



# Spatial and temporal variation of hydrological characteristics and zooplankton community composition influenced by freshwater runoff in the shallow Pechora Sea

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## Abstract

Polar shallow marginal seas are of high importance as they are the most productive regions of the Arctic Ocean and serve as filters for terrestrial runoff. Salinity and turbidity gradients create diverse habitats for planktonic organisms in coastal areas. In the present study we aimed at assessing the degree to which environmental gradients influence the abundance and community structure of the zooplankton in a shallow Arctic sea affected by terrestrial runoff. Zooplankton distribution was studied in a coastal zone in the southeastern part of the Barents Sea (Pechora Sea) in July 2014 and September 2016 along the archipelago that stretches from the continent towards the open sea. The ecosystem was in a spring state in July (2014) and in a summer state in September (2016). A clear positive gradient of salinity and a negative cline of turbidity were revealed, directed from the coast towards the open sea. A horizontal salinity gradient was detected in both seasons. The turbidity gradient was most pronounced during summer. Distribution of several species of marine zooplankton (e.g. *Pseudocalanus* spp., *Temora longicornis*, *Microsetella norvegica*) was associated with the salinity gradient. Parameters of community structure (species richness, diversity, evenness, total zooplankton abundance) correlated with turbidity while only diversity and evenness were influenced by salinity. A gradient was observed from a more diverse and less abundant zooplankton community in areas with high turbidity and low salinity towards a less diverse and more abundant community in the open sea. This heterogeneity influences higher trophic levels including commercial fishes and reflects how marginal filters function.

**Keywords** Arctic · Pechora Sea · Environmental gradients · Zooplankton distribution · Community structure

## Introduction

Zones where fresh and marine waters mix are important barriers as suspended and dissolved matter, including pollutants, moves from land to sea. A specific term “marginal filters” has been introduced to define such areas (Lisitzin 1994, 1999). In these intermixing zones, geochemical transformations and biological processes effectively remove most

suspended and dissolved matter from riverine waters. This process includes several successive stages as freshwater flows into the sea. It begins with gravitational sedimentation followed by coagulation and sorption, and later by bacterial and algal assimilation of a major part of the dissolved matter, including biogenic elements. Further planktonic and benthic filter feeders consume microalgae as well as organic and inorganic detritus, and excrete undigested material as fecal pellets, which settle on the bottom. Particulate and dissolved matter removal from terrestrial runoff reaches 95% and 20–40% efficiency, respectively (Lisitzin 1999). Thus zooplankton plays a key role in biosedimentation processes occurring in estuaries and other mixing zones.

Knowledge on quantitative and qualitative changes in zooplankton communities under the influence of freshwater and suspended matter brought to the sea by rivers is important for understanding how marginal filters function. The abundance and production of phytoplankton are significantly reduced in areas with high turbidity despite nutrient

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sufficiency (Cloern 1987; Northcote et al. 2005). This is due not only to mechanical influence (e.g. by decrease of light penetration into water column), but also to nutrients' absorption into suspended particles (Shi et al. 2017). Environmental heterogeneity, characteristic for estuaries, influences planktonic organisms, horizontal and vertical distributions of which are determined mainly by environmental gradients (Laprise and Dodson 1994; Plourde et al. 2002). Although zooplankton variability in areas where marine and fresh waters mix has drawn the attention of many researchers (Laprise and Dodson 1994; Prudkovsky 2003; DÍaz-Gil et al. 2014; Helenius et al. 2017), its distribution in mixing zones in the open sea, away from narrow estuaries is poorly known (Espinasse et al. 2014).

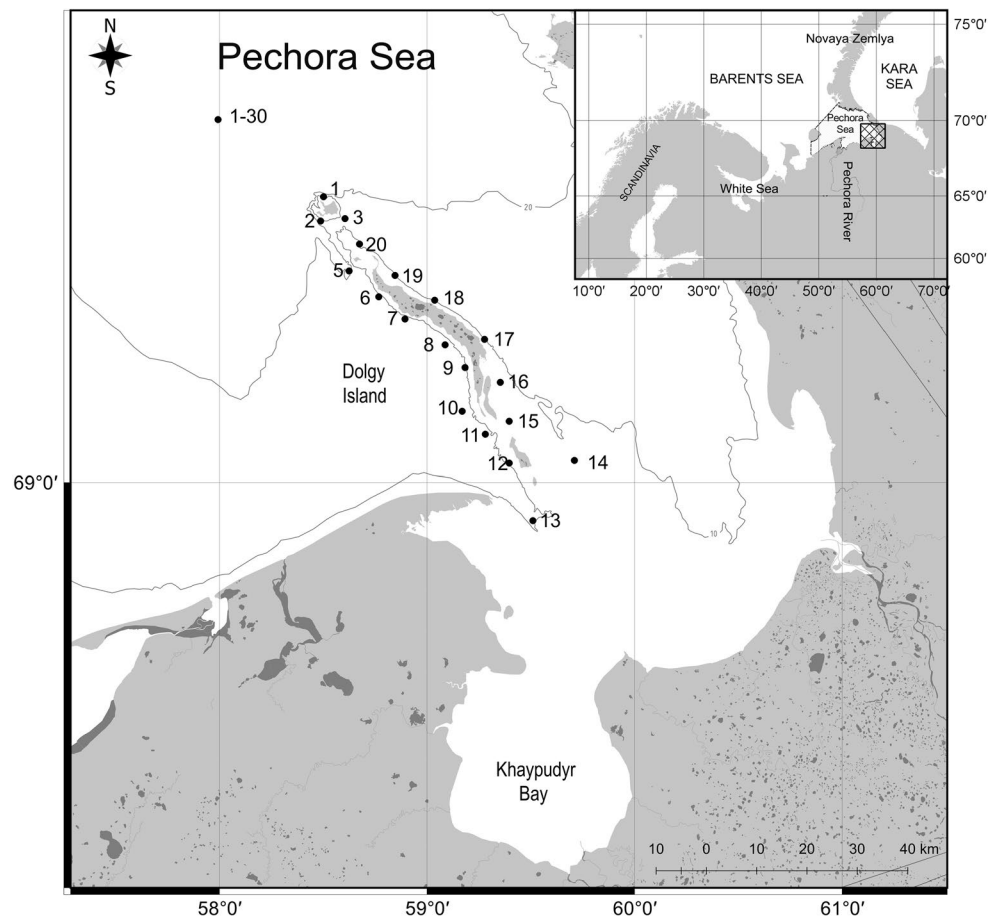
Besides serving as filters for (and partly owing to) terrestrial runoff, the continental shelf is the most productive zone of the oceans. Zooplankton comprises the basic trophic levels of these ecosystems, so knowledge of its abundance, species composition, quantitative and qualitative distribution and functioning is crucial for understanding processes in the whole system (Raymont 1983). Mesozooplankton and copepods may remove up to 50% of primary production in the coastal zone in the Southern Ocean (Atkinson et al. 2012) and in the White Sea (Berger 2007). Zooplankton is

food source of commercially important fish such as herring, Arctic cod and capelin (Podrazhanskaya 1995; Karamushko et al. 1996). Planktivorous fishes account for about 25% of total ichthyofauna in the Barents Sea (Karamushko 2013).

We studied zooplankton abundance and distribution in the shallow coastal area of the Barents Sea—called the Pechora Sea—during two expeditions in 2014 (July) and 2016 (September). The study area is located in a mixing zone strongly influenced by terrestrial runoff.

Russian and American Arctic seas, where many great rivers discharge, are examples of the mixing zones described above. The southernmost parts of these seas, in immediate proximity to river mouths, form marginal filters of great scale. The Pechora Sea, in the southeastern part of the Barents Sea, is one of such systems. This shallow region (Fig. 1) with depths less than 50 m on most of its area experiences substantial continental runoff. In fact, it may serve as a model of the northern marginal seas of Eurasia and America, such as the Kara Sea, the Laptev Sea, the East Siberian Sea, the Chukchi Sea, and the Beaufort Sea, which receive massive river discharge. Besides the runoff itself, the complicated system of local currents significantly influence the hydrological conditions in the Pechora Sea (Byshev et al. 2003; Danilov et al. 2004). Therefore understanding

**Fig. 1** Map of the study area. Position and number of sampling stations are indicated



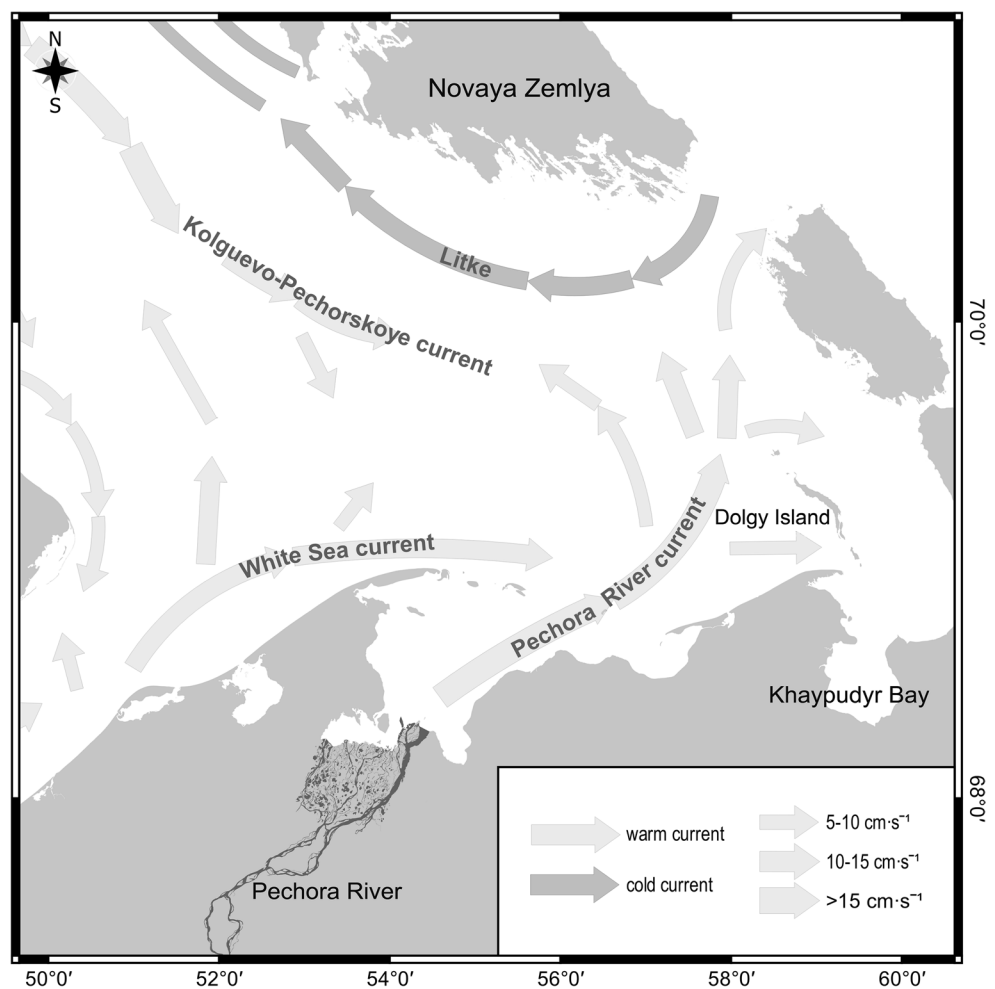
zooplankton interactions with environmental gradients in this area gives insight into the biogeochemical processes in the coastal zone of the Arctic Ocean.

The main currents influencing coastal waters are directed mostly from West to East (Byshev et al. 2003; Danilov et al. 2004) (Fig. 2). The Pechora River and the White Sea waters occupy nearshore areas, while the Kaninskoye and Kolguevo-Pechorskoye currents flow farther from the shore, bringing relatively warm and saline water of Atlantic origin into the Pechora Sea (Byshev et al. 2003). The latter is transformed here through the mixing with the Pechora and White Sea waters. The main source of fresh water in the region is the Pechora River, discharge of which is 130–160 km<sup>3</sup> a year, or about 90% of all freshwater inflow into the Pechora Sea (Matishov et al. 1996; Nikiforov and Dunayev 2003). Thus the area of the Pechora Sea affected by the discharge of the Pechora River is very large because of the shallowness of this sea; the influence of Pechora waters was traced all the way up to Vaygach Island (Byshev et al. 2003). The large freshwater inflow supports the existence of strong vertical and horizontal gradients of abiotic parameters, such as salinity, temperature, suspended and dissolved organic matter,

etc. (Matishov et al. 1996). According to rather scarce publications, a wide (100–150 km) mixing zone exists in this area between local coastal waters and those flowing out of the White Sea (Danilov et al. 2004). During the warm period of the year, this zone is characterized by a thermo- and halocline at 10–20 m depth, this depth increases further from the continent towards the open sea. The temperature changes from 4 to 9 °C above the pycnocline to below 0 °C under it; salinity varies from 26–30 to 32–34, respectively. The area of influence of Pechora River waters declines during the summer period, shifting the zone of mixing with White Sea waters towards the coast and forming complicated spatial patterns of mixing (Musaeva and Suntsov 2001). Seasonal changes in environment may influence zooplankton community, and thus need special investigations.

Zooplanktonic communities in the Pechora Sea are formed mainly by boreal, boreal-Arctic and Arctic species (Zelikman 1966; Musaeva and Suntsov 2001). The average biomass varies from 9 to 180 mg wet weight m<sup>-3</sup> in summer (August–September) to 400–500 mg wet weight m<sup>-3</sup> in spring (July) and autumn (October) (Timofeev and Shirokolobova 1996; Troshkov and Gnetneva 2000; Musaeva and Suntsov

**Fig. 2** Main currents in the Pechora Sea (modified from Byshev et al. 2003 and Danilov et al. 2004)



2003). Copepods dominate zooplankton throughout the entire ice-free period, although Hydrozoa and larvae of benthic animals (meroplankton) are observed in high densities during July–August (Troshkov and Gnetneva 2000; Musaeva and Suntsov 2003).

The Pechora Sea is situated outside of the main commercial fishing areas in the western part of the Barents Sea, which made it relatively understudied until recent decades. However, after finding oil and gas fields in this area in 1989, interest to local fauna and flora increased significantly because of the possible and actual anthropogenic impact on local ecosystems (Plotitsyna and Kilezhenko 1993; Zelenkov and Miskevitch 2000; Novoselov and Studenov 2008). Moreover, an archipelago of small islands in the Pechora Sea and the adjacent sea area, where we worked, belong to the Nenetsky State Nature Reserve and are considered an Important Bird Area (Nikolaeva et al. 2006). They provide habitats for the Pechora Sea population of Atlantic walrus (Born et al. 1995; Boltunov et al. 2010; Semenova et al. in revision), numerous pinnipeds and small whales (Kondakov 1996) and serve as nesting and feeding grounds for many waterfowl as well as stopovers for water birds migrating along the East-Atlantic flyway (Anufriev 2006; Krasnov et al. 2006; Nikolaeva et al. 2006). Increased anthropogenic pressure along with the necessity to protect important populations of marine birds and mammals in the Pechora Sea has led to a rise in scientific interest in this region (e.g., Druzhkov et al. 1997; Dahle et al. 1998; van der Graaf et al. 2004; Denisenko et al. 2007). The main object of our study, zooplankton, is a key link in the trophic chain of the oceanic ecosystems (Raymont 1983). It is a food source for local planktivorous fishes, e.g. herring (*Clupea harengus pallasi n.suworowi*) and Arctic cod (*Boreogadus saida*) (Karamushko et al. 1996), which are important food objects for higher trophic levels, especially marine mammals (Kondakov 1996) and birds (Lønne and Gabrielsen 1992; Borkin 2012). Understanding the mechanisms affecting spatial and temporal distribution and zooplankton community structure parameters is necessary in order to predict possible changes in the Pechora Sea pelagic ecosystems.

Our study aimed at assessing the effect of abiotic factors on zooplankton distribution and its temporal (seasonal) variation in the continent–sea boundary area in the SE part of the Pechora Sea. We hypothesize that hydrological gradients and fields forming in this mixing zone affect zooplankton community structure and quantitative distribution. We also tested whether local or Pechora River runoff exerted more influence on the zooplankton communities in the study area.

## Materials and methods

### Sampling

We conducted zooplankton sampling and hydrological measurements during two cruises, 13–17 July 2014 and 1–7 September 2016, within 15-m isobaths (except two stations—St. 5 and 1–30) around Dolgy Island and adjacent islands in the southeastern part of the Pechora Sea (Fig. 1). The number of stations in 2014 and 2016 differed; only those stations where zooplankton was taken were used in the analysis (Table 1). However all stations are presented in the table to show the spatial distribution of abiotic parameters. The distance between the southernmost and northernmost stations was 97 km. Depth varied from 9 (St. 16) to 31 m (St. 1–30). Data on two upper water layers (above thermocline and the layer of thermocline, which was present at those stations) was used in the analysis at St. 5 and St. 1–30, because they were deeper than others (19 and 31 m respectively) (see Table 1).

### Hydrological parameters

Vertical profiles of temperature (Temp, °C) and salinity (S, PSU) were obtained using a MIDAS CTD + oceanographic probe (Valeport Ltd., UK). Profiles of concentrations of chlorophyll *a* (Chl,  $\mu\text{g L}^{-1}$ ), coloured dissolved organic matter (CDOM, RFU—Relative Fluorescence Units) and turbidity (FTU, Formazin Turbidity Units) were measured with a Cyclops-6 multi-sensor platform (Turner Designs, USA). The average values of these parameters in the upper water layer, corresponding to the zooplankton sampling layer at shallow stations (depth ( $Z$ )  $\leq 13$  m), were calculated. At deep stations ( $Z > 13$  m), zooplankton was collected according to pycnocline position (see below). Tidal height (Tide\_ $H$ , m) was recorded at the time of sampling at each station. Negative and positive values were assigned to tidal height if sampling occurred during ebb and flood, respectively.

### Zooplankton

A Juday net (37 cm mouth diameter and 100  $\mu\text{m}$  mesh size) was used for zooplankton sampling. Vertical hauls were made from the bottom to the surface, or above and below pycnocline: at St. 2 (0–5, 5–13 m) and St. 5 (0–5, 5–10 and 10–19 m) in 2014; at St. 1–30 (0–6, 6–11 and 10–29 m) in 2016. At other stations the total water column was sampled (Table 1). The samples were preserved by formaldehyde addition to the final concentration of 4%. All Copepoda, except rare Harpacticoida, were identified both at the species level and by developmental stage. Other holoplankton organisms were also identified at the species level where possible.

**Table 1** Average values of environmental parameters in the upper water layer in spring (2014) and summer (2016)

Station	Coordinates		Depth, m	Zooplankton sampling layer, m	Station position relative to the islands <sup>a</sup>	Temperature, °C		
	N	E				Spring	Summer	
1	69°29'19"	58°30'18"	15.5	0–11	W	1.7	11.5	
2	69°26'45"	58°29'17"	16.5	0–5, 5–13	W	1.9		
3	69°27'0"	58°36'18"	15.5		W	2.4		
5	69°21'41"	58°37'30"	22.7	0–5, 5–10, 10–19	W	1.2		
6	69°19'0.5"	58°46'5"	18.0	0–13	W	3.1	12.2	
7	69°16'46"	58°53'38"	14.3	0–12	W	3.9		
8	69°14'14"	59°5'24"	13.2	0–10	W	2.9	12.1	
9	69°11'48"	59°10'59"	12.0	0–6	W	2		
10	69°7'40"	59°10'48"	12.5	0–10	W	5.2	12.1	
11	69°4'24"	58°17'24"	13.5		W	6.1		
12	69°1'59"	59°23'46"	11.0		W	3		
13	68°56'8"	59°30'43"	13.5	0–10	W	3.3	12.1	
14	69°2'16"	59°42'36"	12.9	0–10	E	3.6		
15	69°6'27"	59°23'60"	11.4	0–8	E	5.1	12.2	
16	69°10'17"	59°21'11"	9.5	0–5	E	4.3		
17	69°14'42"	59°16'41"	12.0	0–8	E	3.7	11.6	
18	69°18'41"	59°2'13"	12.2	0–10	E	3.8		
19	69°21'19"	58°50'49"	12.5	0–8	E	3.5	11.4	
20	69°24'40"	58°40'52"	13.5	0–10	W	2.2	11.6	
1–30	69°37'0"	57°59'36"	31.0	0–6, 5–11, 10–29	W		11.5	
Average ± SE						3.3 ± 0.29***	11.8 ± 0.11***	
Station	Salinity, PSU		CDOM, RFU		Turbidity, FTU		Chlorophyll <i>a</i> , µg L <sup>-1</sup>	
	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer
1	24.5	25.3	614.7	245.5	2.1	1	2.2	1.1
2	24.5							
3	22.5				1.4		1.2	
5	27.1		676.7		1.8		1.3	
6	22.7	23.8	706.5	360.9	2.8	0.4	1.6	0.8
7	21.7		796.0		1.4		1.4	
8	17.7	23.1	825.8	408.0	2	0.7	1.8	1.1
9	17.8		819.9		1.1		1.9	
10	16.1	22.5		382.6		1.1		0.8
11	17.1				1.3		1.1	
12	16.5				3.5		2	
13	16.1	23.8		360.6	3.5	4	2	1.6
14	16.8		713.8		1.2		1.4	
15	15.6	24.1	842.3		2.2	3.3	1.6	1.3
16	15.2		682.2		0.9		1.2	
17	18	26.1		201.9		3		1.7
18	18.1		708.7		1.8		1.3	
19	19	26.3		214.1	1.7	1.5	1.4	1.2
20	22.3	25.3	655.9	230.9	1.3	1.2	1.2	1.2
1–30		29.6		153.2		0.5		1.1
Average ± SE	19.4 ± 0.82**	25.0 ± 0.65**	731.1 ± 23.23***	284.2 ± 31.16***	1.9 ± 0.20	1.7 ± 0.41	1.5 ± 0.09*	1.2 ± 0.09*

Significant differences between seasons are indicated by asterisks

<sup>a</sup>W to the west from the islands, E to the east from the islands

Mann–Whitney *U*-test: \**U*=23, *p*=0.04, \*\**U*=17, *p*=0.009, \*\*\**U*=0.0, *p*=0.0001

Meroplankton organisms—larvae of benthic and nektonic animals—were identified to the highest taxonomic level. Each sample was concentrated to 100 or 200 mL, depending on the abundance of organisms. Abundant species (> 10 ind. per subsample) were counted in 1-mL subsamples, while rare ones were counted in the total sample in Bogorov chamber. We counted three subsamples per station in order to account for possible splitting errors. Zooplankton abundance (ind. m<sup>-3</sup>) in 0–10 m layer or total sampled depth, if the latter was less than 15 m, was used in the analyses. Zoogeographical attribution (Arctic, boreal-Arctic, cosmopolitan) and ecological traits (cold- and warm-water, marine and brackish-water) were assigned to all species (Musaeva and Suntsov 2001, 2003) (Table 3).

## Data analysis

### Environmental data

The analysis of water mass structure aimed to accomplish three main tasks: (1) to reveal seasonal changes, (2) to search correlation between hydrological parameters, (3) to reveal spatial structure of water masses. Hydrological parameters (Temp, S, Chl, CDOM, Turbidity, Tide\_H) were combined in one matrix, centered to a zero mean and standardized to unit variance, which was analyzed for redundancy (analysis of redundancy, RDA; Legendre and Legendre 2012). Cruises were planned to capture typical spring (late spring) and summer conditions. The season of sampling was used as a constraining factor “Season”, with two gradations: “spring” (July 2014) and “summer” (September 2016). The seasons were determined according to previous studies (Zelikman 1961; Fomin 1985; Matishov et al. 1996; Troshkov and Gnetneva 2000). One constrained axis (RDA1) and five unconstrained axes (PC1–PC5) were extracted. Unconstrained axes characterize variation of water mass parameters after exclusion of the factor “Season”. PC1 and PC2 were the most informative unconstrained axes and thus were chosen for further analysis.

The influence of two main sources of the fresh water was studied: The Pechora River and Khaypudyr Bay. We hypothesized that the influence of the Pechora River, the main source of fresh water and sediments in the Pechora Sea, would lead to differences of hydrological parameters between stations located on different sides of the archipelago. Two regression models of the same type were constructed to examine the influence of geographical position of a station on the variation of unconstrained axes values. PC1 and PC2 were used as the dependent variables. In both models, distance from the southernmost station, St. 13 (reflecting distance from Khaypudyr Bay) and a discrete variable “Group” were used as predictors. The variable “Group” characterized the position of each station relative to the flow

from the Pechora River: whether the station is open to it or is shielded by the islands. “East” group included stations 14–19, while others were attributed to the “West” group. The baseline for the variable “Group” was defined as “East”. Therefore, a negative value for this variable means a negative change compared to the values observed to the east of the archipelago (stations 14–19), and the positive sign means positive change.

### Zooplankton

Before analysis, we divided zooplankton into two constituents: larvae of benthic animals (meroplankton) and true planktonic organisms (holoplankton), which were studied separately. The effect of environmental parameters on the distribution of zooplankton communities was assessed in the following two ways: (1) using multidimensional data—hydrological parameters and abundance of each taxon, and (2) only for holoplankton, using “one-dimensional” variables, which characterize holoplankton community structure—total holoplankton abundance ( $N$ ), number of taxa ( $Sp$ ), Shannon–Wiener diversity index ( $H$ ) and evenness index ( $E$ ). The Shannon–Wiener index was calculated based on holoplankton abundance as follows:

$$H = - \sum [(N_i/N) \times \ln(N_i/N)]$$

where  $N_i$  is abundance of  $i$ th species (ind. m<sup>-3</sup>) and  $N$  is abundance of all species (ind. m<sup>-3</sup>). The evenness ( $E$ ) was calculated as ratio of the actual Shannon–Wiener index to the highest possible value based on the number of species (Pielou 1966):

$$E = H/H_{\max}$$

$$H_{\max} = \ln(Sp)$$

where  $H$ —Shannon–Wiener index;  $H_{\max}$ —highest possible Shannon–Wiener index value for taxa number  $Sp$ .

For the multidimensional analysis we reduced taxa number, leaving out those with low abundance. To find the threshold abundance we calculated average abundance values for each of the 35 taxa using data of both cruises (in 2014 and 2016), and built a diagram depicting frequency distribution of abundance values (not shown). Those taxa which formed a peak in the area of small values ( $\ln(N+1) < 2$ ) were excluded from analysis. After this reduction 16 taxa were used in the analysis. To diminish dispersion between more abundant and less abundant taxa all abundance values were  $[\ln(N+1)]$ -transformed.

Redundancy analysis (RDA) was used for constrained ordination (Legendre and Legendre 2012). As with the hydrological parameters, a matrix of standardized (scaled to zero mean and unit variance) values were used in analysis,

so that the latter was based on the matrix of correlations. The analysis was conducted in two steps. For the first step, we estimated ordination in constrained axes, based on the model, including all studied predictors, some of which are redundant. At the second step, we selected an optimal model of ordination, for which an algorithm of forward stepwise selection was used to select only meaningful predictors (Borcard et al. 2011). This procedure allowed us to only include those predictors which had a significant effect on ordination of stations and taxa in the model. Significance evaluation of the multidimensional model as a whole, and significance of individual ordination axes was accomplished by permutation method (Legendre and Legendre 2012) with 9999 permutations. In all analyses, the season of sampling was included as a discrete predictor.

In the “one-dimensional” analysis, all taxa of holoplankton were used. Multiple regression analysis was applied to study the connection of holoplankton community structure (H, E, N, Sp) to environmental parameters. Evaluation of multicollinearity of predictors (not presented) has shown that CDOM, Temp and Season demonstrated high values of the variance inflation factor. This violation of regression analysis applicability forced us to include in the models only one of the three correlated factors—Season. The baseline value for this factor was defined as spring; the sign before respective coefficient denotes a change relative to the values in spring: “+” means increase, “−”—decrease in summer. Thus, following predictors were used in the models: Season, S, Turbidity, Chl, Tide\_H. Control of conditions of regression analysis applicability was accomplished by visual evaluation of residual diagrams.

Because the studied abiotic and biological parameters had spatial gradients, we analyzed spatial variograms for the control of existence of spatial autocorrelations (Zuur et al. 2009). In cases of significant spatial autocorrelations, we introduced a Gaussian correlation function, which models spatial relationships.

One- and multidimensional analyses were conducted with the use of statistical functions in the R software package (R Core Team 2017). For multidimensional analysis, functions of *vegan* package were used (Oksanen et al. 2018): for the model, which includes all studied predictors, function `rda()` was used; for optimal model selection function `ordisep()` was used. “One-dimensional” analysis was accomplished with the use of functions of *nlme* package (Pinheiro et al. 2017), for model construction we used function `gls()`.

Comparisons of different abiotic parameters, zooplankton abundance and community structure variables in different seasons were made with nonparametric Mann–Whitney *U* statistics. Analysis was conducted in statistical software Statistica (StatSoft Inc.).

In all analyses, statistical significance was evaluated at 0.05 significance level ( $p < 0.05$ ).

## Results

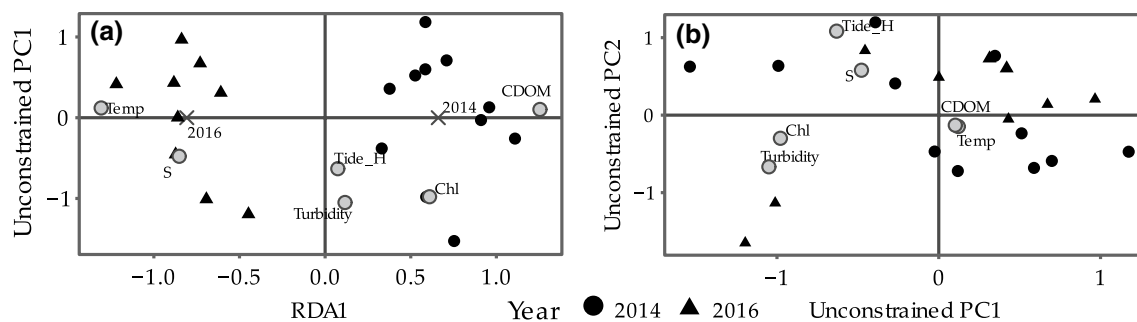
### Spatial and temporal variation of hydrological parameters

Average values of temperature, salinity, chlorophyll *a* concentration and CDOM in the studied area differed significantly in spring (July 2014) and summer (September 2016) (Table 1, Mann–Whitney *U* test). In July 2014 temperature in the 0–10 m water layer varied between 1.2 and 6.1 °C and was much lower than in September 2016, when it was between 11.4 and 12.2 °C at all stations. Salinity showed a similar pattern with more brackish water at stations 8–16 in spring, and much less variation in summer. On the contrary, CDOM was about 2.5 times higher in spring than in summer, while the difference between seasons in chlorophyll *a* concentration was less, albeit significant (Mann–Whitney *U* test,  $p = 0.04$ ). Overall, Chl*a* varied in the studied area from 0.8 to 2.2 µg L<sup>−1</sup>. Turbidity was the only parameter that did not differ significantly in spring and summer, partly because the variation between stations was high (Table 1).

Results of the multidimensional analysis confirmed the existence of seasonal differences. The only constrained axis, RDA1 (permutational  $F = 12.6$ ,  $p < 0.0001$ ), associated with the season of sampling, described 41% of total variability, while the unconstrained five axes together described 59%. All stations were divided into two groups, distributed along RDA1 axis according to the season (Fig. 3a). Water temperature (Temp) and salinity (S) demonstrated the highest negative and CDOM the highest positive loadings on the RDA1 axis, which indicates that these three parameters demonstrated the strongest seasonal changes. The association of chlorophyll concentration with RDA1 (i.e. seasonal variation) was somewhat weaker (Table 1).

Ordination of stations and water parameters in unconstrained axes PC1 and PC2 (Fig. 3b) demonstrated variation excluding the influence of RDA1, i.e. without the influence of factor “Season”. These two unconstrained axes explained 45% of total variability: 25% (PC1) and 20% (PC2), meaning that two more or less equal horizontal gradients existed in the study area. CDOM and temperature were not connected explicitly to PC1 or PC2, which demonstrates that the variability of these factors was almost exclusively explained by seasonal changes.

We cannot unambiguously interpret PC1 and PC2 as gradients of some definite factors. However, PC1 can be linked to the gradient of Turbidity and Chl as they had maximal negative loadings on this axis. Nevertheless nonzero loadings of Tide\_H and S on PC1 did not allow separating input of these parameters from that of Turbidity



**Fig. 3** Ordination of stations (small dark circles and triangles) and water parameters (large grey circles) in the plane of: **a** constrained RDA1 and unconstrained PC1 and **b** unconstrained PC1 and PC2

axes. Dagggers mark the centroids' position. *Temp* temperature, *S* salinity, *Chl* chlorophyll *a* concentration, *CDOM* coloured dissolved organic matter, *Tide\_H* tidal height

**Table 2** Spatial variation of water mass parameters: regression coefficients for two most informative unconstrained axes as a function of distance from Khaypudyr Bay (Distance) and position in relation to the flow from the Pechora River (Group<sub>West</sub>)

Model part	Estimated coefficient	SE	<i>t</i> value	<i>p</i> value
Unconstrained PC1				
Intercept	0.05	0.21	0.24	0.81
Distance	0.0006	0.004	0.15	0.88
Group <sub>West</sub>	-0.11	0.21	-0.55	0.59
Unconstrained PC2				
Intercept	-0.48	0.14	-3.44	<b>0.003</b>
Distance	0.008	0.003	3.06	<b>0.007</b>
Group <sub>West</sub>	0.13	0.13	1.00	0.33

The latter variable shows the change of water parameters at the west side of the archipelago compared to the east side (set as a basic level in the model), and the sign before respective coefficient indicates direction of change. PC1 is linked to the gradient of Turbidity and Chl; PC2 is linked to the gradient between high values of *S* and *Tide\_H* and high values of Turbidity and Chl. *p* values <0.05 are typed in bold

and Chl. Similarly, maximal positive loadings on PC2 belonged to *S* and *Tide\_H*. Nonzero negative loadings of Turbidity and Chl allow us to consider PC2 as the gradient between high values of *S* and *Tide\_H* on the one side and high values of Turbidity and Chl on the other.

Analysis of spatial structure of the two gradients showed a significant latitudinal component (Distance) in the variability of PC2 values (Table 2). PC2 values increased with the distance from Khaypudyr Bay. At the same time no significant connections of both PC1 and PC2 with variable Group (West vs. East side of archipelago) were found, which means, that there was no influence of station position relative to flow from the Pechora River on the measured hydrological parameters at the stations.

Distribution of environmental parameters, which had the highest loadings on the unconstrained axes PC1 and PC2,

is shown on Fig. 3b. No gradients of temperature from the continental coast to the sea, along the chain of islands were observed in spring. Salinity increased in that direction as shown by the linear regression model (Table 2). In summer no gradients of Temp or *S* were detected. A gradient of Turbidity was observed in both seasons, being stronger in summer. A Chlorophyll *a* gradient was also detected in both seasons, but it was in opposite directions in spring and summer (Fig. 4).

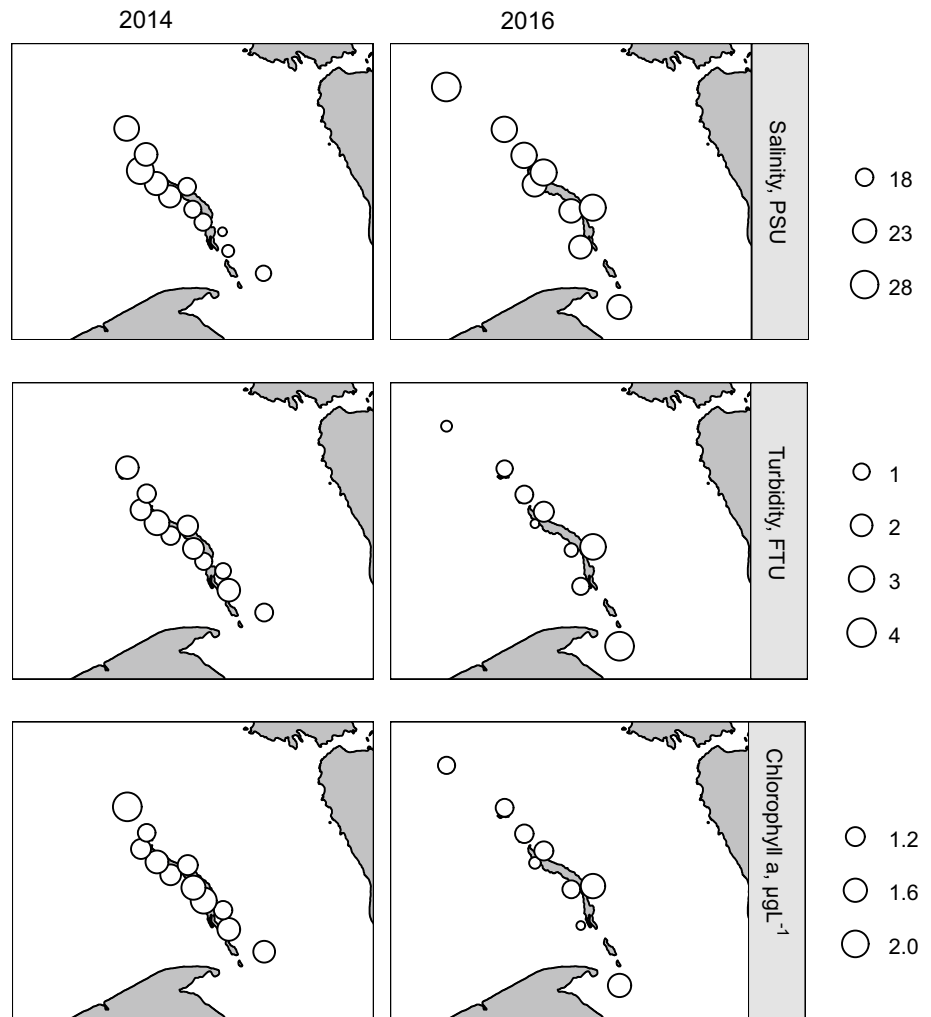
### Spatial and temporal variation of zooplankton communities

During two cruises, in July 2014 and September 2016, we identified a total of 43 taxa (Table 3). Species richness in the two sampling periods differed significantly: 42 taxa were found in spring and only 23—in summer. Only one species found in summer, the copepod *Oithona similis*, was absent in spring. Dominance structure also differed substantially. More than 50% of zooplankton abundance in spring was represented by Bivalvia larvae (46.5%) and *Pseudocalanus* spp. (26.3%). *Oithona similis* absolutely dominated zooplankton in summer (78.4%); the second most abundant species, *Pseudocalanus* spp., accounted for only 5.3%. The other taxa accounted for no more than 5% each. Planktonic Hydrozoa demonstrated the most dramatic difference of taxonomic composition with eight species of this class in spring and only two in summer. Subclass Copepoda was represented by 14 and 9 taxa in spring and summer, respectively (15 taxa in total). Copepods made up 33.9% of total zooplankton abundance in spring and 90% in summer. Meroplankton composition did not differ substantially between the two seasons: larvae of 6 taxa of benthic animals were observed in spring and larvae of 5 taxa were observed in summer, when Nemertea larvae were absent.

Average total zooplankton abundance was (mean  $\pm$  SE)  $20871 \pm 2091$  ind.  $m^{-3}$ ,  $n = 12$  in spring and  $24030 \pm 4686$  ind.  $m^{-3}$ ,  $n = 9$  in summer and did not differ significantly



**Fig. 4** Distribution of hydro-logical parameters which have the highest positive or negative loadings on unconstrained axes PC1 and PC2 around Dolgy Island. Meaning of PC1 and PC2 see in the text



(Mann–Whitney  $U$  statistic = 45.0,  $p = 0.52$ ). However, the ratio of ecological groups in community changed substantially (Table 3). The percentage of cold-water organisms contributing to the overall abundance was much higher in spring: 33.5% versus 5.1% in summer. However, the contribution of warm-water species also decreased in summer: it became 8% compared to 17.1% in spring. Such a dramatic change in these two group's relative abundance was due to the mass appearance of the eurythermal ubiquitous *Oithona similis*, which made up 78.4% of community abundance in summer. Marine species constituted the absolute majority of zooplankton organisms in both seasons. Brackish-water species made up no more than 1% of total abundance.

Meroplankton in spring represented 49% of total zooplankton abundance numbering 10,300 ind. m<sup>-3</sup>, while in summer it represented only 3.6% (870 ind. m<sup>-3</sup>). The difference was due to higher abundance of *Bivalvia* larvae and, to a lesser extent, higher abundance of *Polychaeta* larvae in spring. *Bivalvia* larvae accounted for 97% of the meroplankton in spring (10,000 ind. m<sup>-3</sup>).

Analysis of holoplankton association with all studied predictors (RDA, Fig. 5a) showed that many environmental parameters were highly correlated with the first constrained axis RDA1. This axis, as in the case of analysis of hydro-logic variables, was determined, first of all, by differences between seasons. The only exception was the height of tidal wave (Tide\_H), which did not demonstrate an association with RDA1. As a result of stepwise optimal model selection, the final model of constrained ordination consisted of only three predictors: Season, Salinity and Turbidity (Fig. 5a). This model was statistically significant (Table 4) and explained 75.4% of total variability in terms of total Inertia. All three constrained axes were significant. Ordination of stations in axes RDA2 and RDA3, without the influence of predictor Season, did not show segregation of stations taken in spring and summer (Fig. 5b). RDA2 was associated with salinity (S), and RDA3 demonstrated association with turbidity.

Ordination of taxa in the space of constrained axes (Fig. 6) allowed isolating groups of organisms preferring different environmental conditions. First of all, two distinct

**Table 3** Zooplankton composition, input of different taxa in total abundance and main traits of each taxon at species level

Zooplankton taxa	Species traits	Spring (2014)		Summer (2016)	
		Average abundance* (ind. m <sup>-3</sup> ) ± SE	Ratio, %	Average abundance** (ind. m <sup>-3</sup> ) ± SE	Ratio, %
<b>Infusoria</b>					
<i>Acanthostomella norvegica</i> (Daday)	cw, m	1075 ± 513	5.5	0	0.00
<i>Tintinnopsis tubulosa</i> Levander	ww, m	2156 ± 342	11.0	0	0.00
<b>Hydrozoa</b>					
<i>Obelia longissima</i> Pallas	ww, m	7.03 ± 0.95	0.04	0.22 ± 0.12	0.001
<i>Obelia geniculata</i> (L.)	ww, m	0.54 ± 0.09	0.0	2.5 ± 0.22	0.01
<i>Obelia</i> spp. juveniles		0	0.00	40 ± 0.34	0.19
<i>Halitholus cirratus</i> Hartlaub	cw, m	0.27 ± 0.18	0.001	0	0.00
<i>Hybocodon prolifer</i> Agassiz	ww, m				
<i>Sarsia tubulosa</i> (M. Sars)	ww, m	0.17 ± 0.1	0.001	0	0.00
<i>Rathkea octopunctata</i> (M.Sars)	ww, m	0.05 ± 0.05	0.0003	0	0.00
<i>Euphysa flammea</i> Linko	cw, m	0.06 ± 0.06	0.0003	0	0.00
Ctenophora juveniles		0.02 ± 0.02	0.0001	0	0.00
<b>Rotifera</b>					
Rotifera gen. spp. ( <i>Synchaeta</i> sp.)	ww, br	14.2 ± 8.54	0.1	174 ± 38	0.83
Polychaeta larvae		237 ± 71	1.2	20 ± 5.88	0.10
Nemertea larvae		0.05 ± 0.05	0.0003	0	0.00
<b>Copepoda</b>					
<i>Calanus glacialis</i> Jaschnov	cw, m	2.11 ± 0.69	0.01	0.19 ± 0	0.001
<i>Pseudocalanus</i> spp.	cw, m	5143 ± 1786	26.3	1108 ± 262	5.29
<i>Acartia bifilosa</i> Giesbrecht adults	ww, br	31 ± 8.84	0.2	5.97 ± 5.07	0.03
<i>Acartia longiremis</i> (Lilljeborg) adults	ww, m	24 ± 7.51	0.1	1.23 ± 0.21	0.01
<i>Acartia</i> spp. juveniles	ww,	1197 ± 294	6.1	249 ± 71	1.19
<i>Temora longicornis</i> (Müller)	ww, m	137 ± 50	0.7	889 ± 247	4.24
<i>Centropages hamatus</i> (Lilljeborg)	ww, m	2.41 ± 0.69	0.01	388 ± 126	1.86
<i>Eurytemora affinis</i> (Poppe)	ww, br	6.64 ± 1.99	0.03	0	0.00
<i>Limnocalanus grimaldii</i> (Guerne)	cw, br	2 ± 0.79	0.01	0	0.00
<i>Jaschnovia tolli</i> (Linko)	cw, m	2.79 ± 0.95	0.01	0	0.00
<i>Oithona similis</i> Claus	c, m	6 ± 2.01	0.03	16415 ± 4143	78.36
<i>Oithona atlantica</i> Farran	ww, m	0	0.0	0.03 ± 0.03	0.0001
<i>Cyclopina</i> sp.	ww, m	33 ± 9	0.2	0	0.00
<i>Euryte</i> sp.	ww, m	1 ± 0.22	0.01	0	0.00
<i>Triconia borealis</i> (Sars)	cw, a	0	0.0	0.69 ± 0.69	0.003
<i>Microsetella norvegica</i> Boeck	ww, m	6.94 ± 1.17	0.04	109 ± 49	0.52
<i>Ectinosoma neglectum</i> Sars	ww, m	22 ± 11	0.1	0	0.00
<b>Cladocera</b>					
<i>Podon leuckarti</i> Sars.	ww, m	0.91 ± 0.27	0.005	23.9 ± 11.31	0.11
<i>Evadne nordmanni</i> Lovén	ww, m	0.12 ± 0.04	0.001	94 ± 28	0.45
Cirripecta gen. spp.		35.9 ± 4.5	0.2	2.2 ± 0.65	0.01
Cumacea gen. sp. (larvae)		0.06 ± 0.06	0.0003	0.2 ± 0.17	0.001
Amphipoda gen. sp. (Hyperidea)		1.2 ± 0.56	0.01	0	0.00
Euphausiacea gen. sp.	cw, m	0.15 ± 0.04	0.0008	0	0.00
Decapoda larvae		0.05 ± 0.06	0.0003	0	0.00
Bivalvia larvae		9074 ± 1500	46.5	788 ± 165	3.76
Gastropoda larvae		0.04 ± 0	0.0002	1.51 ± 0.52	0.01
Bryozoa larvae		0.08 ± 0.07	0.0004	2.09 ± 1.03	0.01
<b>Appendicularia</b>					
<i>Fritillaria borealis</i> Lohman	ww, m	15 ± 14.7	0.1	153 ± 78	0.73
<i>Oikopleura</i> sp.	cw, m	0.89 ± 0.69	0.005	0	0.00

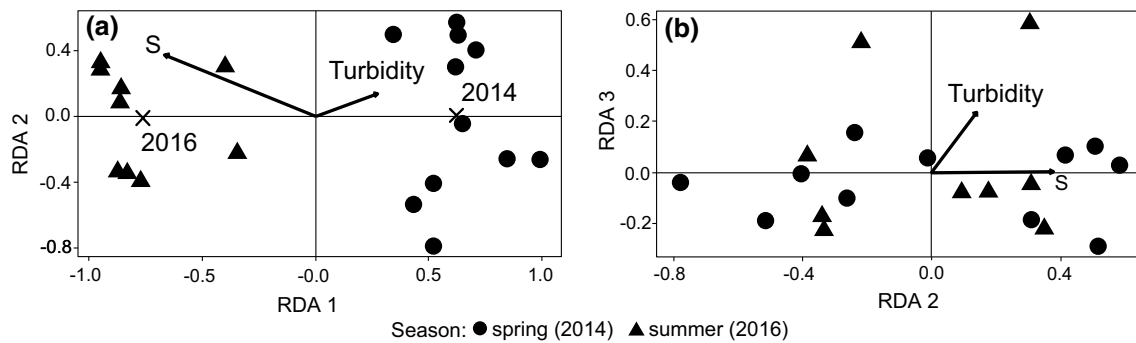
Traits are indicated only for those higher level taxa, which consist of no more than two species known in this area

Ratio proportion in total abundance of zooplankton, SE standard error of mean. Traits: *b* boreal; *a* Arctic; *ba* boreal-Arctic, *c* cosmopolitan, *m*

**Table 3** (continued)

marine, *br* brackish-water, *cw* cold-water, *ww* warm-water

\**n* = 12; \*\**n* = 9



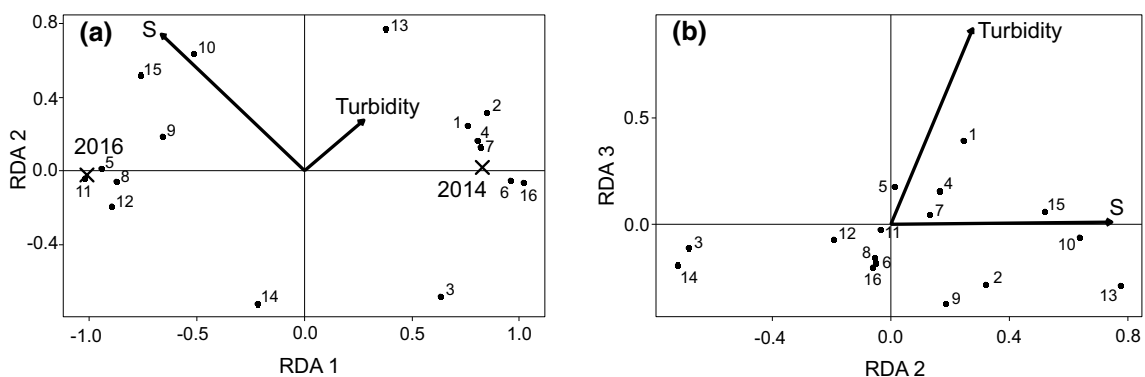
**Fig. 5** Ordination of stations (holoplankton abundance) in the plane of constrained axes: **a** RDA1 versus RDA2 and **b** RDA2 versus RDA3, relative to season, turbidity and salinity. Dagggers mark the centroids' position

**Table 4** Permutational assessment of RDA results

Source of variation	Degrees of freedom	Variance	<i>F</i>	Permutation <i>p</i> level
<b>Whole model</b>				
Model	3	12.06	16.31	0.0001
Residuals	16	3.94		
<b>Constrained axes</b>				
RDA1 (56.9%)	1	9.11	36.97	0.0001
RDA2 (14.6%)	1	2.34	9.50	0.0001
RDA3 (3.8%)	1	0.61	2.47	0.0074
Residuals	16	3.94		

groups were isolated by the position of species along axis RDA1 corresponding to their abundance in different seasons (Fig. 6a, Table 3). The most abundant species in July 2014 were: *Acartia bifilosa*, *A. longiremis*, *Acartia* juveniles, *Cyclopina* sp., *Ectinosoma neglectum*, *Tintinnopsis tubulosa*. In September 2016 *Centropages hamatus*, *Evadne nordmanni*, *Oithona similis* and *Podon leuckarti* were the most numerous.

The next diagram (Fig. 6b) depicts the relationships of species with environmental parameters, excluding the influence of seasonal variation. *Acanthostomella norvegica* and Rotifera preferred less saline water (high negative values of RDA2), while *Pseudocalanus* spp., *Microsetella norvegica* and *Temora longicornis* were found in water with higher



**Fig. 6** Ordination of taxa in the plane of constrained axes: **a** in RDA1 and RDA2; **b** in RDA2 and RDA3 relative to season, turbidity and salinity. Codes for species: 1. *Acartia bifilosa*; 2. *A. longiremis*; 3. *Acanthostomella norvegica*; 4. *Acartia* juveniles; 5. *Centropages*

*hamatus*; 6. *Cyclopina* sp.; 7. *Ectinosoma neglectum*; 8. *Evadne nordmanni*; 9. *Fritillaria borealis*; 10. *Microsetella norvegica*; 11. *Oithona similis*; 12. *Podon leuckarti*; 13. *Pseudocalanus* spp.; 14. *Rotifera*; 15. *Temora longicornis*; 16. *Tintinnopsis tubulosa*

salinity (high positive values of RDA2). More transparent waters (negative loadings on RDA3) were preferred by *Fritillaria borealis*; on the contrary, *Acartia biflosa* was linked to more turbid habitats (positive loadings on RDA3). Ubiquitous *Oithona similis* was positioned closest to the center of both axes (Fig. 6b).

Spatial distribution of the species, most closely connected to major environmental parameters (having maximal loadings on RDA2 and RDA3), is presented on Fig. 7. Rotifera was more abundant at the southernmost part of archipelago, closer to the source of fresh water, but they were not numerous in the immediate proximity to Khaypudyr Bay (Fig. 7a). *Pseudocalanus* spp. preferred the northern part of archipelago with more saline waters. *Fritillaria borealis* was found in spring only at five northernmost stations (St. 1, 2, 5, 6, 20): notably, at St 1 it was two orders of magnitude more abundant than at other stations. This station differed substantially from other stations in that season by chlorophyll *a* concentration (Table 1; Fig. 3). In summer *F. borealis* was most numerous at central stations southwest of the archipelago (Fig. 7b). According to the multidimensional analysis, *Acartia biflosa* preferred more turbid waters, which were more pronounced in summer.

Holoplankton community structure was similar in the two seasons in terms of species diversity (Shannon–Wiener index) and evenness (Table 5). However total holoplankton abundance and especially species number differed significantly from season to season.

Linear models for structure variables (*H*, *E*, *N*, *Sp*) match well with the results of the multidimensional analysis, indicating that variables from the optimal model RDA (Fig. 3) are the most important in this model as well (Table 6). In all cases, significant links of turbidity were found with structural variables: positive with *H* and *E* and negative with *N* and *Sp*. Diversity (*H*) and evenness (*E*) declined with rising salinity (Table 6). Evenness was higher and taxa number was lower in summer compared to spring according to linear model.

Thus, spatial (horizontal) heterogeneity in this shallow nearshore region was expressed in a clear gradient from less salty, more turbid and phytoplankton rich waters near the coast to more transparent and salty waters with less phytoplankton in the open sea. Turbidity and chlorophyll *a* gradients were much stronger in the summer than in the spring. Only the salinity gradient was similarly pronounced during the whole warm period. True marine species was the only ecological group of the zooplankton which demonstrated a clear relationship with the described horizontal gradient of salinity. It means that salinity was one of the main factors determining the distribution of zooplankton in this zone, which is subject to the continental runoff influence. Community structure was determined mostly by the turbidity—salinity axis. The gradient is observed from more

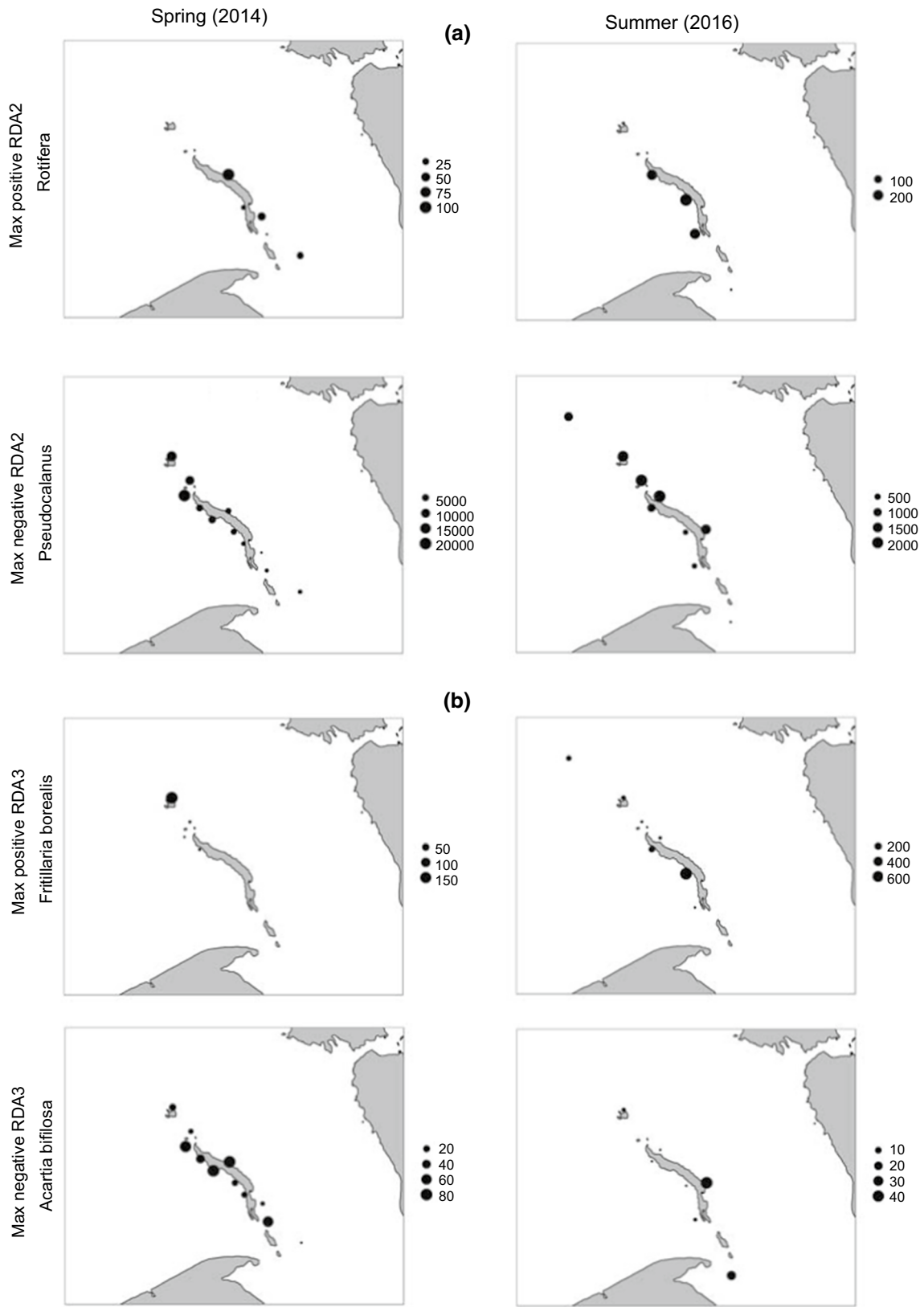
diverse community with evenly represented species in areas with relatively high turbidity and low salinity towards a less diverse community at offshore stations. In places with high turbidity zooplankton also tended to be less abundant.

## Discussion

### Hydrological gradients

Environmental gradients in coastal areas may have different spatial organization. These are either estuaries, where gradients are mostly two-dimensional (Laprise and Dodson 1994; Prudkovsky 2003; Díaz-Gil et al. 2014; Helenius et al. 2017), or open sea near sources of fresh water, where gradients are usually three-dimensional (Espinasse et al. 2014; Bojanić Varezić et al. 2015). In the latter case winds and currents may break the linearity of changes of hydrological parameters (Espinasse et al. 2014). Distribution of environmental parameters near Dolgy Island and adjacent islands resembles this latter type, and patterns of constant currents and gradients are complicated by periodic (tidal) water movements (Byshev et al. 2001). Nevertheless, we detected pronounced horizontal gradients of some environmental parameters.

We worked in the southeastern part of the Pechora Sea, which is subject to the influence of the most intensive fresh-water inflow in the Barents Sea. Almost 90% of fresh water, received by the Pechora Sea, is brought by the Pechora River (Nikiforov and Dunayev 2003). Although the mouth of it is located about 140 km westward of Dolgy and other islands of the archipelago, almost all water discharged from Pechora River flows towards the east—north-east (Fig. 2). We expected an influence of this water on the hydrological characteristics and therefore plankton community around the islands, which were believed to serve as barrier on the way of the flow of Pechora River water. However no significant differences of hydrological parameters were found between the West and East sides of archipelago. The other source of fresh water, Khaypudyr Bay, is located in the immediate proximity to the archipelago (Fig. 1). Khaypudyr Bay receives water from numerous small rivers and streams, and this water heads to the sea through the relatively narrow mouth of the bay. The highest turbidity and the lowest salinity were observed at the southernmost station St. 13, the closest to Khaypudyr Bay. Gradients of increasing salinity and decreasing turbidity were detected, oriented from the continent to the open sea along the chain of islands, suggesting that the flow from Khaypudyr Bay and small streams nearby dominate over the Pechora River's influence in the studied area. Indeed, detailed analysis of thermohaline structure of the Pechora Sea water masses revealed the



**Fig. 7** Distribution of the species, most closely connected to major environmental parameters. **a** having maximal loadings on RDA2 (salinity gradient), **b** having maximal loadings on RDA3 (turbidity gradient). Numbers in legends are given as ind. m<sup>-3</sup>

**Table 5** Holoplankton community structure and abundance at different stations

Station	Sp		N		H		E	
	Spring***	Summer***	Spring*	Summer*	Spring	Summer	Spring	Summer
1	13	12	17,202	28,627	0.72	0.53	0.28	0.21
5	13		24,664		0.62		0.24	
6	12	11	7284	22,355	1.11	0.54	0.45	0.23
7	11		9253		1.03		0.43	
8	13	12	7074	16,415	1.26	0.72	0.49	0.29
9	13		5309		1.42		0.55	
10		11		9433		0.65		0.27
13		10		821		1.63		0.71
14	14		6723		1.15		0.44	
15	13		8141		1.36		0.53	
16	13		9722		0.91		0.36	
17		9		17,511		1.01		0.46
18	14		11,255		1.49		0.57	
19		11		47,579		0.51		0.21
20	12	10	11,592	32,601	0.49	0.56	0.20	0.24
1–30		10		27,887		0.61		0.26

Significant differences between seasons are indicated by asterisks

Sp species number, N holoplankton abundance, H Shannon–Wiener index, E evenness

Mann–Whitney U-test: \* $U=20$ ,  $p=0.015$ ; \*\*\* $U=5.5$ ,  $p=0.0006$

mainstream of the flow from Pechora River to the north of Dolgy Island (Byshev et al. 2003).

Turbidity increased towards the south in both seasons, demonstrating a more pronounced gradient in September 2016. Maximum river discharge in the Pechora Sea is normally observed in June and decreases by September (Nikiforov and Dunayev 2003). Therefore, by the end of summer suspended matter is likely transported closer to the shore than in the spring, and a turbidity gradient can be observed at a relatively short distance from the source. A tight connection between chlorophyll *a* and turbidity distribution may be explained by the fact that phytoplankton is part of the suspended matter. Intensive phytoplankton blooms often follow peaks of river discharge, which is an important source of suspended matter (Guadayol et al. 2009; Bojanić Varezić et al. 2015). Besides that, river discharge causes intensive mixing at coastal shallows, which, in turn, increases turbidity and returns nutrients into photic zone (Guadayol et al. 2009; Espinasse et al. 2014).

Tidal and constant currents are at their highest intensity in the coastal zone of the Pechora Sea and influence horizontal distribution of hydrological parameters (Timofeev and Shirokolobova 1996; Byshev et al. 2001; Musaeva and Suntsov 2001). Coastal waters in the Pechora Sea are formed by the White Sea current and Pechora River discharge, the latter spreading in the surface layer for a distance of 100–150 km from the shore during the warm part of year (Danilov et al. 2004). The strongest vertical gradients of temperature and salinity were detected in

the 0–10 m water layer, however, by the end of summer, because of wind mixing and warming of the deeper layers the distribution becomes more even throughout the water column (Danilov et al. 2004). We also observed almost total vertical homogeneity of temperature and salinity in summer 2016. More off-shore waters and circulation pattern in the Pechora Sea is formed under the influence of the waters of Atlantic origin—Kaninskoye and Kolguyev-Pechorskoe currents (Byshev et al. 2001). Some authors (Musaeva and Suntsov 2001) believe that the mixing zone of the coastal and Atlantic waters begins much closer to the shore, less than 20 km from the coast, implying that Dolgy Island and the other islands of the archipelago lie entirely within this zone. In this mixing zone clear gradients are eroded because of complicated pattern of currents (Musaeva and Suntsov 2001), which supports our observations.

The connection of salinity to the tide height (Tide<sub>H</sub>) may be interpreted as partially functional: more saline waters from the open sea flow towards the coast during flood, while less saline waters flow from the coast during ebb tide.

Thus, water mass variability in the study area has two sources. The first one is connected with saline water inflow from the open sea and fresh (and turbid) water outflow from Khaypudyr Bay and nearby rivers which influence the salinity and turbidity. The second source, according to high loadings of Tide<sub>H</sub> variable on the PC2 axis, includes tidal currents directed along the chain of islands, which redistribute marine and fresh waters.

**Table 6** Parameters of regression models of structural variables of zooplankton community

Parameter	Estimated value	SE	t value	p value
Shannon diversity ( $H$ ) <sup>a</sup>				
Intercept	1.74	0.40	4.38	<b>0.001</b>
Season <sub>summer</sub>	0.15	0.11	1.33	0.21
S	−0.07	0.02	−3.89	<b>0.002</b>
Turbidity	0.22	0.06	3.81	<b>0.002</b>
Chl	0.16	0.16	0.99	0.34
Tide <sub>H</sub>	−0.07	0.10	−0.69	0.50
Evenness ( $E$ ) <sup>a</sup>				
Intercept	0.58	0.14	4.30	<b>0.0007</b>
Season <sub>summer</sub>	0.13	0.03	3.83	<b>0.002</b>
S	−0.02	0.01	−4.05	<b>0.001</b>
Turbidity	0.10	0.02	5.92	<b>&lt;0.0001</b>
Chl	0.05	0.04	1.09	0.30
Tide <sub>H</sub>	−0.03	0.03	−0.98	0.34
Total abundance ( $N$ )				
Intercept	−9051.24	17287.65	−0.52	0.61
Season <sub>summer</sub>	4298.16	5790.93	0.74	0.47
S	1377.24	704.08	1.96	<b>0.07</b>
Turbidity	−4160.25	2772.22	−1.50	<b>&lt;0.0001</b>
Chl	−100.12	7848.66	−0.01	0.99
Tide <sub>H</sub>	4915.30	5216.99	0.94	0.36
Taxa number (Sp)				
Intercept	21.81	3.40	6.42	<b>&lt;0.0001</b>
Season <sub>summer</sub>	−6.78	1.14	−5.96	<b>&lt;0.0001</b>
S	−0.10	0.14	−0.72	0.48
Turbidity	−0.29	0.54	−0.53	<b>&lt;0.0001</b>
Chl	0.28	1.54	0.18	0.86
Tide <sub>H</sub>	1.96	1.02	1.91	0.08

Models for Shannon diversity and Evenness were corrected for spatial autocorrelations

Values of  $p$  in bold and underlined point to significant influence of a specific parameter

Season<sub>summer</sub> change in summer (2016) compared to spring (2014): “+” means increase, “−” decrease in summer

By the end of summer, salinity in the coastal zone of the Pechora Sea increases due to intensive wind-mixing and decrease of freshwater runoff (Danilov et al. 2004). This is what we observed in September 2016 compared to July 2014. The difference in absolute temperatures between the two cruises was observed as well in accordance with the seasonality.

### Spatio-temporal variation of zooplankton

The documented number of zooplankton species in the Pechora Sea is variable, although the lists of taxa in all studies largely overlap. We found 43 zooplanktonic taxa. This number is close to the minimum observed in this region

since 1950s—33 taxa in 1992 (Timofeev and Shirokolobova, 1996). However, our expeditions covered only a relatively small part of the region studied previously. During the first large-scale investigations in the Pechora Sea in 1958–1959, 72 taxa were recorded (Zelikman 1961, 1966). Notably, in those studies no representatives of meroplankton were presented, except for Cirripedia larvae. In the expeditions of 1992, 1998 and 2001 33, 57 and 66 zooplankton taxa were documented, respectively (Timofeev and Shirokolobova 1996; Musaeva and Sunstov 2001; Dvoretzky and Dvoretzky 2009a). The reason for such fluctuations may be in shifts of timing of hydrological and biological seasons, common in high latitudes (Usov et al. 2013)—in different years studies may be conducted in the same time, however the timing of phenological events is not the same from year to year. Number of stations also may influence the completeness of taxonomic list, because of different geographic coverage of cruises.

Distribution of species in hydrological gradients is shaped by their ecological preferences (Fig. 6). *Microsetella norvegica* and *Temora longicornis* are typical marine species (Krause et al. 1995; Razouls et al. 2015), and they preferred saline waters. The abundance of boreal-Arctic marine *Pseudocalanus* spp. tended to rise towards the northern (marine) end of the archipelago both in spring and summer. Some increase in the abundance of cold-water species towards the north was observed earlier in this region (Musaeva and Sunstov 2001), which was explained by increasing depth and average salinity. Such increase of large cold-water copepods' biomass towards the open sea is typical for the Arctic estuarine systems. A similar pattern was also documented along the estuary of Yenisei River from its mouth to the Kara Sea in summer (Kosobokova and Hirche 2016). Appendicularian *Fritillaria borealis*, like all representatives of this taxonomic group, is a marine organism (van der Land 2001). Therefore, it tends to be more abundant in low turbidity habitats which are also more saline. *Synchaeta tamara*, the most numerous Rotifera species in the studied area, is indicated as a brackish water species in some publications (Musaeva and Sunstov 2003), but as true marine in others (Segers 2007). This species is characteristic for ice fauna in the Barents Sea and tolerates a wide range of salinities, from 13 to 32 (Friedrich and De Smet 2000). Unexpectedly, *Acanthostomella norvegica* being a typically marine species (Davis 1985; Scott and Marchant 2005) demonstrated a pronounced negative link to salinity (Fig. 6b). On the other hand, this species showed rather high correlation with the axis RDA1, connected to the season of sampling. Indeed, *A. norvegica* was absent in summer (Table 3). Besides that, this species in spring was distributed very unevenly, being presented only at stations 8–18, around the whole archipelago except its North-Western end, and absent at the “most marine” stations. Tidal phase could be a factor influencing distribution

of *A. norvegica*: at all stations, where this species appeared, except one, we worked during the ebb tide. Absence of *A. norvegica* in September could be explained by its preference for cold waters – it is distributed mostly in high latitudes (Berge et al. 2012; Encyclopedia of Life 2018). We found that turbidity is one of the most important factors for *Acartia biflosa*. In the nearby White Sea *A. biflosa* inhabits mostly estuaries (Prudkovsky 2003), which explains its preference of less saline and more turbid waters. Some authors consider this species brackishwater-marine and also document its presence in estuaries (Collins and Williams 1982; Villate 1991).

All parameters of community structure in the study area were associated with turbidity. In places with high turbidity, zooplankton community contained fewer species, was less abundant, but was more diverse and even in terms of species' abundance (dominance was less pronounced). These results indicate that high turbidity may influence zooplankton in following ways: (1) in turbid waters, mineral particles depress zooplankton development interfering with food particles (Kirk 1991; Jönsson et al. 2011), thus decreasing abundance of animals. (2) In such extreme conditions, not all species typical for this region can survive, so we see a decrease in species number. (3) The zone of high turbidity forms an ecotone—a transitional zone from freshwater to marine habitats. High diversity and lack of dominance are characteristic for such zones (Odum 1971; Naumov 1991).

One of the goals of the present study was to reveal specific seasonal states of the zooplankton community. Low temperature and salinity near the water surface as well as the shallow thermo- and haloclines found in July 2014 are typical for spring in this region (Matishov et al. 1996; Danilov et al. 2004). In addition, in July 2014 the expedition took place soon after ice melt, which normally is observed in the region by the end of June (Danilov et al. 2004). Moreover, floating ice around Dolgy Island was seen in the first half of July during our expedition. According to previous work, spring zooplankton development starts in the Pechora Sea in June–July (Fomin 1985), which confirms that in July 2014 the zooplankton community was in the spring state. Higher temperature and salinity, and deeper thermo- and haloclines in September compared to July indicated a summer state of the environment (Matishov et al. 1996). Not only did species diversity change from season to season: the ratio of main ecological groups also changed substantially. Cold-water species dominated in July among holoplanktonic species (*Pseudocalanus* spp., 26.3%), which is typical for spring. With that, almost a half of the whole community in July consisted of the larvae of bottom animals, primarily bivalve mollusks (46.5%). This situation was also observed in July 1997, when *Bivalvia* larvae made up 20–30% of total zooplankton biomass (Troshkov and Gnetneva 2000). Analysis of species composition of the *Bivalvia* larvae group has shown that almost all belonged to boreal-Arctic *Macoma calcarea* and *Chlamys islandica* (Flyachinskaya LP, pers.

communication). In September 2016 almost 80% of the zooplankton consisted of the ubiquitous *Oithona similis*. Abundance of this species was proved to attain seasonal maxima in Arctic and sub-Arctic coastal areas during the warm period of the year. The seasonal abundance peak of *O. similis* in the Arctic Kola Bay was observed in late summer, in September (Dvoretzky and Dvoretzky 2009b); in the White Sea this species also dominates during summer, from July to September (Prygunkova 1974). *O. similis* was found in the Pechora Sea in the middle of July 2001 at more than 75% of stations and was positively correlated with salinity and depth (Dvoretzky and Dvoretzky 2009a). Hence, the fact that this species was totally absent in spring 2014 leaves a question about existence of year-to-year environmental fluctuations open.

Thus, during the ice-free (warm) season in the coastal zone of the Pechora Sea two communities succeed each other. One develops in the spring and consists of cold-water Arctic and boreal-Arctic species and meroplankton. The other one replaces it in the summer and is dominated by warm-water boreal and ubiquitous (*Oithona similis*) species. Comparing our results to previous investigations in this region, we can conclude, that hydrological conditions and community state are typical for these times of year.

The zooplankton is one of the most important components of the marginal filters (Lisitzin 1994, 1999). All of the mesozooplankton organisms, feeding on the suspended particles (live or dead), add to the clearance of water. The role of the zooplankton is not as important during the first stages of marginal filter functioning, such as gravitational sedimentation and coagulation sorption, as it is later. Water purification is accomplished at this stage mostly due to physical and chemical processes. In the study area these stages probably correspond to the zone with maximal turbidity. Notably, in this very zone the negative impact of the environment on zooplankton is the greatest, judging by its lowest abundance. In places, where the mechanical influence of environment is not as strong (unlike the zone of high turbidity mentioned above) abundance and accordingly the role of zooplankton increase. These places appear to correspond to the third, and final, stage of a marginal filter—biological filtration (Lisitzin 1994, 1999). At this stage the rest of allochthonous suspended matter is precipitated. These waters contained the least suspended material in our case. Thus, the analysis of turbidity and zooplankton distributions may contribute to understanding how marginal filters function.

## Conclusion

Gradients of environmental factors, primarily turbidity and salinity, shape the zooplankton communities in the zones where fresh and marine waters mix. Both abiotic gradients and community structure change from year to year and with



changing climate. These changes may also affect higher trophic levels: fishes, marine mammals and birds, numerous in such areas. High latitudes experience intensive climatic changes (Wassmann et al. 2011), the consequences of which are glacier melting and increased precipitation (IPCC 2014). As most models demonstrate, this trend will persist into the next decades (IPCC 2014). These processes lead to an increase in terrestrial runoff and thus an expansion of high turbidity/low salinity areas near the mouths of Arctic rivers is expected. Storminess and coastal erosion also increase, reinforcing these results in high Arctic coastal regions (Węśławski et al. 2011). The ranges of marine zooplankton will therefore also change, affecting distribution and abundance of planktivorous fishes. For example, our investigation has shown that marine species such as *Temora longicornis* and *Pseudocalanus* spp. prefer more saline and clear waters. These organisms are among the most important food sources of marine fishes such as herring, Arctic cod and capelin (Huse and Toresen 1996; Karamushko et al. 1996). Thus, if tendencies of climate change persist, we may see a corresponding, significant shift in these fishes' ranges. The effectiveness of marginal filters may also influence the turbidity gradient. This effectiveness, itself may be affected by the interannual fluctuations and climate change-induced shifts of the system; hence the efficiency of terrestrial runoff purification may change. This latter effect is of great importance to the whole Arctic Ocean, taking into account increasing human impact on the basins of great rivers flowing into the Arctic Ocean. Thus, further, more detailed studies of the whole ecosystem in this boundary zone are of great importance. Extension of the study area along the gradient from the freshwater sources to the open sea also would contribute to our understanding of the abiotic and biological processes shaping this gradient.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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