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ORIGINAL PAPER

Bacterial community composition in an Arctic phytoplankton mesocosm bloom: the impact of silicate and glucose

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Abstract In order to study interactions between microorganisms at different nutrient conditions in an arctic environment, a mesocosm experiment was performed in Kongsfjorden, Svalbard (79°N). A phytoplankton bloom was initiated by daily additions of mineral nutrients (ammonium and phosphate) to all mesocosm units. The addition of silicate and glucose, forming a factorial design (+Si/+C, +Si/−C, −Si/+C, −Si/−C), was intended to produce different types of growth rate limitation for the bacterial community. We here focus on the response in bacterial community composition to different nutrient situations. Phytoplankton, bacteria and viruses were enumerated by flow cytometry, while denaturing gradient gel electrophoresis (DGGE) was used to track changes in the bacterial community composition. Our results showed that both glucose and silicate addition affected the bacterial community composition, with the largest effect from glucose. The initial increase in bacterial abundance was most pronounced in the glucose units. After silicate addition, highest bacterial abundance was observed in the silicate treatments where mineral nutrient competition by diatoms was expected to be highest. The major effect of glucose was expressed by the significant separation of the +C and the −C samples at the end of the experiment, while silicate addition resulted in a more stable bacterial community structure. In the unit, given both silicate and glucose, the diatoms were totally outcompeted by the bacterial community. The competitive success of the heterotrophic bacteria in C-replete situations allows the conclusion that the bacteria were not more negatively affected by low temperatures than phytoplankton.

Keywords Bacterial community structure · Nutrient competition · DGGE · Phytoplankton · Mesocosm experiment · Arctic Sea

Introduction

Although the role of the bacteria in the microbial food web has been intensely studied in the world oceans over the last three decades, there are relatively few studies from Arctic waters. An enhanced understanding of the microbial system and the carbon flux in polar regions is very important as climate change may have the fastest impact in the Arctic (Manabe and Stouffer 1994). Additionally, it has been suggested that the structure and function of the microbial food web in polar regions may differ from that in warmer waters because some organisms could be more affected by lower temperatures than others (Pomeroy and Deibel 1986; Rose and Caron 2007).

The microbial community structure has been described as "everything is everywhere, but the environment selects" by Baas-Becking 1934. This idea of a universal distribution of microorganisms has recently been debated, but the hypothesis of a selective environment that is responsible for spatial variation in microbial community structure could be confirmed (Martiny et al. 2006). Selective environmental factors that control the bacterial community composition are amongst others nutrient availability, competition for nutrients, predation and viruses.

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The availability of organic carbon (C) in addition to mineral nutrients such as nitrate (N) and phosphate (P) is necessary for the growth of heterotrophic bacteria. Their ability to utilise dissolved organic carbon (DOC) and transform it into particulate carbon (POC) is an important process by which "lost" carbon, which is released by all the organisms as DOC, returns back into the food web. DOC sources released by phytoplankton (Mague et al. 1980; Sharp 1977) may subsequently be utilised by heterotrophic bacteria. This process is of increased significance as ocean warming accelerates the respiratory consumption of dissolved organic matter compared to autotrophic production (Wohlers et al. 2009). It is known that different bacteria prefer different carbon sources (Allers et al. 2007), and that they therefore may be associated with different algae (Sapp et al. 2007). Thus, a change in the phytoplankton community structure may have an impact on the bacterial community structure (Pinhassi et al. 2004).

Competition between phytoplankton and bacteria for N and P sources has already been investigated in several studies (Bratbak and Thingstad 1985; Currie and Kalff 1984b; Currie and Kalff 1984c; Thingstad et al. 1993). Bacteria have a higher surface-volume ratio than eukaryotic phytoplankton and are therefore expected to be more efficient competitors for inorganic nutrients, leading to a competitive advantage where nutrients are limiting (Currie and Kalff 1984a, b, c). On the other hand, bacteria may be more affected by low temperatures than phytoplankton (Pomeroy and Deibel 1986) which could benefit the phytoplankton in the mineral nutrient competition in the Arctic Sea. Domination in terms of population size is, however, the net result of growth and removal, and high grazing pressure on the best competitor may well lead to dominance of the less efficient competitor if this is less grazed (Pengerud et al. 1987).

In a mesocosm study, performed at Søminestationen in Denmark (Havskum et al. 2003), it was shown that the heterotrophic bacteria were able to some extent to outcompete the phytoplankton in mesocosms enriched with mineral nutrients and a supplemental carbon source (glucose). However, when the diatoms were supported by additional silicate, the bacterial consumption of glucose was inhibited, interpreted as diatom success in the phytoplankton–bacteria competition for mineral nutrients. The present study represents a similar experiment, but performed in cold polar water (Ny Ålesund, Svalbard, 79°N). From this experiment, we have previously reported that, in contrast to Havskum et al. (2003), glucose addition successfully promoted the bacteria also when silicate was added in excess, leading to higher mineral nutrient consumption followed by P- and N- limitation. As a consequence, the phytoplankton community was outcompeted by the bacteria in the +Si/+C unit (Thingstad et al. 2008).

In the present study, we have investigated changes in bacterial abundance and composition in the Arctic mesocosms, forming the two-factor design −Si/−C, −Si/+C, +Si/−C and +Si/+C ("C" denoting glucose addition, all four units receiving ammonium and phosphate). One unit without nutrient addition was acting as a control. We have previously argued that the units without glucose entered a state with C-limited bacterial growth, while those with excess glucose addition had mineral nutrient–limited bacteria (Thingstad et al. 2008). The four units are thus argued to give four different situations for bacterial growth:

1. −Si/−C: Carbon-limited bacterial growth—complex C-sources as produced from a flagellate-dominated phytoplankton community.
2. −Si/+C: Mineral nutrient–limited bacterial growth—glucose-dominated organic substrate pool.
3. +Si/−C: Carbon-limited bacterial growth—complex C-source as produced from a *Thalassiosira* sp. dominated diatom community.
4. +Si/+C: Mineral nutrient–limited bacterial growth—glucose-dominated organic substrate pool.

We hypothesise that different types of nutrient limitation will create different bacterial community compositions. If so, one might expect 2 and 4 to be relatively similar due to their mineral nutrient–limited bacterial growth, but different from 1 and 3 with their C-limitation. Situations 1 and 3 may also differ from each other due to differences in the spectrum of C-sources produced from different algal communities—either directly or indirectly via different predatory processes.

Materials and methods

Mesocosm setup

A mesocosm experiment with ten different units (each 700 l initial volume of seawater) was performed in Kongsfjorden (Ny Ålesund, Svalbard, 79°N) in August 2007. For a closer description of the mesocosm setup, see Thingstad et al. (2008). For our studies, samples were collected only from five of the ten units without replication: two units with 0 and two units with 3 times the Redfield ratio glucose (45.5 μM C) in terms of carbon relative to the nitrogen and phosphorus additions and the control unit. The treatments got a daily dose of NH_4^+ (2.3 μM) and PO_4^{3-} (143 nM) in Redfield ratio and were treated identically until day 4 when the naturally available silicate became depleted. Thereafter, two units were kept Si-replete, while the other two units did not receive Si so that a situation without added silicate (−Si/−C, −Si/+C) could be compared with a situation with excess silicate (+Si/−C,

+Si/+C). One unit without any nutrient additions acted as a control. Samples for flow cytometric analysis and DNA extraction were collected once a day for a period of 13 days.

Total number of algae, bacteria and viruses

Phytoplankton, bacteria and virus numbers were determined using a FACSCalibur flow cytometer (Becton–Dickinson) equipped with an air-cooled laser providing 15 mW at 488 nm and with standard filter set-up. Phytoplankton counts were obtained by fresh samples at a high flow rate (approximately 97 µl min^{-1}). The trigger was set on red fluorescence, and the samples were run for 5 min. Discrimination of the phytoplankton populations was based on dot plots of side scatter signal and pigment autofluorescence (chlorophyll, 610 nm and phycoerythrin, 575 nm). Phytoplankton cell numbers were divided into three groups, picoeukaryotes (~1–3 µm), small nanoeukaryotes (~2–5 µm) and large nanoeukaryotes (~5–9 µm). The large nanoeukaryote population was totally dominated by a small (5 µm) diatom (*Thalassiosira* sp.) as it was shown by comparing microscopic and flowcam results with the data obtained from flow cytometry analyses (Egge, University of Bergen, personal communication).

For determination of bacteria and virus numbers, the cells were fixed with glutaraldehyde (final concentration 0.5%). For bacterial counts, the samples were stored at 4°C until analysis the same day, whereas viral samples were fixed for 30 min at 4°C, snap frozen and stored in liquid nitrogen until further analysis. Appropriate dilutions of fixed samples were prepared (10–1,000-fold) in 0.2-µm-filtered TE buffer and stained with SYBR Green I (Invitrogen) for 10 min in the dark, with bacteria at room temperature and viruses at 80°C (Marie et al. 1999). The samples were analysed for 1 min at a flow rate of ~50 µl min^{-1} and events rates between 50 and 1,000 s^{-1} and the discriminator set on green fluorescence. Discrimination of bacteria and virus populations was based on groups observed in scatter plots of SSC signal versus green DNA dye fluorescence (SYBR Green I). The cell numbers of algae, bacteria and viruses were calculated from the instrument flow rate based on volumetric measurements. The data were analysed by using EcoFlow (version 1.0.5).

DNA isolation

Depending on the biomass in the different units, a water volume of 50–140 ml were filtered through a sterile 0.2 µm polycarbonate filter (25 mm) and stored at −80°C until further processing. The DNA isolation was performed using a modified protocol of Bailey et al. (1995). The filters were resuspended in 250 µl lysozyme solution (1 mg ml^{-1} TE buffer (10:1, pH 7.4)). Thereafter, 250 µl of preheated (55°C) lysis buffer (20 µg proteinase K ml^{-1} 0.5% SDS) was added to the solution. After an incubation of 30 min at 55°C, 80 µl 5 M NaCl and 100 µl preheated (55°C) CTAB (10% (w/v) hexadecyltrimethylammonium bromide in 0.7% NaCl) were added. The solution was incubated further for 10 min at 65°C followed by the addition of 500 µl chloroform:isoamylalcohol (24:1). The solution was centrifuged (16,100×*g*, 5 min) to separate the DNA from the rest of the cell material. The top phase was transferred to a fresh tube, DNA was precipitated with isopropanol and later resuspended in TE buffer (pH 7.4).

PCR/DGGE

Partial bacterial 16S rDNA was amplified using the primers EUB-f (Giovannoni et al. 1990) with GC-clamp (*E. coli* position 8–27) (Øvreås et al. 1997) and 518r (*E. coli* position 518–534) (Lane et al. 1985). PCR mixes with a volume of 50 µl contained 5 µl 10× buffer (TaKaRa Bio Inc.), 4 µl dNTP mixture (2.5 mM of each dNTP, TaKaRa Bio Inc.), 2 µl of 2% BSA (Promega), 2.5 µl of each primer (10 µM), 0.25 µl of Taq Polymerase (5 U $µl^{-1}$, TaKaRa Bio Inc.) and 2 µl of template DNA (approximately 10 ng $µl^{-1}$). The PCR program started with an initial denaturation step for 9 min at 94°C. Afterwards, 35 cycles with 30 s 94°C, 1.5 min 54°C and 30 s 72°C followed. Before cooling down to 4°C, an elongation time for 7 min at 72°C was enclosed to the program. The PCR products were verified by gel electrophoresis on 1.5% agarose gels stained with ethidium bromide. DGGE was performed by using the DCode system (BioRad). Equal amounts of PCR products (15 µl) were loaded onto 8% acrylamide gels with a denaturing gradient of 30–55% (where 100% denaturing is defined as 7 M urea and 40% (v/v) formamide (Muyzer et al. 1993)) for optimal separation of the PCR products. An environmental sample with a suitable amount of bands spread from the top to the bottom of the DGGE gels was used as an internal standard on both sides of each DGGE gel. DGGE gels were run for 19 h at 60 V and 60°C in 0.5× TAE buffer and stained for 30 min with SYBR Gold (Invitrogen) diluted 10,000-fold in 1× TAE buffer. Gels were visualised and digitised using the Fujifilm Imaging System (LAS-1000).

Statistical analysis of DGGE images

Digitised DGGE images were analysed using the program Gel 2 K (Svein Norland, Dept. of Biology, University of Bergen), which determines the presence or absence of bands (band patterns) based on grey level units and pixel intensity. The band patterns were transformed into binary data and compared using the program Primer 6 (Primer-E, Plymouth, UK). The DGGE patterns were tested for

similarity by using the Jaccard-Index that calculates the resemblance matrix. This matrix was used for the creation of a non-metric multi-dimensional scaling (MDS) plots. The significance of the results was analysed using the analysis of similarity (ANOSIM) test in the Primer 6 program and a Wilcoxon rank sum test in the program R (function: wilcox.exact).

Results

Total number of algae, bacteria and viruses

Both, the picoeukaryotes (Fig. 1a) and the small nanoeukaryotes (Fig. 1b) were dominated by flagellates. The abundance of picoeukaryotes was similar in the different units, and the cell numbers increased from day 0 ($\sim 2.5 \times 10^4$ cells ml^{-1}) until day 4–5. Highest cell numbers were recorded in the +C units (peak at $\sim 2 \times 10^5$ cells ml^{-1}). After day 5, the picoeukaryote abundance decreased until the end of the experiment. The small nanoeukaryote increased in abundance from day 0 ($\sim 1 \times 10^2$–1×10^3 cells ml^{-1}) until day 6 in the different units. The cell numbers of the four units showed high similarity with a peak at ~ 9–10×10^3 cells ml^{-1}. Only the −Si/+C unit was characterised by lower values with a peak at $\sim 7 \times 10^3$ cells ml^{-1}. After day 6, the abundance of the small nanoeukaryotes decreased in all units. Thereby, the abundances in the −C treatments were higher than in the +C treatments and increased again at the end of the experiment. The diatom abundance was equal in all units until day 5, with values between $\sim 7 \times 10^2$ and 9×10^2 cells ml^{-1} on day 0 and $\sim 2 \times 10^3$ to 3×10^3 cells ml^{-1} on day 5 (Fig. 1c). From day 6 on, a difference between the units emerged. The diatom concentration increased in the units without additional glucose (+Si/−C and −Si/−C), while the numbers decreased in the units that received glucose (+Si/+C and −Si/+C). The increase was most pronounced in the +Si/−C unit with a peak at day 11 ($\sim 3 \times 10^4$ cells ml^{-1}). During the described diatom peak in this unit (+Si/−C), the chlorophyll a fraction >5 µm represented 97% of total chlorophyll a. Microscopic examination of this fraction showed a total dominance of diatoms, particularly the small *Thalassiosira* sp. (personal communication of J. Egge). The diatom abundance in the corresponding unit without silicate (−Si/−C) decreased from day 7 (peak at $\sim 6 \times 10^3$ cells ml^{-1}). Diatom concentrations in the units that received glucose were similar regardless of silicate treatment. Here, the highest concentrations were recorded on day 6 with $\sim 3 \times 10^3$ cells ml^{-1}.

The initial bacterial abundance was approximately 2.2×10^6 cells ml^{-1} (Fig. 1d). In all units, bacterial abundance followed an oscillatory pattern, possibly reflecting a predator/prey-dominated control of bacterial abundance. After day 2, there was, however, also a stimulating effect of glucose on bacterial numbers (−Si/+C > −Si/−C and +Si/+C > +Si/−C) and after day 8, also stimulating effect of silicate (+Si/−C > −Si/−C and +Si/+C > −Si/+C).

The amount of viruses (Fig. 1e) increased from day 0 on with an initial concentration of approximately 2–3 $\times 10^7$ virus ml^{-1} in the different units. The +C units showed higher virus abundances than the −C units, with a pronounced increase in the +Si/+C unit from day 9 on (top at $\sim 2 \times 10^8$ virus ml^{-1} on day 12).

The algal, bacterial and viral concentrations were markedly lower in the control unit than in the nutrient manipulated units, although the dynamics of picoeukaryotes, small nanoeukaryotes and bacteria followed a similar pattern in all units including the control. The dynamics of diatom and virus populations in the control unit differed, however, from the corresponding dynamics in the nutrient-manipulated ones by little or no variation in abundance during the experiment.

DGGE

The DGGE analysis showed that the bacterial community composition changed over time and responded to the different treatments. Between 6 and 24 distinguishable bands were detected in the DGGE profiles (Online Resource 1), and a total of 31 different band positions were observed during the experiment. Although the bacterial community structures in the four treatments showed differences already in the beginning of the experiment (see Fig. 2), each treatment on its own was characterised by a relatively stable bacterial community structure until day 4. After day 4, the bacterial community structure changed and developed in different directions. The most characteristic change was caused by the addition of glucose. The units that received additional glucose (+Si/+C, −Si/+C) showed similar changes in the bacterial community structure after day 5. These changes were different from the changes seen in the units that did not receive glucose (+Si/−C, −Si/−C) (Fig. 2). The ANOSIM test showed a significant separation of the +C samples and the −C samples from day 6 on (Fig. 2; Global $R = 0.794$, $P = 0.01$). Both treatments without silicate addition were characterised by more pronounced changes compared to the silicate treatments. Significantly shorter distances between sample points of the start (day 0–4) and the end (day 6–12) of the experiment in the +Si treatments express a less pronounced shift in bacterial community structure under the presence of silicate (see arrows in Fig. 2; Table 1). Further, also the distances within the two groups (+C/−C) at the end (day 6–12) of the experiment were significantly shorter in the +Si treatments, indicating a stabilising effect of silicate on the bacterial community structure (Fig. 2; Table 1).

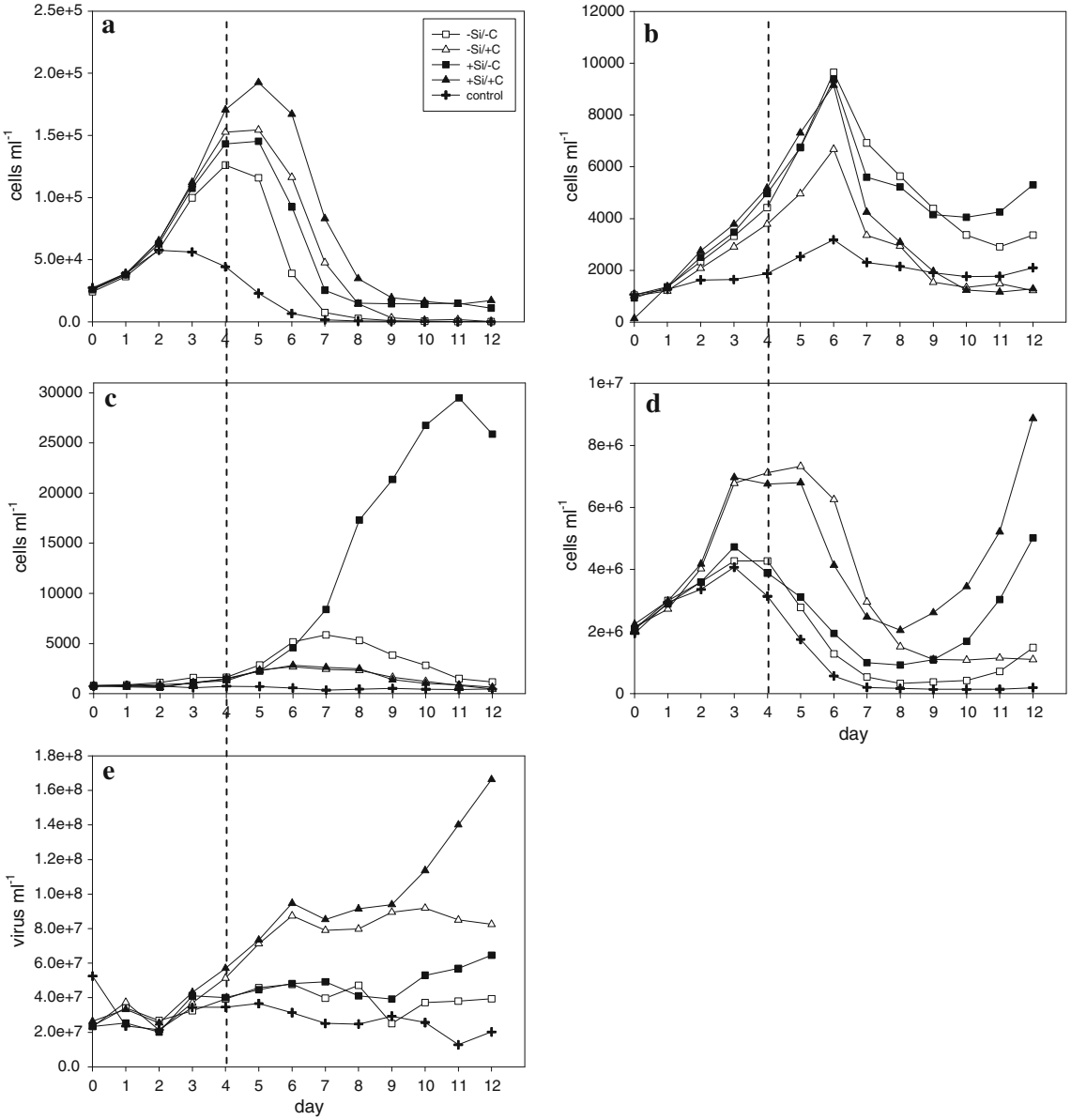

Fig. 1 Abundance of picoeukaryotes (**a**), small nanoeukaryotes (**b**), diatoms (**c**) and bacteria (**d**) in cells ml^{-1} and the abundance of virus (**e**) in virus ml^{-1} determined by flow cytometry. The first silicate dose was added on day 4 (*dashed line*)

Changes in the bacterial community structure were also seen in the control unit during the experiment, but the observed development was different from the development of the samples that were manipulated with nutrient additions (Fig. 2). The sample points of the control show higher similarity to the −C samples than to the +C samples.

Discussion

Our results show that the different nutrient situations in the different treatments resulted in a different responding bacterial community. Major changes in the bacterial community structure were caused by glucose addition. As predicted from our hypothesis, we detected major differences between the +C units (mineral nutrient limited) and the −C units (carbon limited) shown by grouping of the +C samples as well as the −C samples after day 5.

Both glucose treatments (+Si/+C, −Si/+C) suggest P-limitation for bacteria growth, indicated by low concentrations of available phosphate and very fast turnover-times for phosphate in these units (Thingstad et al. 2008). Not only phosphate but also inorganic nitrogen was limiting in these treatments probably due to high consumption by the heterotrophic bacteria. Glucose seems to be an important factor for the nutrient competition between

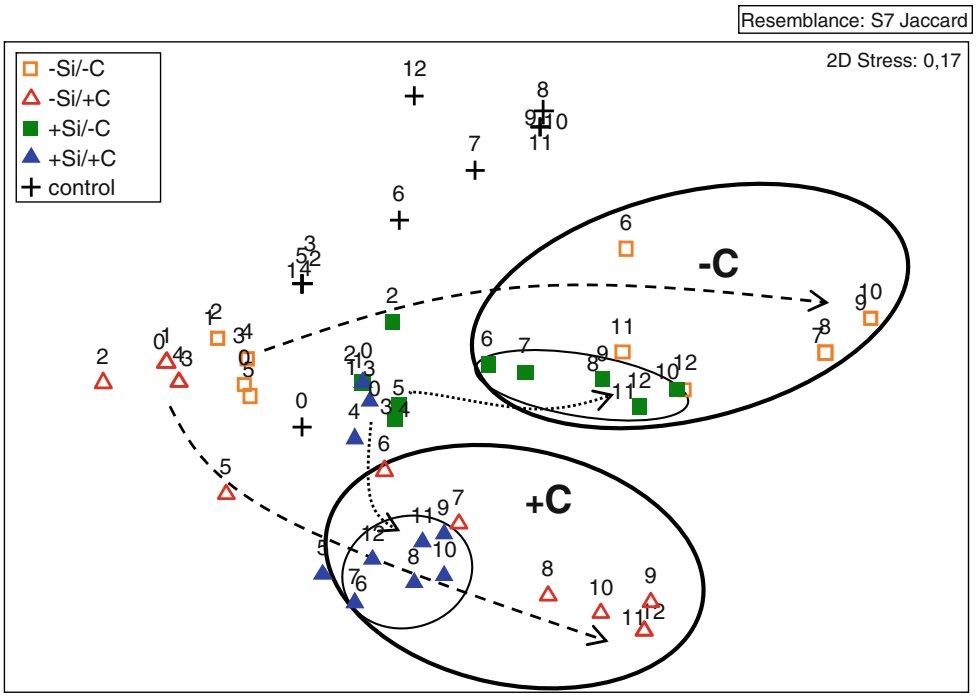

Fig. 2 Multidimensional scaling (MDS) plot; based on the band pattern of the DGGE gels that were transformed into binary data and compared using the program Primer 6 (Primer-E, Plymouth, UK); the similarity test for creating a resemblance matrix was performed by using the Jaccard-Index; sample points are labelled with the number of the sampling day; *big circles underline* the grouping of the +C samples and the −C samples after day 5; *small circles underline* the similarity of the silicate samples within the −C/+C treatments after day 5; the *arrows* describe minor (*small dotted lines*) and major (*big dotted lines*) changes within the bacterial community of the different treatments during the experiment

Table 1 Median distances between sample points in the MDS ordination (Fig. 2) and Wilcoxon test statistics on the effect of silicate

	Glucose	Silicate		W	*n*		*P* value
		−	+		−Si	+Si	
Median distance between start & end groups	−	2.60	1.08	1,225	35	35	<0.001
	+	2.27	0.79	1,225	35	35	<0.001
Median distance within end groups	−	0.69	0.33	322	21	21	<0.01
	+	0.47	0.25	319.5	21	21	<0.05

Distances between the start (day 0–4) and the end (day 6–12) groups as well as within the end groups were calculated for each treatment

bacteria and phytoplankton and also for the composition of the bacterial community. The bacteria managed to outcompete the diatoms for mineral nutrients only when glucose was available (+Si/+C) (Thingstad et al. 2008). In this unit, the numbers of diatoms remained low although silicate was available, while the bacteria abundance increased over time. In the corresponding unit without glucose (+Si/−C), a different bacteria community could be detected that existed together with a high number of diatoms. Increasing bacterial abundance as well as increasing bacterial production and fast phosphate turnover-times at the end of the experiment in this treatment (+Si/−C) (Thingstad et al. 2008) showed that the bacteria were not disadvantaged by the lack of glucose. Other carbon sources must have been available and utilised by the bacterial community in this treatment.

Dissolved organic carbon (DOC) released by the different developing phytoplankton communities may be utilised by the bacterial community and used as carbon source (Bell and Mitchell 1972; Bell et al. 1974). Also the algal bloom break down, as seen for the picoeukaryotes and the small nanoeukaryotes after day 6, might provide the bacterial community with additional DOC that may have had an impact on both bacterial abundance and on the composition of the bacterial community (Bratbak et al. 1998; Castberg et al. 2001; Fukami et al. 1985). Diatoms are supposed to become dominant when mineral nutrients and silicate are available (Egge and Jacobsen 1997) and different studies have shown a tight coupling between diatoms and bacteria (Grossart 1999; Riemann et al. 2000). Stimulated bacterial growth in both silicate units relative to the corresponding units without silicate may suggest a higher production of DOC in the +Si units that could have been utilised by the bacterial community. A more stable bacterial community structure in the +Si treatments, together with an increase in the bacteria abundance at the end of the experiment, leads to the speculation that the silicate treatments promoted the bacterial community compared to situations without silicate. The fact that one diatom species dominated (a small *Thalassiosira* sp. (Egge,

University of Bergen, personal communication)) may have led to more stable environmental conditions for the bacteria, as DOC production seems to be species specific (Chen and Wangersky 1996) and a more homogenous source of algal carbon therefore could be the consequence in these units. However, our results showed that the stabilising and stimulating effect of silicate also was observed in the +Si/+C unit where the diatoms were outcompeted by the bacteria. Eventually, other organisms that require silicate, like silicoflagellates, may have affected the bacterial community structure in this treatment.

Bacterial community structures are also controlled by viral lysis and predation. These two processes provide the bacteria with nutrients (Fuhrman 1999; Nagata and Kirchman 1991) that can in turn, by the process of remineralisation, be recycled to higher levels of the food web (Ducklow 1983). Additional nutrients due to viral lysis and grazing might be of particular relevance for the bacterial community composition in the glucose units as we expect the bacteria to be mineral nutrient limited in these units. In addition to the described bottom-up effect, both viral lysis and grazing can also affect the bacterial community composition as top–down factors. Viruses are known to be host species specific and, as such, have a large impact on the bacterial community structure (Fuhrman 1999; Thingstad 2000). In our study, the viral abundance increased in all the different units, accompanied with a major change in the viral community structure (Sandaa, University of Bergen, unpublished results). Thereby, top–down control by viruses seemed most pronounced in the +Si/+C unit, where both virus abundance and virus diversity were highest. The detection of viruses with larger genome sizes in the +Si treatments (Sandaa, University of Bergen, unpublished results) may have led to more available algal carbon sources for the heterotrophic bacteria, as viruses with large-sized genomes often is associated with viruses infecting phytoplankton species (Sandaa 2008). This may in turn explain the increasing bacterial abundance at the end of the experiment in both silicate treatments, and the more pronounced stability within the bacteria community observed in the +Si units after day 5.

Contrary to viruses, heterotrophic flagellates are not expected to graze species specific but size selective (Gonzalez et al. 1990; Simek and Chrzanowski 1992) and motility dependent (Matz and Jurgens 2003). Nevertheless, it has been shown that they may have specific preferences (Caron 1987) and that they do have an impact on the taxonomic composition of the bacterial community (Juergens et al. 1994; Simek et al. 1997). A grazing experiment that was performed parallel to our mesocosm experiment (see supplementary information of Thingstad et al. 2008) showed an increasing impact of microzooplankton grazing (including heterotrophic flagellates) on the bacterial community after nutrient addition. Hence, the heterotrophic flagellates may have played a role for the bacterial community structure in our experiment, whereas a more pronounced effect is expected by host species-specific viral community (Sandaa et al. 2009).

It has been suggested that bacteria are more adversely affected by low temperatures than phytoplankton (Pomeroy and Deibel 1986), meaning temperature may have an impact on the nutrient competition situation. On the other hand, Kirchman et al. (2005) suggested that microorganisms adapted to cold temperatures in the Arctic should not be more affected by temperature than in warmer regions. Furthermore, low temperature sensitivity of the heterotrophic bacteria was observed by Pomeroy and Wiebe (2001) when nutrients were available in excess, which was also the case in our mesocosms. However, this finding is not consistent with other studies (Kirchman et al. 2009) where the relationship between bacterial growth rates and temperature was not changing with DOC concentration. The water temperature (approximately 6°C) was much lower in our experiment than the water temperatures of a similar experiment by Havskum et al. (2003) performed in Denmark (approximately 17°C). It might be possible that the bacterial dependency on algal carbon sources was different in these two temperature regimes as discussed by Moran et al. (2010). The main difference was the presence of diatoms with larger cell size in the mesocosm experiment performed in warmer water. This would indicate a disadvantage in nutrient uptake because of a smaller surface-volume ratio compared to bacteria, but the diatoms were still able to dominate in the silicate units also when glucose was present. In our experiment, the diatom community was dominated by a small *Thalassiosira* sp. Even though a smaller cell size would indicate an advantage in nutrient-uptake, the diatoms were outcompeted by the bacteria in the presence of glucose in addition to silicate (+Si/+C) (Thingstad et al. 2008). These results suggest that, in terms of nutrient competition, bacteria were not more adversely affected by low temperatures than the phytoplankton community.

Our results show that the bacterial community changed as a consequence of the different treatments, of which glucose had the largest effect on the bacterial community structure. Even though the importance of glucose is emphasised by the fact that the bacteria were able to outcompete the diatoms only when glucose was added, our results demonstrate pronounced bacterial growth when silicate but not glucose was available. The changes in the structure of the phytoplankton community induced by the two different silicate treatments were probably accompanied by variation in algal DOC production (Myklestad 1995), which seems to be an important factor influencing bacterial community dynamics. Nevertheless, the increase in the bacteria abundance in the +Si units at the end of the

experiment and the more stable bacterial community structure in these treatments after silicate addition could not be explained by the presence of diatoms alone, as they were only present in one of the treatments. Further, top–down factors such as viral lysis and grazing could also have played an important role in the regulation of the bacterial community structure in these treatments.

The results strongly indicate the highly dynamic nature of the Arctic bacterial community and shows that nutrient-induced changes in phytoplankton community leads to significant changes in the bacterial community composition that again will influence the rates of bacterial-mediated organic matter cycling. As climate change may have the fastest impact in the Arctic (Manabe and Stouffer 1994), an enhanced understanding of the microbial system and the carbon flux in polar regions is very important. Thus, our results contribute to a better understanding of this nutrient—organic carbon interaction within the Arctic microbial community and emphasise the need to incorporate community composition into our conceptual thinking of the biogeochemical cycling within the marine microbial food web in polar regions.

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