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Original Article

Interannual zooplankton variability in the main pathways of the Atlantic water flow into the Arctic Ocean (Fram Strait and Barents Sea branches)

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Atlantic water (AW) carries large amounts of salt, oceanic heat, and biological richness into the Arctic Ocean. The inflow of AW has a two-branch structure via the West Spitsbergen Current (WSC) in the Fram Strait and the Barents Sea Opening (BSO), and the impact of AW on the Arctic Ocean ecosystem depends on the entrance route. Using data collected during the summers of 2001–2014, the zooplankton standing stock and community structure were studied in these two branches. Generally, there was a higher abundance and biomass of *Calanus finmarchicus* in the BSO than in the WSC, where *Oithona* spp. numerically dominated. The observed AW temperature and volume flux modifications measurably affected zooplankton variability, with additional effects likely related to diverse contributions of advected and local zooplankton production. During the study period, the AW temperature in both branches increased noticeably but in an oscillating manner. This gradual change manifested as *C. finmarchicus* forming an increasing proportion of the biomass. The high abundances of *Oithona* spp. (predominantly *O. similis*) and *C. finmarchicus* were attributed to warm AW temperature anomalies. During the warm event in 2011, predomination of young copepodids of *C. finmarchicus* in the WSC was observed, which represented probably the second generation of the species, reported from this region for the first time. The obtained results show the effects of warming on the zooplankton community transported with the Atlantic water, before they enter the Arctic Ocean. In practical terms, the findings can be used to construct and tune the plankton components of ecosystem models.

Keywords: Atlantic water, Barents Sea, *Calanus*, West Spitsbergen Current, zooplankton.

Introduction

The northward penetration of warm Atlantic water (AW) into the Arctic Ocean not only affects its thermal conditions and the sea ice cover (Beszczynska-Möller *et al.*, 2012; Onarheim *et al.*, 2014) but also determines the stock and structure of primary producers and of secondary and higher trophic level consumers, through its supply of nutrients and drifting organisms (Mumm, 1993; Kosobokova and Hirche, 2000; Bluhm *et al.*, 2015; Wassmann *et al.*, 2015). Atlantic water is carried poleward

through the Nordic Seas by two branches of the Norwegian Atlantic Current (NwAC), a baroclinic branch linked to the Arctic Front and a barotropic shelf break jet (Mork and Skagseth, 2010). Northwest of Norway, the latter flow further splits into two branches. One part of the flow turns eastward into the Barents Sea Opening (BSO) (Ingvaldsen *et al.*, 2004a; Smedsrud *et al.*, 2013), while the larger portion enters the Fram Strait and continues northward along the continental shelf break as the West Spitsbergen Current (WSC) (Gascard *et al.*, 1995;

Walczowski *et al.*, 2005). Most of the AW is transported northward in the WSC core, a fast current confined to the shelf break. On the way through the Fram Strait, the AW flowing towards the Arctic Ocean preserves its warm core while its upper part becomes transformed into a colder and less saline surface layer (Furevik *et al.*, 2002). The AW branch going into the Barents Sea, on the other hand, enters a relatively shallow shelf sea with weak bathymetric gradients, making the AW flow in this region wider and slower than the WSC. When passing through the Barents Sea, the AW is strongly modified by cooling via its interaction with the atmosphere (Schauer *et al.*, 2002). The long-term mean AW inflow to the Barents Sea has been estimated as 1.3 Sv (Ingvaldsen *et al.*, 2004a; Smedsrud *et al.*, 2013), while in the northern Fram Strait, the WSC carries an average of 3.0 Sv of AW (Beszczynska-Möller *et al.*, 2012). In the Nordic Seas, marked increases in the temperature and salinity of AW have been observed since the 1990s (Turrell *et al.*, 2003; Holliday *et al.*, 2008), however, warm AW anomalies and positive linear trends are not necessarily accompanied by similar trends in AW volume transport (Skagseth *et al.*, 2008; Beszczynska-Möller *et al.*, 2012).

It is reasonable to assume that zooplankton production in the Nordic Seas and the Barents Sea, as in other regions, depends on local primary production (Richardson and Schoeman, 2004), but advective transport of organisms also contributes to local zooplankton biomass (Skjoldal and Rey, 1989; Sundby, 2000). Both top-down (predation by fish) and bottom-up (food availability, advection, and temperature changes) processes are known to control zooplankton production and biomass in these regions (Mueter *et al.*, 2009; Drinkwater, 2011). Water temperature strongly influences the geographical, vertical and seasonal distributions as well as the development and physiology of zooplankton and can be particularly important for species at the edges of their thermal niches (Greene *et al.*, 2003). High zooplankton biomass during warm years in the Barents Sea is presumably attributable to large ice-free areas, allowing for higher primary production (Ottersen and Stenseth, 2001), substantial advection of organisms (Dalpadado *et al.*, 2003; Orlova *et al.*, 2005) and high biological activity at all trophic levels (Sakshaug, 1997). The two-branch structure of the AW inflow significantly influences the Arctic ecosystem, as transport along two different pathways allows plankton species to expand their distributions (Speirs *et al.*, 2006), leading to changes in biodiversity, abundance and production levels in these regions. Under warming conditions, increased diversity at each trophic level caused by the expansion of species' ranges may weaken trophic interactions in ecosystems (Johannesen *et al.*, 2012).

The zooplankton community in the Fram Strait and western Barents Sea is characterized by the high dominance of a small number of species (Weydmann *et al.*, 2014). The copepods *Calanus finmarchicus* and *Oithona similis* dominate in terms of abundance, while the biomass of *C. finmarchicus* can be at least one order of magnitude greater than those of other species (Conover, 1988). Several studies in the past few decades have shown that the zooplankton community has changed considerably throughout the North Atlantic in response to changes in temperature (Beaugrand *et al.*, 2002; Beaugrand, 2004; Licandro *et al.*, 2011). There have been also observations of northern shifts in the latitudinal extensions of warm-water boreal species (Weydmann *et al.*, 2014; Busch *et al.*, 2015) and parallel decreases in the numbers of colder-water, subarctic and arctic species. Although zooplankton dynamics have multiple consequences for

ecosystem functions and biogeochemical cycles, the baseline information on the spatial and temporal heterogeneity of zooplankton in the regions of the AW inflow into the Arctic Ocean is insufficient. Previous research on zooplankton has been performed in single pathways of the AW flow (Skjoldal and Rey, 1989; Mumm *et al.*, 1998; Arashkevich *et al.*, 2002; Carstensen *et al.*, 2012; Dalpadado *et al.*, 2012; Weydmann *et al.*, 2014). However, one way to better understand the influence of the hydrographic characteristics of the AW flow on the pelagic ecosystem is to undertake comparative studies, especially those based on long-term data series.

The main goal of this study was to evaluate the effects on the zooplankton community of the interregional and interannual variability in the AW flow through the WSC and BSO branches. Particular attention was paid to *C. finmarchicus* not only because it is among the most abundant zooplankton species in the Nordic Seas but also because it is the most notable example of an Atlantic expatriate into the Arctic Ocean (Hirche and Kosobokova, 2007).

The work was aimed to explore:

- (i) the variation in regional oceanographic conditions in the two branches of the AW inflow using a long-term data series (1998–2014);
- (ii) interregional and interannual differences in the zooplankton composition and standing stock during the study period (2001–2014);
- (iii) links between the regional oceanographic conditions (AW temperature and volume transport) and their changes, and the associated zooplankton community.

Material and methods

Zooplankton sampling and sites

Zooplankton samples were collected at 114 stations located in the WSC (72 stations) and BSO regions (42 stations; Figure 1, Table 1) over a 14-year period (2001–2014). The monitoring cruises were conducted by the Institute of Oceanology of the Polish Academy of Sciences (IO PAN, both regions) and the Institute of Marine Research in Norway (IMR; BSO region) every year from late June to mid-July (Table 1). In this study, the BSO was defined as a part of the section between Fugløya and Bjørnøya (FB), limited by 72°N and 73.5°N latitude, whereas the WSC region was defined as the region in eastern Fram Strait between 75°N and 76.5°N. The zooplankton samples were collected with a WP-2 net (mouth opening 0.25 m², 180 µm mesh), in vertical hauls from a depth of 200 m to the surface (IO PAN stations) and from the bottom to the surface (IMR stations). The zooplankton samples were preserved in a 4% formaldehyde solution in seawater buffered with borax.

The zooplankton were identified to the lowest possible taxonomic level using a sub-sampling method (Postel, 2000). *Calanus* were identified to the species level for each developmental stage (copepodids I–VI, CI–CVI), based on the description in Kwasniewski *et al.* (2003). Copepods of the genus *Oithona* comprised two species: *O. similis* and *O. atlantica*, but due to the low abundance of *O. atlantica*, the two species were grouped and treated as *Oithona* spp. in the long-term analysis. Quantification of the biomass in the IMR samples was done directly, the collected zooplankton were dried and weighed in the laboratory. The sampling procedure is described in more detail in Dalpadado

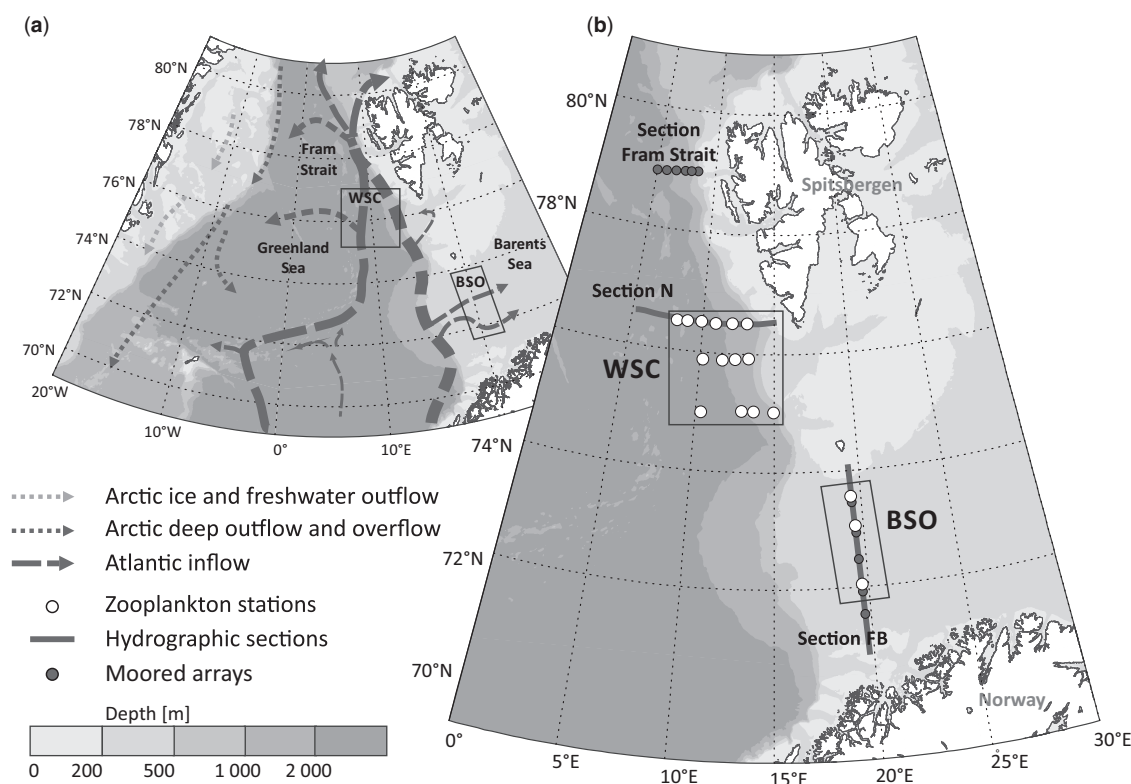


Figure 1. The circulation scheme in the Nordic Seas (simplified after Beszczynska-Möller *et al.*, 2012) (a) and a map of the study area (b) showing the locations of zooplankton sampling stations, the annually repeated hydrographic sections (N and FB) and the locations of the moored arrays monitoring the AW volume flux (sections Fram Strait and FB).

et al. (2012). The zooplankton biomass in the IO PAN samples was calculated from the abundance data and the individual dry mass values or weight-length relationships obtained from the literature (for *Calanus* and *Oithona* species, see Table 2; for other species, see Gluchowska *et al.* (2017) and references therein). The zooplankton abundance and biomass at all stations were expressed as the number of individuals or as mg of dry mass per cubic metre (ind. m⁻³ and mg m⁻³, respectively). The *C. finmarchicus* stage index was calculated as the abundance-weighted mean life stage, with stages given values from 1 (CI) to 6 (CVI).

Regional oceanography

To describe the physical environment in the two studied regions, conductivity-temperature-depth (CTD) measurements from the hydrographic surveys carried out by IO PAN in the studied area since 1997, were employed. A Sea-Bird 911+ CTD instrument mounted on a rosette was used to measure the full depth profiles. The errors were estimated as 1 dbar for pressure, 0.001 °C for temperature, and 0.002 for salinity. We analysed section FB, located between Norway and Bear Island (70°30'–74°15'N, 19–20°E; Figure 1) to characterize the hydrography in the BSO region, while section N (76°30'N, 4–15°E; Figure 1) represented the WSC region.

Time series of the AW volume flux through the Barents Sea and the Fram Strait were obtained from year-round measurements of temperature and sea currents at two moored arrays. One was a moored array in the Barents Sea Opening operated by IMR (Ingvaldsen *et al.*, 2004b), while the other array was maintained in the northern Fram Strait (along 78°50'N, covering the WSC) by

the Alfred Wegener Institute for Polar and Marine Research (Beszczynska-Möller *et al.*, 2015). Details on the data treatment and the calculation of monthly volume fluxes can be found in Ingvaldsen *et al.* (2004b) and Beszczynska-Möller *et al.* (2012). In this study, for each year, the AW volume flux calculated as the March–June average of the monthly mean values was used.

Data analysis

The mean temperature and salinity of the Atlantic water, defined based on Rudels *et al.* (2005) as the water mass with a temperature $T > 2$ °C and a potential density $27.7 > \sigma_\theta > 27.97$, were calculated for the entire FB and N hydrographic sections and for each individual zooplankton station. Additionally, to support the analysis of the zooplankton data, the water temperature and salinity were averaged for each sampled zooplankton depth stratum, regardless of the water mass. To study the interannual variability in the regional oceanography, the AW temperature anomalies from the FB and N sections were obtained by removing the linear trends from the AW temperature time series, using the equation $x_2 = x_1 - (a + bt)$, with coefficients a and b estimated from the data using the least-squares method. 'Warm' and 'cold' summers were selected based on the time series of the AW anomalies in the BSO (FB section) and WSC (N section) regions, for which the AW temperature anomaly was either higher ('warm') or lower ('cold') than 0.75 of the standard deviation of all anomalies in the analysed section (Schlichtholz and Houssais, 2011).

Various descriptors of zooplankton community such as: (1) the zooplankton community structure (restricted to IO PAN

Table 1. Number of stations at which zooplankton samples were collected in the two areas of Atlantic water pathways into the Arctic—the Fram Strait (WSC) and the Barents Sea (BSO).

	Latitude [°N]	Depth [m]	Institution	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
BSO	72.0	310–0	IMR	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	200–0	IO PAN					1	1	1	1	1	1	1	1	1	1	1
	73.0	410–0	IMR				1										
	200–0	IO PAN					1	1	1	1	1	1	1	1	1	1	1
	73.5	480–0	IMR	1	1	1	1	1	1	1	1	1	1	1	1	1	1
WSC	200–0	IO PAN					1	1	1	1	1	1	1	1	1	1	1
	Total			2	2	2	3	3	5	5	4	4	3	4	3	2	5
	Date of sampling			15.06	15.06	15.06	23–24.06		17–21.06	20–29.06	22–27.06	21–26.06	19–22.06	6–29.06	27.06	29.06	18–29.06
	75.0	200–0	IO PAN	3	2	2	1	3	2	1	1	3	2	2	3	3	3
	75.9	200–0	IO PAN	2	1	1	1	1	1	1	2	2	1	1	1	1	2
Date of sampling	76.5	200–0	IO PAN	2	2	2	2	3	1	1	2	2	2	1	6	4	4
	Total			7	5	5	3	7	3	3	5	7	5	4	9	9	9
	1–7.07			1–7.07	2–6.07	1–6.07	2–4.07	30.06–5.07	6–7.07	29.06–13.07	29.06–5.07	27.06–3.07	28.06–8.07	1–12.07	27.06–12.07		1–10.07

Table 2. Dry mass of *Calanus* and *Oithona* species and the prosome lengths used to calculate these biomass estimates.

Species	Copepodid	Mean length of prosome		Dry mass	
		[mm]	Source	[mg]	Source
<i>C. finmarchicus</i>	CI	0.680	1–7	0.005	5, 8–10
	CII	0.926	1–6	0.011	5, 8–10
	CIII	1.315	1–6	0.029	5, 8–10
	CIV	1.734	1–2, 4–7, 11	0.075	5, 8–10
	CV	2.330	1, 4–7, 11	0.214	5, 8–10
	CVI F	2.562	1, 4–6, 11	0.282	5, 8–10
<i>C. glacialis</i>	CVI M	2.253	5–6, 12	0.139	5, 8–10
	CI	0.927	2–4, 13	0.009	5, 8–10
	CII	1.306	2–4, 13	0.022	5, 8–10
	CIII	1.813	2–4, 13	0.062	5, 8–10
	CIV	2.481	2, 4, 11, 13	0.198	5, 8–10
	CV	3.337	1, 4, 11, 13	0.620	5, 8–10
<i>C. hyperboreus</i>	CVI F	3.887	1, 4, 11, 13	1.303	5, 8–10
	CVI M	3.650	12	0.987	5, 8–10
	CI	1.039	4, 14	0.011	5, 8–10
	CII	1.633	4, 14	0.029	5, 8–10
	CIII	2.474	4, 13–14	0.112	5, 8–10
	CIV	3.520	7, 12, 13–14	0.378	5, 8–10
<i>O. similis</i>	CV	4.920	7, 12, 13–14	1.209	5, 8–10
	CVI F	6.721	7, 11–14	3.293	5, 8–10
<i>O. atlantica</i>	CVI M	4.720	12	0.874	5, 8–10
		0.500	15	0.002	16
		0.690	15	0.007	16

Sources: 1. J. Koszteyn and S. Kwasniewski—WSC (unpublished data); 2. Kwasniewski et al., 2003; 3. Grainger, 1963 4. Hirche et al., 1994 5. Hay et al., 1991 6. Karlson and Båmstedt, 1994 7. Diel and Breteler, 1986 8. Hirche et al., 1991 9. Mumm, 1991; data converted from ash free dry mass (AFDM), assuming AFDM/dry mass = 0.9 (Båmstedt, 1986) 10. Båmstedt et al., 1991 11. S. Kwasniewski—WSC, Bear Island (unpublished data) 12. Brodsky, 1983 13. Koszteyn and Kwasniewski, 1992 14. Sømme, 1934 15. S. Kwasniewski—WSC, west of Spitsbergen (unpublished data); 16. Hopcroft et al., 1998.

collections), (2) the zooplankton standing stock (total zooplankton abundance and biomass), (3) *C. finmarchicus* abundance and biomass, (4) *C. finmarchicus* stage composition and stage index and (5) *Oithona* spp. abundance; were used to test for inter-regional and interannual differences.

Non-parametric permutational ANOVA (PERMANOVA) (Anderson et al., 2008), with two fixed factors was used to test for differences in the zooplankton community structure (full and complete data available only for IO PAN data) between the regions (WSC and BSO) and among years (2006–2014). The Bray-Curtis similarity was used to calculate the resemblance matrix for the relative abundance data. The calculation of pseudo-F and *p*-values was based using type III sums of squares, to account for unbalanced data (varying number of stations for each region x-year combination), and 999 permutations of the residuals under a reduced model. Unbiased estimates of each of the components of the variation (ECVs) were calculated from mean squares to compare the amounts of variation attributable to different factors in the model. The PERMDISP test was used to test the homogeneity of multivariate sample dispersions between the studied regions (Anderson et al., 2008). Additionally, one-way PERMANOVAs were used to test for differences in the zooplankton community structure among years separately for each region, using the full available time series data (WSC: 2001–2014; BSO: 2006–2014). The pattern of multivariate zooplankton community

Table 3. Comparison of hydrographic properties and selected descriptors of the zooplankton community in the WSC and BSO regions pooled for all available years.

	WSC			BSO			Mann-Whitney U-test	
	<i>n</i>	Mean \pm SE	Min.–Max.	<i>n</i>	Mean \pm SE	Min.–Max.	<i>Z</i>	<i>p</i>
Temperature [°C]	72	4.94 \pm 0.09	3.52–6.6	42	5.87 \pm 0.10	4.50–6.81	–5.82	<0.001
Salinity	72	35.12 \pm 0.01	35.03–35.18	42	35.12 \pm 0.01	35.00–35.18	–0.29	0.773
AW temperature [°C]	72	4.01 \pm 0.06	3.23–5.12	42	5.19 \pm 0.13	3.79–6.45	–6.95	<0.001
AW salinity	72	35.10 \pm 0.01	35.04–35.15	42	35.11 \pm 0.01	35.04–35.16	–2.64	0.008
AW volume transport [Sv]	15	2.90 \pm 0.15	1.80–3.82	17	1.72 \pm 0.15	0.78–3.10	4.08	<0.001
Total zooplankton abundance ^a [ind. m ^{–3}]	72	883.6 \pm 66.1	153–2924	22	1066.5 \pm 152.6	265–2736	–0.42	0.678
<i>C. finmarchicus</i> abundance [ind. m ^{–3}]	72	129.0 \pm 13.7	13–527	42	357.3 \pm 61.9	17–1920	–3.56	<0.001
<i>Oithona</i> spp. abundance [ind. m ^{–3}]	72	411.7 \pm 29.2	28–1016	42	244.6 \pm 38.5	16–1125	4.06	<0.001
Total zooplankton biomass [mg m ^{–3}]	72	36.7 \pm 2.7	7–132	42	40.9 \pm 5.3	5–192	0.11	0.911
<i>C. finmarchicus</i> biomass [mg m ^{–3}]	72	20.9 \pm 2.4	1–110	42	30.2 \pm 4.2	3–145	–2.13	0.033
<i>Oithona</i> spp. biomass [mg m ^{–3}]	72	1.2 \pm 0.1	1–3	42	0.7 \pm 0.1	0–3	4.24	<0.001

^aTotal zooplankton abundance only for IO PAN data. Statistically significant ($p < 0.05$) U-test values are shown in bold.

structure was illustrated using metric multidimensional scaling (mMDS) ordination. Additionally, canonical analysis of principal coordinates (CAP) was used to visualize the variability along the two axes that best discriminated among the groups of samples defined by years (separately for each region). Spearman rank correlation vectors of species relative abundances with axes were overlaid on the mMDS and CAP plots.

To test for differences between the regions in the hydrographic properties and the selected univariate descriptors of zooplankton (standing stock, *C. finmarchicus* abundance and biomass, *C. finmarchicus* stage index, *Oithona* spp. abundance), a nonparametric Mann-Whitney U-test was used. The relationships between AW temperature, AW volume transport and the selected univariate zooplankton characteristics were examined using Pearson's product-moment correlation.

All described statistical analyses were performed using PRIMER 6 and PERMANOVA+ (Clarke and Warwick, 2001; Anderson *et al.*, 2008) and STATISTICA 10 (StatSoft, Inc.). The significance level for all statistical tests used was $p = 0.05$.

Results

Interregional variability

During the study period of 2001–2014, the mean seawater temperature, as well as the mean AW temperature, within the zooplankton sampled depth stratum as well as the mean AW temperature, were significantly higher in the BSO than in the WSC region, whereas the AW transport was greater in the WSC region. The mean salinity in the zooplankton sampled depth stratum was comparable between the two regions, while the mean AW salinity was slightly higher in the BSO than in the WSC region (Table 3).

There was no definite pattern in the variation of the total zooplankton abundance and biomass across the two regions (Table 3), however, the PERMANOVA analysis indicated significant effects of both REGION (MS = 15875.0, pseudo- F = 19.33, p = 0.001) and YEAR (MS = 2114.4, pseudo- F = 2.58, p = 0.001) on the zooplankton community structure studied over 2006–2014. REGION had a stronger effect than YEAR, as indicated by the higher ECV (29.8% vs. 17.5%), but both shaped the observed zooplankton variability. The vectors of the species plotted on the mMDS plot (Figure 2a) indicated that *C. finmarchicus*, *Oikopleura* spp., *Fritillaria borealis* and *Pseudocalanus* spp. were

the most important in shaping the zooplankton community in the BSO region, whilst *Oithona* spp. and *Triconia borealis* were the most significant for the zooplankton in the WSC region. Comparison of the zooplankton data confirmed that indeed, the abundance and biomass of *C. finmarchicus*, were higher in the BSO, while the abundance of *Oithona* spp. was twice as high in the WSC (Table 3, Figure 2b). Considering the entire study period and both regions, the abundance of *C. finmarchicus* was positively correlated with the AW temperature ($R = 0.34$, $p < 0.001$) while the abundance of *Oithona* spp. correlated negatively ($R = -0.30$, $p = 0.001$). However, a significant REGION \times YEAR interaction (PERMANOVA; MS = 1618.2, pseudo- F = 1.97, $p = 0.007$) indicated that the interregional variability in the zooplankton communities was dependent on year. Additionally, the PERMDISP analysis revealed significant differences in the dispersion of zooplankton community structure between REGIONS ($F = 11.74$, $p = 0.001$; Figure 2c), with greater variability in the BSO compared to the WSC regions, suggesting that the significant PERMANOVA results were due to a combination of REGION, YEAR, and dispersion effects. Furthermore, a high ECV value for the residuals (34.1%) indicated large variability among the replicate samples.

Interannual variability–WSC region

During the years 1997–2014, positive linear trends were observed in both the AW temperature and salinity (Figure 3a; Pearson's product-moment correlation: $R = 0.83$, $p < 0.001$, and $R = 0.92$, $p < 0.001$, respectively), overlaid on periodically occurring increases and decreases in both properties. The time series of the summer AW temperature showed a positive trend of ~ 0.56 °C per decade (black line). There was a statistically significant relationship between AW volume transport (measured at moorings in the northern Fram Strait) and AW temperature at the section N (in the southern Fram Strait); therefore, on the interannual time scale, high AW temperatures are linked to increased mean March–June AW transport (Pearson's product-moment correlation: $R = 0.52$, $p = 0.032$). During the period 1998–2012, the mean AW volume flux into the Fram Strait varied from 1.80 Sv to 3.82 Sv (Table 3).

Changes in the zooplankton community were assessed using year-oriented canonical analysis of principal coordinates, CAP

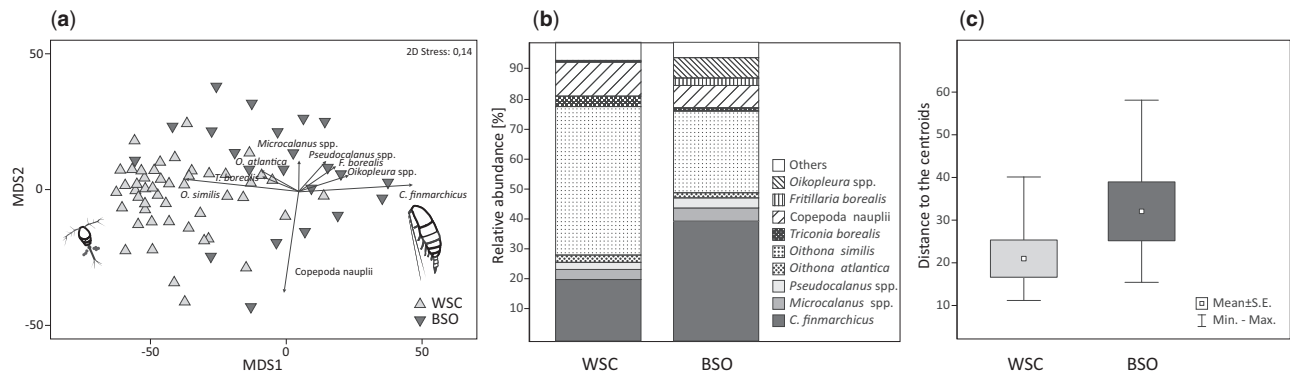


Figure 2. Two-dimensional metric multidimensional scaling (mMDS) ordination of the zooplankton samples collected from 2006 to 2014 (only for IO PAN data). Symbols represent the WSC and BSO regions (a), the average zooplankton community structure (b) for each region and the results of the PERMDISP analysis (c) comparing the homogeneity of multivariate dispersions between the regions.

(Figure 4), which showed a gradual modification of the community structure from 2001 to 2014 (PERMANOVA: $MS = 1365.2$, pseudo- $F = 2.54$, $p = 0.001$). During 2001–2005 more important in the communities were *Aglantha digitale*, *Oikopleura* spp., *Triconia borealis* and *Oithona atlantica*, while after 2006, the zooplankton communities were characterised, among others, by higher contributions of *C. finmarchicus*, *Microcalanus* spp., Bivalvia and Gastropoda veligers. This gradual change also manifested in changes in the zooplankton biomass. During the study period, both the total zooplankton biomass (Figure 5a) and the proportion of biomass of *C. finmarchicus* (Figure 5b) gradually increased (Pearson's product-moment correlation: $R = 0.36$, $p = 0.002$, 19.2 mg m^{-3} per decade and $R = 0.59$, $p < 0.001$, 27.5% per decade, respectively), and both characteristics were positively correlated with the AW temperature (total zooplankton biomass, $R = 0.47$, $p = 0.046$; proportion of biomass of *C. finmarchicus*, $R = 0.60$, $p = 0.031$).

During the last two decades, four 'cold' (1997–1998, 2003, 2009, 2013) and three 'warm' (1999–2000, 2005–2006, 2011) events were distinguished in the hydrography of the WSC region, with two 'cold' and two 'warm' events taking place within the zooplankton study period of 2001–2014 (Figure 3b). For the WSC 'cold' summers and the WSC 'warm' summers, the AW temperature deviated from its long-term mean by approximately 0.4°C . In 2005–2006 (W1), the seawater temperature at the zooplankton stations varied between 4.55 and 6.60°C (with a mean of 1.73°C higher than during C1), and the salinity ranged between 35.12 and 35.16 (Table 4). The total zooplankton abundance during W1 fluctuated between 278 – 1158 ind. m^{-3} and was predominantly represented by *Oithona* spp. (52.1%, Figure 6), which occurred in higher absolute and relative abundances during W1 than during the rest of the study period. The abundance of *C. finmarchicus* was comparable between the W1 'warm' and WSC 'cold' summers (Figure 7), and the populations were composed predominantly of CV-CVI copepodids (67–83%, Figure 8). The second warm event W2 was observed in 2011, with a temperature ranging between 4.53 and 6.13°C (the mean was 0.84°C higher than during the C2 event). The total abundances of zooplankton exceeded those during the cold events and varied between 606 and 1024 ind. m^{-3} (Table 4). *Calanus finmarchicus* was the most numerous species during W2 (Figure 6), and the population was composed predominantly of copepodids CI–CIII (59%). Due to predominance of young copepodids during W2,

the contribution of *C. finmarchicus* to the total zooplankton biomass was relatively low (43.6–59.7%), despite the high abundance of this species, and the total zooplankton biomass was comparable to previous years (Table 4).

Interannual variability–BSO region

During the years 1998–2014, positive linear trends were observed for both the AW temperature and salinity (Figure 3a; Pearson's product-moment correlation: $R = 0.68$, $p = 0.004$, and $R = 0.80$, $p < 0.001$, respectively), and the AW temperature showed a positive trend of $\sim 0.45^\circ\text{C}$ per decade (black line). The standard deviation of the AW temperature anomalies for the BSO was $\sim 0.25^\circ\text{C}$, which was slightly larger than that for the WSC (0.19°C). The mean AW volume flux into the Barents Sea was lower than that through the Fram Strait, and during 1998–2014 the mean March–June volume flux varied from 0.78 Sv to 3.10 Sv (Figure 3c). No significant relationship between AW volume transport and the AW temperature was observed (Pearson's product-moment correlation: $R = 0.58$, $p = 0.101$).

Examination of the changes in the zooplankton community indicated a marked separation among the studied years (2006–2014; PERMANOVA: $MS = 1797.7$, pseudo- $F = 1.58$, $p = 0.043$) and a gradual modification was clearly illustrated by the year-oriented CAP ordination (Figure 4). Taxa such as *Oikopleura* spp., Bivalvia veligers, Echinodermata larvae, and *C. glacialis* were more abundant during 2006–2008, while *Oithona similis*, *O. atlantica*, and *Microcalanus* spp. predominated during 2010–2014. During the study period, the zooplankton biomass in the BSO was positively correlated with the AW volume transport (Pearson's product-moment correlation: $R = 0.70$, $p = 0.037$). The gradual changes in the AW temperature, on the other hand, manifested as changes in the zooplankton biomass structure, marked first of all in a gradual increase of the contribution of *C. finmarchicus* to the zooplankton biomass (Pearson's product-moment correlation: $R = 0.46$, $p = 0.002$, 22.8% per decade).

Two 'warm' (2006, 2011–2012) and two 'cold' (2001, 2009) events were identified in the BSO during the study period of 2001–2014. The differences in the AW temperature between the BSO 'cold' and 'warm' summers appeared to be almost twice of the magnitude (0.6°C) observed in the WSC region (Figure 3b). During W1 (2006), the seawater temperature at the zooplankton

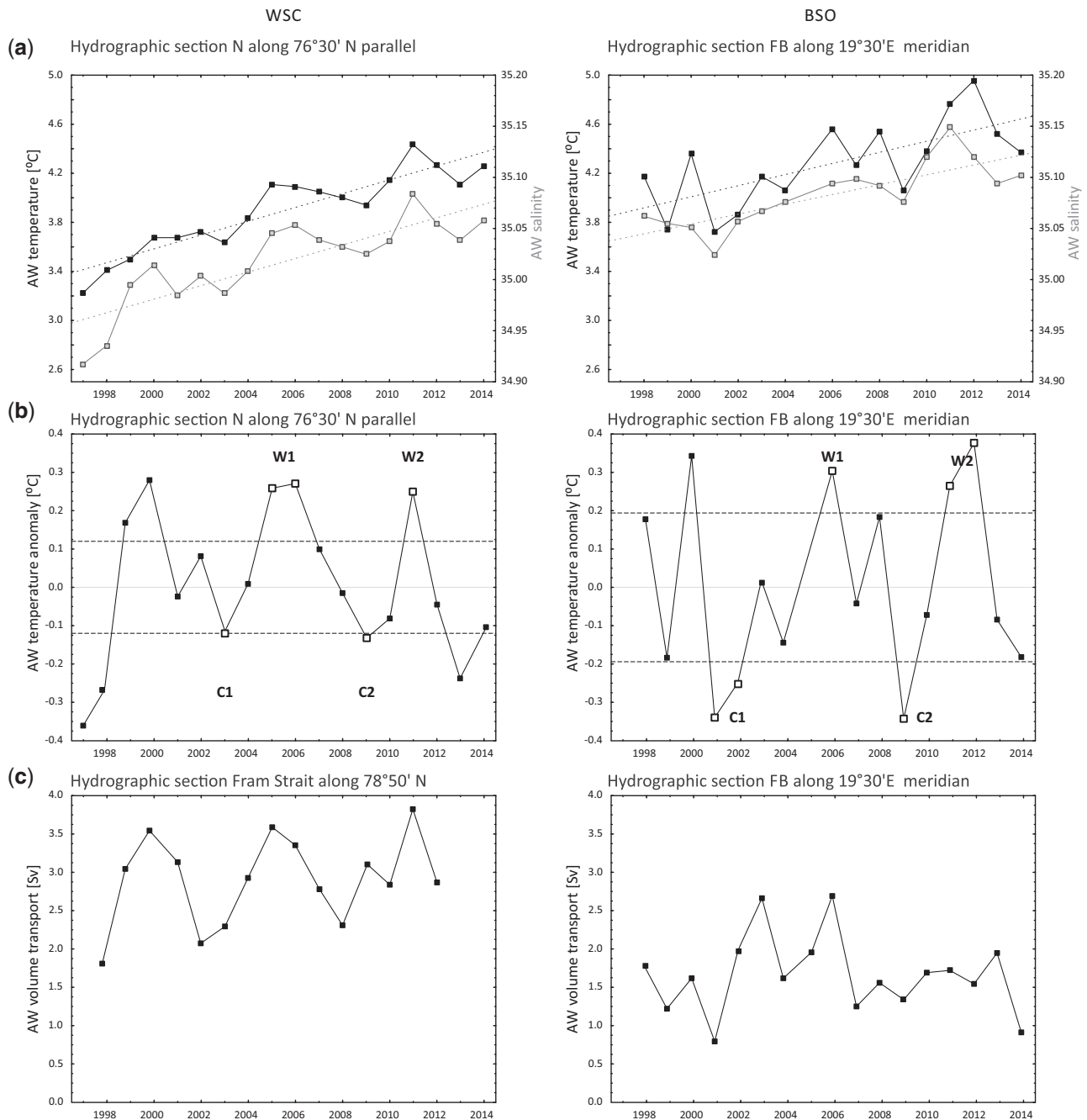


Figure 3. The time series of summer AW temperatures (filled squares) and salinities (open squares) in the hydrographic sections representing the WSC (left, section N) and BSO (right, section FB) regions (a). The dashed lines denote the linear trends. The detrended anomalies of AW temperature and ± 0.75 of their standard deviations (marked by dashed horizontal lines; C1, W1, C2, W2, and C3 indicate the cold and warm events discussed in the text) (b). Mean AW volume fluxes averaged for March–June for the areas of mooring stations representing the WSC (left, Fram Strait) and BSO (right, section FB) regions (c).

stations varied between 5.88 and 6.69 °C, and the salinity ranged between 35.12 and 35.16 (Table 4). The high total zooplankton abundance observed in W1 was due to extremely high numbers of both *C. finmarchicus* and *Oithona* spp., which exceeded five times those in C1 (Figure 7). In that summer *C. finmarchicus* constituted 42.8% of the zooplankton community (Figure 6). The

total zooplankton biomass during W1 was four times higher than in the previous cold event and was dominated by *C. finmarchicus* (79.4%, Table 4). High abundances of *C. finmarchicus* and *Oithona* spp. were also observed during the second ‘warm’ event W2 (2011–2012), during which the seawater temperature ranged between 4.71 °C and 6.37 °C, whereas the abundances of the

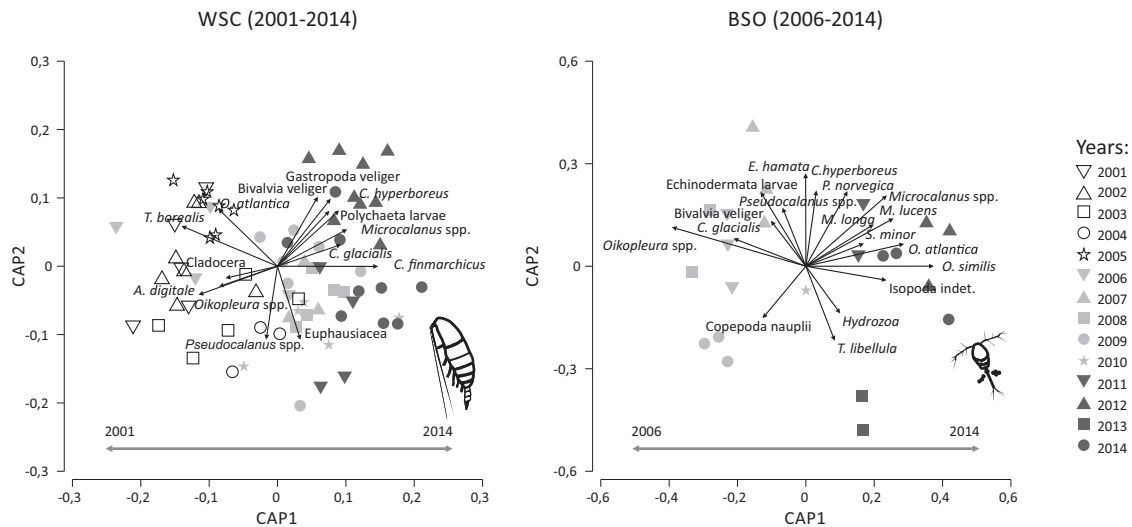


Figure 4. CAP ordinations showing the groups of samples providing the best discrimination, defined by years and based on Bray-Curtis similarities of zooplankton species relative abundances (only for IO PAN data), in the WSC (left) and BSO regions (right). Symbols represent years. Vectors indicate the species best correlated with the ordination coordinates ($r > 0.3$). Vector length corresponds to the correlation value.

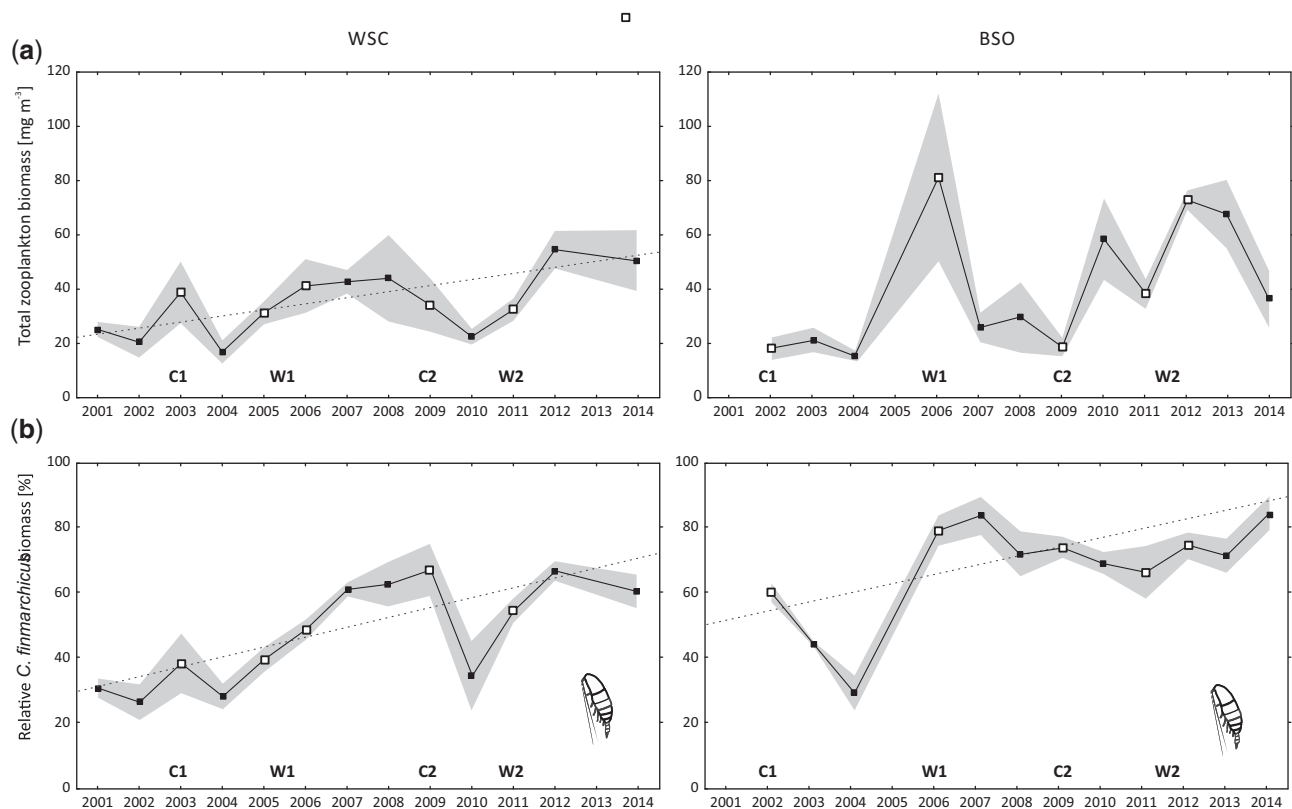


Figure 5. Time series of total zooplankton biomass (a) and relative *Calanus finmarchicus* biomass (b) in the WSC (left) and BSO (right) regions. Means and \pm standard error are presented. The dashed lines denote the linear trends. No significant trend was found between for total zooplankton biomass for the time series from the BSO.

copepods were only twice as high as in C2 (Figure 7). For total zooplankton abundance, the relative proportions of *C. finmarchicus* and *Oithona* spp. were comparable during W2 (Figure 6, 27.3 and 28.1%, respectively), but *C. finmarchicus* was the most

important species in terms of biomass (70%, Table 4). The stage index of *C. finmarchicus* was similar between ‘cold’ and ‘warm’ summers in the BSO (Figure 8), and the populations were composed predominantly of CIV-CV copepodids (66–86%).

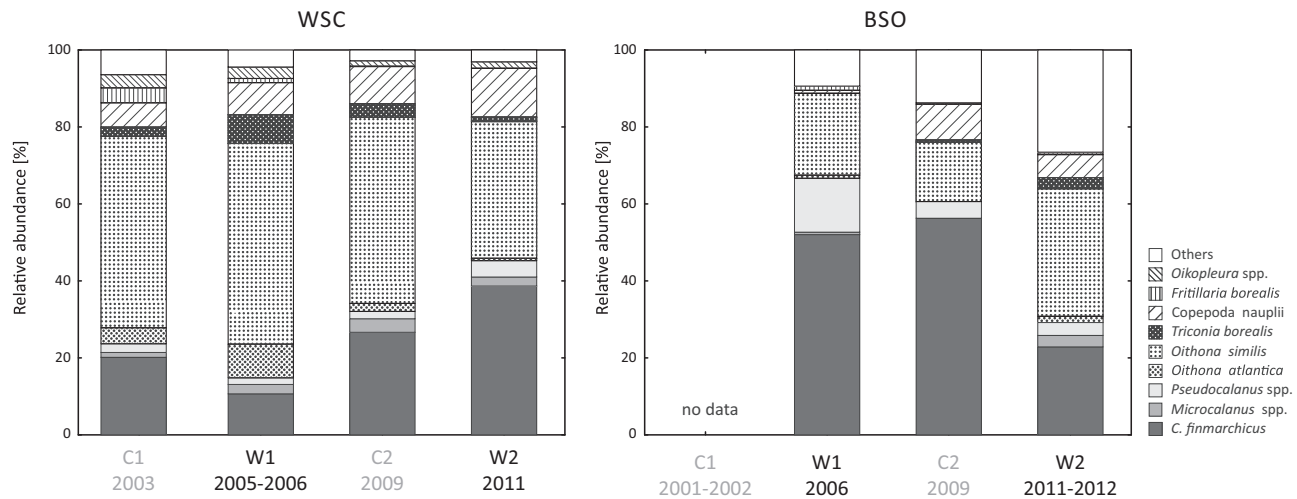


Figure 6. Relative abundance of zooplankton taxa in the WSC (left) and BSO (right) regions during 'warm' (W1, W2) and 'cold' (C1, C2) events (only for IO PAN data).

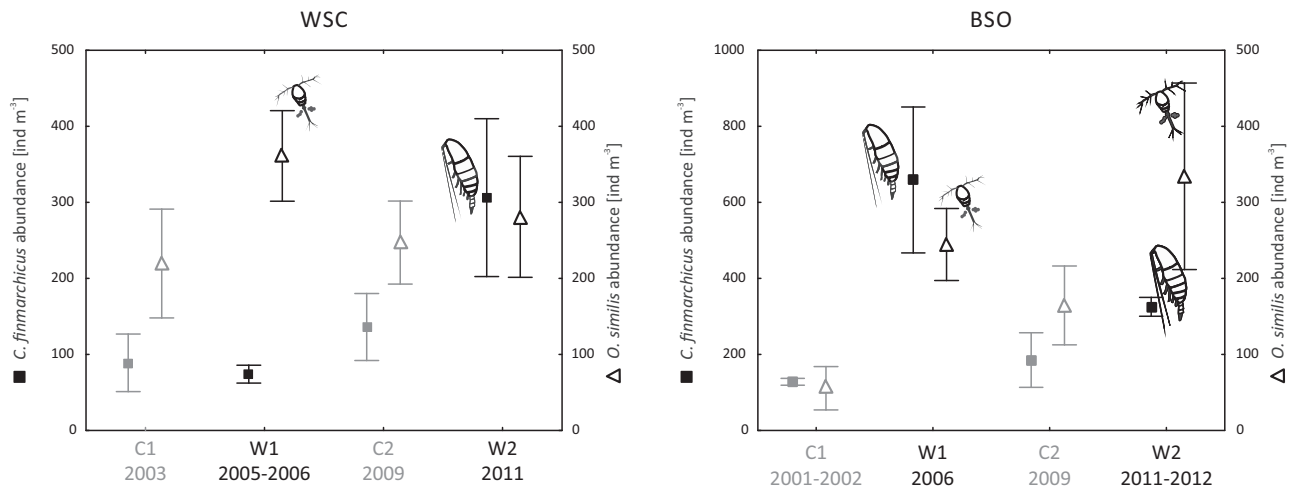


Figure 7. Abundance of *Calanus finmarchicus* (squares, solid line) and *Oithona* spp. (triangles, dashed line) in the WSC (left) and BSO (right) regions during 'warm' (W1, W2) and 'cold' (C1, C2) events. Means and \pm standard error are presented.

Discussion

Using the results of summer observations, this paper presents new information on the spatial and temporal heterogeneity of zooplankton in the regions of the AW flow through the WSC and the BSO paths. The results showed that within each of these regions the AW temperature increased noticeably. This gradual change induced the increase in total zooplankton biomass as well as in the proportion of biomass contributed by Atlantic-associated *C. finmarchicus*.

Effects of sampling strategies

Long-term studies in the marine realm, especially in Arctic ecosystems, involve trade-offs among time, extent and resolution (Hewitt *et al.*, 1998). To reduce the influence of seasonal variability on the results, zooplankton sampling was performed at the same time of the year—from late June to mid-July. The chosen sampling strategy, moving from south (BSO, late June) to north (WSC, early July), followed the expected latitudinal

differences in pelagic bloom (Leu *et al.*, 2011), and therefore seem appropriate for observing and concluding about zooplankton after the peak of pelagic production. Previous studies conducted in the adjacent seas (Dalpadado *et al.*, 2003; Weydmann *et al.*, 2014) indicated considerable regional differences in the zooplankton community structure, and the observed spatial variabilities were related to environmental discontinuities as well as to the generally heterogeneous nature of zooplankton distribution (Folt and Burns, 1999). The practical problems of sampling, and not fully understood patterns of zooplankton distribution, made that our time series were spatially limited and therefore unbalanced, like most of the zooplankton time series (Mackas *et al.*, 2012). Moreover, the WSC and BSO regions differ in terms of bottom topography. The AW branch crossing the shallow Barents Sea occupies the entire 450 m depth of the water column (average 230 m), whereas in the WSC, the AW layer extends down to 700–800 m (Beszczynska-Möller *et al.*, 2011). Therefore, we focused our research in the WSC region on the epipelagic layer based on the general pattern of zooplankton

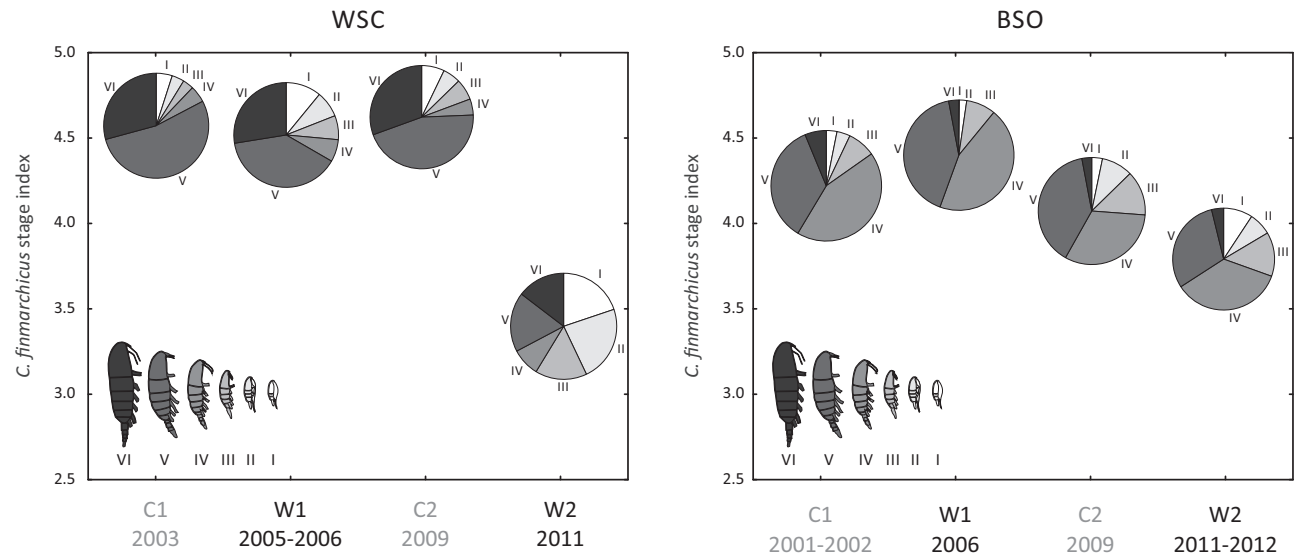


Figure 8. Mean *Calanus finmarchicus* stage indices together with stage compositions in the WSC (left) and BSO (right) regions during ‘warm’ (W1, W2) and ‘cold’ (C1, C2) events.

Table 4. Hydrographic properties and selected descriptors for the zooplankton communities in the WSC and BSO regions during ‘warm’ (W1, W2) and ‘cold’ (C1, C2) events.

	C1			W1			C2			W2		
	<i>n</i>	Mean	Min.–Max.	<i>n</i>	Mean	Min.–Max.	<i>n</i>	Mean	Min.–Max.	<i>n</i>	Mean	Min.–Max.
WSC												
Temperature [°C]	5	3.91	3.26–4.33	10	5.64	4.55–6.60	7	4.14	3.29–6.17	4	4.98	4.53–6.13
Salinity	5	35.08	35.06–35.10	10	35.14	35.12–35.16	7	35.20	35.10–35.13	4	35.16	35.15–35.18
Total abundance [ind. m ⁻³]	5	441.0	228–664	10	692.7	278–1158	7	511.5	153–684	4	792.0	606–1024
<i>C. finmarchicus</i> abundance [ind. m ⁻³]	5	89.0	28–227	10	74.1	37–168	7	136.2	24–369	4	306.3	101–527
<i>Oithona</i> spp. abundance [ind. m ⁻³]	5	219.6	90–493	10	361.1	68–633	7	247.2	28–431	4	281.0	56–425
Total biomass [mg m ⁻³]	5	38.9	16.4–68.8	10	34.3	17.3–59.2	7	34.2	14.5–88.7	4	32.5	26.7–44.3
<i>C. finmarchicus</i> biomass [%]	5	38.6	13.8–69.9	10	42.6	26.1–58.1	7	67.3	35.9–88.4	4	54.7	43.6–59.7
<i>Oithona</i> spp. biomass [%]	5	2.9	0.5–7.9	10	4.4	1.5–9.3	7	2.9	0.6–6.8	4	2.3	0.4–4.4
BSO												
Temperature [°C]	2	5.61	4.64–6.59	5	6.33	5.88–6.69	4	5.73	4.63–6.21	7	5.83	4.71–6.37
Salinity	2	35.05	35.02–35.07	5	35.14	35.13–35.16	4	35.12	35.07–35.15	7	35.16	35.12–35.18
Total abundance [ind. m ⁻³] ^a				3	1540.3	1308–1965	3	449.0	265–621	5	1189.8	530–2736
<i>C. finmarchicus</i> abundance [ind. m ⁻³]	2	128.0	119–137	5	659.0	147–1070	4	185.2	27–352	7	325.3	201–383
<i>Oithona</i> spp. abundance [ind. m ⁻³]	2	55.5	27–84	5	244.6	72–360	4	164.5	52–299	7	334.3	71–966
Total biomass [mg m ⁻³]	2	18.1	13.9–22.2	5	81.2	23.7–91.2	4	18.7	12.5–26.0	7	53.1	30.6–79.0
<i>C. finmarchicus</i> biomass [%]	2	60.2	57.4–63.1	5	79.4	62.7–88.6	4	74.2	65.5–80.8	7	70.0	52.9–85.9
<i>Oithona</i> spp. biomass [%]	2	0.7	0.5–0.9	5	1.1	0.4–2.1	4	3.4	0.8–6.2	7	2.0	0.5–4.6

^aTotal zooplankton abundance only for IO PAN data.

distribution during the Arctic summer (Richter, 1994; Kosobokova and Hopcroft, 2010). Consequently, our zooplankton studies covered most or even the entirety of the AW flow through the BSO and only part of it in the case of the WSC region. In most of published results from the same or adjacent waters, zooplankton standing stocks, especially during summer, concentrated in the top 200 m (Sameoto, 1984; Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Blachowiak-Samolyk *et al.*, 2007; Kosobokova and Hopcroft, 2010). Carstensen *et al.* (2012) even found that most of the *Calanus* biomass in the NwAC and in the WSC from late June to mid-July concentrated in the uppermost 100 m (above the seasonal pycnocline), which suggests that the chosen sampling strategy was appropriate for

characterising the *Calanus* populations during the study periods. However, recent study on zooplankton in the WSC region, based on samples collected down to 1000 m (Gluchowska *et al.*, 2017), indicated that a substantial biomass of zooplankton, including that of *C. finmarchicus*, can be distributed below 200 m, in the mesopelagial (200–1000 m). The distribution of *C. finmarchicus* in the deeper water layers was attributed, by the authors, to the fact that parts of the populations had most probably begun their seasonal migrations at the time of sampling (Pedersen *et al.*, 1995; Hirche, 1996). Therefore, an underestimating of the *C. finmarchicus* standing stock in the WSC region, especially in cases when the population consisted of older copepodids, was possible in this study.

Interregional variations in zooplankton in relation to regional oceanography

The shelves and slopes along the Atlantic inflow in the Nordic Seas are among the highest primary and secondary production areas of the world's oceans (Sakshaug, 2004; Carmack and Wassmann, 2006; Skaret *et al.*, 2014). High annual primary production (above $100 \text{ g C m}^{-2} \text{ y}^{-1}$; Hill *et al.*, 2013) is most likely crucial for maintaining high *C. finmarchicus* stocks (Skjoldal and Rey, 1989; Falk-Petersen *et al.*, 2000; Dalpadado *et al.*, 2012). Although both studied regions are strongly influenced by warm and saline AW, and are located relatively near each other, differences between them were noted in *C. finmarchicus* abundance and biomass during the study period, with higher values in the BSO (Table 3). The latitudinal range sampled in this study was small (less than three degrees), but the AW is significantly cooled during its northward flow, most likely influencing the spatial biological heterogeneity of this region. Higher AW temperatures in the BSO than in the WSC may contribute to higher production and consequently higher *C. finmarchicus* abundance and biomass in the BSO. It has been shown, for example, that a temperature increase in the Barents Sea from 3 to 5°C can result in a doubling of the production (from 4 to 8 g C m^{-2}) during summer (Tande, 1991). Our observations suggest that the regions differed likely also in terms of different contributions of advective processes to the total zooplankton production. Calculations conducted for the entire Barents Sea indicate that contributions of advected biomass are important for maintaining high zooplankton production levels in the Barents Sea (Skjoldal and Rey, 1989; Edvardsen *et al.*, 2003). However, the most important factor is local production, which can provide almost 70% of the total production (Dalpadado *et al.*, 2012). The local production is probably also important in the WSC, but the higher current speed, and bigger depth of the sea, likely lead to weaker retention and/or higher diffusion of the plankton, resulting in lower *C. finmarchicus* abundance per cubic metre for the studied epipelagic layer (200–0 m). Additionally, it is worth noting that the difference in *C. finmarchicus* biomass between the regions, due to the differences in stage composition, was smaller than the difference in the abundance (Table 3). It is therefore likely that the differences in sea ice cover and spring bloom dynamics between the regions, resulted in variability in the zooplankton community time changes. The onset and growth of the phytoplankton is not only related to the availability of nutrients and light but also to water stratification, winds, surface-water transport, and the activity of grazers (Cherkasheva *et al.*, 2014). Stabilization of the upper water column is likely to occur first along the ice edge in the Fram Strait, and phytoplankton likely start growing earlier in the WSC region than in the permanently ice-free BSO area, like in the scenario of phytoplankton bloom development along the latitudinal gradient described in Skjoldal *et al.* (1987) and Leu *et al.* (2011). One can speculate, therefore, that *C. finmarchicus* development had started earlier and thus had progressed further in the WSC region (populations were composed predominantly of CV–CVI copepodids) than in the BSO (populations were composed mostly of CIV and CV copepodids), at the time of sampling. However, the observed interregional differences could also be related to the slight time lag between sampling campaigns.

In terms of biomass, the zooplankton communities in both regions were dominated by *C. finmarchicus*, but there were relatively large interregional differences in zooplankton community

structure considered in terms of abundance (Figure 2a). The high abundances of *Oithona* spp. (especially *O. similis*) in the WSC compared to the BSO, indicated that the development of small copepods such as *Oithona* spp. in the WSC might be stimulated after the large copepods, like *C. finmarchicus*, left the photic zone (Hansen *et al.*, 1999). The increasing importance of small copepods in the upper water layer during the period of *Calanus* spp. dormancy has been reported across the Fram Strait (Svensen *et al.*, 2011), in Disco Bay (Madsen *et al.*, 2008), on the western coast of Greenland (Hansen *et al.*, 1999) and in the Barents Sea (Arashkevich *et al.*, 2002). Despite the relatively minor contribution of *Oithona* spp. to the zooplankton biomass, due to high turnover rates, these smaller organisms can contribute considerably to an overall higher production in some regions, e.g. the Southern Ocean (Fransz and Gonzalez, 1995). Recently, the importance of small copepod species had been recognized and their ecology had been studied with more effort (Nielsen *et al.*, 2002; Lischka and Hagen, 2005; Narcy *et al.*, 2009). However, the inadequate sampling methods for this kind of organisms still results in an underestimation of their quantitative contribution and functional role (Gallienne and Robins, 2001). The role of *Oithona* spp. may become even more important in future ocean, because cyclopoid species can survive a wide range of changes in environmental factors (Hansen *et al.*, 2003; Ward and Hirst, 2007), thus, *Oithona* spp. may actually benefit from increasing temperatures in the Arctic seas (Narcy *et al.*, 2009).

In the BSO region *C. finmarchicus* numerically dominated, nevertheless, large spatial and temporal variations in the zooplankton community structure were observed (Figure 2a and c), most likely due to high variability in oceanographic conditions. Although AW usually dominates in this region (Dalpadado *et al.*, 2012), the influence of Arctic and Polar Front waters can also be important. Increased productivity of phytoplankton and zooplankton in frontal systems, manifested in elevated abundance of both planktonic communities, is a well-documented phenomenon (Franks, 2005; Basedow *et al.*, 2014; Trudnowska *et al.*, 2016). Such dynamic conditions likely contributed also to the increased abundances of appendicularians in the BSO region (Figure 2b), thanks to high small particles concentrations. Appendicularians have been shown to be common in the Arctic (Kosobokova and Hirche, 2000; Auel and Hagen, 2002), but despite their potentially high role in transferring the particles from the pelagic to benthic ecosystems, they are only occasionally studied, most probably due to difficulties in sampling (Hopcroft *et al.*, 2005).

Interannual variability in zooplankton community and regional oceanography

The series of AW temperatures in the WSC and BSO regions showed positive trends of ~ 0.56 and $\sim 0.45^\circ \text{C}$ per decade, respectively. These trends were similar to the trend observed in the northern Fram Strait ($\sim 0.06^\circ \text{C}$ per year) over the period of 1997–2010 (Beszczynska-Möller *et al.*, 2012), larger than the trend reported by Schlichtholz and Houssais, 2011) in the BSO area ($\sim 0.25^\circ \text{C}$ per decade, 1982–2005) and much larger than the trend in the global mean temperature from 1955 to 2003, which was $\sim 0.04^\circ \text{C}$ per decade (Levitus *et al.*, 2005). Our time series are relatively short, and the trends should be considered carefully, as they may represent interannual variability and anomalies

rather than the real long-term trends. Analyses of the variability in the interannual water temperature across the AW inflow in the Nordic Seas (Furevik, 2001) have shown several cold and warm events, varying between 2 and 7 years in duration. Such oscillatory patterns were also observed in the AW temperature and salinity monitored in the N (WSC region) and FB (BSO) sections in this study. Variations in the AW volume fluxes into the Barents Sea and the Fram Strait were also observed. In the WSC region, the AW volume transport changed together with the AW temperature, despite the data were obtained from distant sections (in the southern Fram Strait and in the northern Fram Strait, Figure 1). At the beginning of the 21st century, the early summer temperatures were relatively low in the studied BSO (2001–2002) and WSC (2003) regions, followed by warm events in 2005–2006, which were associated with anomalously large volume fluxes of AW observed in both areas (3.59–3.36 Sv in WSC and 2.68 in BSO, Figure 3c). During the ‘warm’ event of 2006, the 5 °C isotherm shifted in the WSC region by more than 350 km to the north in comparison with the ‘cold’ summer of 2003, and warmer-than-usual AW extended northward into the Fram Strait (Walczowski et al., 2012). During the ‘warm’ event in 2011–2012, a higher-than-average AW volume transport was observed only in the WSC region (3.82 Sv in 2011, mean 2.90 Sv), while in the BSO, the values were similar to the long-term average (Figure 3c). Thus, although ‘warm’ and ‘cold’ events occurred in both regions, their timing, scales, and characteristics seemed to have some differences between the regions.

Over the study period, increasing zooplankton biomass was observed in both regions, mainly due to increasing contributions of *C. finmarchicus*. This is consistent with findings in other studies (Reygondedeau and Beaugrand, 2011; Weydmann et al., 2014), suggesting that shifts towards the dominance of boreal species in the Arctic are mainly due to increased role of *C. finmarchicus*. The observed increasing trends in the numbers of boreal copepods are consistent with biogeographic shifts in copepod assemblages and with the northward extension of warm-water species observed in the eastern North Atlantic and European shelf seas (Beaugrand et al., 2002). The correlations between AW temperature and the selected univariate zooplankton characteristics, such as the proportion of biomass contributed by *C. finmarchicus*, indicated that water temperature measurably affected the zooplankton community in the study area. Similar to other studies (Daase and Eiane, 2007; Blachowiak-Samolyk et al., 2008; Kwasniewski et al., 2010; Estrada et al., 2012; Gluchowska et al., 2016), this study also showed that the environmental conditions had led to the spatial and temporal differentiations of zooplankton communities. The biomass of Atlantic-associated *C. finmarchicus* increased with increasing AW temperatures, most likely by regulating the rate of metabolic processes (Ikeda et al., 2001), development (Huntley and Lopez, 1992; Møller et al., 2012) or increasing the trophic efficiency of plankton communities (Richardson, 2008). The increased biomass of *C. finmarchicus* provides advantageous feeding and growth conditions for several ecologically and economically important fish, such as herring, cod, and capelin (Dalpadado et al., 2012). The effects of top-down processes (predation) on the zooplankton community structure were not addressed in this study. The Atlantic *C. finmarchicus* introduced into the Arctic marine ecosystem will face competition from its congener *C. glacialis*, and may be less successful as long as the presence of ice, lower temperatures and lower salinity favour its Arctic counterpart (Søreide et al., 2008; 2010). However, with the continued warming trend in the Arctic, the replacement of *C.*

glacialis by *C. finmarchicus* may cause redirection of the Arctic food chain from plankton-eating seabirds to plankton-eating fish and fish-eating birds (Stempniewicz et al., 2007).

During the ‘warm’ events, increasing abundances of *Oithona* spp. and/or *C. finmarchicus* in both AW branches were observed in this study, indicating that the ocean circulation system and its associated water mass characteristics, exert important influences on the distribution, physiology, and life history of these species. The abundance of *Oithona* spp. seems to have gradually increased in the BSO since 2010, and the consequences of the changes in the abundance of small-sized zooplankton species, leading to changes in the size structure of zooplankton communities, seem to be more important than changes in the absolute zooplankton biomass (Richardson and Schoeman, 2004; Lane et al., 2008). On the other hand, high abundances of *C. finmarchicus* in the BSO during ‘warm’ events can be linked not only to high AW volume transport, which increased the contribution of advected *C. finmarchicus* biomass, but also to increased AW temperatures, which may affect both, local and advected populations.

Generation cycles of *C. finmarchicus*

During the warm event in the WSC region in 2011, a young developmental status of *C. finmarchicus* was observed (with copepodids CI–CIII representing almost 60% of the population). This suggested a possibility that the young copepodids represented the second generation (G2) of the species, which would be the offspring of the first generation (G1), still present in the population as the older stages. *Calanus finmarchicus* produces 1–3 generations per year along the Norwegian coast (Pedersen et al., 2000), but in the northern parts of the Norwegian Sea and in the Arctic ecosystems, where waters temperatures are lower, 1-year reproductive cycle is typically observed (Falk-Petersen et al., 2009 and references therein). Previous studies in the WSC region indicated that during summer, older overwintering developmental stages of *C. finmarchicus* (CIV–CVI) dominated (Hirche and Kosobokova, 2007). It was also found that G1 individuals can develop into stage CV and adults within 1.5 months (Hygum et al., 2000), and under favourable conditions (temperature, food), this generation could spawn and give rise to a new generation (G2) in July/August (Dalpadado et al., 2012). The samples which contained young copepodids of presumably G2 were collected from 1 to 12 July (Table 1). Using the fundamental relation between *C. finmarchicus* development rate and temperature (Corkett et al., 1986), the time needed for development from egg to CI or CII at 4 °C is 26–33 days. That means that spawning, which gave rise to this offspring, should take place in early June. If this were to be the reproduction performed by G0, it would have been much delayed in comparison to the regular reproduction of G0 (April–May) reported in earlier studies (Hopkins et al., 1984; Hirche, 1996; Hirche et al., 2001). The number of *C. finmarchicus* generations may vary not only among regions but also among years at the same location (Irigoien, 2000). Water temperature together with synchronization of the timings of food availability and development to maturity and spawning, may be the primary factors in reproduction regulation (Hirche and Kosobokova, 2007; Skaret et al., 2014).

Summary

In this study, it was demonstrated that, in the regions of Atlantic water inflow into the Arctic, the effects of water mass

modifications on zooplankton communities vary in both space and time. During the study period, the AW temperature steadily increased in both the BSO and WSC branches and this gradual change also manifested as changes in the zooplankton community structure, including the increase in proportion of Atlantic-associated *C. finmarchicus* in the zooplankton biomass and the increase in role of small-sized *Oithona* species. These findings support the notion of an ongoing 'Atlantification' of the regions and hence possibly of the Arctic Ocean. Further long-term studies of zooplankton in the main pathways of the Atlantic water flow into the Arctic are strongly recommended, especially in other seasons and with a greater focus on sub-dominant and rare taxa. Extended observations and experimental studies are indispensable for better understanding the actual role of advective transport in structuring zooplankton communities in the Arctic marine ecosystems.

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