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Arctic fjord during warming: Planktonic point of view

Abstract. The climate affects aquatic ecosystems worldwide, yet the most dramatic impact has been observed in Polar Regions. The presented study aimed to test the hypothesis that changes in biodiversity are linked to changes in the food web functioning under different temperature conditions, with large species dominant in cold waters and smaller species dominant in warmer waters. Two sites with contrasting hydrology were surveyed in summer 2005 in Hornsund (west Spitsbergen). The first site was located close to the fjord entrance and was strongly influenced by the Atlantic waters (WARM). The second was located deep inside the fjord, where the water is fresher and colder due to glacier meltwater runoff (COLD). Temperature, salinity and photosynthetic active radiation were measured, nutrient concentrations and chlorophyll *a* were analyzed. Plankton biota, including different fractions of zooplankton, phytoplankton and bacteria was collected and enumerated. The temperature differences were the most pronounced out of the abiotic parameters measured. In particular, the COLD site was characterized by lower water temperature and higher turbidity due to the influence of meltwater. Significant differences in the composition and the quantitative ratios of plankton biota were noted, with the most dramatic variation in the number of microplankton taxa and their biomass. The overall plankton biomass at the WARM site (91 mg C · m^{-3}) was higher than that at the COLD site (71 mg C · m^{-3}), as well as the primary production rates. Microplanktonic assemblages at the WARM site included twice as many taxa. The protists constituted more than half of the plankton biomass at the WARM site (53.2%), whereas their share at the COLD site was slightly higher (63.6%). The nanoplankton fraction was numerically dominant among the protists, whereas copepods were the main component of the zooplankton biomass. The differences in planktonic communities' compositions observed between the two sites might have arisen due to the influence of turbid meltwater runoff, which eliminates larger, strictly autotrophic and decreases primary production.

Keywords: Arctic fjord, bacteria, climate change, Hornsund, protists, zooplankton

1 Introduction

Climate change leading to the Earth warming has been observed since the 1920s, but it has been accelerating since the 1980s (Macdonald et al., 2005). Although the consequences of these changes are documented worldwide, they are seen most dramatically in the Polar Regions. This is because of the high latitudes' peculiarity; vast amounts of freshwater are deposited there in a frozen state (Carmack & Wassmann, 2006). Glaciers store 3.1 · 10^6 km^3 of frozen fresh water (Dowdeswell & Hagen, 2004), while permafrost stores 10.8—35.5 · 10^3 km^3 (Zhang et al., 2000), and sea ice — ~7—15 · 10^6 km^2 (Parkinson et al., 1999). Even small increases in the mean temperature result in dramatic changes throughout polar aquatic ecosystems by the triggering of massive freshwater runoffs (Gordeev, 2006).

Heat transport in the marine Arctic is increased by the North Atlantic Current (Walczowski & Piechura, 2007) and the atmosphere (Graversen et al., 2008), which results in particular, in increased water temperatures (Macdonald et al., 2005) and shrinking sea-ice cover.

The main hypothesis of the current study was that changes in biodiversity are linked to changes in food web functioning, with large species dominant in cold waters and smaller species dominant in warmer waters.

This hypothesis was tested in Hornsund Fjord located in West Spitsbergen (Svalbard). For this area there are available long-term hydrological (Swerpel, 1985) and biological data on the pelagic and benthic associations (Węsławski et al., 1991). The warm North Atlantic waters entering the fjord along the southern bank are cooled and flow out of the fjord along the northern bank, so there are 'warm' areas with temperatures >5 °C in the outer part of the fjord and 'cold' waters in the inner part (Piwosz et al., 2009).

The main question of the current study was if and how the differences in hydrology are reflected in the size structure of the planktonic compartment. Warming influences the physiology of aquatic organisms by inducing altered metabolic rates (López-Urrutia et al., 2006) or by shifting the taxonomic and size structures of communities, which then impact food quality (Richardson & Schoeman, 2004). As warm water advanced, shifts from large taxa to smaller ones were observed in the North Sea (Beaugrand et al., 2003).

Not many investigations of the planktonic communities' whole size spectrum have been performed to date in Svalbard fjords, although preliminary results are available for the higher trophic levels (Węsławski et al., 1999). Although research has been conducted on the development and distribution of phytoplankton and mesozooplankton, primary production, and the sedimentation of organic carbon (Eilertsen et al., 1989; Koszteyn & Kwasniewski, 1989; Węsławski et al., 1991; Keck et al., 1999; Wiktor, 1999; Karnovsky et al., 2003; Wiktor & Wojciechowska, 2005; Walkusz et al., 2007; Piwosz et al., 2009; Koziorowska et al., 2016), no complete picture of size distribution is available. The current study results supplement the knowledge of the distribution of all planktonic fractions from bacteria to macrozooplankton.

2 Materials and methods

Based on previous studies, two suitable sites were designated for testing the hypothesis of the current study. The warm site was located on the southern shore close to the fjord mouth at 76°57′ N 015°46′ E (90 m depth; WARM). The second site was designated on the northern side of the fjord at 77°02.185′ N; 16°00.527′ E (70 m depth; COLD).

Salinity and water temperature, photosynthetic active radiation (PAR), and water transparency measurements were taken before biological samples were collected.

Salinity and temperature were measured with a CTD probe (Seabird 19), while PAR was measured with an LI-190 Quantum Sensor, and incident and underwater PAR with an LI 193 Underwater Spherical Sensor.

The samples used for the enumerations of protists and analysis of nutrient concentrations were collected with a 30 dm^3 Niskin bottle at light levels of 100% (surface), 75%, 50%, 25%, 10%, and 1% of incident PAR. They were also collected at two levels below the euphotic zone (20 m and 70 m at the COLD site; 50 m and 90 m at the WARM site). Subsamples from each sampling event were used to analyze chlorophyll *a* concentrations, estimate primary production, determine and enumerate the fraction below 20 m, and analyze nutrient concentrations for enumerations of protists <20 μm, an additional 30 m^3 of seawater from each level was filtered through a 20 μm net to obtain approximately 100 ml of a concentrated sample.

Zooplankton samples were collected using plankton nets (mesh sizes of 60 μm, 180 μm, 500 μm, 1000 μm) that were hauled vertically through the water column.

The following procedures were implemented for each of the preceding parameters. Subsamples for the analyses of macronutrient (DIN, P-PO_4, SiO_4) concentrations were placed in acid-washed polypropylene bottles with a volume of 250 ml and frozen immediately at –20 °C. The samples were analyzed at the laboratory of the Sea Fisheries Institute within three months according to procedures described in (Grasshoff et al., 1983) and (Intergovernmental Oceanographic Commission, 1983).

Chlorophyll *a* analysis was performed on 50 ml of seawater that was run through filters with different

pore sizes using the 'semi cascade' method. Water was filtered subsequently through 3 μm, 0.7 μm, and 0.22 μm filters. These were frozen at −80 °C, and chlorophyll *a* concentrations were analyzed within three months with a Turner Designs 10 AU fluorimeter after 24 h extraction in 10 ml of 90% acetone at 5 °C in the dark (Arar & Collins, 1997).

Specimens for bacteria enumerations were prepared using 1—5 ml of seawater filtered through nucleopore filters with a 0.2 μm pore size (Porter & Feig, 1980), and then stained with 4.6-diamidino-2-phenyl-indol (DAPI, final concentration 2 μg/ml). The filters were placed on microscope slides with AF3 antifadent (Citifluor Ltd.), and covered with cover glasses. The bacteria were counted using an epifluorescence Nikon 80i microscope (excitation filter — 365 nm, barrier filter — 420 nm, dichromatic mirror — 400 nm) at a magnification of 1200×. Bacterial cells were counted in at least twenty fields of view, and their biomass was calculated using the formula by (Norland, 1993).

Subsamples of 20—60 ml of seawater were fixed with 10% glutaraldehyde solution (to a final concentration of 1%), and subsequently filtered through black, polycarbonate filters with a pore size of 0.22 μm (Millipore). After filtration, the cells were stained with 2 ml of DAPI solution (1 μg ml^{-1}) for 10 minutes in the dark and then air-dried. Next, the filters were placed on microscopic slides, mounted in Citifluor (Citifluor Ltd.), secured with cover glasses, and stored at −20 °C in the dark until further processing. The samples were examined for all eukaryotic cells with a fluorescence microscope at UV/Blue excitation/emission wavelengths at a magnification of 1000×, and at Green/Red excitation/emission wavelengths for autotrophs at a magnification of 1000×.

Nanoplankton was analyzed using 250 ml volume subsamples fixed immediately after collection in acidified Lugol's solution, to which formaldehyde was added after 24 hours to comprise a final concentration of 1—2% of each fixative. Enumeration and taxonomic analysis were performed under an inverted Nikon TE-300 microscope according to methods described by Utermöhl (1958). At least 300 units (cells) were counted, and the cell volumes were calculated based on size measurements of at least ten individual cells using conversion factors for carbon content by Menden-Deuer and Lessard (2000).

Microplankton samples were enumerated and measured with the same procedure used for the nanoplankton samples, but the concentration factor was considered.

Phytoplankton primary production measurements were conducted with the ^{14}C method described by Strickland and Parsons (1972) and Nielsen and Bresta (1984). Subsamples of 100 ml volume were inoculated with $Na^{14}CO_3$ to the radioactivity of 8 μCi per sample and incubated *in situ* at midday in transparent glass bottles for 4.5 h (COLD site) or 5.3 h (WARM site). Dark bottles were also incubated at the surface and at the deepest layer to estimate the dark carbon fixation. After incubation, formaldehyde was added to stop assimilation and the samples were put through 3 μm, 0.7 μm, and 0.22 μm filters (as was done with the chlorophyll *a* samples) at a pressure of <0.4 atm. The filters were exposed to fuming HCl vapour for 5 min in a desiccator to remove extracellular ^{14}C exudates. The filters were dissolved in Ready Value Light Scintillation Cocktail for Aqueous Samples (Beckman, USA), and stored in the dark at 4 °C until analysis on a BETA scintillation counter (Beckman LS 6000IC, USA) to determine the radioactivity of the samples. All handling prior to and after incubation was performed in dimmed light, and the bottles were stored in the dark. The carbon fixation rate was calculated according to procedures in Strickland and Parsons (1972).

Zooplankton samples were collected in triplicate vertical hauls at different water column strata that were determined with CTD profiling. At the WARM site these were 0—10 m, 10—75 m, and 75—90 m, and at the COLD site — 0—20 m and 20—65 m. The volume of the filtered water was calculated from readings of flow meters attached to the nets. The samples were fixed immediately with 4% borax-buffered formaldehyde to a final concentration of 4%.

The organisms were identified and counted under a stereomicroscope equipped with an ocular micrometer (Falk-Petersen et al., 1999; Harris et al., 2000). Small-sized zooplankters (mostly Copepoda, Cirripedia, juvenile stages of Pteropoda, Euphausiacea, Amphipoda, Chaetognatha) were identified and counted

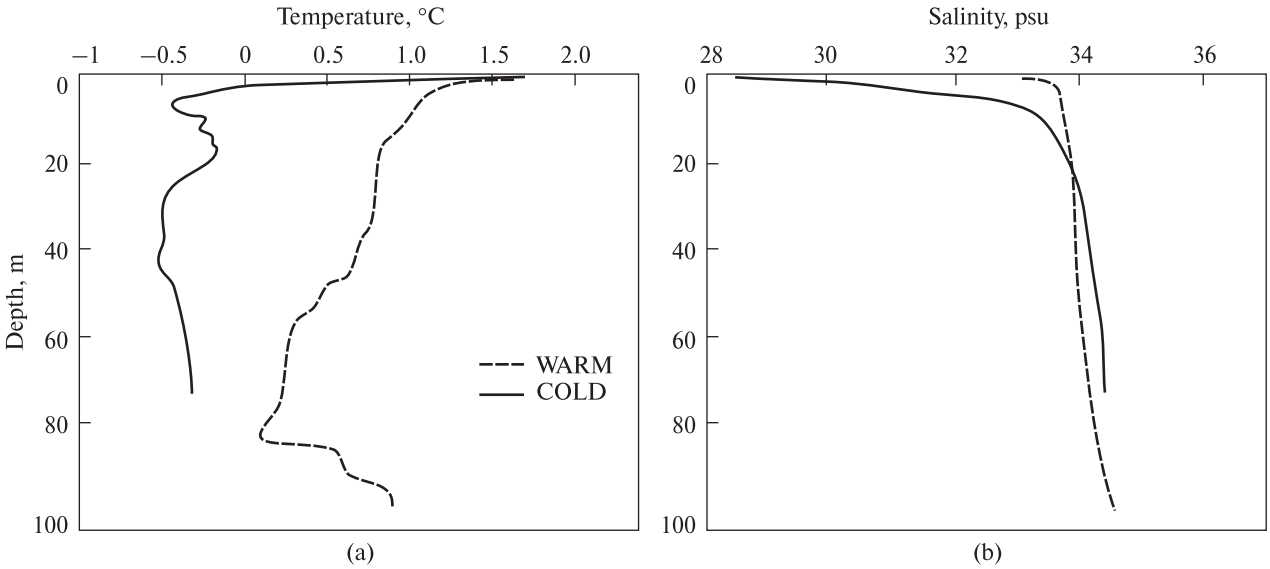

Figure 1. Vertical distribution of water temperature (a) and salinity (b) at the sites studied

Table 1. Hydrochemical parameters of seawater at the WARM and COLD sites, Hornsund, July 2005

Site/ Parameter range	WARM	COLD
Salinity [psu]		
mean	34.0	33.7
max/min	34.6—33.0	34.4—28.4
Temperature [°C]		
mean	0.63	−0.31
max/min	1.6—0.1	1.7—−0.53
$P\text{-}PO_4$ [μmol · dm^{-3}]		
mean	0.3	0.34
max/min	1—0.1	0.7—0.1
DIN [μmol · dm^{-3}]		
mean	2.2	3.8
max/min	5.2—0.8	5.7—2.2
SiO_4 [μmol · dm^{-3}]		
mean	2.2	3.8
max/min	5.2—0.8	5.7—2.2
Secchi Disc depth [m]		
	5	~2

in sub-samples with volumes that permitted counts of approximately 500 individuals. Large zooplankters (Copepoda, Pteropoda, Euphausiacea, Amphipoda, Decapoda, Appendicularia, Chaetognatha, Pisces) were segregated from whole samples and identified separately. The species *Calanus* were identified based on morphology and the prosome lengths of individual copepodid stages (Tande, 1991; Kwasniewski et al., 2003).

Biomass was calculated based on abundance data by applying individual dry mass (DM) values derived from species-specific length-mass relationships or by using published (Uye, 1982; Hirche, 1991; Mumm, 1991; Richter, 1994; Hanssen, 1997; Kosobokova et al., 1997; Karnovsky et al., 2003; Blachowiak-Samolyk et al., 2008) estimates. The values of organic carbon were obtained by multiplying DM by a factor of 0.5.

Zooplankters were classified by trophic level (herbivorous, omnivorous, carnivorous feeders) according to (Blachowiak-Samolyk et al., 2007) and citations therein.

3 Results

Salinity and temperature

The seawater temperature ranged from –0.5 to 1.7 °C, while the surface temperatures were similar (<1.5 °C)

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at the two sites (Table 1). The deeper layers varied; water temperature never exceeded 0 °C at the COLD station, whereas it was higher than 0 °C at the WARM site throughout the water column (Fig. 1a). The waters at the WARM site were more saline at a mean value of 34.0 psu versus 33.7 psu at the COLD site (Table 1). The deeper waters were well below 30 psu at the COLD site, but the surface layers did not vary between the sites at values of 34 psu to 34.5 psu in both locations (Fig. 1b).

The waters at the COLD site were more turbid than those at the WARM site. Secchi disc depth did not exceed 2 m, while transparency at the WARM site was approximately twice higher at 5 m.

Macronutrients

The dissolved inorganic nitrogen compounds' (DIN) concentrations varied from 0.83 to 5.73 μmol · dm^{-3} depending on site and depth. The minimum concentration occurred at the surface, whereas the maximum was noted in the bottom layers (Fig. 2). Concentrations at the COLD site never dropped below 2 μmol × × dm^{-3}, with a maximum of 5.7 μmol · dm^{-3} at the bottom and a minimum of 2.2 μmol · dm^{-3} in the upper layer. The concentrations in the surface waters of the WARM site were twice as low as those at the COLD site, but the values near the bottom were at the same level (Fig. 2, Table 1).

Inorganic phosphorus concentrations (P-PO4) were similar at both stations (Fig. 3), and ranged from 0.13 to 1.0 μmol · dm^{-3}. The concentration peak occurred 3 m beneath the surface at the WARM site (1 μmol × × dm^{-3}) and 7 m below the surface level at the COLD site (0.67 μmol · dm^{-3}).

Silicate (SiO_4) concentrations were higher at the COLD site (from 8.4 μmol · dm^{-3} to 0.9 μmol · dm^{-3}) than in the WARM waters (3.6 μmol · dm^{-3} to 0.3 μmol · dm^{-3}). While the maximum occurred at the surface in the COLD waters, the richest water was in the lower part of the euphotic zone at 10 m at the WARM site (Fig. 4).

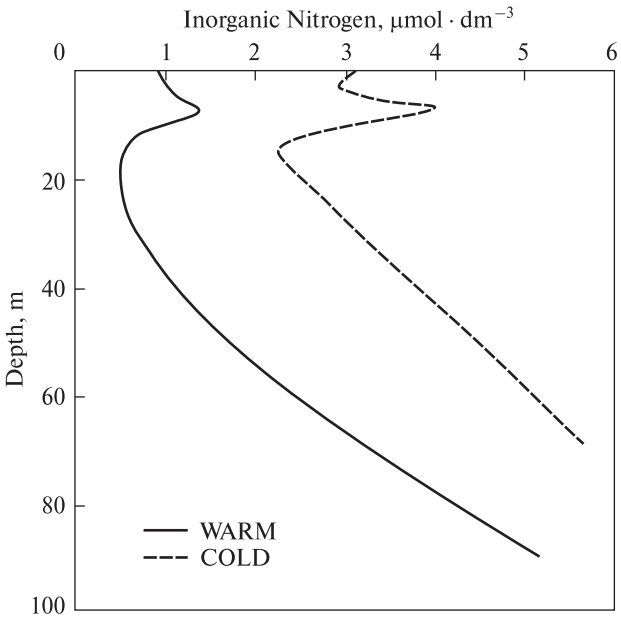

Figure 2. Distribution of inorganic nitrogen in the water column at the sites studied

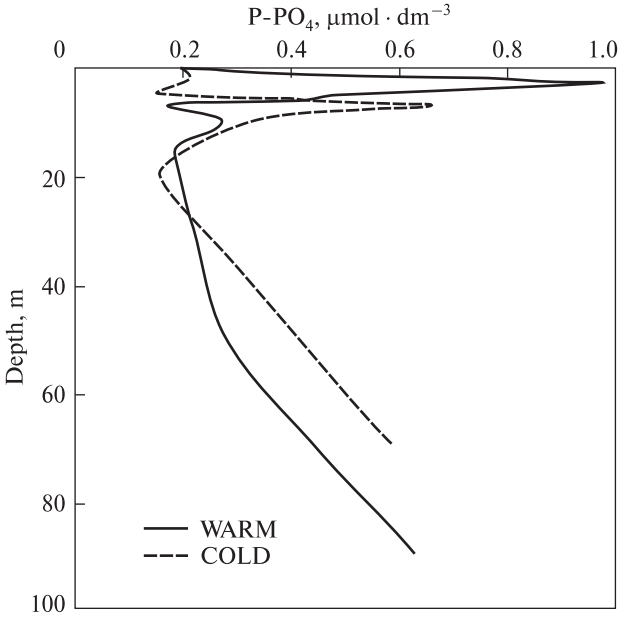

Figure 3. Distribution of inorganic phosphorus in the water column at the sites studied

Photosynthetic pigments

Concentrations of chlorophyll *a* ranged from 0.12 mg × × m^{-3} to 4.38 mg · m^{-3}. The overall amount of chlorophyll was considerably higher at the WARM site ranging from 0.6 to 4.4 mg · m^{-3}, while at the COLD site it was from 0.12 to 1.9 mg · m^{-3} (Fig. 5a, b; Table 2).

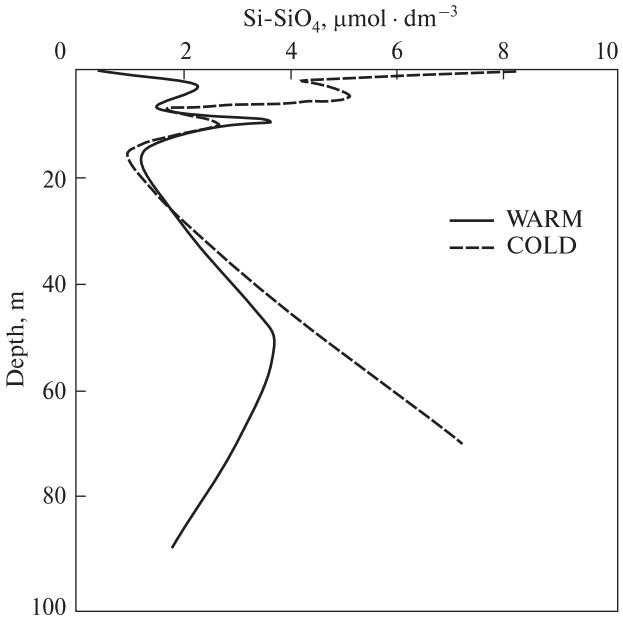

Figure 4. Distribution of silicates in the water column at the sites studied

Moreover, there were two concentration peaks at the COLD site at the surface (0—2 m) and at 20 m. In contrast, the maximum concentration occurred far deeper on the opposite side of the fjord at 40 m (Fig. 5). The mean values throughout the water column were three times higher at the WARM site than at the COLD site and were 2.9 and 0.7 mg · m^{-3}, respectively (Table 2). At both sites chlorophyll *a* was mainly associated with protists larger than 3 μm, and their share never fell below 60% at the COLD site or 80% at the WARM site (Fig. 5a, b). While the maximum share of the <3 μm fraction was the highest in the surface waters of the WARM site, at the COLD site the contribution of this fraction increased in the lower part of the euphotic zone or even just below it (Fig. 5a).

Table 2. Chlorophyll *a* and carbon fixation at the WARM and COLD sites, Hornsund, July 2005

Site/Parameter range	WARM	COLD
Chlorophyll *a* total [mg · m^{-3}]		
Mean	3.0	0.7
(euphotic zone)	(2.8)	(0.3)
max/min (whole column)	4.4—0.6	2.0—0.1
Primary production [mgC · h^{-1} · m^{-2}]		
mean	37.3	7.4
max/min [mgC · h^{-1} · m^{-3}]	3.4—0.1	2.4—0.1
Share of <3 μm [%]	91	7.4

Bacteria

The abundance of bacteria ranged from $12 \cdot 10^{11}$ cells × × m^{-3} at the surface layer of the COLD site to $3.4 \times \times 10^{11}$ cells · m^{-3} in the lowermost layer of the water column at the WARM site. The mean biomass of bacterial cells was as low as 0.016 pgC · $cell^{-1}$ at the COLD site, while being 0.019 pgC · $cell^{-1}$ at the WARM site (Table 3). Total biomass ranged from $6.04 \cdot 10^{-3}$ mg · m^{-3} to $1.8 \cdot 10^{-2}$ mg · m^{-3} (WARM) and $6.6 \cdot 10^{-3}$—$1.7 \cdot 10^{-2}$ mg · m^{-3} (COLD) (Fig. 6). Despite the differences in the vertical distribution, the mean bacterial biomass (for the whole water column) was not significantly different at the two sites studied at $1.2 \cdot 10^{-2}$ mgC · m^{-3} (COLD) and $1.0 \cdot 10^{-2}$ mgC · m^{-3} (WARM).

Eukaryotic Protists

The total number of planktonic protists ranged from $3 \cdot 10^{8}$ to $1 \cdot 10^{10}$ cells · m^{-3}, representing a biomass range of 4—76 mg per m^3. During the survey, three fractions (picoplankton, nanoplankton, microplankton) were taken into consideration.

Picoplankton

The total number of picoplankton cells per m^3 ranged from $70 \cdot 10^{6}$ to $10 \cdot 10^{9}$, representing a biomass range of 0.07 to 1.0 mgCorg · m^{-3}. These values varied depending on the level and site, and were higher at the WARM site at 0.3 to 0.6 mgC · m^{-3} than at the COLD site at 0.07 to 0.2 mgC · m^{-3} (Fig. 7). The picoplanktonic biomass contributed plastidic and aplastidic taxa, and the share of heterotrophic (aplastidic) was always higher than 50% (Fig. 7), but the contribution was slightly higher at the COLD site (82% and 72%) than at the WARM site when integrated biomass is taken under consideration. The mean biomass of heterotrophic picoplankters was as low as 0.01 pgC · $cell^{-1}$,

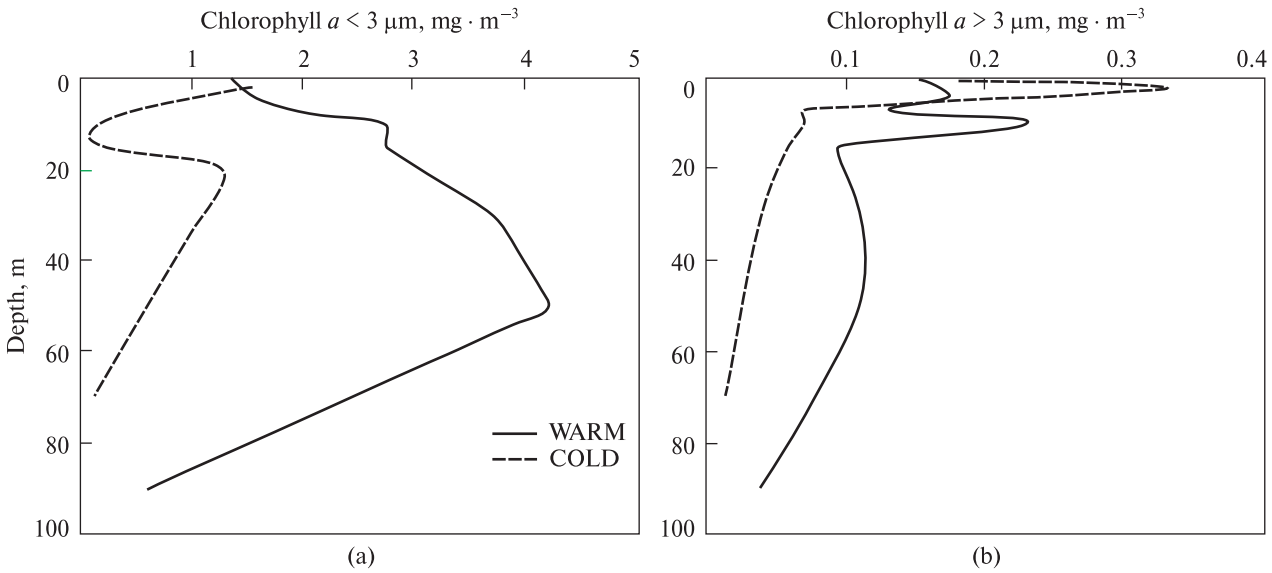

Figure 5. Chlorophyll *a* vertical distribution, (a) — associated with cells <3 μm; (b) — associated with cells >3 μm; note change of scale

while that of autotrophic picoplankters was one order of magnitude higher at 0.1 pgC · cell^{-1}.

Nanoplankton

Thirty-nine nanoplanktonic taxa representing eight higher taxonomic groups and groups of unidentified nanoflagellates in three size classes were identified during the study. Similar numbers of taxa occurred at both sites, but only 14 taxa were common for the two sites. Most of the taxa represented the classes Dinophyceae (mainly the family Gymnodiniaceae), Cryptophyceae, and a group of undetermined flagellates.

Throughout the study, the overall abundances ranged from 100 million to 3 billion cells per m^3 (Table 4). Nanoplankton occurred more abundantly in the waters of the COLD site (Table 4). Biomass was also higher, not only because of higher abundance but also because the mean cell biomass was higher as well (Table 4). In both cases, this formation was dominated by plastidic (or at least mixotrophic) protists (Table 4). In addition to differences in abundance and biomass, vertical distribution also differed. While the biomass at the COLD site is mainly concentrated at the surface and at 20 m, at the WARM site the biomass concentration increased gradually from the minimum at the surface to the maximum at ~50 m (Fig. 8). The biomass of autotrophic nanoplankton dwarfed that of heterotrophic nanoplankton at both sites throughout the water column (Table 4).

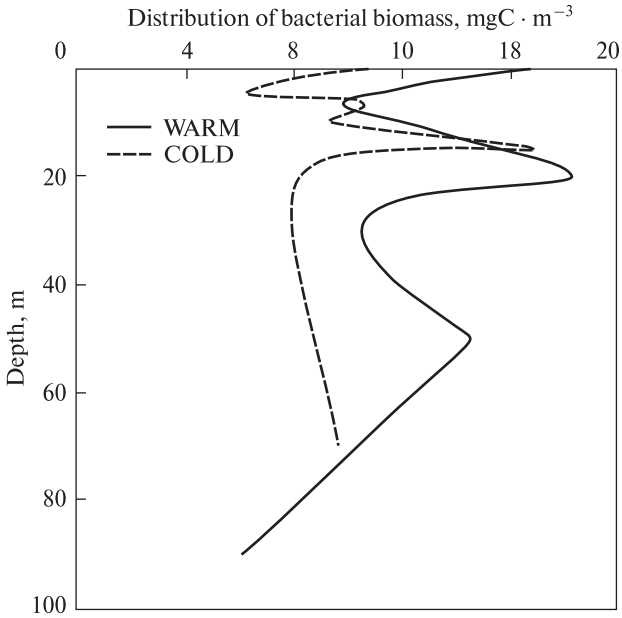

Figure 6. Vertical distribution of bacterial biomass

Microplankton

The microplanktonic fraction comprised 57 protistan taxa. Fifty taxa occurred at the WARM site, while 28

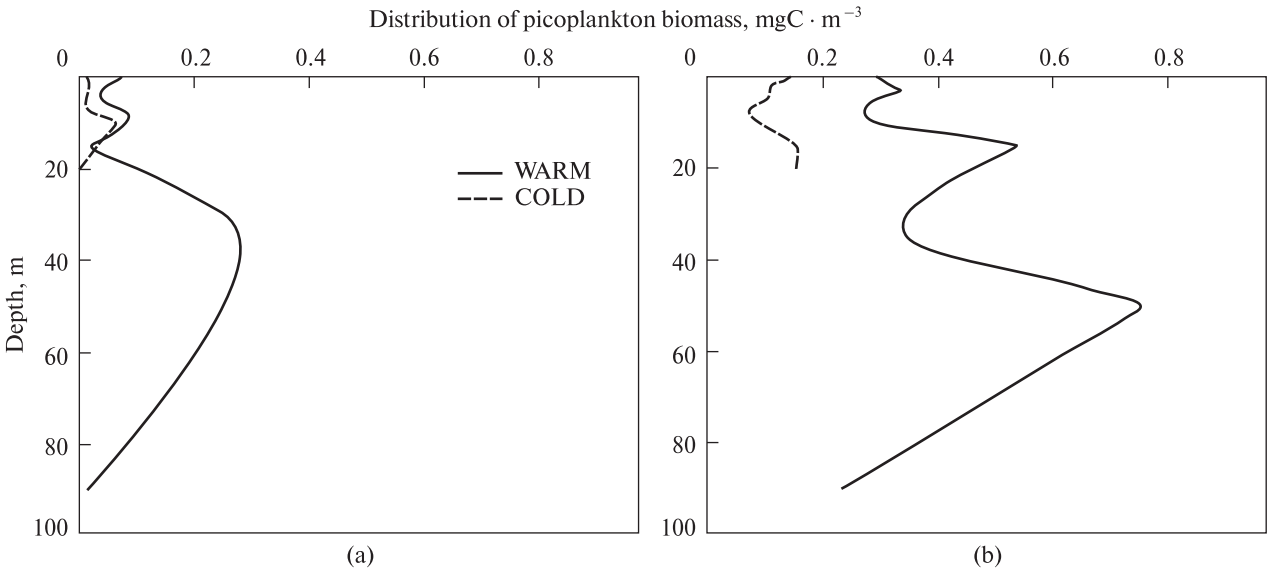

Figure 7. Distribution of picoplankton biomass — (a) autotrophic; (b) heterotrophic

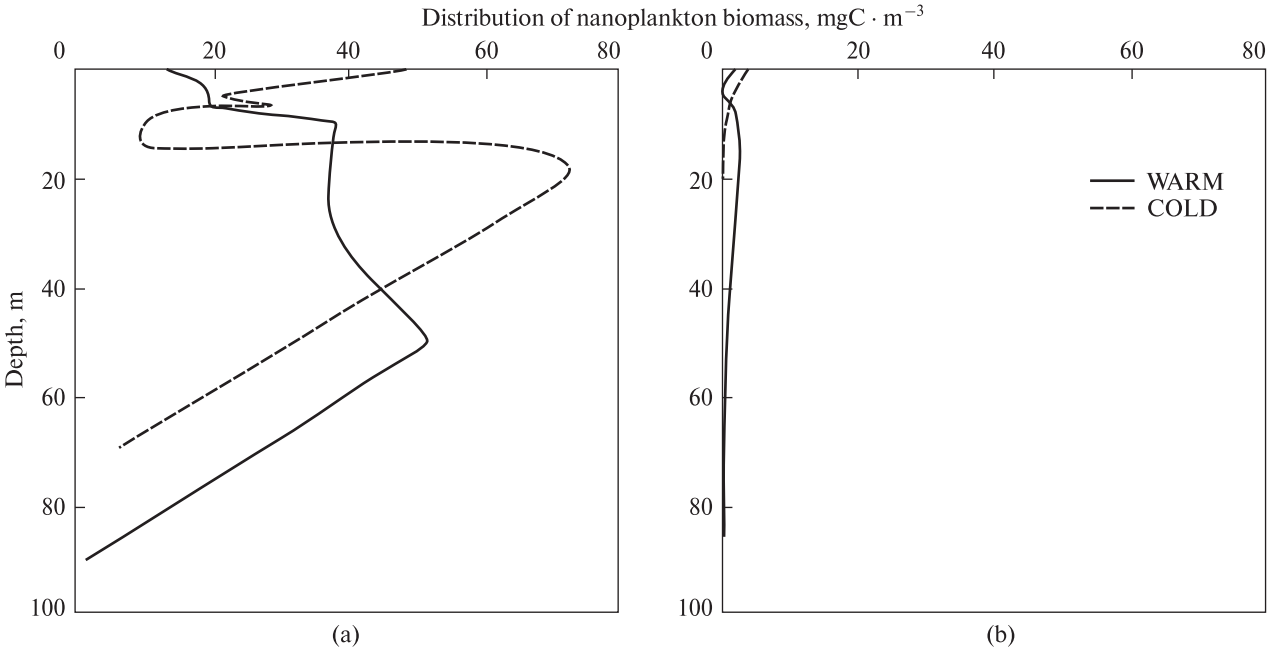

Figure 8. Distribution of nanoplankton biomass — (a) autotophic; (b) heterotrophic

taxa occurred at the COLD site. Diatom taxa were the most numerous (28), followed by Dinophyceae (19), and Ciliophora (10). Only 21 taxa were common to both sites. Abundances were lower than those of nanoplankton, and ranged from less than 40×10^3 cells per m^3 to almost 20×10^6 cells per m^3 depending on the site and level (Table 5). Generally, microplankton was less abundant at the COLD site (mean 90×10^3) than at the WARM site (~60×10^3). The biomass range was almost a thousandfold from well below

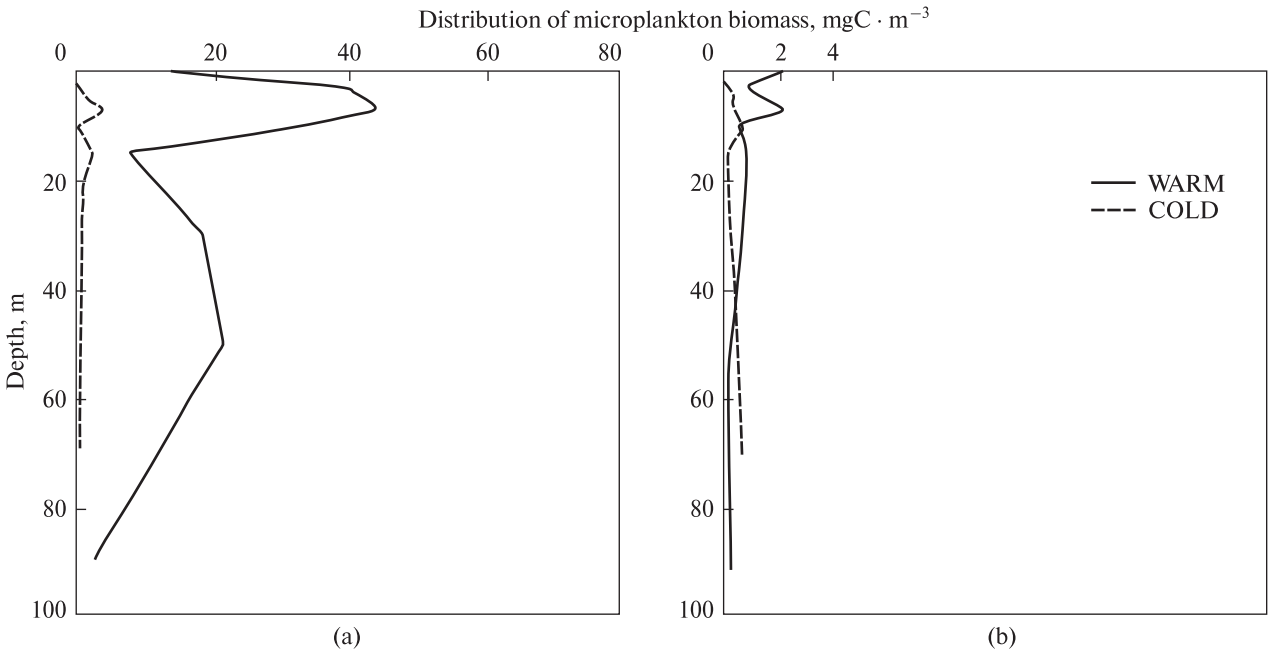

Figure 9. Distribution of microplankton biomass — (a) autotrophic; (b) heterotrophic

0.1 mg to almost 50 mg per cubic meter depending on location. At the WARM site it was significantly higher (tenfold) than at the COLD site, where the mean cell was almost 1.5-fold heavier (Table 5). Apart from biomass differences, the composition of the autotroph/heterotroph ratio was significantly lower (more than fivefold) at the WARM site (Table 5; Fig. 9a, b).

Table 3. Bacteria count at the WARM and COLD sites, Hornsund, July 2005

Site/Parameter range	WARM	COLD
Bacteria abundance [cells · m^{-3}]		
mean	$4 \cdot 10^{11}$	$5 \cdot 10^{11}$
max/min	$9 \cdot 10^{11}$—$3 \cdot 10^{11}$	$1 \cdot 10^{12}$—$14 \cdot 10^{11}$
Biomass [mgC · m^{-3}]		
mean	8	9
max/min	18—6	17—6
mean ind. biomass [pgC · $cell^{-1}$]	0.02	0.02

Primary production

Primary production ranged from 0.01 to 3.52 mgC × × $m^{-3} \cdot hr^{-1}$. At the COLD site, carbon fixation was at a similar level (above 1 mgC · $m^{-3} \cdot h^{-1}$) to that at the WARM site in the very upper layer only, while below 7 m it dropped to almost undetectable values. At the WARM site, autotrophs were most active in deeper

Table 4. Nanoplankton assemblage parameters at the WARM and COLD sites, Hornsund, July 2005

Site/Parameter range	WARM	COLD
Number of taxa	28	29
Abundance [cells · m^{-3}]		
mean	$1.96 \cdot 10^{8}$	$1.1 \cdot 10^{8}$
max/min	$2.4 \cdot 10^{9}$—$1 \cdot 10^{6}$	$1.5 \cdot 10^{9}$—$4.4 \cdot 10^{5}$
Biomass [mgC · m^{-3}]		
mean	34	36
max/min	59—0.01	44—0.01
Share of autotrophs [%]	96	98
mean ind. biomass [pgC · $cell^{-1}$]	$6.3 \cdot 10^{1}$	$3.5 \cdot 10^{1}$

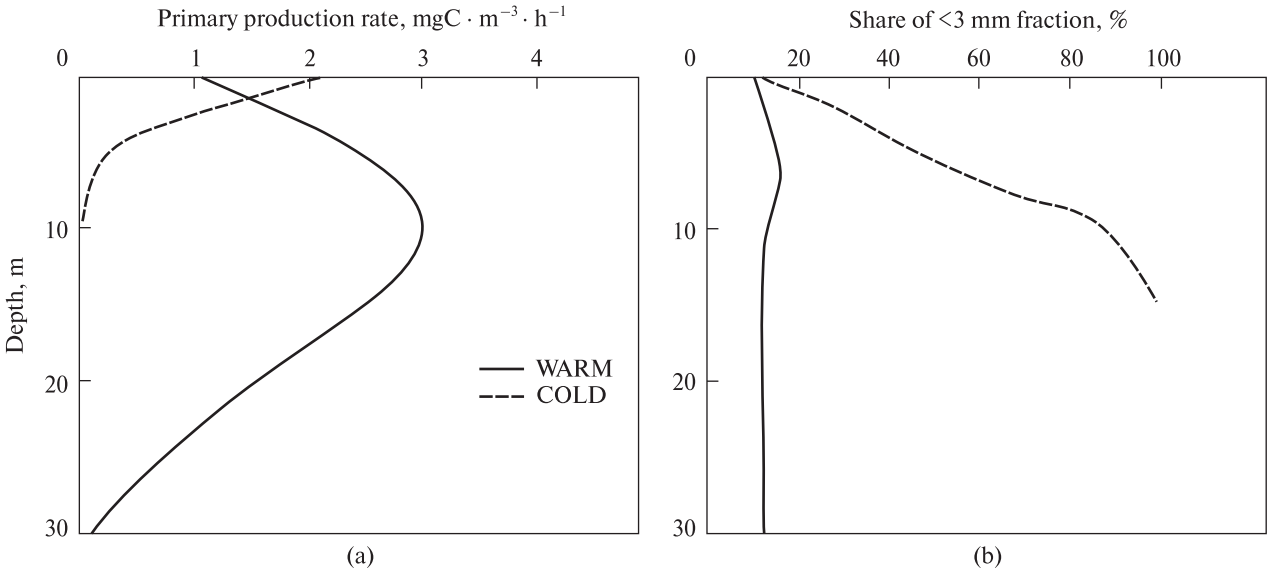

Figure 10. Primary production rates of plankton autotrophs, (a) — total Pp; (b) — share [%] of fraction below 3 μm

layers between 5 and 15 m (Fig. 10). This resulted in nearly sixfold lesser production at the COLD site than at the WARM site at 7.7 and 37.3 mgC · m^{-3} · h^{-1}, respectively (Table 2).

When the size fraction share is taken into consideration, the differences are also meaningful, and at the COLD site the share of autotrophs smaller than 3 μm increases with depth (Fig. 10b).

Table 5. Microplanktonic assemblage parameters at the WARM and COLD sites, Hornsund, July 2005

Site/Parameter range	WARM	COLD
Number of taxa	50	29
Abundance [cells · m^{-3}]		
Mean (Integr.)	$2.1 \cdot 10^5$	$9.4 \cdot 10^4$
max/min	$1.4 \cdot 10^7$—$4.6 \cdot 10^2$	$2.4 \cdot 10^6$—$3.4 \cdot 10^2$
Biomass [mgC · m^{-3}]		
mean	18	1
maximum	43—>$1 \cdot 10^{-3}$	3.6—>$1 \cdot 10^{-3}$
Share of autotrophs [%]	97	67
mean ind. biomass [pgC · $cell^{-1}$]	$0.9 \cdot 10^4$	$1 \cdot 10^4$

Table 6. Taxonomic composition (number of species in major groups) of the zooplankton at the WARM and COLD sites, Hornsund, July 2005

Taxon	WARM	COLD
Chaetognatha	2	2
Copepoda	17	16
Copepoda naupli	1	1
Ctenophora	1	1
Echinodermata (larvae)	1	1
Eumalacostraca	4	4
Gastropoda	1	1
Hydrozoa	3	3
Mollusca	2	1
Pisces indet. (larvae)	1	–
Polychaeta	1	1
Rotifera	1	1
Thecostraca	1	1
Tintinnina > 400 μm	1	1
Tunicata	2	2
Total	38*	35*

Note: * excluding Copepoda naupli

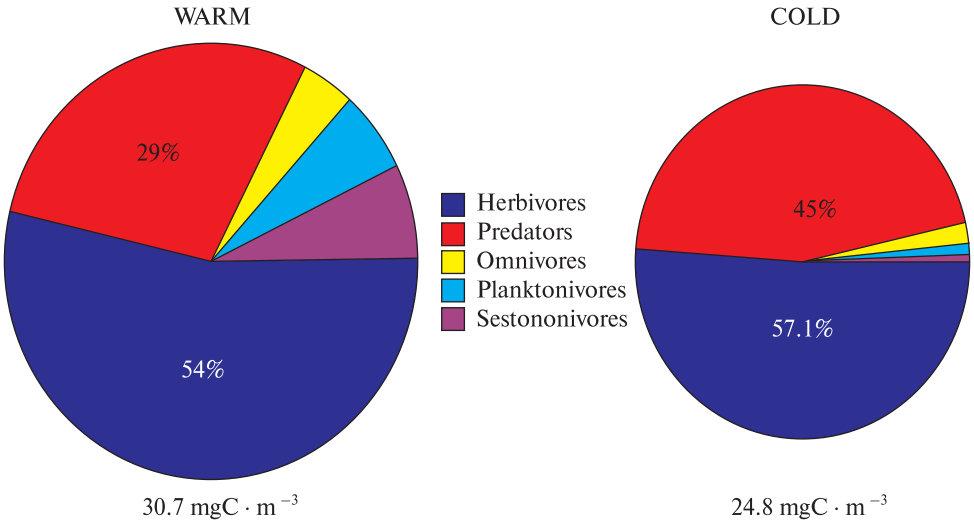

Figure 11. Total biomasses and trophic group shares of zooplankton

Table 7. Abundances and biomasses of main trophic groups of the zooplankton collected at the WARM and COLD sites (the share of the total abundance/biomass in brackets)

Trophic group	WARM		COLD	
	Abundance [ind · m^{-3}]	Biomass [mgC · m^{-3}]	Abundance [ind · m^{-3}]	Biomass [mgC · m^{-3}]
Herbivores	1.6 · 10^3 (85.0%)	16.5 (54%)	2.9 · 10^3 (87%)	12.7 (51%)
Predators	3.3 · 10^1 (2.0%)	9.0 (29%)	4.1 · 10^1 (1.4%)	11.2 (45%)
Omnivores	1.4 · 10^2 (7.5%)	1.3 (4.1%)	1.4 · 10^2 (3.6%)	0.5 (2.0%)
Planktonivores	9.0 · 10^2 (4.8 %)	1.9 (6.0%)	2.1 · 10^2 (7.1%)	0.2 (1%)
Sestonofeeders	1.3 · 10^1 (0.7%)	2.1 (6.9%)	1.9 · 10^1 (0.7%)	0.2 (1%)
Total	1.9 · 10^3	30.8	2.9 · 10^3	24.8
mean ind. biomass [mgC · ind^{-1}]	16.2		8.5	

Table 8. Share of size classes of zooplankters at the WARM and COLD sites

Size class	WARM		COLD	
	Abundance, %	Biomass, %	Abundance,%	Biomass,%
<1 mm	66.8	7.3	46.8	7.6
1—5 mm	32.4	43.2	52.8	53.8
5—10 mm	0.6	15.0	0.3	5.5
>10 mm	0.2	34.6	0.1	33.1

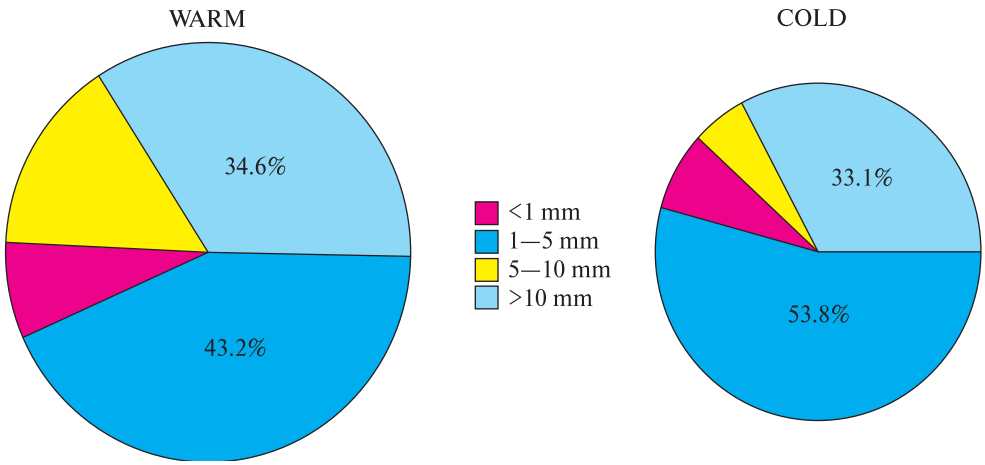

Figure 12. Size class shares of the total zooplankton biomass at the WARM and COLD sites, Hornsund, July 2005

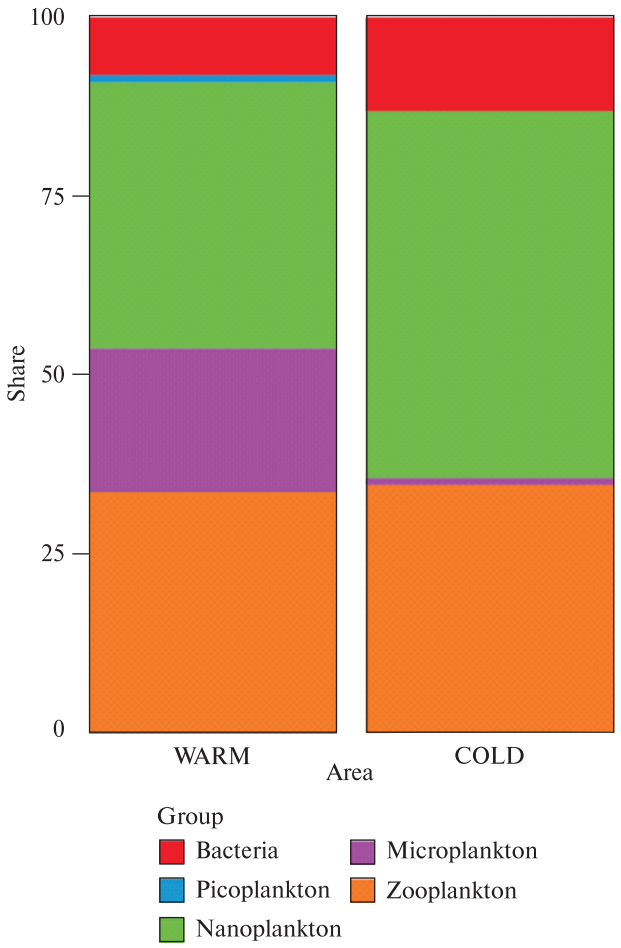

Figure 13. Main plankton component shares of the total biomass at the WARM and COLD sites, Hornsund, July 2005

Zooplankton

The zooplankton community comprised 41 taxa representing Copepoda (54%), Eumalacostraca (9.8%), and Hydrozoa (7.3%). Thirty-eight taxa were noted at the WARM site, against 35 at the COLD site. The majority of these taxa (34) occurred at both sites (Table 6). The mean abundance per m^3 was higher at the COLD site (<50%; Table 7); however, biomass was higher at the WARM site since mean individual biomass was 50% higher at 30.8 mgC · m^{-3} in comparison to 24.8 mgC · m^{-3} at the COLD site.

Herbivores dominated at both sites, but the share of herbivore biomass was most prominent (53%) at the COLD site, while being slightly lower at the WARM site (43%; Fig. 12). Predatory zooplankton had the second highest share of total biomass, which was also higher at the COLD site (39%) than at the WARM site (32%). At the COLD site, the biomass of these two trophic formations was dominated by omnivores, sestonivores, and planktonivores, where as at the WARM site, these were present in higher proportions (Fig. 11).

If size is considered, organisms in the 1 mm — 5 mm and >10 mm size classes dominated the total biomass at both of the sites studied (Fig. 12). The share of the second class exceeded 50% at the COLD water site (Table 8).

4 Discussion

Mean salinity and phosphate concentrations did not differ significantly, but the temperature did. The mean water temperature at the COLD site was 0.31 °C, which was almost 1 °C lower than at the WARM site. The waters at the COLD site were also more turbid. In terms of salinity and temperature, this hydrological state reflects typical fjord circulation (Svendsen & Thompson, 1978), in which shelf waters enter the fjord along the southern coast and circulate cyclonally and then exit the fjord along the northern bank. As waters circulate along the fjord in the location studied, they become colder and less saline as they mix with the meltwaters of the numerous glaciers. Melting during summer releases approximately 1.3 km^3 of freshwater into the innermost part of Hornsund fjord (Weslawski et al., 1995). Since this process is accelerating, the amount of freshwater discharged at the time of the study was likely greater. Hence, the water temperature was lower in the northern part of the fjord (COLD site) and had a distinctive layer of low-saline water. As the meltwaters carried vast amounts of mineral matter, turbidity was higher in this area, which was also observed by e.g. Piwosz et al. (2009).

The water nutrient concentrations did not exceed the range typical of the fjords of west Spitsbergen (Eilertsen et al., 1989) or the oceanic waters of northwest Spitsbergen (Owrid et al., 2000). The vertical distribution of nutrient concentrations suggested they were partially depleted by primary production at the WARM site. In contrast, higher levels of silicate concentrations at the COLD site might have resulted from the massive load of mineral suspensions.

Total concentrations of chlorophyll *a,* the distribution of chlorophyll biomass, and primary production rates were similar to those observed in 2002 by Piwosz et al. (2009), which suggests that this is typical of the summer period in this region. The lack of data renders it impossible to perform a correlation analysis of the suspended matter—chlorophyll *a* concentration and primary production rates. The regularity in the spatial distribution of the photosynthetic pigments is, however, sufficient to permit concluding that meltwaters carrying large amounts of mineral suspensions impact autotrophic organisms. Primary production rates, which were fivefold higher at the WARM site compared to those at the COLD site, supported this.

The current investigations of bacteria and picoplankton eukaryotes are novel in contrast to the previous studies of the Hornsund region, and are particularly rare for adjacent waters. The scarcity of data concerning these fractions, their abundance and biomass and their share in total primary production stem from the lack of scientific interest prior to the late 1970s when the concept of the microbial loop was introduced by Azam et al. (1983), inspired by the ideas of Pomeroy (1974).

The bacterial abundance determined in the current study was one order of magnitude higher in comparison with the data reported by Zajaczkowska and Zajączkowski (1989). Jankowska et al. (2005) reported far lower bacterial abundances in Kongsfjorden than the current investigation.

Picoeucariota abundance was, in turn, one order of magnitude lower than that measured south of Spitsbergen (Not et al., 2005). Biomass was also lower in comparison to that in the waters of the central Barents Sea (Rat'kova & Wassmann, 2002). Values observed in the Central Arctic Basin (Sherr et al., 1997) and Kongsfjord (Wang et al., 2009) were similar to those observed during the current investigation (10^9—10^{11} cells · m^{-3}).

Nanoplankton abundance in Kongsfjorden (Piwosz et al., 2009) was two- to threefold greater compared to that in the Central Arctic Basin (Sherr et al., 2003). Although Wang et al. (2009) noted similar nanoplankton abundance in Kongsfjorden, the overall biomass they reported was tenfold higher at ~306 mgC · m^{-3} in the outer fjord to 35 mgC · m^{-3} in the innermost part where highly turbid water occurred. The higher overall nanoplankton biomass could have been anticipated since these authors only considered heterotrophic nanoflagellates. Unfortunately, the authors did not report the taxonomic composition, but according to the biomass abundances communicated, individual cells had higher biomass than did those in Hornsund. The mean, individual biomass may be derivative of water temperature because, in Horn-

sund, where the overall biomass did not differ considerably, the carbon per unit was almost half lower than that at the WARM site.

The most dramatic differences were noted in microplankton biodiversity (numbers of taxa) and biomass. As at the WARM site, this formation was an important component of the planktonic realm, while at the COLD site the microplankton was only a minor part of the total plankton-bound organic carbon. There, the low microplanktonic biomass comprised larger individuals than that at the WARM site. The current study noted higher biomass comprising mainly autotrophs at the WARM site. However, at the COLD site, the taxonomic diversity of the microplankton and the share of heterotrophs were both higher.

The overall zooplankton abundance did not diverge from values reported in the same area in summer of 2002, namely the densities ranging from ~2000 ind · m^{-3} in the outer part of Hornsund to ~2500 ind · m^{-3} in the inner part (Piwosz et al., 2009). To date, zooplankton investigations have focused only on size classes above 180 μm, so precise comparisons are impossible. In the present study, the differences in zooplankton abundance and biomass were minor as were the shares of size classes and trophic groups.

The overall picture of the pelagic ecosystem did not differ from that of adjacent waters. Most of the biotic parameters differed significantly between the two fjord sites with higher total abundance and biomass at the WARM site. Although it was impossible to perform statistical analyses because of the lack of repetitions, the comparison presented in Figure 13 illustrates this persuasively.

Does global warming really cause a planktonic shift towards the dominance of the smaller-sized fraction? Or was the COLD site not cold enough for arctic conditions? The mean values for water temperature and salinity at this site differed from those at the WARM site, yet this was the effect of the cooler and less saline meltwater. Finkel et al. (2005) found that sea-ice melt, which results in stronger stratification, favors smaller-sized autotrophs. This contradicts the scenario proposed by Arrigo et al. (2008), in which Arctic marine primary production increased from 2003 to 2006—2007 by almost 10 TgC · yr^{-1}, and 30% of this was because of the summer sea-ice shrinkage. In theory, free water areas opening mean more available light. However, it must be noted that warming causes both sea-ice and terrestrial ice to thaw. Throughout the Arctic, huge quantities of freshwater are discharged from melting terrestrial ice-cover –$3.1 \cdot 10^6$ km^3 (Dowdeswell & Hagen, 2004), permafrost — ~36×10^6 km^2 (Walsh et al., 2011), and sea ice ~7—15×10^6 km^2 (Parkinson et al., 1999). Terrestrial storage discharges 3559 $km^3 \cdot y^{-1}$ (Carmack et al., 2006) of freshwater that usually carries high sediment loads (Gordeev, 2006); thus, these affect water column stability (Strass & Nöthig, 1996). All of the above appears to apply to Hornsund, where the COLD site is occupied by turbid meltwater discharged by warmed, tidal glaciers. The low primary production and overall biomass are constructed in higher proportions by fractions smaller than 3 μm.

A clear picture of the selective influence of the turbid meltwaters on protistan plankton is presented in the previously mentioned Kongsfjorden (Keck et al., 1999). The share of ubiquitous flagellates that are resistant to unfavorable light conditions decreased with distance from the glacier front (Keck et al., 1999; Wiktor, 1999), whereas autotrophs increased significantly. Despite the lack of differences in bacterioplanktonic biomass and abundance in Hornsund, a strong spatial gradient from highly turbid water near the glacier front (0.16 mgC · m^{-3}) to the outside of the fiord (0.03 mgC · m^{-3}) was noted in Kongsfjorden (Jankowska et al., 2005).

To summarize, the results of the current study indicated that water turbidity caused by meltwater runoff had a pronounced influence on pelagic systems by eliminating larger autotrophs and decreasing primary production. Extrapolating this situation to the Arctic as a whole permits predicting that progressive Arctic warming, at least that in shelf areas, will result in decreased production and a shift to planktonic mixotrophic and heterotrophic flagellates.

Author contributions. JW — fieldwork, phytoplankton & chlorophyll *a* samples analyses, manuscript preparation; MG — zooplankton and sediment sampling, and preliminary data processing; KBS — zoo-

plankton samples analyses; KP — sampling, picoplankton samples preparations and analyses; SK — supervision of zooplankton analyses; KJ — DOC and bacteria samples analyses and data processing; KD — zooplankton analyses, biomass evaluations; JMW — project leader, sampling.

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Арктичний фіорд під час потепління: планктонна точка зору

Реферат. Клімат впливає на водні екосистеми в усьому світі, але найбільший вплив спостерігається в полярних регіонах. Це дослідження спрямоване на перевірку гіпотези про те, що зміни в біорізноманітті пов'язані зі змінами, яких за різних температурних умов зазнає планктонна біота, при чому її великі за розміром види домінують у холодних водах, а менші — у теплих. Улітку 2005 року у фіорді Хорнсунд (західний Шпіцберген) було обстежено дві ділянки з контрастною гідрологією. Перша ділянка розташована поблизу входу в фіорд, вона зазнала сильного впливу атлантичних вод (WARM). Друга ділянка розташована глибоко всередині фіорду, де вода більш прісна й холодніша через стік талих льодовикових вод (COLD). Виміряно температуру, солоність та фотосинтетично активну радіацію, проаналізовано концентрацію поживних речовин та хлорофілу *a*. Зібрано та перераховано планктонну біоту, що включає різні фракції зоопланктону, фітопланктону та бактерій. Серед виміряних абіотичних параметрів різниця температур була найбільш вираженою. Зокрема, ділянка COLD характеризувалася нижчою температурою та більшою каламутністю через вплив талої води. Виявлено значні відмінності у складі та кількісних співвідношеннях планктонної біоти, при чому найбільш різкі зміни були в кількості мікропланктонних таксонів та їх біомаси. Загальна біомаса планктону на ділянці WARM (91 мгС · м$^{-3}$) була вищою, ніж на ділянці COLD (71 мгС · м$^{-3}$), як і первинні показники. Мікропланктонне різноманіття на ділянці WARM було рясне і містило вдвічі більше таксонів, ніж на ділянці COLD. Найпростіші організми (протисти) становили більше половини планктонної біомаси на ділянці WARM (53,2%), в той час як їхня частка на ділянці COLD була дещо вищою (63,6%). Серед найпростіших домінувала фракція нанопланктону, а основною складовою біомаси зоопланктону були копеподи. Відмінності у складі планктонних спільнот, виявлені між двома ділянками, могли виникнути через різний вплив стоку талих вод, що усуває більші, виключно автотрофні організми та зменшує первинне продукування.

Ключові слова: арктичний фіорд, бактерії, зміна клімату, зоопланктон, протисти, Хорнсунд