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ORIGINAL RESEARCH ARTICLE

Comparison of bacterial production in the water column between two Arctic fjords, Hornsund and Kongsfjorden (West Spitsbergen)

Anetta Ameryk [a], **Katarzyna M. Jankowska** [b,*], **Agnieszka Kalinowska** [b], **Jan M. Węsławski** [c]

[a] *National Marine Fisheries Research Institute, Gdynia, Poland*
[b] *Gdańsk University of Technology, Gdańsk, Poland*
[c] *Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland*

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Summary Bacterial production and the accompanying environmental factors were measured in the water columns of two Arctic fjords during the cruise in July and August 2013. Water samples were collected at six stations located in the central part of Hornsund and Kongsfjorden. In Hornsund, where average water temperatures were 1.25-fold lower than in Kongsfjorden, the bacterial production was twice as high (0.116 ± 0.102 vs 0.05 ± 0.03 mg C m^{-3} h^{-1}). Statistical analysis indicated that chlorophyll *a* concentration itself was not a significant factor that affected bacterial production, in contrast to its decomposition product, pheophytin, originating from senescent algal cells or herbivorous activity of zooplankton. Single and multiple regression analysis revealed that water temperature, dissolved organic carbon (DOC), and pheophytin concentration were the main factors affecting bacterial production in both fjords.

* Corresponding author at: Gdańsk University of Technology, Narutowicza 11/12 Street 80-233 Gdańsk, Poland. Fax: +58 347 20 44.
E-mail addresses: aameryk@mir.gdynia.pl (A. Ameryk), kjank@pg.gda.pl (K.M. Jankowska), agnieszka.kalinowska@poczta.onet.pl (A. Kalinowska), weslaw@iopan.gda.pl (J.M. Węsławski).
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1. Introduction

Polar regions are extremely important research fields because of their unique vulnerability to climate change. One of the already visible and predicted signs of global warming is intensive retreat of glaciers. Due to glacial meltwater inflow, and therefore particulate matter (Urbański et al., 2017) and freshwater introduction, changes were observed in the microbial community composition in the Arctic fjords (Piquet et al., 2010, 2016).

Fjords of Hornsund (located on the south-west coast of Spitsbergen, Fig. 1) and Kongsfjorden (located on the north-west coast of Spitsbergen) were selected as sites where monitoring of the implications of climate change is possible (Warwick et al., 2003) due to their location in the area of increasing air temperature as well as inflow of Atlantic Waters (AW) (Serreze et al., 2000; Walczowski and Piechura, 2006, 2007, 2011; Walczowski et al., 2012). Kongsfjorden remains under strong influence of warm and saline West Spitsbergen Current. It follows the deeper part of the Fram Strait, and often enters the fjord, causing warming of its environment (Cottier et al., 2005; Svendsen et al., 2002). The South West coast of Spitsbergen is more affected by coastal Arctic waters from the Barents Sea which are less saline (Skagseth et al., 2008). This so called Sørkapp Current has great influence on the Hornsund Fjord (Cottier et al., 2005; Swerpel, 1985).

Research carried out in recent years in the polar regions shows that low temperature is not a limiting factor of bacterial activity (Kirchman et al., 2005; Rivkin et al., 1996). Many authors highlight the need to combine conventional techniques of determining bacterial production (based on the incorporation of ^{3}H-thymidine or ^{3}H-leucine) (Fuhrman and Azam, 1982; Kirchman et al., 1985; Simon and Azam, 1989) with single-cell analysis to identify the capability for assimilation of dissolved organic matter (DOM) by individual groups of bacteria (Elifantz et al., 2007).

The total abundance, biomass, and morphological structure of bacterioplankton can be evaluated by means of the direct cell counting technique, without the need of bacteria cultivation (Amann et al., 1995). In recent years, intensive development of non-cultivating techniques has contributed significantly to the expansion of knowledge on microbial diversity and community composition in the environment (Piquet et al., 2010, 2016; Zengler, 2009).

Although Kongsfjorden BP data are available for several seasons and years (Engel et al., 2013; Iversen and Seuthe, 2011; Motegi et al., 2013; Piquet et al., 2016; Wängberg et al., 2008), no information is to date available on BP in Hornsund. Experiments regarding the impact of climate change on microorganisms also were conducted in Isfjorden, under the influence of the Atlantic Waters (Lara et al., 2013).

Despite this multi-annual overview on the functioning of West Spitsbergen fjords, the details of microbial processes are still not fully understood. An interdisciplinary approach, combining hydrology, chemical composition of glacial and surface runoff, as well as and metagenomic data, is necessary to establish the scale of impact of biotic and abiotic factors

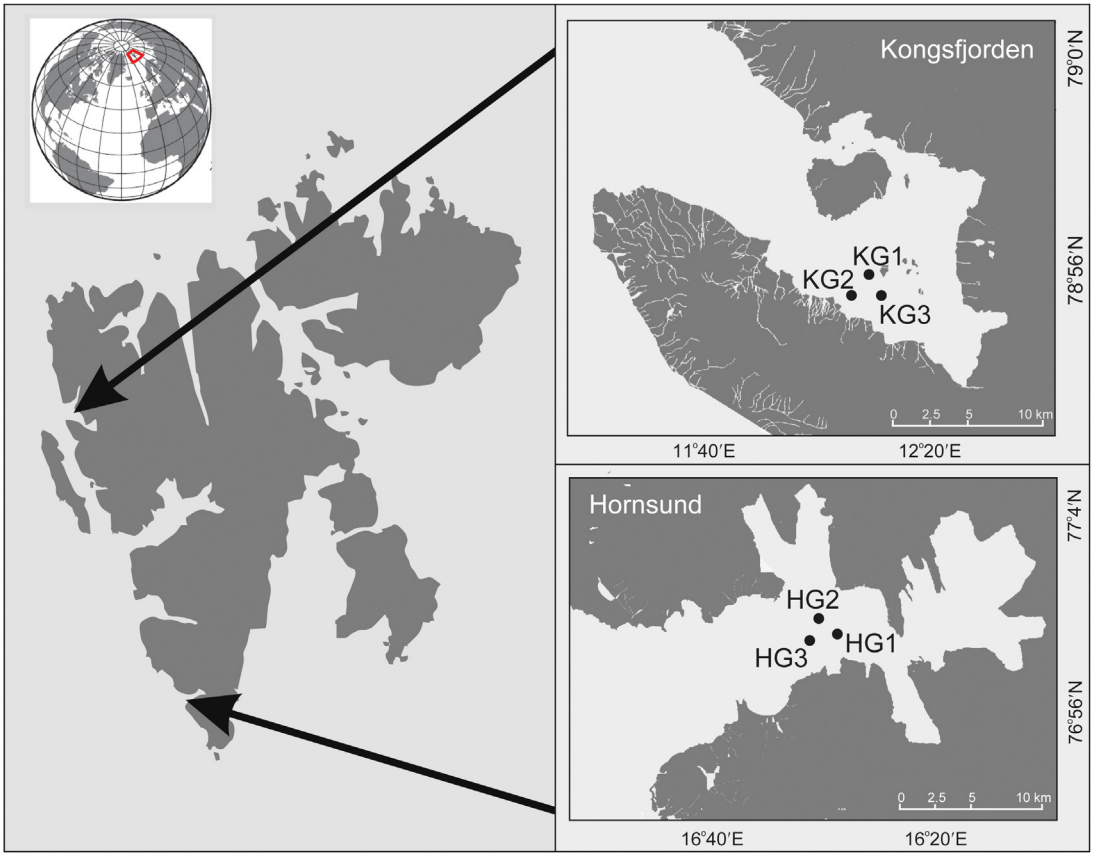

Figure 1 Maps of sampling points (GAME data).

on microbial life in marine ecosystems. Therefore, the primary objective of the study was to compare bacterial production in two Arctic fjords, and to determine the factors influencing it.

2. Material and methods

2.1. Study area and sampling

Marine water was sampled in the scope of GAME project on 29–30.07.2013 in Hornsund, and on 7–9.08.2013 in Kongsfjorden during a cruise of *r/v Oceania* (Institute of Oceanology, Polish Academy of Sciences). Samples were taken at three stations in each of the two fjords, HG1, HG2, and HG3 in Hornsund, and KG1, KG2, and KG3 in Kongsfjorden (Fig. 1). Separate samples were collected for measurements of bacterial production (BP) and determination of total bacterial number (TBN), biomass (BBM), average cell volume (ACV), and morphological form (MF).

Samples for the determination of bacterial production were collected at 4–5 depths in the water column: surface, 10 m, 25 m, 75 m (HG1 at 50 m instead of 75 m), and bottom in Hornsund; surface (0 m), 10 m, 15 m, 35 m, 75 m, and bottom in Kongsfjorden. Total bacterial number, biomass, and cell volume were determined in samples from 5 to 8 depths (see Tables 1 and 2). Surface water samples were collected by means of a bucket, and the others by Niskin bottles.

2.2. Bacterial production

For all the samples, four 10 ml subsamples were prepared: triplicates and one blank. To avoid any bacterial growth in the blank, 100 μl of 36% formaldehyde was added immediately after sampling. 200 μl leucine was then added to the samples (final solution of 20 nM). 100 nM leucine was added to the bottom water sample. Leucine reagent was a mixture of ^{3}H-leucine (SA = 54.1 Ci mmol^{-1}) and L-leucine in ratio 1:9. Incubation held in in situ temperature (range between 1.7 and 5.4°C) lasted for 3 h. To finish the incubation, 100 μl of formaldehyde was added to samples. Samples were filtered through 0.2 μm nitrocellulose filters. Prior to filtration, chimneys were cooled in the freezer. Filters were rinsed with 10× 1 ml of cold (0°C) trichloroacetic acid and 10× 1 ml of 80% ethanol. They were stored in scintillation vials, dried, and frozen at −20°C until further processing. Unfrozen filters were dissolved in 0.5 ml ethyl acetate, and 6 ml of scintillation cocktail was added to the vials. Well mixed samples were counted on a scintillation counter Beckmann LS 6000IC twice: after one and after four days after the addition of the scintillation cocktail.

Table 1 Values of all measured bacterial parameters in the waters of Hornsund (total bacterial number (TBN) and bacterial biomass (BBM) already published by Kalinowska et al., 2015).

	Depth	BP [mg C m^{-3} h^{-1}]	ACV [μm^3]	MF [%]			TBN [10^5 cells cm^{-3}]	BBM [mg C m^{-3}]
				R	C	O		
HG1	0 m	0.319	0.27	48	49	3	3.46	14.73
	5 m	n.d.	0.07	75	19	6	4.11	8.06
	10 m	0.123	0.10	68	27	5	3.16	7.28
	15 m	n.d.	0.04	67	30	3	2.15	3.15
	25 m	0.160	0.27	36	63	1	2.94	12.09
	35 m	n.d.	0.02	73	26	1	2.23	2.20
	50 m	0.032	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	75 m	n.d.	0.03	70	29	1	1.71	2.08
	Bottom (77 m)	0.085	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
HG2	0 m	0.330	0.16	60	34	6	3.94	12.06
	5 m	n.d.	0.04	68	25	7	2.14	2.99
	10 m	0.051	0.33	44	52	4	3.21	14.01
	15 m	n.d.	0.16	43	53	4	2.55	7.96
	25 m	0.127	0.31	38	58	4	3.62	16.14
	35 m	n.d.	0.12	47	49	4	3.19	8.24
	75 m	0.023	0.27	41	55	4	3.56	14.62
	Bottom (103 m)	0.022	0.10	48	49	3	2.11	4.85
HG3	0 m	0.118	0.26	46	50	4	2.36	9.74
	5 m	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	10 m	0.037	0.24	52	44	4	3.03	11.83
	15 m	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	25 m	0.215	0.22	52	44	4	3.29	12.33
	35 m	n.d.	0.07	64	30	6	3.36	6.48
	75 m	0.027	0.20	47	50	3	3.62	12.73
	Bottom (105 m)	0.065	0.25	42	56	2	2.60	10.17

HG1, HG2, HG3 name of stations in Hornsund; BP, bacterial production; ACV, average cell volume; MF, morphological form; R, rods; C, cocci; O, others; n.d., not determined.

Table 2 Values of all measured bacterial parameters in the waters of Kongsfjorden (total bacterial number (TBN) and bacterial biomass (BBM) already published by Kalinowska et al., 2015).

	Depth	BP [mg C m^{-3} h^{-1}]	ACV [μm^3]	MF [%]			TBN [10^5 cells cm^{-3}]	BBM [mg C m^{-3}]
				R	C	O		
KG1	0 m	0.055	0.31	42	37	21	1.55	7.72
	5 m	n.d.	0.29	49	42	9	1.67	6.75
	10 m	0.030	0.21	42	50	8	1.55	5.76
	15 m	0.048	0.30	31	66	3	1.84	8.16
	25 m	n.d.	0.07	63	32	5	1.09	2.02
	35 m	0.015	0.03	76	21	3	1.16	1.36
	75 m	0.012	0.05	66	29	5	1.55	2.30
	Bottom (105 m)	0.015	0.23	38	60	2	2.02	7.66
KG2	0 m	0.041	0.21	50	44	6	1.21	4.49
	5 m	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	10 m	0.047	0.18	47	48	5	2.70	8.87
	15 m	0.141	0.15	51	46	3	4.25	12.42
	25 m	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	35 m	0.039	0.14	47	50	3	1.76	4.83
	75 m	0.013	0.10	53	44	3	1.53	3.50
	Bottom (118 m)	0.117	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
KG3	0 m	0.052	0.20	48	41	11	1.86	6.79
	5 m	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	10 m	0.106	0.45	17	81	2	1.52	8.47
	15 m	0.082	0.16	44	52	4	1.81	5.53
	25 m	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	35 m	0.021	0.34	28	64	8	1.77	8.13
	75 m	0.012	0.16	30	68	2	1.81	5.53
	Bottom (96 m)	0.060	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

KG1, KG2, KG3 name of stations in Kongsfjorden; BP, bacterial production; ACV, average cell volume; MF, morphological form; R, rods; C, cocci; O, others; n.d., not determined.

Due to the lack of access to the scintillation counter during the cruise, the concentration of leucine applied in the study was chosen based on literature data. In order to verify the value of the concentration, a saturation curve was prepared. Water samples used for that purpose were from 10 m, HG1 station. Several leucine concentrations were added to the consecutive sub-samples: 2.5 nM, 5 nM, 10 nM, 20 nM, 40 nM, and 80 nM. The water saturation curve shows that 20 nM was the appropriate concentration of leucine. 3.1 kg C mol Leu^{-1} conversion factor (Kirchman, 1992) was applied.

2.3. Total bacterial number, biomass, average cell number, and morphological structure

Water samples were fixed immediately after collection with particle-free formaldehyde solution to a final concentration of 2%. The samples were kept at +4°C until further analyses. The DAPI (4′,6-diamidino-2-phenylindole) direct count method (Porter and Feig, 1980) was used for microscopic analysis: the samples were stained for 10–15 min with DAPI solution to a final concentration of 1 $\mu g\ ml^{-1}$ and filtered on 25 mm polycarbonate filters (Millipore, 0.2 μm pore diameter).

Microscopic slides were observed under an epifluorescence microscope Nikon Eclipse 80i under 1000-fold magnification (HBO-103W high pressure mercury burner, 330–380 nm excitation filter, 420 nm barrier filter, and 400 nm dichroic mirror). A PC coupled with high resolution CCD digital camera Nikon DS-5 Mc-U2 and MultiScan v.14.02 counting program with the modification of Świątecki (1997) were used for the image analysis.

Total bacterial number, biomass, average cell volume, and morphological structure were obtained based on the mean value from 2 series of photos (10 fields each). Bacterial cells were classified to three morphological types: cocci, rods, and others (vibrio). Total bacterial number and biomass were calculated after Norland (1993), as presented in Kalinowska et al. (2015).

2.4. Additional analyses

Analyses of chlorophyll *a*, pheophytin, nutrients, and dissolved organic and inorganic carbon (DOC and DIC) concentrations were also performed in the scope of the GAME project. The detailed methodology was described by Wiktor et al. (2017) and Zaborska et al. (2016). Salinity and water temperature were measured by means of a CTD probe SEA-BIRD SBE 49.

For statistical calculations, the majority of the data, apart from temperature and salinity, were converted by a natural logarithm. DIC values were transformed by an exponential function: *e* to the power *x*. For the comparison of the mean values between the fjords Student's *t*-test was applied.

3. Results

Bacterial production values determined in Hornsund were higher than in Kongsfjorden. In Hornsund, bacterial production ranged from 0.022 to 0.33 mg C m^{-3} h^{-1}, whereas in Kongsfjorden BP varied from only 0.012 to 0.141 mg C m^{-3} h^{-1}, and averaged 2× higher (av. = 0.116 ± SD 0.102 mg C m^{-3} h^{-1} in Hornsund vs. 0.050 ± 0.038 mg C m^{-3} h^{-1} in Kongsfjorden). The coefficient variation (CV = SD/Av) in Hornsund exceeded 88%. This suggests a larger fluctuation in bacterial production than in the Kongsfjorden, where CV is 76.4%.

Depth profiles of bacterial production in the water column show two maxima in Hornsund: at the surface and at a depth of 25 m, and at 10—15 m in Kongsfjorden (Fig. 2a, Tables 1 and 2). These depths correspond to fluorescence maxima and location of the thermocline. Bacterial production decreased to the minimum at a depth of 50—75 m. In the bottom layer, bacterial production usually slightly increased. The values corresponding to the surface water layer on stations HG1 and HG2 clearly diverged from the remaining data, as seen in detail in Fig. 2a. Student's *t*-test results showed a statistically significant difference between bacterial production in both fjords (Fig. 3). Despite the observed difference between the fjords in terms of bacterial abundance (Kalinowska et al., 2015), no correlation was found between the abundance and average cell volume.

Temperature ranged from 1.63 to 5.43°C, av. 2.90 ± 1.02°C in the colder Hornsund Fjord. In the warmer Kongsfjorden, it varied from 1.78 to 5.48°C, av. 3.63 ± 0.88°C. CV in Hornsund was higher (35.2%) than in Kongsfjorden (24.1%), again showing a higher fluctuation of the parameter in the colder fjord. Temperature was rising with depth, reaching its maximum at approximately 25 m in Hornsund, and at approximately 20 m in Kongsfjorden, and then dropping till the bottom (Fig. 2b).

Salinity ranged from 30.17 to 31.02 (av. 33.8 ± 1.33 SD) in Hornsund, and from 34.79 to 34.86 (av. 34.2 ± 0.91) in the more saline Kongsfjorden. The coefficient variation was low, and showed no considerable difference between the fjords, amounting to 3.94% in the southern fjord, and 2.66% in the northern one. Salinity was constantly increasing with depth in the water column (Fig. 2c).

Detailed values of chlorophyll *a*, pheophytin, DIC, DOC, and nutrients are published in Zaborska et al. (2016) and Wiktor et al. (2017).

The analysis of single regression equations of bacterial production with other parameters (Table 3) showed that BP variability was accounted for to the greatest extent by the concentration of pheophytin and dissolved organic carbon, whether each fjord was considered separately or together. Pheophytin, which is a product of chlorophyll decay, accounted for 47% of bacterial production variability in Hornsund, 52% in Kongsfjorden, and 56% for samples from both fjords combined (Fig. 4). No significant differences were observed between the fjords in terms of average pheophytin concentrations, but the highest values of bacterial production in the surface layer at HG1 and HG2 stations correspond to very high pheophytin concentrations.

Chlorophyll *a*, indicating the presence of living phytoplankton, accounted for only 20% of bacterial production variation. The strong correlation of BP and DIC (R^2 = 0.52 for Hornsund; R^2 = 0.33 for Kongsfjorden; and R^2 = 0.45 for all the data) is inversely proportional (Fig. 5). At the same time, differences in the average concentrations of DIC between the fjords were not statistically significant (Table 3). Dissolved

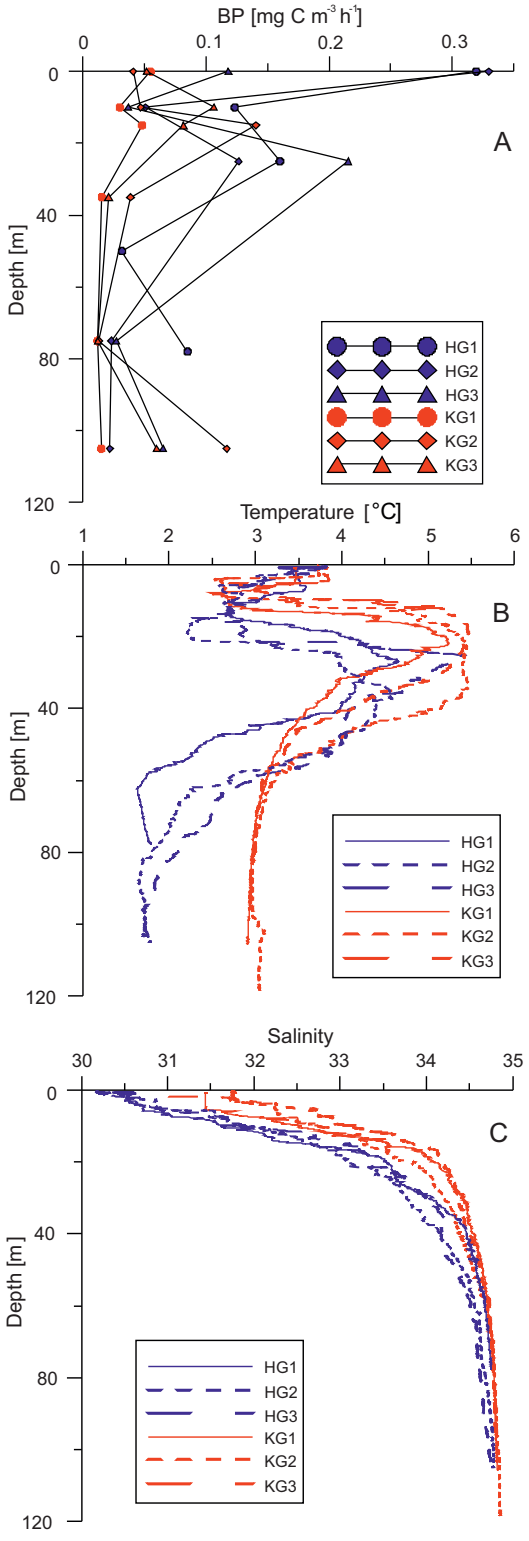

Figure 2 Depth profiles of bacterial production (a), salinity and (b) temperature in (c) Hornsund (HG1, HG2, HG3) and Kongsfjorden (KG1, KG2, KG3) waters.

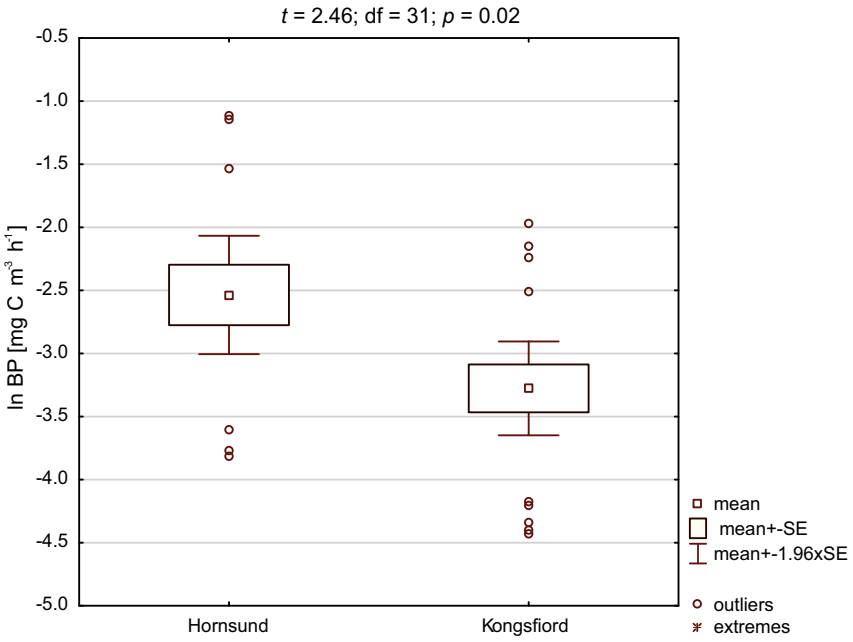

Figure 3 Difference between bacterial production in the water columns of Hornsund and Kongsfjorden (Student's *t*-test for equal variance).

organic carbon had no statistically significant effect on the BP in each of the fjords separately, but significantly accounted for 14% of the variation in the total set of data. Nutrients in the form of phosphate, nitrate, and ammonium were inversely proportional, and significant only for bacterial production in Hornsund.

Temperature accounted for 13% of the variability in bacterial production in both fjords simultaneously. However, based on the scatter plot, a regression line for each of the fjords can be plotted separately (Fig. 6). At a lower temperature, BP is higher in Hornsund. Temperature in Hornsund accounts for 57% of bacterial production variation, and is statistically significant. In Kongsfjorden, no statistical significance of temperature was found. Both temperature and salinity played a greater role in explaining the variability of BP in Hornsund, as well as in the data from both fjords combined. BP was directly proportional to temperature and inversely proportional to salinity.

Table 3 Single regression in separate fjords and in combined material — bacterial production [mg C m^{-3} h^{-1}] (ln transformed) versus different variables.

Parameter	Hornsund $N = 15$		Kongsfjorden $N = 18$		Both fjords $N = 33$	
	R^2 R^{-2}_{adj}	p	R^2 R^{-2}_{adj}	p	R^2 R^{-2}_{adj}	p
ln Pheoph	0.47/0.43	**	0.52/0.48	**	0.56/0.54	***
eDIC	0.52/0.48	**	0.33/0.28	**	0.45/0.43	***
ln Chlor		ns		ns	0.20/0.17	*
Temperature	0.57/0.54	**		ns	0.13/0.10	*
Salinity	0.37/0.32	*		ns	0.30/0.27	**
ln DOC		ns		ns	0.14/0.11	*
ln PO_4	0.32/0.27	*		ns		ns
ln NO_3	0.55/0.52	**		ns		ns
ln NH_4	0.55/0.52	**		ns		ns
ln TBN		ns		ns	0.30/0.27	**
ln BBM		ns	0.39/0.35	**	0.37/0.35	***

Pheoph, concentration of pheophytin [mg m^{-3}]; DIC, conc. of dissolved inorganic carbon [mg C dm^{-3}]; Chlor, conc. of chlorophyll *a* [mg m^{-3}]; DOC, conc. of dissolved organic carbon [mg C dm^{-3}]; PO_4, conc. of phosphates [mmol m^{-3}]; NO_3, conc. of nitrates [mmol m^{-3}]; NH_4, conc. of ammonium [mmol m^{-3}]; TBN, total bacterial number [10^5 cells cm^{-3}]; BBM, bacterial biomass [mg C m^{-3}]; ln, natural log transformed; *e*, transformed by an exponential function: *e* to the power *x*. *N*, number of measurements; R^2 R^{-2}_{adj}, determination coefficient/adjusted determination coefficient; *p*, level of significance; ns, not significant.

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

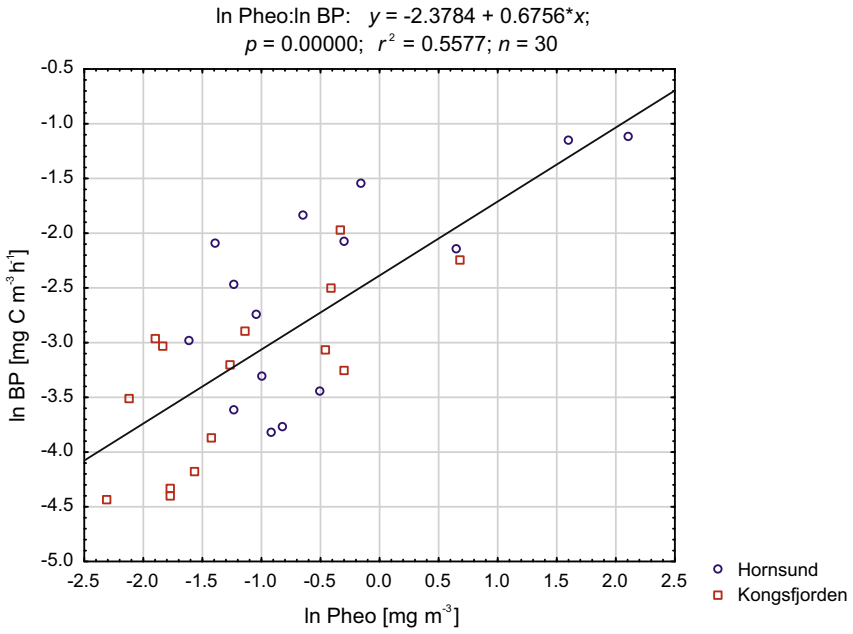

Figure 4 Relationship between bacterial production (BP) and concentrations of pheophytin in both fiords (different colours and shapes show values in each fiord).

Bacterial production showed no statistically significant dependence on bacterial abundance in each of the fjords separately. Considering all the data together, however, TBN accounted for 30% of BP variation. Higher bacterial production in Hornsund is followed by higher bacterial abundance in the fjord, and analogically: lower production corresponds to lower abundance in Kongsfjorden (Fig. 7). Bacterial biomass partially accounted for bacterial production variability in Kongsfjorden (39%) and in all the data (37%) (Fig. 8).

The results of multiple regression analysis for BP values from both fjords suggested that temperature, salinity, dissolved organic carbon, chlorophyll *a* concentrations, and total bacterial number combined account for 92% of bacterial production variability in both fjords (Table 4). Three regression factors: TBN, temperature, and pheophytin accounted for 69% of BP variability, while variables independent from bacterial number, namely temperature, pheophytin, and DOC explained a comparable value of 68% of results.

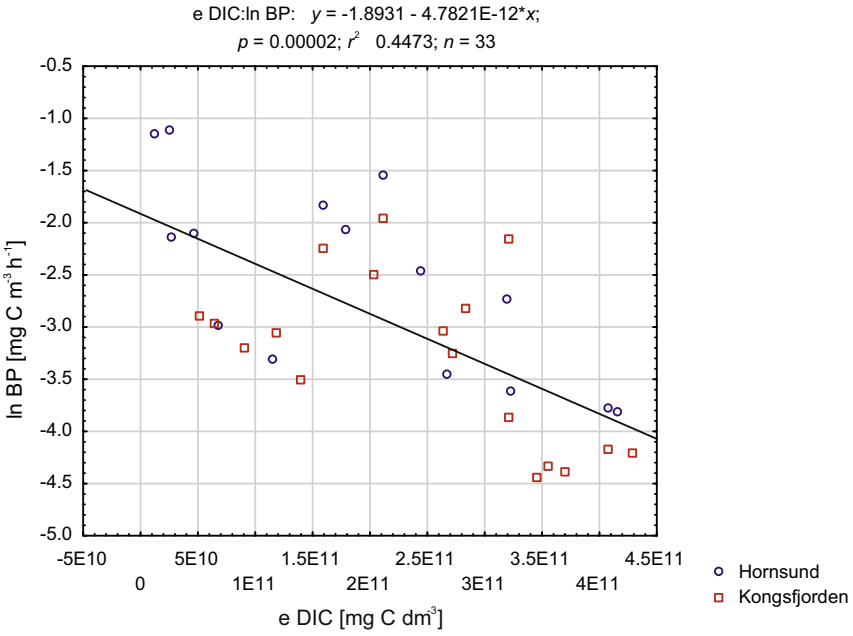

Figure 5 Relationship between bacterial production (BP) and concentrations of dissolved inorganic carbon (DIC) in both fiords (different colours and shapes show values in each fiord).

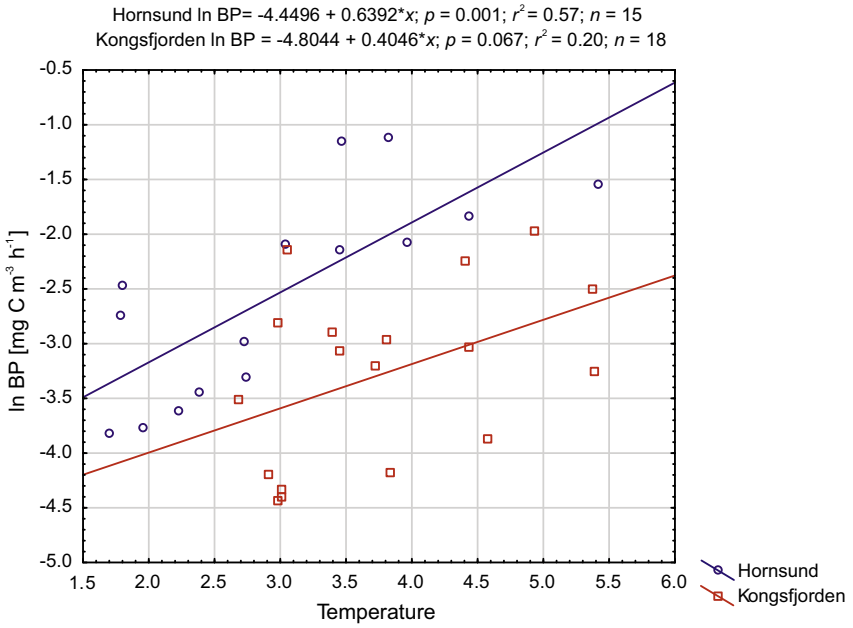

Figure 6 Dependence between bacterial production (BP) and water temperature in Hornsund and Kongsfjorden.

4. Discussion

It should be mentioned that the regression analyses shown in this study are based on a limited amount of data. Our results present temporary conditions, "a snapshot", and do not necessarily depict the general or multi-annual dependencies in the study environment. In the context of the comprehensive and simultaneous analysis of multiple biological and physicochemical parameters (GAME project), an attempt was made to estimate the relationship between bacterial production and environmental factors. In both fjords described in this study, sampling was carried out on three reference stations best characterising the areas of interest, and permitting mutual comparison (Węsławski et al., 2017).

The Kongsfjorden is strongly influenced by warm and saline waters of the West Spitsbergen Current (WSC) (Hop et al., 2002; Piquet et al., 2010, 2016; Svendsen et al., 2002; Wiencke and Hop, 2016). It shows hydrographic characteristics specific for both Arctic and broad fjords, related to water temperature, most frequent wind directions, freshwater inflow, and Coriolis effect, affecting the dynamics in the fjord (Svendsen et al., 2002). Water entering the

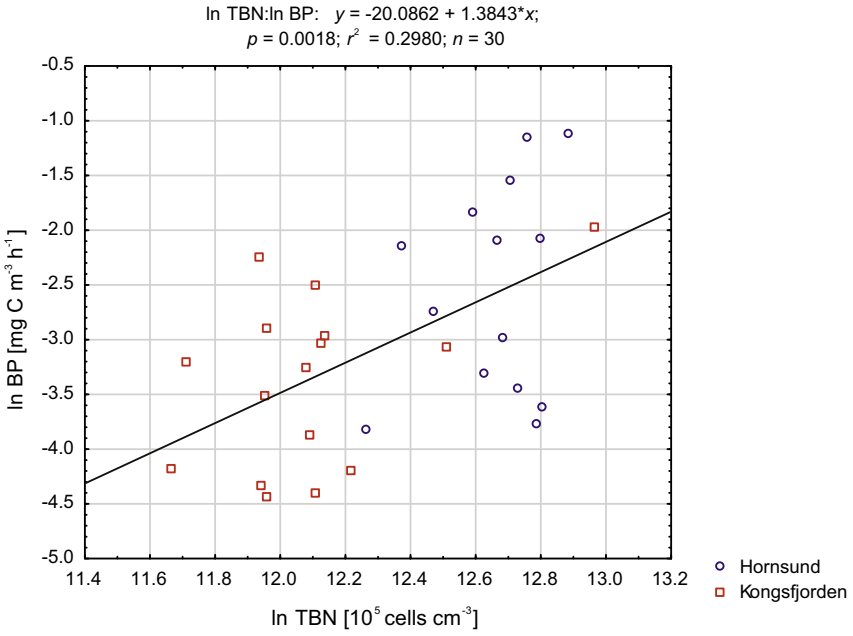

Figure 7 Relationship between bacterial production (BP) and total bacterial numbers (TBN) in water in both fiords (different colours and shapes show values in each fiord).

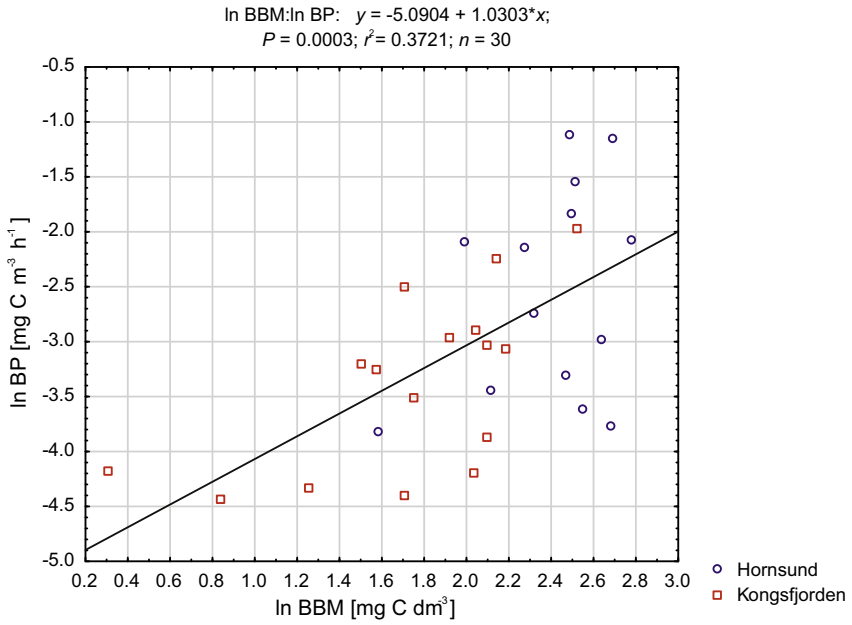

Figure 8 Relationship between bacterial production (BP) and bacterial biomass (BBM) in water in both fiords (different colours and shapes show values in each fiord).

Hornsund fjord will tend to inflow along the southern coast, and outflow along the northern coast of the basin (Cottier et al., 2007). Water of Atlantic origin (modified by mixing with Arctic Water) is usually observed as a bottom inflow. All of the water formations found in the fjord depend on Atlantic, Arctic, and glacial water mixing, and show seasonal variability (Cottier et al., 2005; Drewnik et al., 2016; Svendsen et al., 2002). Seasonal occurrence of local upwellings has been observed at glacier faces in both fjords (Węsławski et al., 1991). Upwelling processes were also clearly reported in Kongsfjorden in winter, during the occurrence of northern winds (Cottier et al., 2007). According to Divya and Krishnan (2017) and Promińska (unpublished data), summer 2013 was extraordinary in terms of hydrographic

Table 4 Multiple regression between ln BP [mg C m^{-3} h^{-1}] and physical and biological variables in the water column in both of the fjords.

	Term	<beta>	R^2 R^{-2}_{adj}	*p*	*N*
A					
ln BP	Intercept	−5.561	0.94/0.92	<0.00001	24
	Temp	0.746			
	Salinity	−0.346			
	ln DOC	1.268			
	ln Chlor	−0.267			
	ln TBN	0.852			
B					
ln BP	Intercept	−14.564	0.72/0.68	<0.00001	29
	ln TBN	0.885			
	Temp	0.298			
	ln Pheoph	0.453			
C					
ln BP	Intercept	−4.448	0.71/0.67	<0.00001	30
	Temp	0.352			
	ln Pheoph	0.378			
	ln DOC	1.362			

A, the best equation to all of the factors; *B*, the second best equation; *C*, the third best equation; Temp., temperature; DOC, conc. of dissolved organic carbon [mg C dm^{-3}]; Chlor, conc. of chlorophyll *a* [mg m^{-3}]; Pheoph, concentration of pheophytin [mg m^{-3}]; TBN, total bacterial number [10^5 cells cm^{-3}]; ln, natural log transformed; <beta> standardised coefficient of regression; R^2 R^{-2}_{adj}, determination coefficient/adjusted determination coefficient; *p*, level of significance; *N*, number of measurements.

conditions in West Spitsbergen fjords. Driven by climate change, high inter-annual variabilities in water masses in Kongsfjorden suggest that in the era of ongoing global warming, Hornsund might also soon become more influenced by the Atlantic Waters, and reveal hydrographic patterns similar to those of Kongsjforden.

Bacterial production values presented in this study do not deviate from the values representative of Svalbard, presented in other studies (Boras et al., 2010; Iversen and Seuthe, 2011; Lara et al., 2013; Piquet et al., 2016; Wängberg et al., 2008). However, statistically significant differences were observed between the two fjords. Both BP values (presented in this article) as well as bacterioplankton abundance and biomass values (Kalinowska et al., 2015) were higher in Hornsund than in Kongsfjorden. Higher values of microbiological parameters in the colder fjord raise a question about the reason of this phenomenon, especially that statistical analysis also shows a faster increase of bacterial production at lower temperature.

The answer might be the adaptation ability of typical arctic bacterioplankton to lower temperatures, and/or higher availability of organic matter (OM) supplied from the land (especially from bird colonies, numerously localised in Hornsund), which is more widely discussed by Kalinowska et al. (2015). Although low salinity differences do not influence bacterial physiology, they can be an indicator of freshwater inflow of glacial or land origin. In our study, bacterial production was inversely proportional to salinity. Therefore, we speculate that bacteria might have developed owing to the organic matter coming from such runoff, especially that Zaborska et al. (2016) reported a significantly greater share of OM of terrestrial origin in the waters of Hornsund (50–70% C_{org}) than in those of Kongsfjorden (20–40% C_{org}). Dissolved organic carbon (DOC) values, measured in the same samples as microbiological parameters, were also significantly higher in Hornsund than Kongsfjorden (Zaborska et al., 2016).

According to De Corte et al. (2011), the high particle load associated with the melting of ice from the surrounding glaciers, and high radiation conditions during the summer might play a key role in the structuring of the microbial food web in the coastal Arctic regions. Jankowska et al. (2005) suggests that higher organic matter concentrations in the inshore areas corresponded with higher bacterial biomass and abundance. Piquet et al. (2010) also suggested that freshwater originating from melting glaciers might introduce non-marine species, and simultaneously displace typical marine microorganisms to deeper water layers, where they receive less light. That, in turn, could limit primary production, similarly as high sediment input reducing the transparency of the water column. Urbański et al. (2017) points out extremely high suspended particulate matter concentrations at the glacier front, correlating with the feeding birds aggregation. This may indicate both high ecosystem richness and biodiversity in that spot, as well as possible introduction of large amounts of bird faeces to the waters in front of glaciers which may constitute a highly important food source for microorganisms. All of the above suggests that the activity of glaciers may significantly influence marine microbial communities. The exact scale of the phenomenon and detailed processes, however, are still unknown.

According to Maranger et al. (2015), next to temperature, bacterioplankton abundance and chlorophyll *a* concentration are also parameters affecting bacterial production in the Arctic. Among 720 samples collected throughout the Arctic, these parameters accounted for the variability of bacterial production in 57%. Phytoplankton growth is directly related to light availability, i.e. the depth of the euphotic zone where photosynthesis is possible. Bacterioplankton, in turn, is related to phytoplankton abundance, and the possibility to use its secretions as a food source.

Because phytoplankton utilises dissolved inorganic carbon, the correlation between primary production and DIC is expected to be inversely proportional. On the other hand, an increase in primary production results in increased bacterial production. Because the inverse proportion between BP and DIC reported in this study was considered as mediated by phytoplankton and therefore as an indirect relationship, DIC was not taken into account in the multiple regressions.

The range of the euphotic zone (1% PAR) is different in both fjords. It averages 16.21 m in Kongsfjorden, and 9.56 m in Hornsund (Smoła et al., 2017). Literature data show that primary production is higher by an order of magnitude in Kongsfjorden than in Hornsund. This is directly related to the turbulence and depth of the euphotic zone (Piwosz et al., 2009). While the species composition for planktonic protists differs between fjords, a higher number of taxa and biomass were recorded in Hornsund (Wiktor et al., 2017).

Bertilsson et al. (2004) suggests that solar radiation exerted a minor influence on the bioavailability of total DOM of the Southern Ocean. In this study, the analysis of bacterial production at all sampled depths from both fjords (N = 30) showed that the content of chlorophyll *a*, combined in the equation with temperature and total bacterial number (TBN), was not statistically significant. Instead of chlorophyll, pheophytin concentration was added to the regression with temperature and TBN. Pheophytin is a chlorophyll decomposition product derived from senescent algal cells, or released from phytoplankton cells due to the herbivorous activity of zooplankton (Welschmeyer et al., 1984). Together, temperature, TBN and pheophytin concentration accounted for 68% of the variability of BP. Also, the maximum BP values detected in the surface layer in Hornsund (stations HG1 and HG2) were followed by the maximum values of pheophytin concentrations. In the case of this study, the dependence of BP on phytoplankton could have only occurred in samples from the two most shallow layers. The deeper ones were already below the range of euphotic layer.

Although bacterial production is much higher in the euphotic zone, the microbial processes in the aphotic zone play a greater role in the entire ecosystem. The primary role in the intensity of microbial processes in the aphotic zone is played by the accessibility of organic matter (OM) derived from the decomposition of faecal pellets of zooplankton feeding on phytoplankton, and decomposition of phytoplankton itself. In the euphotic zone, however, organic matter comes from secretions of living phytoplankton.

Better understanding of the impact of the environmental conditions on marine microbial communities in polar ecosystems requires long-term monitoring. The interdisciplinary approach, combining data regarding glacial meltwater inflow, hydrological parameters, and co-functioning of microorganisms, phytoplankton, and zooplankton in the Arctic fjords, should be applied.

5. Conclusions

The study results show higher bacterial production in the waters of the colder Hornsund Fjord, compared to the waters of Kongsfjorden, considered as a warmer fjord. A similar trend has been reported in the case of bacterioplankton abundance and biomass. Apart from temperature, the waters of both fjords differ in the amount and availability of dissolved organic matter (DOM). It may originate from primary production or surface runoff from land during the polar summer. High amounts of biogenic compounds can originate from the tundra, melting glaciers and numerous bird colonies, and are flushed out to the waters of the Hornsund Fjord.

The results show that in both fjords, the most important factors influencing marine bacterioplankton production include temperature, pheophytin (the product of phytoplankton degradation) concentration, and the content of dissolved organic carbon. DOM can be either originating from faecal pellets of herbivorous zooplankton, or from surface runoff.

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