



Shift towards the dominance of boreal species in the Arctic: inter-annual and spatial zooplankton variability in the West Spitsbergen Current

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ABSTRACT: We studied summer mesozooplankton composition between 2001 and 2009, in the epipelagic zone of the West Spitsbergen Current (WSC) and adjacent areas, which constitute a transition zone between warmer Atlantic and cold Arctic waters. According to hydrography and species composition, this region could be divided into 4 main areas: western and eastern branches of the WSC, the Greenland Sea together with Fram Strait, and the shelf areas of Spitsbergen and the Barents Sea. The most abundant species was *Oithona similis* and the most important, in terms of biomass, was *Calanus finmarchicus*; both species were found at all stations. The novel spatial analysis method of principal coordinates of neighbour matrices (PCNM) and the following variation partitioning were applied to disentangle the contributions of environmental variables and spatial differences in explaining mesozooplankton community variation. In spite of the large geographic area covered, environmental factors used in redundancy analysis (RDA) explained 30.6 % of zooplankton variability, while the spatial distribution of sampling stations was responsible for 27.2 %, and 12.5 % was a common share of both predictors, coming from their correlations. We observed a smooth change from dominance of ubiquitous and boreo-Arctic taxa such as *O. similis* and *Triconia* sp. in the beginning of the study period towards stronger dominance of boreal taxa such as *C. finmarchicus*, which was the most abundant species in 2009.

KEY WORDS: North Atlantic · Mesozooplankton · *Calanus finmarchicus* · Redundancy analysis · Variation partitioning · Principal coordinates of neighbour matrices · Long-term data series

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INTRODUCTION

The West Spitsbergen Current (WSC), which is the continuation of the Norwegian Atlantic Current, transports Atlantic waters (AW) and associated biota through the Norwegian and Greenland Seas, and thus influences both physical and biological properties of the Arctic Ocean (Piechura & Walczowski 2009). The WSC is a transition zone between the considerably warmer Atlantic and the cold Arctic domains, and as such it is a suitable place to study effects of climate change in Arctic and sub-Arctic marine ecosystems. Warming of the

WSC waters has been observed recently with maximum high AW temperature and salinity recorded in summer 2006. In the following 2 years, both variables decreased rapidly, but AW temperature and salinity were high again in summer 2009 (Piechura & Walczowski 2009, Walczowski et al. 2012). On the basis of these observations, Spielhagen et al. (2011) suggested that AW temperatures observed west of Spitsbergen in the beginning of the 21st century may have been the warmest of the past 2000 yr.

Knowing that temperature has increased significantly in the Arctic over the last 3 to 4 decades (IPCC

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[Intergovernmental Panel on Climate Change] 2007, Stroeve et al. 2007), it has been hypothesised that effects of temperature increases could be assessed from biological long-term monitoring data in the Arctic region (Hughes 2000, Hays et al. 2005, Kirby & Beaugrand 2009, Carstensen et al. 2012). However, most of the existing biological data sets from the Arctic have a much shorter time scale of monitoring and are without a consistent spatial factor (i.e. sampling is not repeated at the same locations through time). This complicates the analyses of such data and diminishes the possibility to extract time series that are not biased by changes in spatial sampling pattern (Beare & McKenzie 1999, deYoung et al. 2004).

Nonetheless, Carstensen et al. (2012) investigated the effects of environmental conditions on the biomass of *Calanus* spp. in the Nordic Seas in 2001 to 2009 and reported significant relationships with temperature, including a critical threshold around 6°C, above which the presence and biomass of *C. glacialis* decreased. Mumm et al. (1998), in their 5 yr study of transpolar distribution of mesozooplankton, found out that mesozooplankton in the WSC was evenly distributed throughout the upper 500 m, with *C. finmarchicus* as the prevailing species. Recently, Kwasniewski et al. (2012) studied inter-annual changes (2001 to 2008) in zooplankton composition in relation to hydrography on the West Spitsbergen Shelf as well as their connection to the North Atlantic Oscillation (NAO), and identified time lags of 4 to 7 yr between changes in NAO and the biological response. However, zooplankton from the WSC has not been thoroughly investigated in the whole area of its influence, because most data sets are confined spatially or temporally, and consequently, long-term studies of a broader geographic area are especially sparse.

The goal of this study was to describe the inter-annual and spatial variability of the mesozooplankton community in the Atlantic–Arctic transition zone, using an almost decadal long and spatially comprehensive monitoring data set from the West Spitsbergen Current. We also wanted to distinguish the effects of 2 sets of explanatory variables, environmental factors and spatial distribution of sampling stations, on the variation of zooplankton taxonomic composition and its demographic structure. We applied a novel statistical method following variation partitioning, principal coordinates of neighbour matrices (PCNM), which provides a powerful tool for analysing the spatial variation in species composition and has mainly been applied in terrestrial studies (Legendre et al. 2009, Peres-Neto & Legendre 2010).

MATERIALS AND METHODS

Sample collection and analysis

Zooplankton was sampled annually at the end of June and beginning of July, within a 3 wk time window from 2001 until 2009, usually during or slightly after the spring bloom, from RV ‘Oceania’ (Table 1). The spatial extent of this data set covers multiple sampling stations in the area from 73° 30′ to 78° 50′ N and from 3° to 19° E, including eastern and western branches of the WSC, shelf areas of Spitsbergen and the Barents Sea, and the Greenland Sea with Fram Strait (Fig. 1). Twenty stations (A to U), which were sampled for at least 5 yr during the study period, were selected for further analysis (Fig. 1). This resulted in 138 sample collections in total. Due to the ship’s drift and sea conditions, the exact geographic position of a sampling station may differ slightly between years.

Mesozooplankton was collected with a WP2 net, equipped with 180 µm filtering gauze, in a vertically stratified manner within the epipelagic zone of the sea (Table 1). Water temperature and salinity were measured prior to zooplankton sampling using the Sea-Bird Electronics CTD (SBE 911*plus*) system with temperature and conductivity sensors, in order to investigate the origin of the different water masses.

Zooplankton samples were preserved in a 4% solution of buffered formaldehyde in seawater immediately after sampling. Most of the copepods were identified to species or genus level, and for larger copepods that were collected representatively (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa* and *Pseudocalanus* spp.), the copepodite developmental stages were also identified. To discriminate between specific *Calanus* species, the prosome length was measured following the procedure described by Weydmann & Kwasniewski (2008). Copepod biomasses were calculated from the abundance data and individual dry mass (DM) values, according to Błachowiak-Samołyk et al. (2008). To study the contribution of species originating from different zoogeographical ranges, all holoplankton taxa identified to species level were assigned into 4 categories according to their centres of distribution: ubiquitous, Arctic, boreal and boreo-Arctic (Jaschnov 1970, Lindley 1977, Corkett & McLaren 1979, Park 1994, Razouls et al. 2005–2012, Kosobokova et al. 2011; and the World Register of Marine Species [WoRMS], www.marinespecies.org).

Table 1. Sampling details: stations with their geographic position, mean water depth, median sampling depth of the sampling period, dates (given as dd.mm.) and years of sampling at a certain station

Stn	Latitude °N	Longitude °E	Mean water depth (m)	Median sampling depth (m)	Sampling date	Sampling years
A	73°30	09°50	2240	95	23–26.06.	2001, 2002, 2006–2009
B	73°30	13°05	1596	60	22–27.06.	2001–2005, 2007, 2009
C	73°30	15°00	659	55	22–27.06.	2001–2007, 2009
D	73°30	19°20	470	200	21–27.06.	2005–2009
E	75°00	05°00	2747	60	25.06.–02.07.	2005–2009
F	75°00	10°25	2532	100	27.06.–04.07.	2001, 2004–2006, 2009
G	75°00	13°00	1972	60	27.06.–04.07.	2001–2003, 2005, 2009
H	75°00	15°00	1113	60	28.06.–05.07.	2001–2003, 2005–2009
I	76°00	13°00	1511	72.5	29.06.–03.07.	2001–2005, 2007–2009
J	76°00	15°00	334	80	29.06.–04.07.	2001–2009
K	76°08	17°00	300	200	28.06.–07.07.	2001–2009
L	76°30	04°00	2575	60	02–11.07.	2004, 2006–2009
M	76°30	09°00	2269	200	03–13.07.	2001–2009
N	76°30	13°00	1728	80	03–07.07.	2001–2005, 2008, 2009
O	76°30	15°00	172	120	04–14.07.	2001–2007, 2009
P	77°14	03°00	2767	200	03–10.07.	2003–2009
R	77°00	06°00	2540	62.5	03–12.07.	2001, 2003–2009
S	77°24	08°00	2181	72.5	02–07.07.	2004–2009
T	78°50	05°00	2191	70	10–17.07.	2001, 2002, 2004, 2006–2008
U	78°50	09°15	203	60	10–15.07.	2001, 2002, 2004–2006, 2008, 2009

Data analysis

Data analysis focused on the epipelagic zone by integrating the surface and subsurface sampling layers (the median depth of these layers was 60 m), which represented mostly surface AW. Species abundance data (individuals [ind.] m^{-2}) were $\log(x + 1)$ -transformed prior to all following analyses to allow identification of the possible influence of numerically less important taxa. To reveal similarities between years and sampling locations for both hydrographical conditions and zooplankton community composition, significance tests for differences between separated groups of samples were performed using the 1-way analysis of similarities (ANOSIM) permutation tests in PRIMER 6.0 (Plymouth Marine Laboratory).

To study the relationships between the mesozooplankton community and both environmental variables and spatial distribution of sampling sites, constrained ordination techniques were applied in CANOCO 4.5 (Leps & Smilauer 2003). Redundancy analysis (RDA) was performed using environmental variables as predictors (water depth at a station, actual sampling depth, water temperature, salinity, sea ice concentrations and monthly chlorophyll *a* concentrations from June and July), ranked according to their quantitative importance by forward selection. Chlorophyll *a* concentrations were taken from SeaWiFS 9 km (2001 to 2002) and MODIS-Aqua

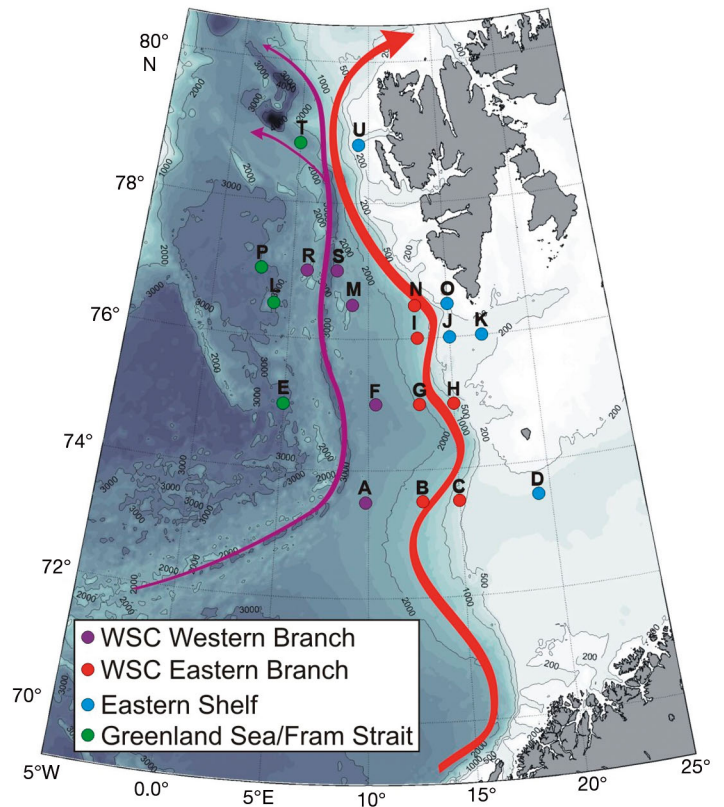


Fig. 1. Location of zooplankton sampling stations in the West Spitsbergen Current (WSC) used in the present study, partitioned into 4 distinct areas influenced by different water masses. The general flow of the WSC eastern and western branches is illustrated with arrows

4 km (2003 to 2009) data from an online Giovanni application (disc.sci.gsfc.nasa.gov/giovanni/; Acker & Leptoukh 2007). To illustrate the geographic distribution of species, the parallels of latitudes based on the generalised linear model (GLM) were added to the RDA ordination plot.

To detect and quantify spatial patterns in the meso-zooplankton community over such a large sampling area as the WSC and adjacent waters, the novel method of PCNM was employed. This method can be applied to any set of sites providing a good coverage of the geographic sampling area in order to quantify spatial structuring of ecological data, which originates either from the physical forcing of environmental variables or from community processes (Borcard & Legendre 2002). In the first step, a truncated Euclidian distance matrix among the sampling sites was constructed on the basis of their geographic coordinates. In the second step, principal coordinates of the distance matrix were computed by principal coordinate analysis in order to represent the spatial information in a form compatible with canonical ordination (in this study it was RDA), and as a result, 82 PCNM eigenfunctions with positive eigenvalues were generated. Then the principal coordinates, derived from these positive eigenvalues, were used as explanatory variables in RDA (for details of the method see Borcard & Legendre 2002). Additionally, forward selection was applied to the PCNM results to determine whether the WSC mesozooplankton spatial structure was mostly broad-, middle- or fine-scaled (Legendre et al. 2009).

Variation partitioning for RDA was applied to compare the mesozooplankton variability connected with the influence of environmental factors with effects of their spatial distribution, using 1 set of response variables (mesozooplankton community composition) and 2 sets of predictors: environmental variables (water and sampling depth, temperature, salinity, sea ice and chlorophyll *a* concentrations) and significant spatial descriptors derived from PCNM (Legendre et al. 2009, Peres-Neto & Legendre 2010).

Similarity percentages (SIMPER) analysis was used to decompose average Bray-Curtis dissimilarities between different years in terms of species composition, and to determine the contribution of each species to the within-groups similarity. In addition to the above calculations, the second stage analysis (2STAGE) based on weighted Spearman's correlations was applied to taxa abundances at the sampling stations (inner factor) over the years (outer factor) in PRIMER 6.0, and illustrated by a non-metric multi-

dimensional scaling (MDS) plot in order to reveal differences and similarities in zooplankton community composition between sampling years (Clarke et al. 2006).

RESULTS

Hydrographical and ice conditions

Stations were partitioned into 4 different types (Fig. 1) according to their geographic position as well as to hydrographical conditions characterised by environmental variables (temperature, salinity, sea ice concentration and water depth): western (stations A, F, M, R, S) and eastern (B, C, G, H, I, N) branches of the WSC, eastern shelf area (D, J, K, O, U) and stations influenced by water masses from the Greenland Sea and Fram Strait (E, L, P, T) (1-way ANOSIM, global test $p = 0.001$, global $R = 0.488$), with all the pairwise tests being significant.

Since environmental variables, like zooplankton samples, were integrated for the surface and subsurface layers (median extension of the integrated layer from 60 m to the surface), they mostly captured characteristics of the surface water, which only partially characterises the entire AW flow into the WSC. However, temperature and salinity of the surface AW displayed fluctuations from year to year, similar to those of the AW core below (Walczowski et al. 2012), with maximum values of temperature and salinity in 2002, 2006, 2009 and lower values in 2001, 2004 and 2008 (Fig. 2).

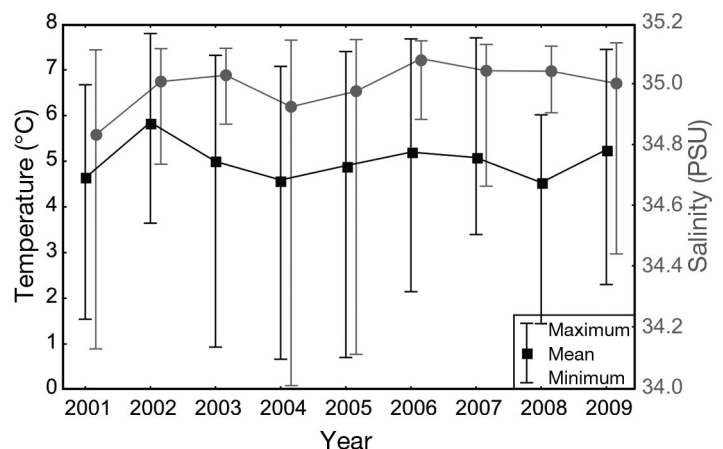


Fig. 2. Means of temperature and salinity of sampling layers (median extension of the integrated layer from 60 m to the surface) at stations

Species composition

The mesozooplankton community in the study area included over 100 taxa originating from 3 biogeographic domains: boreal, boreo-Arctic and Arctic, as well as ubiquitous species (Table 2). However, both in terms of abundance and biomass, the community was dominated by a few species. *Oithona similis* was generally the most abundant, with typically around 30 000 ind. m⁻². However, in terms of biomass, *Calanus finmarchicus* was the most important, with values around 1200 mg DM m⁻², an order of magnitude higher than other species (Table 2). In general, *C. finmarchicus*, *Pseudocalanus* spp., *O. similis* and copepoda nauplii (mainly *Calanus* spp.) were the most frequently occurring taxa, found in every single sample across the entire study area.

Comparison of the mesozooplankton composition among stations revealed that the community could be grouped similarly to the types based on hydrography: western and eastern branches of WSC, eastern shelf area and the Arctic-type stations from the Greenland Sea and Fram Strait (1-way ANOSIM, global test $p = 0.001$, global $R = 0.419$), with all pairwise tests between groups being significant. Except for taxa present in all geographic groups, the following taxa contributed mostly to the similarities of zooplankton communities within the indicated hydrographical regions and were characteristic for them: *Aglantha digitale* and *Oikopleura* spp. for the eastern branch of WSC, *Calanus glacialis* and Echinodermata larvae for the shelf region, and *C. hyperboreus* for the Arctic-type and western branch.

Influence of environmental variables

Environmental variables explained 30.6% of the variation in species–environment relationships in the RDA model ($p = 0.001$). The most important predictors were station water depth and water temperature, explaining 13% and 9% of species variability, respectively (Table 3). Only satellite chlorophyll *a* concentration data from June were significant and explained 2% of zooplankton variability in addition to the other environmental variables. The gradient between the northern and southern part of the study area is clearly seen along the temperature eigenvector in the ordination plot, illustrating the relationship between zooplankton taxa abundances (ind. m⁻²) and environmental variables, as well as the latitudinal range based on GLM (Fig. 3). The RDA analysis revealed that higher abundances of *Calanus fin-*

marchicus males, *Aglantha digitale*, *Limacina retro-versa*, and Bryozoa larvae, which were recorded in the southern part of the WSC, corresponded with higher temperatures. The presence of *C. hyperboreus*, older copepodite stages of *Pseudocalanus* spp. and *Themisto libellula* was associated with deep stations in the Greenland Sea and Fram Strait, located in the north-western part of the study area, while *Parasagitta elegans*, *Frittilaria borealis* and the larvae of echinoderms and cirripedes preferred eastern shelf areas. The presence of nearly all stages of *C. glacialis* was highly correlated with increasing sea-ice concentrations along the Spitsbergen shelf in the north-eastern part of the study area.

Spatial distribution and variation partitioning

PCNM analysis resulted in 82 PCNM eigenfunctions with positive eigenvalues, of which 20 were significant according to the forward selection procedure in RDA. The significant eigenfunctions were equally distributed among the 82 PCNM functions, representing mesozooplankton spatial variation from broad to local scale. The RDA model ($p = 0.001$) based on these 20 significant PCNMs used as predictors allowed explanation of 27.2% of the mesozooplankton community variation.

As mentioned above, 27.2% of the variation of the community composition data was spatially structured and explained by the PCNM eigenfunctions, while 30.6% of the variation was explained by the environmental variables. However, after applying variation partitioning for RDA, these proportions changed to 18.1% of variation being explained by environmental factors alone, 14.7% by the spatial distribution alone, and 12.5% being common to both (Fig. 4). The results indicate that variation resulting from changes in water and sampling depth, temperature, salinity, chlorophyll *a* and sea ice concentrations was more important for the WSC mesozooplankton community than that explained by the spatial distribution of sampling stations, in spite of the large geographic extent of the study area.

Inter-annual zooplankton variability

In 2001, 2002 and 2004, the highest total abundances of almost all species were observed (Table 4), which was especially visible for the small copepods such as *Oithona similis*, *O. atlantica*, *Triconia* (= *Oncaea*) *borealis* and Copepoda nauplii. In terms

Table 2. Taxa found in this study, with their minimum, median and maximum values for abundance and biomass (dry mass, DM) across all stations. Biomasses of taxa with large size variance have not been calculated. For holoplankton species the biogeographic origin is given

Species	Biogeographic origin	Abundance (ind. m ⁻²)			Biomass (mg DM m ⁻²)		
		Min.	Median	Max.	Min.	Median	Max.
<i>Calanus finmarchicus</i>	Boreal	2131	12464	520100	0.4	1164.3	45016.4
<i>Calanus glacialis</i>	Arctic	0	97	25285	0	36.3	5467.1
<i>Calanus hyperboreus</i>	Arctic	0	130	11817	0	44.84	7882.5
<i>Microcalanus</i> spp.	Boreo-Arctic	0	146	7209	0	1.0	50.5
<i>Pseudocalanus</i> spp.	Boreo-Arctic	200	2641	104316	1.5	15.9	393.2
<i>Metridia longa</i>	Boreo-Arctic	0	28	2440	0	3.7	495.5
<i>Paraeuchaeta norvegica</i>	Boreal	0	20	370	0	0	74.0
<i>Acartia longiremis</i>	Boreo-Arctic	0	0	773	0	0	11.1
<i>Gaetanus tenuispinus</i>	Ubiquitous	0	0	24	0	0	0.07
Aetideidae	Boreo-Arctic	0	0	4	0	0	0.04
<i>Heterorhabdus norvegicus</i>	Boreal	0	0	32	0	0	6.4
<i>Metridia lucens</i>	Boreal	0	0	182	0	0	0.57
<i>Temora longicornis</i>	Boreal	0	0	4.0	0	0	0.01
<i>Scolecithricella minor</i>	Ubiquitous	0	0	137	0	0	0.86
<i>Microsetella norvegica</i>	Ubiquitous	0	510.0	3257	0	0	3.4
Harpacticoida indet.		0	0	61	0	0	0.35
<i>Oithona atlantica</i>	Boreal	0	529	9600	0	3.6	65.9
<i>Oithona similis</i>	Ubiquitous	1500	30717	245440	3.7	76.2	608.8
<i>Triconia (=Oncaea) borealis</i>	Boreo-Arctic	0	781	93338	0	1.6	190.4
Copepoda nauplii		140	6747	256667	0.6	30.1	1143.4
<i>Evadne nordmanni</i>	Ubiquitous	0	0	3567			
Ostracoda		0	3	195	0	0.2	12.9
Cirripedia nauplii		0	0	827	0	0	17.4
Cirripedia cypris		0	0	1663	0	0	34.9
Cirripedia Facetotecta nauplii		0	0	26			
<i>Themisto abyssorum</i>	Boreo-Arctic	0	93	1005			
<i>Themisto libellula</i>	Arctic	0	8	878			
Isopoda Bopyridae		0	0	67			
Isopoda		0	0	44			
<i>Thysanoessa inermis</i>	Boreo-Arctic	0	0	364			
<i>Thysanoessa longicaudata</i>	Boreal	0	0	616			
<i>Thysanoessa raschii</i>	Boreo-Arctic	0	0	356			
Euphausiacea nauplii		0	0	1304			
Euphausiacea calyptopis		0	72	1745	0	49.8	1200.2
Euphausiacea furcilia		0	47	1900			
<i>Eupagurus zoea</i>		0	0	7			
<i>Hyas</i> sp. zoea		0	0	100			
<i>Hyas</i> sp. megalopa		0	0	8			
<i>Pandalus borealis</i> zoea		0	0	1			
<i>Munida</i> zoea		0	0	4			
Decapoda larvae		0	4.0	4.0			
<i>Aglantha digitale</i>	Boreo-Arctic	0	42	19455	0	17.9	8242.6
<i>Halopsis ocellata</i>	Boreo-Arctic	0	0	4.0			
<i>Dimophyes arctica</i>	Boreo-Arctic	0	0	15			
<i>Beroë cucumis</i>	Ubiquitous	0	0	224			
<i>Mertensia ovum</i>	Arctic	0	0	96			
Ctenophora larvae		0	0	533			
Ctenophora indet.		0	0	257			
Tornaria larvae		0	19.0	60.0			
<i>Clione limacina</i>	Arctic	0	0	133	0	0	1410.8
<i>Limacina helicina</i>	Arctic	0	74	8800	0	13.2	1578.3
<i>Limacina retroversa</i>	Boreal	0	0	365	0	0	65.5
Gastropoda veliger		0	0	218			
Bivalvia veliger		0	67	9003			
<i>Tomopteris helgolandica</i>	Boreal	0	0	8			
Polychaeta larvae		0	0	125			
Polychaeta indet.		0	0	490			
Echinodermata larvae		0	94	20805	0	0.1	20.8
Bryozoa larvae		0	0	438			
<i>Eukrohnna hamata</i>	Boreo-Arctic	0	576	5504			
<i>Parasagitta elegans</i>	Arctic	0	6	1416			
<i>Fritillaria borealis</i>	Boreal	0	0	8600	0	0	4.8
<i>Oikopleura</i> spp.	Boreo-Arctic	0	292	22886			

of relative abundance, copepoda nauplii was the second most important taxa, after *O. similis*, in the first 2 yr (8.5 and 10.17%), while this role was overtaken by *Calanus finmarchicus* in the following years. In

Table 3. Conditional effects of explanatory environmental variables from the redundancy analysis (RDA). Lambda A values are the canonical eigenvalues with *F*- and *p*-statistics obtained by means of permutation tests

Explanatory variables	Lambda A	<i>F</i>	<i>p</i>
Sea depth	0.13	19.69	0.001
Temperature	0.09	17.13	0.001
Sampling depth	0.04	6.38	0.001
Salinity	0.02	3.63	0.001
Sea-ice concentration	0.01	2.86	0.001
Chlorophyll <i>a</i>	0.02	2.00	0.015

fact, 2009 was the first year when the most abundant species was not the ubiquitous *O. similis*, comprising a proportion of around 10 to 11% of all taxa in the previous years, but the boreal *C. finmarchicus*, reaching a relative abundance of 12%. In 2004, 2005 and 2006, boreal species, such as *O. atlantica*, were observed in relatively higher numbers. *C. glacialis* was observed in the WSC mainly in 2004 and 2009, while *C. hyperboreus* was found mostly in 2007 and 2008. Overall, the sum of these species-specific observations could suggest an increasing abundance of boreal taxa in the WSC and adjacent areas.

Supporting trends can be seen in relative abundances and biomasses of holoplankton (Fig. 5). Ubiquitous species were most abundant, with the exception of 2006 and 2009, with relative contributions ranging from 45.1% in 2004 to 65.9% in 2002. In

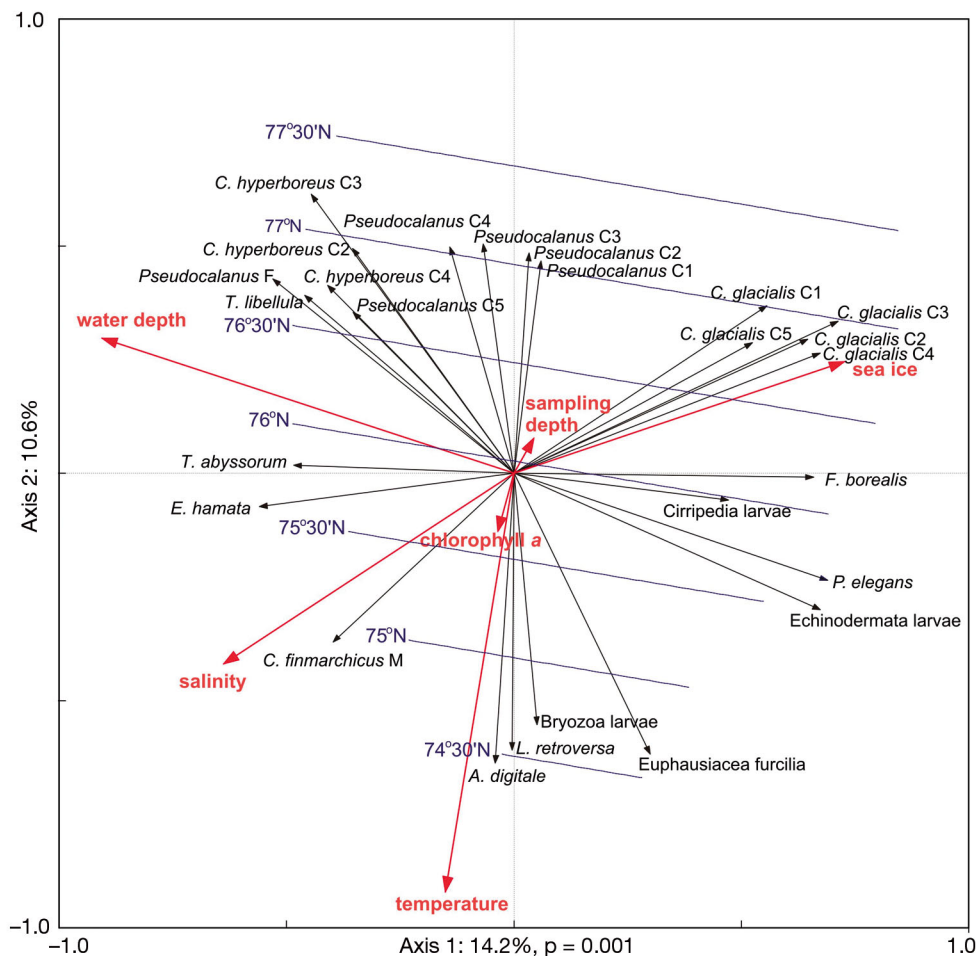


Fig. 3. Ordination plot from redundancy analysis (RDA) on mesozooplankton taxa abundances (black arrows) and their relation to environmental variables (red arrows). The 21 best fitted taxa are shown in the plot. Blue lines represent the parallels of latitude of the sampling sites. See Table 2 for species names

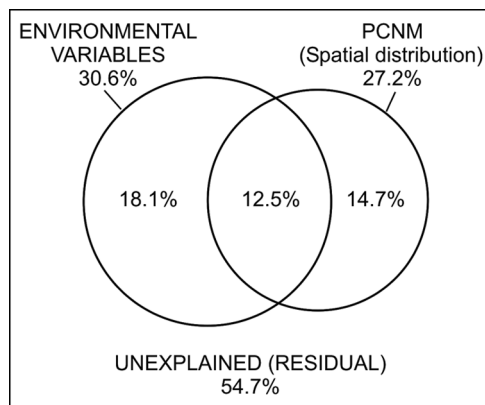


Fig. 4. Venn diagram representing the partition of the variation of zooplankton community composition between 2 sets of explanatory variables: environmental factors (left circle) and principal coordinates of neighbour matrices (PCNM) eigenfunctions representing spatial distribution (right circle). The box represents 100% of the variation

2006 and 2009, the highest fractions of boreal species were observed (48.2% and 45.2%, respectively). Boreo-Arctic species were the second-most abundant group only in 2001 and 2002, whereas the group of boreal species became more dominant in 2003 to 2009. The shift towards increasing dominance of boreal taxa was even clearer in holoplankton biomass; the relative biomass of boreo-Arctic species was the highest only in 2001 and 2002, while boreal species gradually increased their relative proportion in the following years, reaching 84.3% of the zooplankton biomass in 2009.

Based on weighted Spearman's correlations of the abundances of species and their life stage composition at sampling stations between each pair of sampling years, the 2STAGE analysis revealed the presence of 2 groups with the computed correlations $r^2 > 0.6$, illustrated by MDS plot (Fig. 6). The first group included 2001, 2003, 2004, 2006, 2007, and the sec-

Table 4. Results of similarity percentages (SIMPER) analysis: relative abundances of selected taxa which contributed most to the dissimilarities between years, and to the within-groups similarities, with a cut-off at 50%. MEAN is the average total mesozooplankton abundance (ind. m⁻²) across stations in a given year

Species	2001	2002	2003	2004	2005	2006	2007	2008	2009
<i>Oithona similis</i>	9.20	11.70	10.04	10.14	10.84	10.37	10.91	10.64	11.60
Copepoda nauplii	8.50	10.17	8.47	8.61	8.35	8.12	8.71	8.65	9.98
<i>Calanus finmarchicus</i>	7.63	9.82	9.46	9.29	10.44	9.45	10.36	9.66	11.99
<i>Triconia borealis</i>	7.14	8.18	4.66	5.99	5.13	5.56		6.54	
<i>Pseudocalanus</i> spp.	7.08	8.33	6.98	7.90	7.80	7.41	8.11	8.56	8.85
<i>Oikopleura</i> spp.	6.07		4.43						
<i>Oithona atlantica</i>	5.78			6.17	4.59	5.54			
<i>Agathidium digitale</i>		4.85							
<i>Eukrohnia hamata</i>			6.13	6.19	5.59	5.56	6.68	5.82	6.11
<i>Calanus hyperboreus</i>							6.20	5.24	
<i>Calanus glacialis</i>									5.13
MEAN	2958	2170	1182	2454	1139	1547	1144	1175	1285

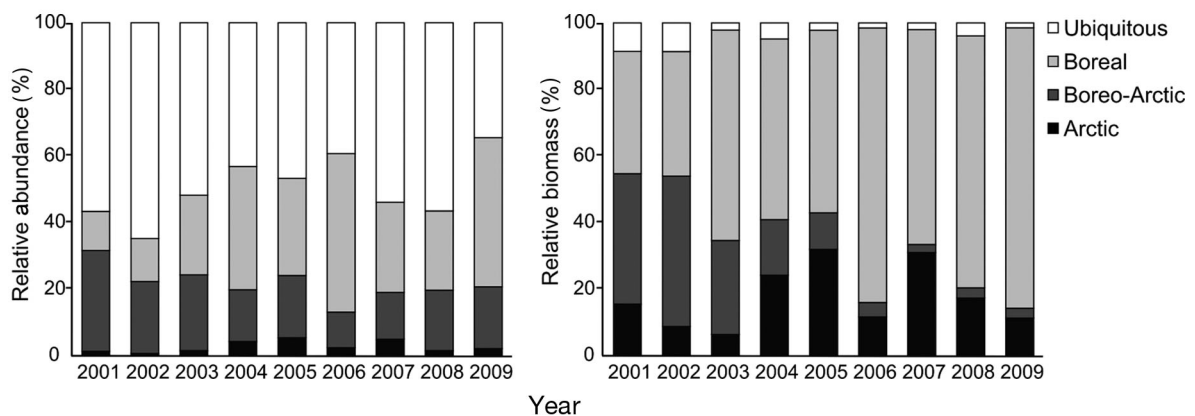


Fig. 5. Changes in relative abundances and biomasses of holoplankton species groups over the study period

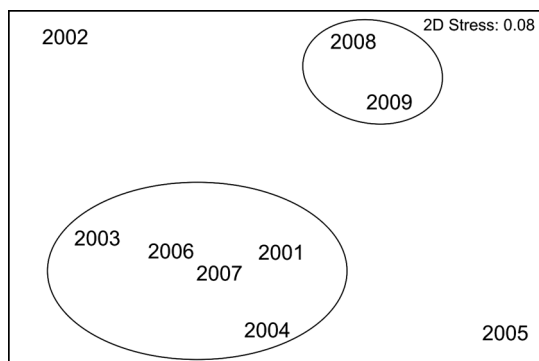


Fig. 6. MDS plot showing differences between years, derived from 2STAGE analysis computed for patterns in abundances of taxa (ind. m^{-2}) among stations

and one consisted of 2008 and 2009, while 2002 and 2005 were defined as outliers (Fig. 6).

DISCUSSION

Zooplankton spatial distribution

The mesozooplankton community in the study area, including the WSC, shelf areas of Spitsbergen and the Barents Sea, and the Greenland Sea with the Fram Strait, was a mixture of boreal, boreo-Arctic, Arctic and ubiquitous species, with large spatial and interannual variations. The main environmental factors driving zooplankton variability were temperature and water depth at stations, despite the fact that sampling only took place in the upper part of the water column. The role of these variables in explaining zooplankton variability can be attributed to the species' biology, as discussed below. The WSC transports great amounts of heat northwards (Piechura & Walczowski 2009); therefore, the area of the southern stations is ice free during most of the year (Svendsen et al. 2002), and was characterised mainly by the presence of boreal species, such as *Aglantha digitale*, *Limacina retroversa* or *Calanus finmarchicus*. The stations in the eastern part of the study area, on the Spitsbergen shelf, which were located in the flow of fresher and colder Arctic waters associated with the coastal South Cape Current, had an increasing number of *C. glacialis* and meroplanktonic Echinodermata larvae. *C. glacialis* is a cold-water Arctic shelf species, predominating the *Calanus* stock in the northern Barents Sea (Tande 1991). The species' predominance in the Arctic may be related to its use of

ice algae as an important food source, especially by females during spawning (Tourangeau & Runge 1991, Søreide et al. 2010, Weydmann et al. 2013). This could explain the positive relation between *C. glacialis* abundance and sea ice concentrations in our analyses. The stations in the north-western part of the study area, where the water masses of the WSC mix with fresher and colder waters originating from the Greenland Sea (Boreal Basin Gyre) or the Fram Strait (Loeng & Drinkwater 2007, Oliver et al. 2008), had increasing water depth and, consequently, characteristic species at these stations, *Calanus hyperboreus* and *Themisto libellula*, are typically associated with deep waters of the Greenland Sea (Hirche 1997), supporting the relationships found in our analyses.

PCNM is a powerful tool for analysing the spatial variation in species composition, although so far it has been mostly used in terrestrial ecology (Borcard & Legendre 2002, Legendre et al. 2009). This study demonstrated that it can be successfully applied to ocean studies as well. The PCNM results showed that the zooplankton community exhibits large spatial variations in the study area, from local to broad scale. Apart from the differences between the sampling years, the small scale variation could be ascribed to the mesoscale features observed within the WSC and in the frontal zones between Atlantic and Arctic-type waters. Mesoscale physical dynamics are known to govern the major time and spatial scales of biological variability in terms of biomass, production and export, and they seem to have a strong impact on ecosystem structure and functioning, although observational evidence in the NE Atlantic is still rather limited (Garcon et al. 2001, Yebra et al. 2009). The large scale variation was connected to the huge geographic range of our sampling stations, especially its latitudinal extent.

Ecologists use variation partitioning in order to understand the contribution of the environment, independent of spatial distribution, and vice versa, as well as to control for inflated type I error in assessing the environmental component under spatial autocorrelation (Legendre et al. 2009, Peres-Neto & Legendre 2010). In this study, this method allowed us to determine that variation in zooplankton explained by environmental factors was higher than that explained by the spatial distribution of sampling stations, in spite of the large geographic extent of the study area. However, some variation remained that could not be partitioned and was explained by both factors together, most likely due to a correlation between them. For example, water temperature and

salinity decrease as the WSC penetrates northwards, as a result of water transformation (Piechura & Walczowski 2009), resulting in a correlation between environmental variables and spatial distribution of stations. The analytical tools used in the study explained most of the linear, explainable variation, and the remaining unexplained variance was most likely associated with sampling and the large spatial–temporal heterogeneity of the mesozooplankton community in the water column or stochastic processes such as dispersal, establishment and mortality, or noise (ter Braak 1994).

Zooplankton inter-annual variability

The zooplankton community inhabiting the WSC displayed significant year-to-year variability, with a gradual transition from dominance of ubiquitous and boreo-Arctic species towards an increasing contribution of boreal ones, rather than an abrupt regime shift or tipping point as described by Carstensen & Weydmann (2012). Parallel to the changes observed in zooplankton, positive trends in temperature and salinity of the AW were observed in 2000 to 2009, based on measurements conducted at the same time as the zooplankton sampling (Walczowski et al. 2012), whereas June to July sea ice extent in the study area and the spring bloom varied substantially between 2001 and 2009 (Acker & Leptoukh 2007, Fetterer et al. 2002, updated 2009).

The beginning of the zooplankton sampling period coincided with small changes in the mean temperature of the AW layer during the summers of 2001 and 2002 (Piechura & Walczowski 2009) and wide open waters found in the Fram Strait, especially in 2001 (Fetterer et al. 2002, updated 2009). The spring bloom began in the Eastern Shelf in May in these years, spread towards western stations in June and finished by the end of sampling period in July (Acker & Leptoukh 2007). During these years the zooplankton was characterised by high abundances of almost all taxa, but small copepods such as the ubiquitous *Oithona similis* and boreo-Arctic *Triconia borealis* declined after 2002. Similar observations of regime changes were made in the Gulf of Maine by Pershing et al. (2005), who described a common pattern of interdecadal variability for a number of taxa including *Oithona* spp. and *Pseudocalanus* spp., and noted a dramatic increase in these taxa around 1990, followed by a rapid decline in 2002 driven by large-scale changes in the salinity of the Northwest Atlantic Shelf.

In contrast, 2003 was considered a cold year by Walczowski et al. (2012), the marginal ice zone appeared close to the north-western part of the study area (Fetterer et al. 2002, updated 2009) and the spring bloom did not coincide with zooplankton sampling apart from at the southernmost stations. Heavy ice conditions around the southern part of Spitsbergen in 2004 (Fetterer et al. 2002, updated 2009) and advection of the Arctic waters from shelf areas of the Barents Sea into the eastern branch of the WSC caused both the delay in spring bloom in this area and peak abundances of Arctic species such as *Calanus glacialis* and *Clione limacina*, as well as larval stages of benthic echinoderms, where these taxa were usually marginal.

Between 2004 and 2006, significant increases in AW temperature and salinity were observed, together with the northward shift of warm water resulting in the highest AW salinity in 2005 and the highest AW temperature recorded in summer 2006. The northward advance of AW in 2006 was an unprecedented event: the position of the warm-water tongue shifted more than 350 km to the north, and temperatures in the WSC reached the highest values ever recorded (Walczowski et al. 2012). Also, the spring bloom lasted longer compared to other sampling years. The increased occurrence of *Oithona atlantica*, especially pronounced in 2006, indicates an increased contribution of Atlantic fauna to the zooplankton community in the WSC area.

After 2006, the AW temperature and salinity decreased rapidly and peaked again in 2009 (Walczowski et al. 2012). In 2008 and 2009, the spring bloom coincided with the sampling time apart from at the eastern shelf stations (Acker & Leptoukh 2007). The increasing proportions of boreal species over the study period and the shift to their dominance in 2009 were mainly due to high counts of *Calanus finmarchicus*. This observation is consistent with the findings of Reygondeau & Beaugrand (2011) which suggested that *C. finmarchicus* would increase its abundance at the northern edge of its spatial distribution.

This data set is too short to assess if the observed increasing dominance of boreal species in the WSC and adjacent areas is just a temporary phenomenon or constitutes a more persistent trend. The higher proportion of boreal species could have been a result of stronger advection of AW northwards, like in 2006, although the following years did not show any extreme hydrographical properties (Walczowski et al. 2012). Alternatively, the high proportion of boreal species in recent years could be part of an inter-

decadal oscillating behaviour, similar to what was observed in the Gulf of Maine (Pershing et al. 2005). However, the hydrographical data from the WSC, which were collected simultaneously with the presented zooplankton data and in the years before zooplankton sampling started, indicate positive trends in summer AW salinity and temperature over the last 15 yr (Walczowski et al. 2012), which could suggest that this trend is indeed persistent.

Rising water temperature results in increasing marine copepod metabolic processes such as respiration and oxygen consumption (Hirche 1987, Ikeda et al. 2001). Temperature also affects the growth of Atlantic and Arctic zooplankton directly through regulation of development time and final weight (Huntley & Lopez 1992), and development rates (Møller et al. 2012), or indirectly by influencing relationships among species including primary producers, as well as zooplankton consumers or competitors (Kirby & Beaugrand 2009), which in turn affect the distribution of zooplankton development stages and community composition (Ji et al. 2012). The above processes may lead to ecological regime shifts such as the climate-induced regime shift in the North Atlantic and the high Arctic that occurred in the 1920s and 1930s and involved changes in cod and capelin distribution and a northward expansion of boreal invertebrates (Drinkwater 2006) or a dramatic shift from benthic fish to a pelagic fish/macroinvertebrate-dominated system in the Northwest Atlantic in the late 1980s and early 1990s (Frank et al. 2005).

The observed trend in the increasing numbers of boreal copepods at the gateway to the Arctic is consistent with strong biogeographic shifts in all copepod assemblages and the northward extension of warm-water species by more than 10° latitude, associated with a decrease in the number of colder-water species, described in the eastern North Atlantic and European shelf seas (Beaugrand et al. 2002). The shifts in geographic ranges may mean more possibilities for hybridisation between Arctic and Atlantic species, as observed for *Calanus finmarchicus* and *C. glacialis* by Parent et al. (2012) in the Arctic and Northwest Atlantic. The 'warmer Arctic' scenarios also forecast a switch in the Arctic marine food web from large, lipid-rich Arctic herbivores to boreal grazers, which could mean that primary production will be utilised by smaller, faster-growing and less lipid-rich species (Søreide et al. 2010) and consequently, the food resources available to the top Arctic predators such as seabirds, seals, and whales would be reduced (Weslawski et al. 2009).

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