund and Kongsfjorden, respectively. Overall, their contribution to the total zooplankton standing stock biomass was 58% and 65%, which confirms that these copepods are the most important species in the marine ecosystems of Svalbard (e.g., Daase et al., 2007; Hop et al., 2006). The lower biomass of *C. finmarchicus* in Hornsund ( $10.71 \text{ mg DM m}^{-3}$ ) than in Kongsfjorden ( $24.19 \text{ mg DM m}^{-3}$ ) corresponds to the anticipated more Atlantic character of the latter fjord. However, some of this difference could be caused by differences in population stage composition that result from differences in seasonality between the fjords (this study, Gluchowska et al., 2016). On the other hand, higher amounts of *C. finmarchicus* in Kongsfjorden could stem from the advection of a probably more developed oceanic population (Willis et al., 2006, 2008).

The constituents of the LZ size fraction were about two orders of magnitude less numerous than the constituents of SZ and MZ, yet their abundances were about the same as those found in earlier studies on macrozooplankton in Svalbard waters (Buchholz et al., 2010; Dalpadado et al., 2016; Weslawski et al., 2000). The abundances of LZ in the present study could have been underestimated as sampling with the TT was not done in trawling mode but in vertical tow mode at the stations and also because approximately the 10 m layer above the seabed was omitted during sampling to avoid

damaging the net and contaminating the catch with bottom sediments. Recently euphausiids and amphipods were found to aggregate close to the seabed in fjords (Hirche et al., 2015), so parts of their populations could have been omitted by the sampling method. Large zooplankton organisms can be good indicators of different water masses, even if they are not very diverse (e.g., Buchholz et al., 2010). The higher abundance of *T. abyssorum* in Kongsfjorden concurred with the findings of Dalpadado et al. (2016) and was also in line with observations of Atlantic euphausiid species such as *M. norvegica* and *N. megalops* in this fjord, which suggests that AW has a marked impact on the pelagic environment of Kongsfjorden (Buchholz et al., 2010; Weslawski et al., 1991, 2000). In turn, the higher relative abundance of *T. libellula* among hyperiid amphipods and of *T. inermis* among euphausiids could be a manifestation of the more cold water character of the Hornsund environment (Buchholz et al., 2010; Dalpadado et al., 2016; Koszteyn et al., 1995). Another observation that also supports this was the higher abundance of hermit crab (*P. pubescens*) larvae in this fjord. Balazy et al. (2015) showed that this species inhabits the shallow rocky bottom south of Hornsund, from where its larvae could be transported to the fjord with the cold, coastal Sørkapp Current. This species is not as abundant on the AW-influenced coasts in the vicinity of Kongsfjorden. Hydromedusae were generally more important and diverse in Hornsund, probably because this fjord preserved a more coastal character, in contrast to the more oceanic one in Kongsfjorden, which was subjected to stronger advective flushing. Hydromedusae fauna can be richer in coastal rather than in open sea waters in this region. The finding of the Arctic-associated *H. cirratus* (Kramp, 1959; Manko, 2015) only in Hornsund and the Atlantic-associated *A. digitale* (Kramp, 1959; Manko, 2015) predominating among the hydromedusae in Kongsfjorden, adds more evidence in support of the overarching conclusion of this study which is that the pelagic ecosystem in Hornsund is of a more Arctic character while that of Kongsfjorden is more Atlantic. This concurs with the hypothesized “Atlantification” of the Kongsfjorden ecosystem (Dalpadado et al., 2016; Prominska et al., 2017a).

#### 4.3. Zooplankton interannual variability

This study found that the zooplankton communities in Hornsund and Kongsfjorden were composed of species of Arctic, boreo-Arctic, boreal, and ubiquitous biogeographic affinities that contributed different proportions in the two fjords in different years, which is an observation that corroborates the results of earlier research (Gluchowska et al., 2016; Kwasiński et al., 2003; Piwosz et al., 2009; Trudnowska et al., 2014; Walkusz et al., 2009). The comparison of the interannual changes in the composition of mesozooplankton suggests that in Hornsund between 2002 and 2012 the contribution of Arctic and boreo-Arctic species was higher than in Kongsfjorden, whereas it diminished substantially in 2013. Simultaneously, in previous years the contribution of Arctic and boreo-Arctic species was lower in Kongsfjorden than in Hornsund on account of the important admixture of boreal (Atlantic) and ubiquitous species, while in the year of the study it was equal to that in Hornsund. The changes observed in zooplankton biogeographic composition are supported by hydrographic observations (Prominska et al., 2017b).

The high percentages of Arctic and boreo-Arctic species in Hornsund between 2002 and 2012 occurred during a time when AW inflows into the fjord were low, while the lowest contribution of these species in 2013 coincided with the highest influx of AW masses observed during the hydrographic time series (2001–2013). An analogous relationship was observed between the biogeographic composition of the zooplankton and the hydrography in Kongsfjorden. In years when the contribution of Arctic and boreo-Arctic species was relatively low, the presence of AW in the fjord was low. When an exceptionally high proportion of Arctic species represented mainly by *C. glacialis* was noted in 2012, the hydrographic data showed the lowest amount of AW in Kongsfjorden. The return to an increased proportion of boreal (Atlantic) and ubiquitous species in 2013 was associated with the marked presence of AW in the fjord.

Changes in total zooplankton abundance and biomass in the years studied oscillated somewhat and were statistically significant only in the very dynamic environment of Kongsfjorden. Variations in total biomass could suggest decreasing biomass in Hornsund and increasing in Kongsfjorden. These fluctuations were mainly associated with variations in the biomass of Arctic species. The general reason for increasing zooplankton biomass in Kongsfjorden could be its higher phytoplankton productivity (Hop et al., 2002; Piwosz et al., 2009; Smola et al., in press). Arctic species could benefit from increased food availability or from increased temperature if it remained within their range of tolerance, so they could perform at higher rates (Weydmann et al., 2015) and achieve higher productivity. In contrast, the strongest AW influx in 2013 in Hornsund coincided with decreased total zooplankton biomass and also the lower biomass of Arctic species. This could be interpreted as a short term effect of disturbance (Lindahl and Perissinotto, 1987), which was manifested as the removal of the original, Hornsund, Arctic fauna and the replacement of it with advected, WSC Atlantic fauna, followed by a lack of acclimation allowing the components of one or both of the biota to take advantage of the new circumstances, such as increased productivity, similar to that suggested for the Kongsfjorden ecosystem (Piwosz et al., 2009).

In polar marine ecosystems, in which food webs can comprise fewer components, but in which the key species are highly specialized, changes in species composition can have cascading effects and impact various trophic levels (Drinkwater, 2006; Falk-Petersen et al., 1990, 2007; Frank et al., 2005; Grebmeier, 2012; Jackson et al., 2001). The shift toward a higher contribution of boreal *C. finmarchicus* would directly alter the feeding conditions of the little auk, *Alle alle* (Jakubas et al., 2011; Kwasniewski et al., 2010). Another important effect of changes in the taxonomic composition of the zooplankton community associated with changes in hydrography, appears to be the increase in the proportion of ubiquitous species, mainly small *O. similis* that is linked with a higher admixture of AW. Small-sized copepods do not contribute as much to the zooplankton biomass in high latitude regions as do the larger species of the genus *Calanus* and *Metridia* (Ashjian et al., 2003; Hopcroft et al., 2005; Svensen et al., 2011; present study); however, this is expected to change along with the warming of Arctic ecosystems. Studies suggest the role of small copepods in ecosystem functioning is essential (e.g., Gallienne and Robins,

2001). The advantage of small taxa in future warmer systems, in addition to the general rule of biota responding positively to temperature (Huntley and Lopez, 1992), is their high fecundity and fast growth rates, which are possible because of their effective feeding on small-sized particles and omnivory. These features mean small species are less affected by rapid changes in environmental conditions (Ward and Hirst, 2007), which would favor an increase in their importance in warming, Arctic seas. Changes in size structure of zooplankton communities are suggested to be of greater importance to ecosystem functioning than changes in the zooplankton biomass (Lane et al., 2008; Richardson and Schoeman, 2004). One of the reasons for this could be the potential role of small copepods, like *O. similis*, as mediators between microbial and classical food webs (Svensen et al., 2011). Hence, more focus should be put on determining the roles of the small size fraction of zooplankton since their role in future Arctic ecosystem functioning would increase.

The trophic composition of the zooplankton communities in both the fjords was predominated by herbivorous species. In Hornsund, a somewhat higher contribution of carnivores represented by the chaetognaths *P. elegans* and *E. hamata* was observed. In contrast, carnivores were less abundant in Kongsfjorden, and they were mainly represented by *P. elegans* and *T. abyssorum*. Blachowiak-Samolyk et al. (2007) and Hirche et al. (1994) found chaetognaths and hyperiid amphipods to be the most numerous carnivores in Arctic pelagic ecosystems. Comparisons of holozooplankton trophic composition over the years suggest decreasing contributions of carnivorous taxa in both of the fjords studied. This could suggest a modification toward the growing importance of smaller, omnivorous zooplankton and, as a consequence, the greater dissipation of carbon in the environment (e.g. Wassmann et al., 2011; Weslawski et al., 2011).

## 5. Conclusions

The results of our study corroborate with earlier findings and confirm that historically the zooplankton communities in Hornsund and Kongsfjorden have been formed by a mixture of organisms originating from the Atlantic Subarctic Province and the Boreal Polar Province. In recent years, however, the faunal composition, abundance, and biomass of zooplankton have undergone changes linked to variations in hydrographic conditions. This study indicates the possible directions of modifications in zooplankton communities in Arctic shelf seas impacted by 'Atlantification', a phenomenon related to increasing advection of Atlantic-origin waters and their biota to Arctic systems. The observed differences between zooplankton communities from Hornsund and Kongsfjorden were substantial and concerned every zooplankton size fraction. We conclude that the results of this study confirm the working hypothesis that Atlantic water influence supports higher concentrations of small and medium zooplankton, mainly of boreal and ubiquitous affinity, a feature observed primarily in Kongsfjorden. The study also found an increase of the biomass of zooplankton in Atlantic influenced Kongsfjorden, possibly because of positive effect on Arctic fauna of increasing temperature, which changed within the species tolerance range. In case of Hornsund, the strong impact of waters of Atlantic origin in 2013 left a visible mark on the pelagic environment and the zooplankton community,

weakening its typical Arctic character and decreasing biomass, most likely due to disturbance effect.

The results of the study do not signal that the environmental changes observed as a consequence of the increasing impact of Atlantic waters on Arctic shelf ecosystems will have immediate negative effects on Arctic zooplankton. However, scales of these effects most likely depend on extent of the temperature increase, rate of water mass exchange, and perseverance of the phenomena. The effects can also have a tendency to accumulate, leading to a tipping point and changes which will be irreversible and negative.

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