**FEATURE ARTICLE**

Plankton patchiness in the Polar Front region of the West Spitsbergen Shelf

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ABSTRACT: Plankton patchiness, a widely known but poorly studied phenomenon, was investigated concurrently with measurements of environmental conditions in the Polar Front region west of Spitsbergen in summer (June–July) 2012. Continuous high-resolution observations were made using a laser optical plankton counter, a fluorometer and CTD along several sections in the surface 50 m of the sea with additional data from zooplankton net sampling and full-depth range hydrographical measurements at stations. The observed patches differed in terms of size, number and distribution patterns. They occupied only a minor portion of the studied ocean area (2–17%), but contained plankton concentrations that were 3–17 times higher than the concentrations in the background waters. The generation and existence of patches was associated with particular conditions created by increased primary production, optimal hydrography, discontinuities in the density field and/or the presence of meanders or eddies. The distribution of small size fraction patches, consisting of the phytoplankton, inorganic particles and detritus, was closely related to specific patterns in hydrography. The medium-size zooplankton and marine snow were concentrated mainly in conjunction with discontinuities in density field. The distribution of the large copepods was independent of any oceanographic feature detected in this study, which points towards biological cues as factors regulating zooplankton aggregation processes. Diverse mechanisms of patch formation as well as their ecological significance are discussed in the context of planktonic responses to the structured environment in the region of the Polar Front.

KEY WORDS: Zooplankton · Patchiness · Zooplankton distribution · Laser optical plankton counter · Eddy · Polar Front · West Spitsbergen Current
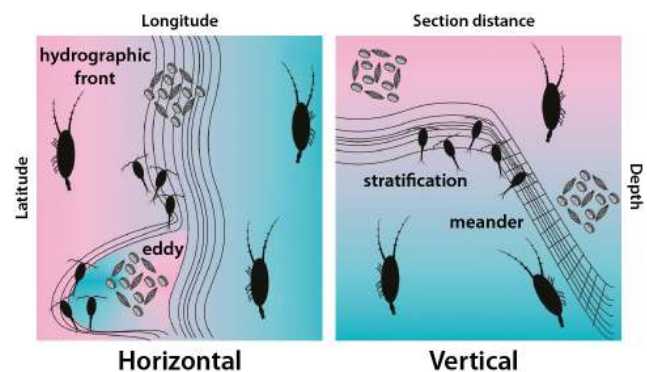
Schematic plankton patchiness in Polar Front surface waters. Response of the size-fractionated plankton (small, medium, large) distribution patterns to a structured environment is presented in both horizontal (hydrographic front and eddy) and vertical (stratification and meander) planes.

Graphic: Emilia Trudnowska

INTRODUCTION

Plankton patchiness is a well-known phenomenon, although it is poorly characterized and understood (Haury et al. 1978, Franks 2005). Patchiness, or heterogeneity, is defined as a discontinuous distribution of individual organisms through space (Smith 1972) and is often a result of the interaction between physical and biological processes (Haury et al. 1978, Omori & Hamner 1982, Folt & Burns 1999). Plankton aggregations can arise as responses to temperature and salinity gradients or discontinuities, water motion, variation in light intensity, food and/or predator concentrations as well as from complex social and reproduction behaviours (Deutschman et al. 1993, Cowles & Desiderio 1998, Ambler 2002). Patches can differ greatly in terms of their size, shape

and generative processes, their species- and size-specific compositions, as well as the concentrations of individuals within aggregations (Omori & Hamner 1982, Pinel-Alloul 1995, Folt & Burns 1999). The role of patches in enhancing trophic transfer has been widely demonstrated (e.g. Wishner et al. 1988, Godø et al. 2012, Majaneva et al. 2013). Thus, spatial variability in the abundance of plankton is an essential theme in marine ecology.

There is a great variety of methodological approaches to adequately detect patchiness in zooplankton distribution, e.g. by net sampling (Wiebe 1970, Vogedes et al. 2014), continuous water pumping (Piontkovski et al. 1997, Molinero et al. 2008), acoustics (Zhou & Huntley 1996, Genin et al. 2005), optical counters (Basedow et al. 2006, Trudnowska et al. 2012), video recording (Benfield et al. 1996, Davis et al. 2004), laboratory experiments (Dagg 1977) or modelling (Riley 1976, Woodson et al. 2005). Nevertheless, this phenomenon remains more a topic of speculation than one of actual measurements and documentation. When studying plankton distribution, one of the main challenges is achieving appropriate spatial resolution. This problem has been tackled in our study by the use of continuous and automatic measurements by an *in situ* laser optical plankton counter (LOPC), which has enabled the high-resolution mapping of size-fractionated plankton together with simultaneous measurements of water mass characteristics. A further problem in patchiness studies arises from the lack of clear criteria to distinguish between a plankton patch and the ambient water. Among the existing approaches to define a patch, various thresholds have been applied (George 1981, Pinel-Alloul 1995, Dormann et al. 2007), such as the concentration of individuals exceeding the median value (Wiebe 1970, Mehlum et al. 1999); the local maximum, that is, a point in a data series at which the concentration of a particular category/type of particles and plankton exceeds the concentration at the preceding point by 30–50% (Gallager et al. 2004, Sullivan et al. 2010); and a density of individuals that is several orders of magnitude higher than the density at the remaining points from the observation series (Wiebe 1970, Wishner et al. 1988, Alldredge et al. 2002). There are also studies that have applied the Moran's *I* spatial autocorrelation coefficient (Kaltenberg & Benoit-Bird 2013, Vogedes et al. 2014), which determines whether the studied elements of an ecosystem are dependent or independent of each other (Pinca & Huntley 2000, Dormann et al. 2007, Molinero et al. 2008). An alternative to Moran's *I* is the Mahalanobis generalized distance

(D^2) coefficient, which allows the identification of observations far from the centre of the data cloud (Molinero et al. 2008). In the present study, following the approach used by Wiebe (1970) and Piontkovski et al. (1997), a patch was defined by data points in an observation series for which the abundance of plankton was >1 SD above the mean abundance recorded within the specified study area.

The ocean is highly structured, both horizontally and vertically, and this is most pronounced in coastal waters. Hence, shelf waters provide a patterned habitat in which the distribution of marine life is patchy on a range of scales (Woodson et al. 2005). The pelagic habitat on the West Spitsbergen Shelf (WSS) area is highly structured, mainly due to the interactions between water masses of Arctic and Atlantic origin associated with the presence of a pronounced hydrographic front. Moreover, the concurrence of steep horizontal gradients of temperature and density, along with barotropic and baroclinic instabilities that develop due to the presence of topographic discontinuities, results in the formation of diverse mesoscale water structures (e.g. meanders and eddies) (Nilsen et al. 2006, Teigen et al. 2010). Such ocean structures cause particle concentration and retention, and they enhance biological productivity (Franks 1992, Labat et al. 2009, Godø et al. 2012). The impact of such structures on phytoplankton has been clearly shown by remote sensing (e.g. Riandey et al. 2005, d'Ovidio et al. 2010), but their influence on zooplankton still needs to be assessed through *in situ* sampling, because zooplankton can exhibit much more fine-scale variation in their spatial distribution than phytoplankton (Levin 1992).

The convergence, mixing and exchange of the Atlantic- and Arctic-origin water masses on the WSS (Saloranta & Svendsen 2001) results in a complex hydrography. On its offshore side, the West Spitsbergen Current (WSC) carries warm and saline Atlantic water into the Arctic Ocean (Saloranta & Haugan 2001, Walczowski et al. 2005). The highest Atlantic water temperature and current speed are observed in the WSC core, which is confined to the upper part of the continental slope (Beszczyńska-Möller et al. 2012). The colder and fresher Arctic-type water advected from Storfjorden around the southern tip of Spitsbergen is transported northward along the coast by the Sørkapp Current (SC). This current carries mainly Storfjorden surface water, which is a mixture of local meltwater that has been heated by solar radiation and Arctic water that has already been warmed in the shallow Barents Sea and advected into Storfjorden by the East Spitsbergen

Current (Haarpaintner et al. 2001, Skogseth et al. 2005). Therefore, the Arctic-type water occupying the WSS is warmer and fresher than typical Arctic water (colder than 0°C and saltier than 34.8). The Arctic-type water carried over the shelf and the Atlantic water transported above the upper slope are typically separated by a frontal zone, which is a part of the larger-scale Polar Front system (Loeng 1991, Saloranta & Svendsen 2001, Walczowski 2013). The Polar Front west of Spitsbergen is characterized by a density gradient only in the fresher surface water layer of approximately 50 m, while beneath this layer, the front is density compensated and manifested through strong temperature and salinity gradients (Saloranta & Svendsen 2001, Walczowski 2013).

The goal of this study was to investigate the phenomenon of plankton patchiness by the simultaneous detection of plankton patches and the environmental conditions under which they occur in the upper 50 m layer of the sea in the Polar Front region. The purpose was to find out whether particles and plankton accumulate within specific water masses or at characteristic discontinuity zones or whether they are formed irrespective of water mass structures. It was assumed that the distribution of particles and various plankton size fractions would differ because of their different mobility abilities. Our hypothesis was that small size fraction patches would be strongly related to the heterogeneity of the environment, whereas the patches of larger organisms would be more independent from the direct influence of the physical environment. By verifying the issues raised, we expected to provide new data for a discussion about the ecological significance of particles and plankton patchiness and their relation to physical features such as fronts and eddies.

MATERIALS AND METHODS

Instrumentation and study design

The distribution of particles, plankton and selected environmental variables was examined in summer 2012 within the frontal zone between the Arctic and Atlantic waters as well as along the sections in the core areas of these 2 domains in the area of the WSS (Fig. 1).

Continuous automatic measurements along sections were surveyed with the towed instrument platform carrying an LOPC (Brooke Ocean Technology), a conductivity-temperature-depth (CTD) sensor (SBE 911plus, Seabird Electronics) and a fluorometer (Seapoint Sensors). The details regarding the principles of the LOPC are presented elsewhere (e.g. Herman et al. 2004, Basedow et al. 2010, Trudnowska et al. 2014). The LOPC detects particles and plankton in a size range from 0.1 to 35.0 mm equivalent spherical diameter (ESD), which will henceforth be referred to as the size range of the total abundance. The LOPC counts were first integrated into 50 consecutive size classes, equally spaced along a $\log_{10}$ axis, and then re-grouped into 3 size fractions: small (S: 0.1−0.3 mm ESD), medium (M: 0.3−0.8 mm ESD) and large (L: 0.8−5.0 mm ESD). The measurements of the smallest size fractions (<0.25, <0.3 or <0.5 mm ESD) are often neglected in zooplankton studies at high latitudes (Basedow et al. 2010, Trudnowska et al. 2012, 2014) because they theoretically include phytoplankton aggregations, marine snow or suspended matter from glaciers, sea ice or sea bed sediments. In this study, however, this smallest size fraction (S) was also included in the analyses as a real and potentially important constituent of the pelagic ecosystem. The
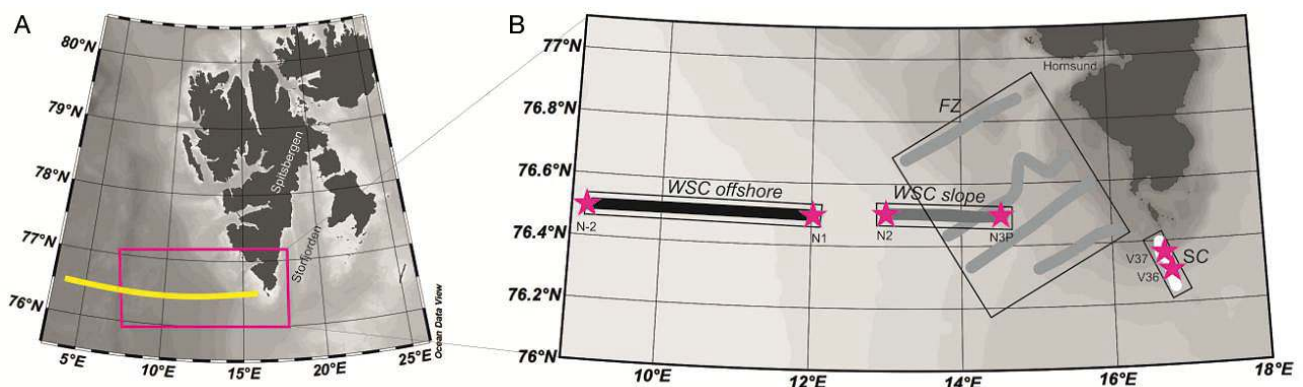

Fig. 1. Study area. (A) Svalbard archipelago with the West Spitsbergen Shelf region. Pink rectangle indicates the area of the laser optical plankton counter (LOPC) surveys; yellow line indicates the route of the full-depth hydrographic stations. (B) Survey area. Grey, black and white lines indicate routes of the individual LOPC-CTD-fluorometer sections; pink stars indicate net sampling stations. FZ: frontal zone; SC: Sørkapp Current; WSC: West Spitsbergen Current

larger size fractions (M and L) represent mainly mesozooplankton, for which LOPC is well suited, and consist of medium-sized zooplankton such as *Oithona*, *Triconia*, *Microcalanus* and nauplii copepods, and various benthic larvae as well as large-sized *Pseudocalanus*, *Metridia* and *Calanus* copepods. The occasional counts of macrozooplankton, i.e. organisms >5.0 mm ESD (euphausiids, amphipods), were included in the total abundance calculations.

In the frontal zone area (FZ sections), the continuous automatic measurements were made along 4 sections at a constant depth of approximately 25 m (Table 1, Fig. 1). In the SC, WSC slope and WSC offshore sections, the measurements were performed in an undulating mode, spanning the layer from the subsurface (approximately 2 m) down to 50 m depth. The SC section (~20 km long) across the southernmost part of the Spitsbergen shelf was set in the area of Arctic-type water inflow onto the WSS. The WSC slope (~40 km long) and offshore (~70 km long) sections were set in the Atlantic WSC water flow.

Data processing and statistics

LOPC counts were divided by the volume of the water passing through the sampling tunnel and were averaged horizontally over 5 m distance intervals for constant-depth horizontal tows (FZ sections) and vertically over 1 m depth intervals for the undulating sampling mode tows (SC and WSC sections). The counts that exceeded the mean abundance by >1 SD in the selected size categories (S, M or L) were interpreted as counts of the particle and/or plankton patches (Wiebe 1970, Piontkovski et al. 1997),

whereas the remaining lower abundance counts were regarded as background (Wiebe 1970). The threshold values of particle and plankton abundance used to discriminate between a patch and the background were established individually for each section (FZ, SC, WSC slope and WSC offshore). A dedicated MATLAB programme was employed to calculate, detect and extract all patches and background water measurements that met these criteria.

To analyse the relationships between plankton distribution and hydrography, each variable was interpolated using a Kriging routine (Surfer 8.0, Golden Software) in 1 m vertical and 0.5 km horizontal distance gridding. The standardized anomalies of the plankton abundances and environmental parameters were calculated by subtracting the horizontal sample average and dividing it by the corresponding sample standard deviation. Non-parametric Spearman's rank-order correlations (Sokal & Rohlf 1981; Statistica 10.0, StatSoft) were used to test the pairwise relationships between vertically averaged (over each separate depth profile) zooplankton abundances in the selected size categories (S, M, L) and environmental variables (temperature, salinity, density, chlorophyll fluorescence).

Seawater density was calculated from salinity, temperature and pressure using the MATLAB seawater toolbox (http://mooring.ucsd.edu/software/matlab/doc/toolbox/ocean/swstate.html). Chlorophyll *a* concentration was determined fluorometrically by an *in situ* sensor. The Ocean Data View software programme (Schlitzer 2015) was used to prepare figures.

In addition to the high-resolution particle and plankton distribution measurements, full-depth hydrographic measurements were performed at fixed stations along the section crossing the WSC at 76° 30′ N.

Table 1. Sections and stations, sampling dates, times, locations and bottom depths. FZ: frontal zone; LOPC: laser optical plankton counter; SC: Sørkapp Current; WSC: West Spitsbergen Current

LOPC section	Net station		Date	Time (UTC)	Latitude	Longitude	Bottom depth (m)
FZ		Start	27.07.2012	16:00	76°26.91′N	016°05.56′E	
		End	29.07.2012	16:20	76°51.62′N	014°42.18′E	
SC		Start	29.06.2012	02:42	76°15.07′N	016°50.18′E	
	V36			03:43	76°18.94′N	016°47.03′E	106
	V37			04:50	76°20.81′N	016°44.18′E	110
		End	29.06.2012	06:12	76°23.81′N	016°38.38′E	
WSC slope	N3P	Start	11.07.2012	01:25	76°29.83′N	014°31.50′E	212
	N2	End	11.07.2012	08:55	76°30.00′N	013°03.86′E	1519
WSC offshore	N1	Start	11.07.2012	19:26	76°29.92′N	011°59.04′E	1888
	N-2	End	12.07.2012	09:12	76°30.19′N	009°04.54′E	2250

Hydrographic data were collected using a SeaBird SBE911plus CTD, equipped with duplicate temperature and conductivity sensors. The data were processed in a standard manner (Walczowski 2013).

Zooplankton net samples

Continuous measurements of the plankton distribution were supplemented with zooplankton net samples collected at stations located in the SC, WSC slope and WSC offshore sections (Table 1, Fig. 1). The zooplankton samples were collected in vertically stratified net hauls (from 2 to 5 layers distinguished within the upper 50 m), made with a Multiple Plankton Sampler (MPS; Hydro-Bios) or WP2 net, both equipped with net bags of 180 µm mesh size. Net samples were preserved in a 4 % formaldehyde-in-seawater solution buffered with borax. In the laboratory, the zooplankton samples were examined for taxonomic composition and abundance following the protocols described in Postel (2000). First, large organisms (>5.0 mm) were picked out, identified and counted. The remaining zooplankton were suspended in a fixed volume of water, from which 2 ml subsamples were taken with a large-volume automatic pipette, and examined thoroughly under a stereomicroscope. The number of subsamples was determined individually such that at least 500 individuals per sample were identified and counted. At the end, the remaining volume of the sample was scanned to find and identify taxa that had not been found previously. Zooplankton organisms

were identified to species or the lowest taxonomic level possible, including, where feasible, identification of the developmental stages. *Calanus* species were identified based on morphology and size according to criteria from Kwasniewski et al. (2003). Zooplankton abundance was expressed as the number of individuals in a cubic metre (ind. m^{-3}) of seawater.

RESULTS

Frontal zone sections

The water temperature, salinity, density and chlorophyll fluorescence, as well as the particles and plankton concentrations at the 25 m depth in the FZ sections, were higher in the Atlantic than in the Arctic water domain (Fig. 2).

Patches of the small size fraction were located mainly near the front along the whole investigated area (55 km, the distance between the southern and northern sections) and extended for ca. 2–5 km. A few patches of the medium and large size fractions were observed adjacent to the hydrographic front, while others were located farther out. They typically extended for a few kilometres along the survey route and continued in the parallel sections, suggesting they could reach more than 15 km in length. The mean concentrations of particles and plankton estimated within the patches in the FZ sections were 3.5 (S), 7.5 (M) and 16.7 (L) times higher than within the background waters (Table 2).
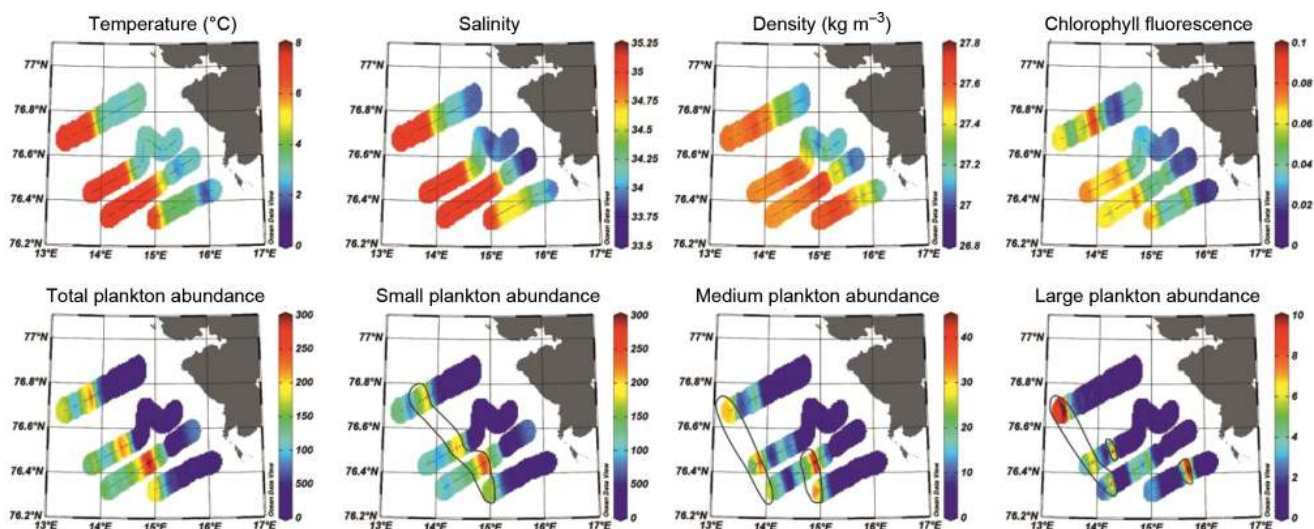

Fig. 2. Frontal zone (FZ) sections, approximately 25 m depth. Top: Distribution of temperature, salinity, density and chlorophyll fluorescence along the FZ sections. Bottom: Abundances (ind. m^{-3} × 10^3) of total (0.1–35 mm equivalent spherical diameter [ESD]), small (0.1–0.3 mm ESD), medium (0.3–0.8 mm ESD) and large (0.8–5.0 mm ESD) size fractions along the FZ sections. The identified patches are outlined by solid black lines

Sørkapp Current section

The upper 50 m layer in the SC section was stratified. The surface 10–20 m was occupied by warm and fresh waters, exhibiting a signature of local meltwater, while the layer underneath contained cold and more saline waters, most likely originating from the East Spitsbergen Current (Fig. 3). Elevated values of chlorophyll fluorescence and a higher total abundance of particles and plankton in the SC section were found generally in the cold lower layer.

The patches of the small and medium size fractions were mainly distributed in the lower, cold-water part of the SC section. They had a horizontal dimension of a few kilometres and a vertical dimension ranging from a few metres to 10 m. Additionally, one pronounced abundance peak, formed mainly by small size particles, was registered in the northern shallow part of the section (Fig. 3). The patches of the large fraction were found in the lower layer, in water pockets with high chlorophyll fluorescence, or in the upper 10 m layer in waters characterized by low salinity, density and chlorophyll fluorescence. They were, on average, 5 km in the horizontal dimension and varied between a few and more than 20 m in the vertical dimension. The mean concentrations of particles and plankton estimated within the patches in the SC section were 4.8 (S), 6.3 (M) and 3.4 (L) times higher than in the background waters (Table 2).

WSC slope section

Two distinct hydrographic structures were observed in the WSC slope section (Fig. 4). One was a small but pronounced intrusion of colder and less saline water, found in the middle portion of the section, occupying the entire 45 m span of the studied layer. The other was a doming of denser water with lower temperature observed on the western side of the section. A similar, albeit smaller, upward shift of denser and colder water was recognized in the

eastern part of the section. Full-depth hydrographic measurements at the fixed stations revealed the presence of an anticyclonic mesoscale baroclinic eddy with a diameter of approximately 30–40 km and a vertical extent of approximately 700 m (Fig. 5). The eddy was characterized by a warm and salty core and occupied most of the WSC slope section. The western intrusion found in the WSC slope section coincided with the western edge of the observed eddy structure, while the colder and fresher eastern intrusion was enclosed within the eddy.

Very high chlorophyll fluorescence was measured inside the eddy structure between the cold intrusion and the doming structure, and it was associated with extremely high total particle and plankton abundance. Most of the observed patches in the selected size categories (S, M, L) extended vertically throughout the entire 50 m layer and spread horizontally from 2 km up to 11 km. The conspicuous aggregations of the medium and large size fractions clung to the peripheries of the observed hydrographic structures (Figs. 4 & 6). In addition, a few other patches of the large size fraction with various spatial dimensions were dispersed regularly along the entire WSC slope section. The mean abundances of particles and plankton within the patches were 3.2 (S), 3.9 (M) and 5.4 (L) times higher than in the background waters (Table 2).

WSC offshore section

The water in the eastern part of the WSC offshore section was warmer and more saline than in the western part (Fig. 6). The hydrographic measurements made over the full depth range along this section (Fig. 5) suggest that the elevated temperature and salinity in the eastern part of the WSC offshore section may have resulted from the presence of shallow meanders or a very weak eddy in the upper 40–50 m layer filled with the Atlantic water from the WSC core flowing over the slope.

The vertical distribution of chlorophyll fluorescence along the WSC offshore section was relatively uniform, with peak values at 10–30 m depth. Horizontally, however, the chlorophyll fluorescence values decreased towards the centres of the southward flow of the supposed meanders. Large and pronounced patches of the small size fraction were observed in the upper part of the studied water column in the WSC offshore section, extend-

Table 2. Mean abundance (ind. $m^{-3} \times 10^3$) of particles and plankton within the patches of small (S), medium (M) and large (L) size fractions and background (Bgr.) waters of different sections studied (see Fig. 1)

Size fraction	FZ Patch	FZ Bgr.	SC Patch	SC Bgr.	WSC slope Patch	WSC slope Bgr.	WSC offshore Patch	WSC offshore Bgr.
S	212.0	61.1	192.2	40.3	552.2	171.9	187.1	69.9
M	41.5	5.5	44.4	7.0	116.9	30.2	27.0	2.7
L	14.6	0.9	2.4	0.7	8.1	1.5	3.5	0.2

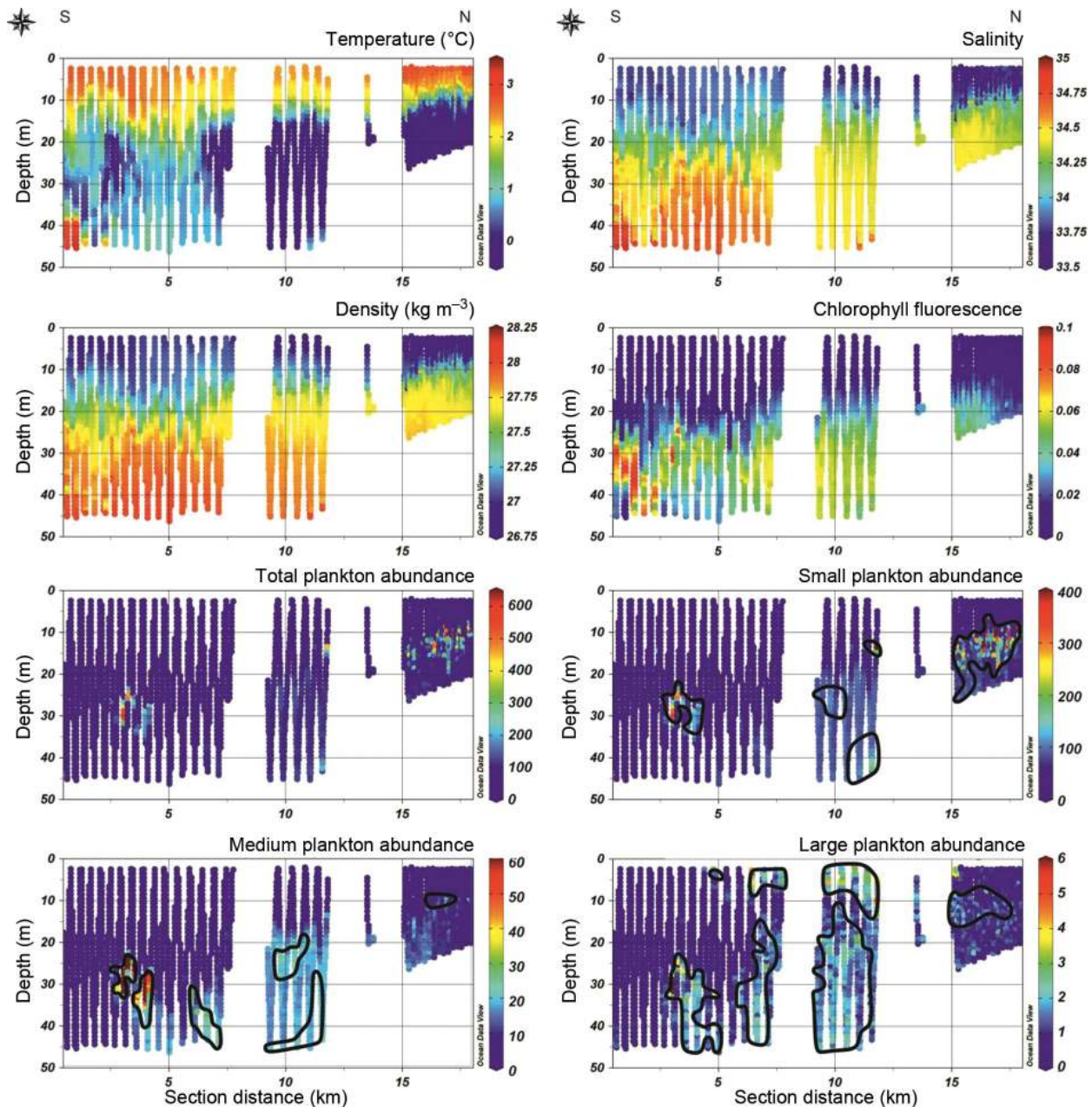Fig. 3. Sørkapp Current (SC) section. Distribution of temperature, salinity, density, chlorophyll fluorescence and plankton abundance (ind. m^{-3} × 10^3) of total, small, medium and large size fractions along the section. The identified patches are outlined by solid black lines

ing vertically down to 30 m and coinciding with the eastern warm branch of the meander. The medium size fraction patches extended vertically for at least 20 m and were relatively narrow in the horizontal plane. They were found in the western part of the section, at the periphery of a pocket of denser, slightly colder and more saline water, which was assumed to be associated with sloping isopycnals and a wedge-shaped Atlantic water layer in the WSC

offshore branch. The numerous patches of the large plankton were not associated with any of the hydrographic features. They concentrated mainly within the upper 10 m layer in the eastern part and within the upper 30 m layer in the western part of the WSC offshore section. The mean concentrations of particles and plankton found within the patches were 2.7 (S), 9.0 (M) and 17.5 (L) times higher than the concentrations in the background waters (Table 2).
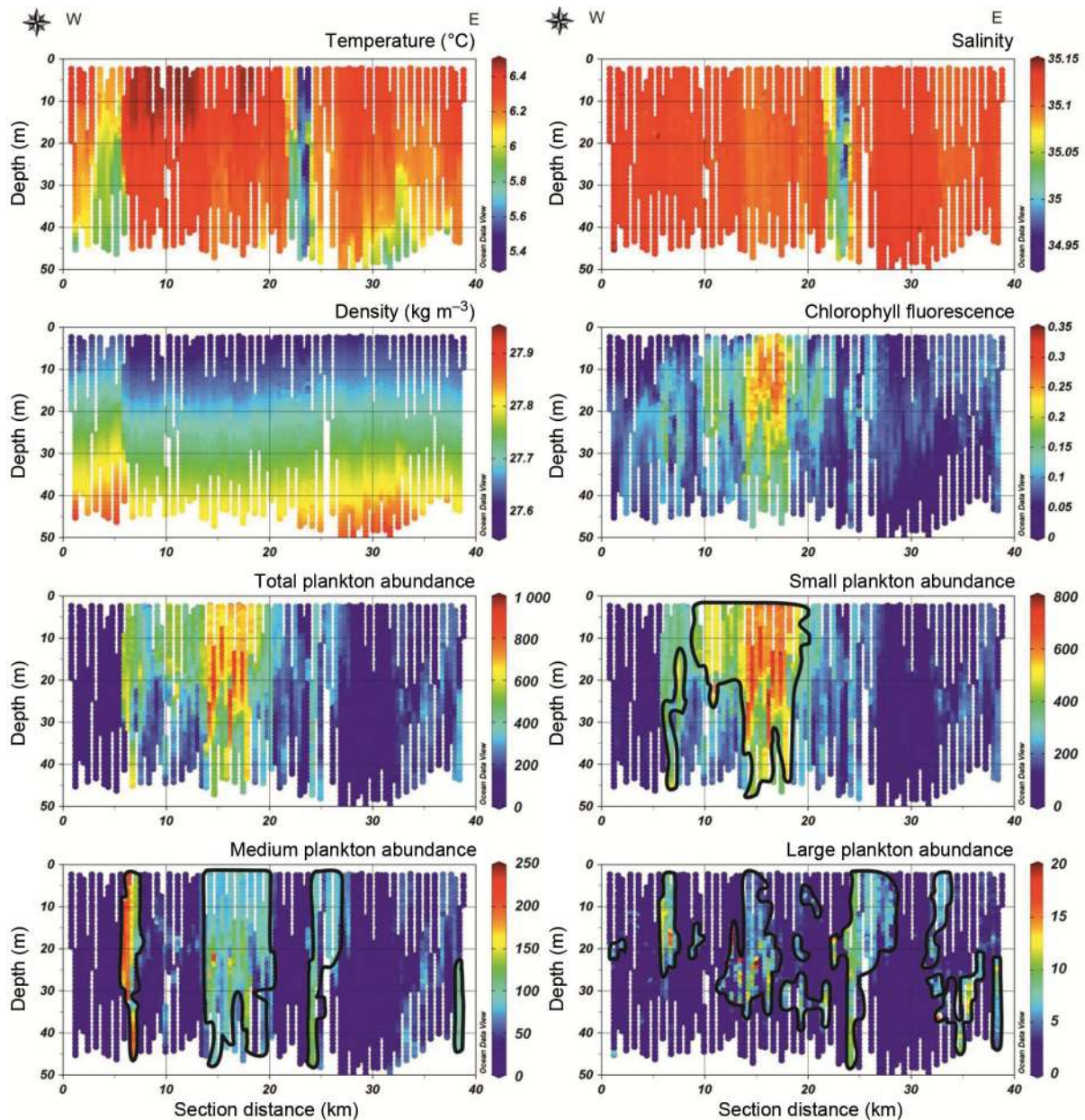
Fig. 4. West Spitsbergen Current (WSC) slope section. Distribution of temperature, salinity, density, chlorophyll fluorescence and plankton abundance (ind. m^{-3} × 10^3) of total, small, medium and large size fractions along the section. The identified patches are outlined by solid black lines

Relationships with water characteristics and discontinuities

The correlations between vertically averaged zooplankton abundances in the selected size categories (S, M, L) and the environmental variables (temperature, salinity, density, chlorophyll fluorescence) were analysed to verify whether there are statistical relationships between the observed patchiness patterns and the water characteristics (Table 3).

The abundance and distribution of the small size fraction was highly correlated with all measured characteristics of the water masses (temperature, salinity, density and chlorophyll fluorescence). In particular, a strong correlation was found between the abundance of small particles and water density (positive trend in FZ and SC sections and negative in both WSC sections). The strongest correlations between the abundance of the medium size fraction and the environmental variables were found in the
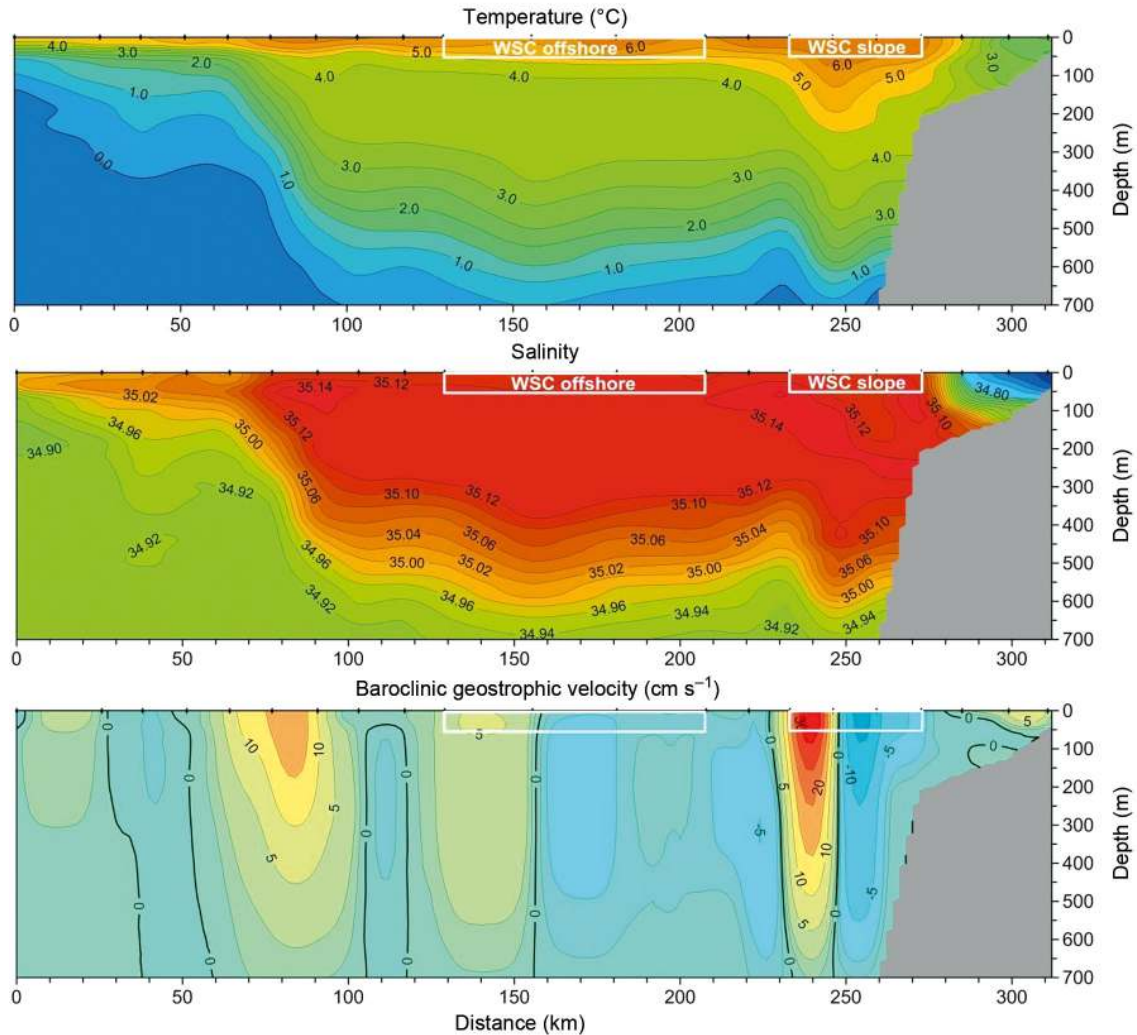
Fig. 5. Distribution of temperature, salinity and baroclinic geostrophic velocity in the upper 700 m layer. The locations of the West Spitsbergen Current (WSC) slope and WSC offshore laser optical plankton counter (LOPC) sections are indicated by white rectangles

sections in which large hydrographic gradients were observed (FZ and WSC slope sections). The correlations between the large size zooplankton abundance and the environmental variables were generally weak, except for in the SC and FZ sections.

The distribution of anomalies from average values over distance for individual sections, for particle and plankton abundance, and for the measured environmental variables showed a correlation between the occurrence of the peak abundance anomalies and the positions of the supposed water structures, such as increased pelagic system productivity (chlorophyll distribution) and water mass dynamics (hydrographical fronts, eddies or meanders). The largest anomalies in the distribution of all measured variables were observed in the FZ region, where the positive anomalies of particle and plankton abundance were located

mainly in the Atlantic water domain near the front (Fig. 7). In the SC section, higher-than-average abundances of all size fractions (S, M, L) coincided with higher-than-average salinity, density and chlorophyll and lower-than-average temperature (Fig. 7). In the southern part of the SC section (0–12 km), the abundance of small size fraction particles was positively correlated with chlorophyll fluorescence, while in the northern shallow part of the section, this correlation was negative. In the WSC slope and offshore sections, a strong, negative relationship was recorded between the anomalies of small size fraction abundance and water density. In the WSC slope section, positive abundance anomalies of the medium and, to some extent, large size fractions were observed close to the eastern edges of the 2 most pronounced temperature anomalies. Relationships between the anomalies of
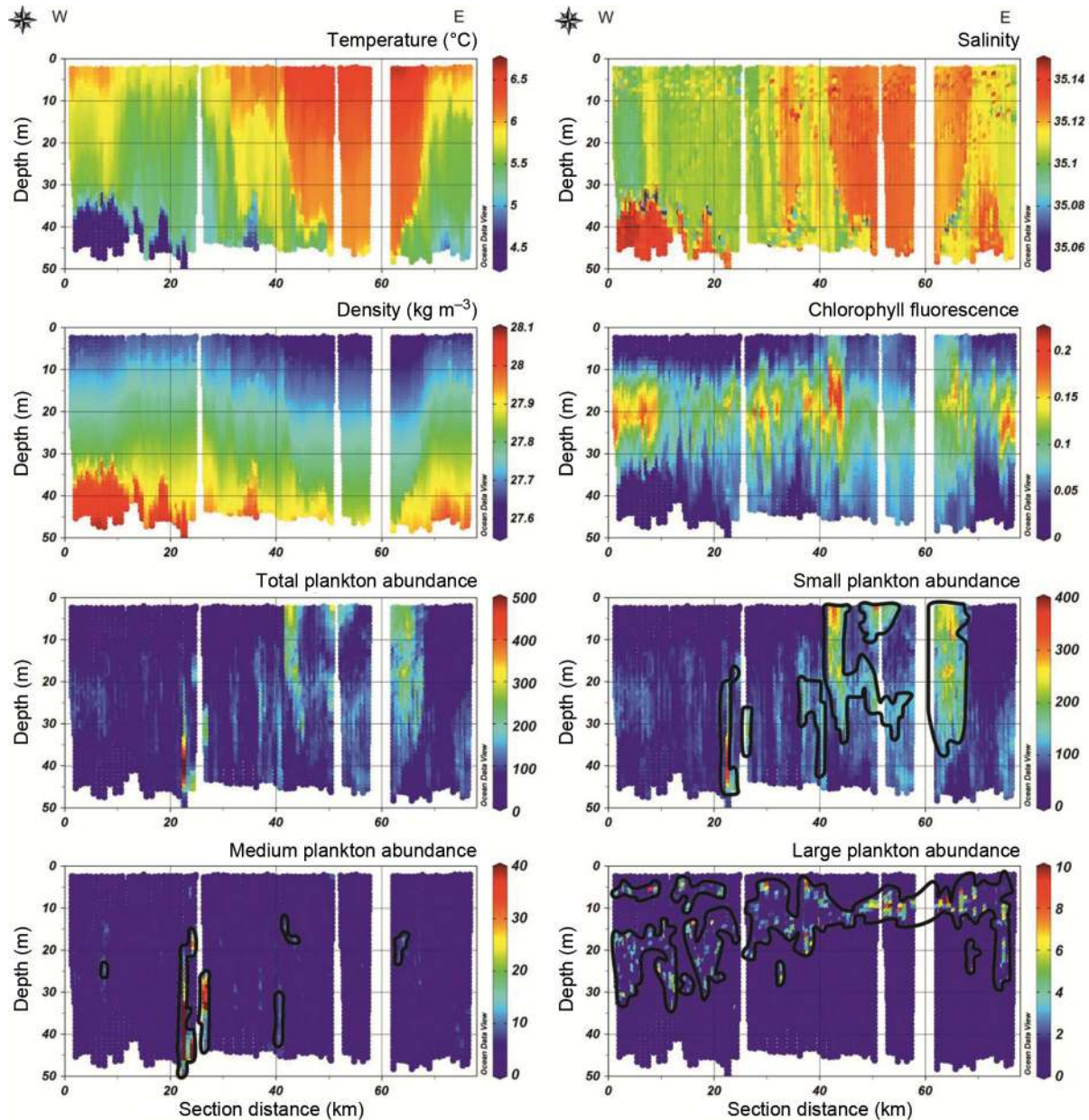
Fig. 6. West Spitsbergen Current (WSC) offshore section. Distribution of temperature, salinity, density, chlorophyll fluorescence and plankton abundance (ind. m^{-3} × 10^3) of total, small, medium and large size fractions along the section. The identified patches are outlined by solid black lines

large size fraction abundance and environmental variables in both WSC survey sections were the least pronounced.

Species composition

The results of the net sampling indicated that the zooplankton were very abundant in the SC section

(Table 4) and consisted mainly of calanoid copepods (*Calanus glacialis*, *C. finmarchicus* and *Pseudocalanus* spp.) and copepod nauplii. The copepods were found predominantly in the lower part of the studied layer, below 20 m. The zooplankton of the SC also included another calanoid copepod, *Acartia longiremis*, as well as the ctenophore *Mertensia ovum*, the appendicularian *Fritillaria borealis* and the chaetognath *Parasagitta elegans*.

Table 3. Non-parametric Spearman's rank-order correlations testing the pair-wise relationships between vertically averaged particle and plankton abundances in the selected size categories (small, medium and large) and environmental variables (temperature, salinity, density, chlorophyll fluorescence)

Section	Small		Medium		Large	
	R	p	R	p	R	p
FZ (n = 85)						
Temperature	0.70	<0.001	0.82	<0.001	0.63	<0.001
Salinity	0.83	<0.001	0.80	<0.001	0.48	<0.001
Density	0.84	<0.001	0.75	<0.001	0.35	0.001
Chlorophyll	0.62	<0.001	0.69	<0.001	0.43	<0.001
SC (n = 25)						
Temperature	−0.84	<0.001	−0.67	<0.001	−0.84	<0.001
Salinity	−0.17	0.414	−0.36	0.080	−0.14	0.495
Density	0.74	<0.001	0.44	0.028	0.76	<0.001
Chlorophyll	0.62	0.001	0.35	0.086	0.60	0.001
WSC slope (n = 77)						
Temperature	0.62	<0.001	0.36	0.001	−0.01	0.904
Salinity	−0.66	<0.001	−0.60	<0.001	−0.53	<0.001
Density	−0.91	<0.001	−0.61	<0.001	−0.27	0.019
Chlorophyll	0.86	<0.001	0.63	<0.001	0.28	0.015
WSC offshore (n = 153)						
Temperature	0.72	<0.001	−0.03	0.724	−0.20	0.012
Salinity	0.50	<0.001	−0.29	<0.001	−0.28	<0.001
Density	−0.76	<0.001	−0.02	0.841	0.18	0.024
Chlorophyll	0.57	<0.001	0.54	<0.001	0.10	0.215

The net zooplankton in the WSC slope section were more abundant in the eastern part (station N3P) than in the western part (station N2), where zooplankton were dominated by the cyclopoid copepod *Oithona similis*, younger life stages of *C. finmarchicus* and copepod nauplii. In the western part of this section, older life stages of *C. finmarchicus* were more abundant.

The zooplankton in the WSC offshore section were more abundant in the western part (N-2) and consisted mainly of *O. similis* and all developmental stages of *C. finmarchicus.* In the eastern part of the WSC offshore section (N1), the predominant zooplankton included older life stages of *C. finmarchicus* in the upper layer and *O. similis* in the lower layer (Table 4). Furthermore, in this section, the contribution of less-numerous taxa such as *C. glacialis*, *Triconia* spp. and meroplankton (e.g. Echinodermata and Bivalvia larvae) decreased compared with in the WSC slope section, whereas the contribution of *Pseudocalanus* spp. increased.

DISCUSSION

The present study contributes to the research on summer plankton distribution patterns in the dy-namic region of the Polar Front. Through high-resolution measurements, it was possible to detect particles and plankton patches concurrently with the environmental conditions under which they occurred. The distinguished patches differed in terms of their number, extent, spatial distribution, particle and plankton concentration as well as their relationships to the structured physical environment.

The earliest investigations of zooplankton patchiness assumed that zooplankton patches are circular (Wiebe 1970), but most of the latest investigations have shown that they are rather elongated structures, i.e. are much longer in the horizontal than in the vertical dimension. Most of the patches found in our study were a few kilometres long horizontally, which is in agreement with the results of an earlier study on the WSS (Trudnowska et al. 2012) as well as with a study in the Mediterranean Sea (Molinero et al. 2008) that investigated the size of *Calanus* and *Oithona* patches (6 and 12 km, respectively). According to Pinca & Huntley (2000), patches of this size are considered small. However, Vogedes et al. (2014) found that in Svalbard fjord the zooplankton patches can be even smaller (1.2 km). In contrast, patches of large size are known to spread horizontally over many kilometres, that is between 30 and 60 km (Huntley et al. 1995) or even >100 km in case of the largest patches (Pinca & Huntley 2000). Patches of *C. finmarchicus* along the New England coast occupied 2500 km^2 (Wishner et al. 1988). The vertical extension of the patches observed in the present study, from 5 to approximately 50 m (the entire studied water column), was within the typical range of regular patches (Pinca & Huntley 2000), but much greater than typical patch thicknesses recorded for thin plankton layers (Dekshenieks et al. 2001, Benoit-Bird et al. 2009). The size of plankton patches and their variability generally scale inversely with the organism's size (Levin 1992), and because the swimming capability of zooplankton is directly proportional to its size (Pearre 1979), the size-fractionated approach to the analysis of particles and plankton patches was applied in the present study. However, the variability and size of the patches observed generally did not differ among various size fractions. Instead, the hypothesis proposed for this
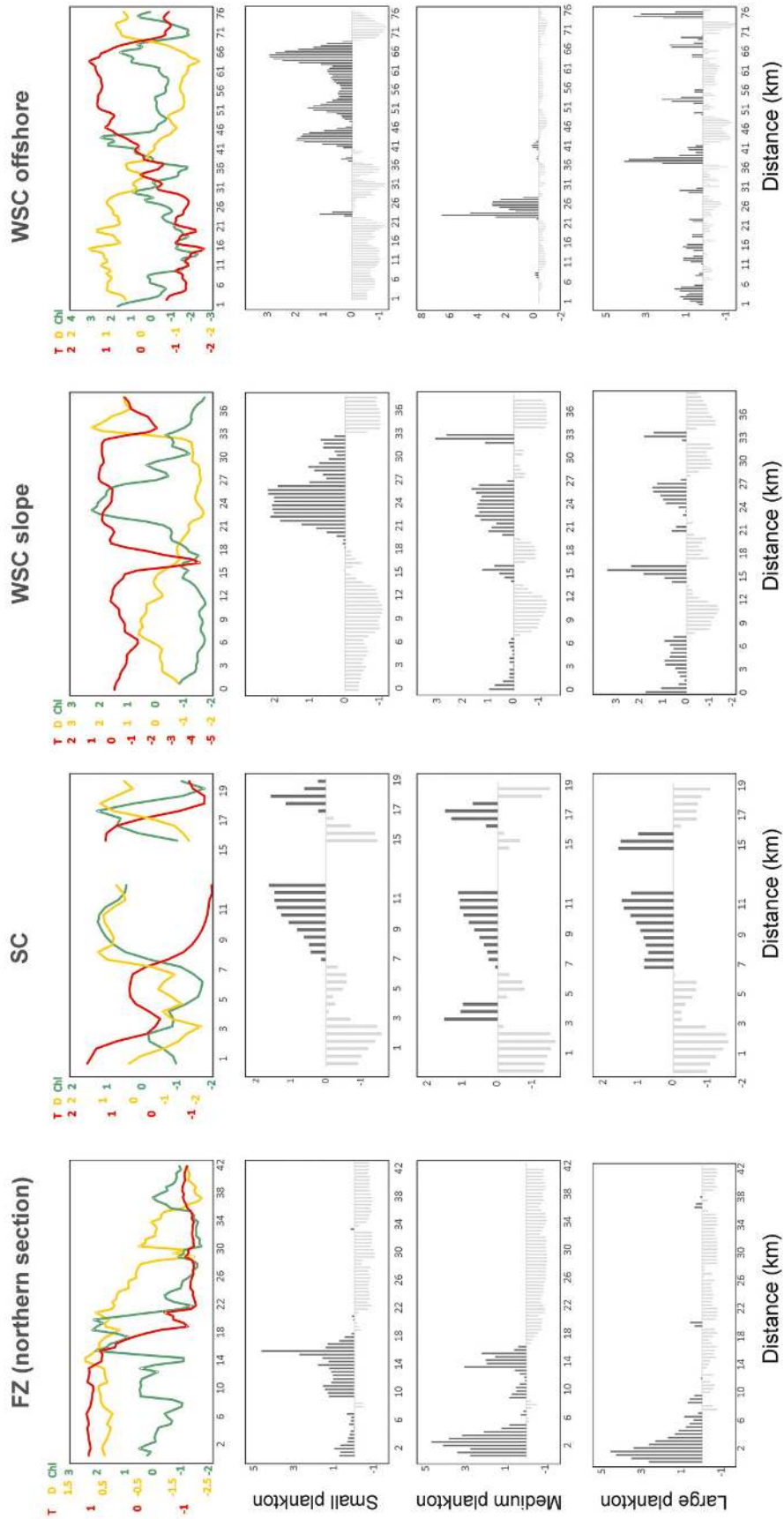
Fig. 7. Standardized anomalies in the abundance of the small (0.1–0.3 mm equivalent spherical diameter [ESD]), medium (0.3–0.8 mm ESD) and large (0.8–5.0 mm ESD) particle and plankton size fractions (grey columns) as well as in water temperature (red lines), density (yellow lines) and chlorophyll fluorescence (green lines) calculated for a 1 m vertical and 0.5 km horizontal distance gridding dataset. FZ: frontal zone; SC: Sørkapp Current; WSC: West Spitsbergen Current

Table 4. Taxonomic composition of net zooplankton (abundance ind. m^{-3})

Taxon	SC				WSC slope				WSC offshore			
	Stn V36		Stn V37		Stn N3P		Stn N2		Stn N1		Stn N-2	
	45–20m	20–0m	50–20m	20–0m	50–25m	25–0m	50–25m	25–0m	50–25m	25–0m	50–25m	25–0m
Calanus finmarchicus I–III	115	104	147	94	251	552	67	4	83	36	219	447
C. finmarchicus CIV–CVI	19	11	12	18	48	413	875	715	34	333	82	428
C. glacialis I–III	2456	1063	3204	1903	13	26	0	1	2	1	0	0
C. glacialis CIV–CVI	56	189	162	269	18	66	13	49	0	40	2	83
Pseudocalanus spp. CI–CIII	176	85	557	263	5	3	6	2	9	0	5	1
Pseudocalanus spp. CV–CVIF	19	24	109	47	17	3	21	5	33	6	38	53
Acartia longiremis	3	31	6	66	0	0	0	0	0	0	0	0
Oithona similis	80	73	239	153	1669	903	417	60	1086	122	1268	708
Copepoda nauplii	624	740	1055	862	162	279	46	7	52	27	75	100
Triconia spp.	0	2	5	0	57	8	11	12	4	4	2	6
Meroplankton	51	50	133	235	30	32	9	33	5	4	1	3
Mertensia ovum	6	10	7	77	0	0	0	0	0	0	0	0
Eukrohnia hamata	0	0	0	2	17	2	25	1	36	3	55	5
Parasagitta elegans	1	3	13	18	0	0	0	0	0	0	0	0
Appendicularia	32	46	10	51	5	7	0	0	0	0	0	1
Others	38	55	78	312	14	27	20	16	44	33	27	37
Total	3675	2485	5738	4370	2305	2322	1509	906	1389	610	1775	1871

study was supported by the tendency for the patches of smaller size particles and plankton to have a stronger relationship to the controlling physical conditions.

The method of averaged abundance and biomass over an area or a part of the water column (arbitrarily defined gridding) often fails to recognize the existence of plankton patches. This can only be achieved by high-resolution measurements of abundance or biomass rates of change over space (Benoit-Bird et al. 2009) or time, because the plankton patches occupy only a minor part of the ocean (2–17% in the present study; ~12% in the NE Pacific, Menden-Deuer 2012; 2–29% in Monterey Bay, Benoit-Bird et al. 2009). However, the importance of patches results from the fact that the concentrations of plankton and particles in patches are generally a few times higher than in the background waters (3–17 orders higher in the present study). Such high plankton concentrations, compared to those in the surrounding water, were observed in earlier studies in thin plankton layers consisting of phytoplankton, bacteria, marine snow and zooplankton (Dekshenieks et al. 2001, Alldredge et al. 2002, Benoit-Bird et al. 2010).

The LOPC detects and counts all objects suspended in the sampled water volume. Most of the particle counts include biological elements (phytoplankton, zooplankton, faecal pellets), but may also incorporate inorganic suspended matter from a river (Schultes & Lopes 2009) or a glacier plume (Trudnowska et al. 2014). Such material can constitute a

substantial part of the counts and it may also have contributed to the composition of the small size fraction patch detected above the sea bottom in the shallow part of the SC section (Fig. 3). Supporting evidence for this conclusion may be that this patch, unlike other patches of the small size fraction, was not associated with detectable chlorophyll fluorescence. The high abundance of particles in this patch most probably consisted mainly of sea-bottom sediments resuspended by storm-induced wave action over a shallow part of the shelf or of terrigenous material brought into the sea by terrestrial or glacial freshwater run-off (Trudnowska et al. 2015). Differentiation of the relative composition of phytoplankton and detritus in oceanic suspended matter can be confirmed by the simultaneous measurement of the light-scattering and absorption characteristics of the particles (Stramski et al. 2001, Trudnowska et al. 2015), although these techniques were not available for the present survey.

One of the possible mechanisms of patch formation may be related to the existence of local areas of higher primary production or standing stock, resulting in a subsequent concentration of potential grazers (e.g. Basedow et al. 2006, Norrbin et al. 2009, Menden-Deuer 2012). Indeed, the distribution of particles and plankton patches in the present study was often correlated with chlorophyll fluorescence maxima, as has been similarly demonstrated by, for example, Benoit-Bird & McManus (2012). The high, positive correlation between chlorophyll fluorescence and the abundance

of the small size fraction, especially in the WSC slope section, implies that a substantial part of the patch found there could comprise phytoplankton cells (Fig. 4, Table 3).

Particles and plankton are also known to concentrate and/or gather at density gradients (Woodson et al. 2005, Prairie et al. 2012). Patches of the medium size fraction taxa that are predominant in the study region (e.g. *Oithona*, *Triconia*, *Acartia*, young *Pseudocalanus*, copepod nauplii, benthic larvae) were frequently found concomitant with density discontinuities, such as the horizontal density gradient on the hydrographic front, the vertical density gradient at the pycnocline or the density gradients at the boundaries of pockets of hydrographically different waters. The density gradients may act as a barrier to particle and copepod movement and may facilitate the maintenance of their position near preferred habitats. Gallager et al. (2004) have shown that *Calanus* copepods occur in high numbers on the fringes of hydrographic gradients, as was also observed in the present study in the WSC slope section (large size fraction; see Figs. 4 & 7).

It is possible that the formation of the large size fraction patches, the distribution of which was not clearly associated with any detected oceanographic feature, could result from the migratory capabilities of the zooplankton due to habitat selection, forced by ontogenetic, diel and foraging migrations as well as predator avoidance (Falkenhaug et al. 1997, Folt & Burns 1999, Ambler 2002, Prairie et al. 2012). The biological cues could partly be modified by a lack of synchrony in daily vertical migrations, most likely present during midnight sun conditions (June–July). Previous studies either from the beginning (Blachowiak-Samolyk et al. 2006) or the end (Berge et al. 2014) of the productive season have indicated that vertical migration is not performed or is weakly pronounced in majority of the mesozooplankton taxa in the study region. The results of collecting zooplankton in the study area by nets suggest that the patches of the large size fraction consisted mainly of *C. finmarchicus* and *C. glacialis*, distribution of which also exhibited no evidence of dependence on environmental cues over small spatial scales in the northern North Sea (Solow & Steele 1995).

The large size fraction patch in the WSC slope section, which could be attributed to elevated concentrations of *C. finmarchicus*, was located at the periphery of the intrusion of low salinity and cold water at the edge of the anticyclonic eddy. Eddy-like mesoscale structures are commonly observed in

WSC waters (Gascard et al. 1995, Walczowski 2013), and peak zooplankton abundances are often found inside or on the peripheries of eddies (Riandey et al. 2005, Labat et al. 2009, Godø et al. 2012, Samuelsen et al. 2012). The high-resolution sections in the present study did not extend deep enough to detect the structure of the eddy; however, the analysis of full-depth hydrographic point measurements, carried out in parallel to the continuous survey, confirmed the occurrence of a mesoscale anticyclonic baroclinic eddy, extending down to approximately 700 m (WSC slope section). Eddies can extend to depths greater than 500 m (Smith 1988), but the most pronounced contrasts in temperature are mostly found in the upper 25–50 m, as in cyclonic eddies in the Fram Strait (Johannessen et al. 1987). The eddy observed in the present survey reached a diameter of approximately 30 km, which is a typical size for mesoscale eddies in the Fram Strait (Walczowski 2013), where the Rossby radius of deformation is on the order of 10 km. Eddies larger than the Rossby radius have an aggregating effect when rotating anticyclonically and a dispersive effect under cyclonic rotation. The aggregating effect of the anticyclonic rotation was confirmed in the present study, because the detected eddy contained extremely high particle and plankton concentrations. This eddy had a warm and salty core, similar to a 15-km-wide eddy that was previously observed near the surface in the vicinity of the Polar Front in the Barents Sea (Våge et al. 2014). A mesoscale eddy of this kind was also found over the continental slope of the northern Chukchi Shelf (Llinas et al. 2009). The eddy had a radius of 8 km and was associated with elevated concentrations of zooplankton, represented mainly by *C. glacialis* and *M. longa*. The aggregation of *C. glacialis* due to anti-cyclonic eddy circulation has also been observed in Academy Bay in the Sea of Okhotsk (Rogachev et al. 2008). Another eddy-like structure, with a cold-water core, was observed in the southern FZ sections. It was located at nearly the same location as a similar structure, containing almost exclusively the large copepod *C. glacialis*, that was found the previous year by Jakubas et al. (2013), which suggests a repeatable tendency for eddy formation in this region.

The Polar Front is a critical climatic feature for the dynamics of the Arctic region. To date, most studies of this feature have focused on the Barents Sea region (e.g. Loeng 1991, Parsons et al. 1996, Våge et al. 2014) while, in contrast, the Polar Front west of Spitsbergen has received substantial attention only recently. The recent studies reflect the understanding of the role of the Polar Front in modifying the heat

exchange by the WSC and in controlling environmental conditions in the Spitsbergen fjords (Saloranta & Svendsen 2001, Tverberg & Nøst 2009, Walczowski 2013). Increased productivity of plankton autotrophs and zooplankton in frontal systems, manifested by their elevated abundance, is a well-documented phenomenon (Franks 1992, Molinero et al. 2008, Schultes et al. 2013). Observations in the FZ sections of the present study, showed elevated densities of various plankton size fractions in relation to the front line and are in agreement with other *in situ* data obtained in the Polar Front region of the Barents Sea (Basedow et al. 2010, 2014). Similar increases in concentrations of phytoplankton and zooplankton have been detected in association with a front over a narrow continental shelf off northern Norway (Skarðhamar et al. 2007) and also in the Gulf of Maine (Beardsley et al. 1996). Such peak concentrations of particles and plankton at fronts often persist in the form of convex doming structures (Molinero et al. 2008, Trudnowska et al. 2012).

Physical features in the form of fronts or eddies create attractive feeding habitats for higher trophic levels (e.g. Bakun 2006, Godø et al. 2012). For the WSS, the importance of the Arctic side of the Polar Front as the main foraging site for the little auk *Alle alle* has been recorded by Stempniewicz et al. (2007) and Kwasniewski et al. (2010). The results of at-sea bird tracking studies showed that birds are able to sight the patches of potential prey and intensify foraging in these regions (WSS, Jakubas et al. 2013; Fram Strait, Joiris & Falck 2011). The higher overall particle and plankton abundances in the Atlantic offshore waters, in comparison to the Arctic waters on the shelf, are consistent with the results of previous studies in the frontal zone on the WSS (e.g. Kwasniewski et al. 2010, Dvoretsky & Dvoretsky 2013, Jakubas et al. 2013). In contrast, which fish components of the marine food web (e.g. capelin *Molotus villosus*, herring *Clupea herrengus*, possibly also Atlantic cod *Gadus morhua* or haddock *Melanogramus aeglefinus*) take advantage of higher concentrations of plankton on the Atlantic side of the Polar Front in the WSS region is still to be confirmed from direct observations. The results of the present investigation highlight the link between environmental gradients and the distribution of microhabitats in the Polar Front area in the vicinity of Spitsbergen. In turn, the differentiation of the pelagic habitat has consequences for ecosystem structure and functioning, due to its direct impact on spatial species distribution and trophic interactions.

CONCLUSIONS

This study highlights the mosaic nature of the distribution pattern of particles and plankton, as well as its response to a structured environment. It shows that the generation and existence of patches could be associated with peculiar conditions created by increased primary production, optimal hydrography, discontinuities in the density field and/or the presence of meanders or eddies.

The distribution of the small size fraction patches, comprising either phytoplankton (WSC sections) or non-living particles (SC section), was closely related to specific patterns in hydrography. The patches of the medium size fractions, consisting of small zooplankton and marine snow, concentrated predominately at discontinuities in density field. The distribution of the large size fraction patches, which comprised mostly *Calanus* copepods, was not associated with any specific hydrographic or hydrodynamic feature detected in this study and it is thus assumed that biological factors were the major causes responsible for their migration and aggregation processes.

The observations on different relationships between the environmental structures and diverse, size-specific particle and plankton distribution patterns provide new data for discussions about the concepts of marine ecosystem structure and functioning. However, several aspects remain to be studied, such as patch persistence, details of patch composition and origin, and their ecological consequences. Recently improved ability to observe patches of plankton with increased resolution, owing to the application of acoustic and optical methods, should further facilitate studies enabling a comprehensive understanding and explanation of the spatial and temporal variability of plankton distribution under the dynamic conditions of the Arctic Ocean. These investigations will require synchronised measurements and sampling using these modern and advanced *in situ* optical and acoustical sensors, together with satellite observations to allow proper spatial and/or temporal resolution of the investigations.

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