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Primary production and the relevance of small autotrophic and heterotrophic cells in arctic marine ecosystems

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Abstract

The Arctic is one of the least studied regions in the world and large changes in marine ecosystem dynamic are expected here because of the increasing air and ocean temperature. The central Arctic Ocean has for a long time been considered as a very low productive ecosystem, but recent estimates of primary production gives relatively high values. The shelves surrounding the Arctic Ocean are highly productive areas, especially the Barents Sea region, and a large part of arctic primary production occurs in these seasonally ice-covered regions. The relevance of small cells in arctic ecosystems has received increased attention the last two decades, and it is now accepted that the microbial food web play an important role also in the Arctic.

To increase the knowledge on primary production and the relevance of small autotrophic and heterotrophic cells in the Arctic different field studies were conducted. Spring bloom dynamics (nutrients, phytoplankton, protozoans and *in situ* primary production) were investigated in Kongsfjorden (Svalbard) in April and May in 2002. During the multidisciplinary CABANERA-project three field campaigns in 2003-2005 to the marginal ice zone of the northern Barents Sea were conducted. Primary production was measured *in situ* for 24 hours at different stages of ice-edge blooms. Primary production and chlorophyll *a* measurements were fractionated in small (<10µm) and large cells (>10µm). During an expedition across the Arctic Ocean in August and September 2005 different biological parameters were measured (chlorophyll *a*, biogenic silica, particulate carbon and nitrogen, few zooplankton samples) together with the distribution of autotrophic and heterotrophic microbial biomass. Bacteria abundance was estimated using flow-cytometry and protists abundance was analyzed by epifluorescence microscopy after staining with DAPI. Protists were divided in different size categorize: < 2µm, 2-5µm, 5-10µm and 10-20µm. A seasonally study (January-September) of bacteria community structure and activity was conducted in a cold high latitude fjord (Balsfjord, northern Norway) in 2009 using fluorescence *in situ* hybridization (FISH) combined with microautoradiography (micro-FISH).

In Kongsfjorden we found that the onset of the spring bloom was linked to the hydrographical situation during the sea ice break up. The peak of the spring bloom was found to vary between different years in both timing and intensity but will most probably occur between the middle-end of April and the middle of May. Primary production in 2002 persisted for a long time due to mixing with nutrient rich water masses. The ice edge phytoplankton bloom in the

marginal ice zone of the northern Barents Sea was very heterogenic and no patterns in integrated primary production could be assigned to stages or latitudes. Subsurface (20-60m) primary production contributed with 24% to the total integrated primary production during ice edge blooms in the marginal ice zone, illustrating the importance of sampling in subsurface maxima. Small cells contributed with 46% to total primary production during ice edge blooms underlining the important role small cells can play as primary producers. Picoplankton (<2µm) abundance was high in the Arctic Ocean, and in the central part heterotrophic cells dominated (72%). Bacteria abundance was very low in the central part of the Arctic Ocean, but it is unknown whether this was caused by low growth rates or by high predation pressure. Bacteria were found to be highly active during summer in the Balsfjord underlining the important role they play in carbon turnover in the ocean. Bacteria belonging to *Roseobacter* were very active in assimilating DOM but they were not very abundant. This suggests that species specific predation may regulate the abundance of active bacteria.

The main conclusion from the work included in this synthesis is that small cells are an important component of arctic food webs. Small cells need to be considered as important primary producers, also during spring blooms and ice edge blooms. We also found that bacteria need to be studied on single cell level to understand the underlying reasons for the dynamics that are observed on community levels.

Contents

List of publications

This synthesis is based on the following papers, which are referred to as **paper I-IV**.

Paper I

Hodal H, Falk-Petersen S, Hop H, Kristiansen S, Reigstad M (2011) Spring bloom dynamics in Kongsfjorden, Svalbard: Nutrients, phytoplankton, protozoans and primary production. Polar Biology. DOI 10.1007/s00300-011-1053-7

Paper II

Hodal H and Kristiansen S (2008) The importance of small-celled phytoplankton in spring blooms at the marginal ice zone in the northern Barents Sea. Deep-Sea Research Part II 55: 2176-2185.

Paper III

Kristiansen S, **Hodal H**, Reigstad M. Autotrophic and heterotrophic microbial biomass across the Arctic Ocean. Manuscript

Paper IV

Hodal H, Kirchman D, Kristiansen S, Straza T. Bacteria diversity and single-cell activity in a cold high latitude fjord (Balsfjord) from winter to late summer 2009. Manuscript

1. Introduction

The Polar Regions are expected to experience some of the largest temperature effects of global climate change (ACIA 2004). As a result, sea ice cover in the Arctic Ocean has decreased over the past three decades (Levi 2000; Parkinson 2000) and the length of the ice melt season has increased (Comiso 2006; Serreze et al. 2007; Comiso et al. 2008). The seasonally ice-covered regions in the Arctic hold a large part of the arctic primary production (Sakshaug 2004). These regions are also highly dynamic. However, because of their remote location, they are far less understood than what is required to comprehend the influence climate change will have on seasonally ice-covered ecosystems in the future (Wassmann et al. 2008). The Barents Sea and Svalbard waters are highly productive shelf regions, accounting for approximately 50% of the total pan-Arctic shelf primary production (Sakshaug 2004). Even though the Barents Sea belongs to the best investigated shelves in the pan-Arctic, basic information from the ice-covered and seasonally ice-covered areas is still missing (Wassmann et al. 2008). Only few *in situ* measurements of pelagic primary production have been published from the Barents Sea (Ellertsen et al. 1981; Rey and Loeng 1985; Vernet et al. 1998), the northern Barents Sea (Hegseth 1998; **Paper II**) and fjords in Svalbard (Eilertsen et al. 1989; Hop et al. 2002; Piwosz et al. 2009; Rokkan Iversen and Seuthe 2010; **Paper I**).

For a long time, arctic ecosystems were considered to be dominated by a short and simple food chain with large diatoms dominating the primary production during a short and intense spring bloom. Even though the microbial food web was found to be important in marine ecosystems, mediating fluxes of carbon and nutrients (Azam et al. 1983), it was considered less important in the Arctic due to low temperatures and substrate limitation on bacteria growth rates (Pomeroy and Deibel 1986; Pomeroy et al. 1990). However, Thingstad and Martinussen (1991) found that the bacteria community in the cold pelagic ecosystem of the Barents Sea was very active at the end of the spring bloom and in subsurface blooms during summer. Later studies have supported this and shown that the relationship between temperature and bacteria activity is complex (Rivkin et al. 1996; Yager and Deming 1999; Pomeroy and Wiebe 2001; Kirchman et al. 2005; Kirchman et al. 2009a, b) and the microbial food web has been found to be important also in arctic ecosystems throughout the year (Levinsen et al. 2000; Sherr and Sherr 2003; Sherr et al. 2003; Garneau et al. 2008; Terrado et al. 2008; Vaqué et al. 2008; Rokkan Iversen and Seuthe 2010). So far the microbial contribution to primary production has been little studied. Primary production is highly

variable both temporally and spatially in the Arctic and more knowledge is needed about the relatively short productive period, particularly on the onset, range and development of primary production. Increasing evidence of a complex food chain in the Arctic require quantification of the importance of distribution and production of small cells.

Implementation of molecular genetic tools in microbial ecology has revealed new dimensions of microbial communities. We now consider the group Bacteria to be highly heterogenic and to include several clades and subclades suggested to play different roles in the carbon turnover (Giovannoni and Stingl 2005). The *Alphaproteobacteria* are for example thought to be more important in the uptake of low molecular weight dissolved organic matter (DOM) (Cottrell and Kirchman 2000; Malmstrom et al. 2004; Elifantz et al. 2007) while the *Cytophage*-like bacteria are suggested to be more important in uptake of high molecular weight DOM (Cottrell and Kirchman 2000; Elifantz et al. 2007). Whether these observations can be generally applied are still uncertain, and more work is needed to reveal the ecological function of the various phylogenetic groups until we can make general conclusions for specific bacteria groups.

By understanding the dynamics of autotrophic and heterotrophic organisms in the whole Arctic, their relative importance and the pan-Arctic variation we can be able to identify similarities and differences and merge knowledge from different regions to a larger extent than today to better understand the function of the Arctic microbial community.

2. General background

2.1. Measuring primary production

There exists no single method or series of observations that provide aquatic scientists with an absolute measure of primary production in the ocean. All methods and all approaches are approximations (Marra 2002). Primary production is typically measured as time dependent rates of O_2-evolution or ^{14}C-assimilation. The techniques, however, measure different products of the photosynthetic pathway and reflect different physiological processes (Falkowski and Raven 2007). Using the O_2-method with dark and light bottles, it is possible to obtain both net community production and gross primary production (Marra 2002). Results from ^{14}C-assimilation are more difficult to interpret since the respiration rate can not be separated (Falkowski and Raven 2007). This method however, is less time consuming and has a very low detection limit. An outline of the ^{14}C-method is described in Box 1. All primary production measurements in this thesis were done using the ^{14}C-method based on *in situ* incubations for 24 hours (**Paper I and II)**.

In most rate measurements incubation is part of the process, which means removal from the environment. Even if the samples are incubated *in situ,* they are removed for a while from the initial quantity and quality of light they were living in (Marra 2002). Because of factors like water mass movement and sinking of cells, it is not very likely that an organism will stay for a long time at one fixed depth. Incubation in incubators either with artificial light or natural light adjusted to a decreasing light intensity arise further problems. It can be difficult to find an artificial light source mimicking the natural light regime, and temperature control can be difficult and may lead to disruption of the autotrophic and heterotrophic community within the bottles (Marra et al. 1988). Working with environmental monitoring data, including primary production measurements, Larsson et al. (2010) revealed large differences between *in situ* incubations and incubations with artificial light. In a study 24 different laboratories were involved in an intercomparison exercise (Richardson 1991). Different incubators were used and the results revealed large variations between different incubators. Marra (1995) argued that incubation times should be kept to 24 hours to avoid any extrapolations of the data. He also argued that incubation times longer than a day include changes in biomass and interactions between trophic levels that would affect the results. Using incubation times shorter than 24 hours one would have to understand the physiology of the

different phytoplankton. Figure 1 illustrates the concept of distance between the "real primary production rate" and different approaches to measure it. The results from this thesis fit in the box named "*in situ* experiments" close to the "real rate of carbon assimilation". Because of the high temporal and spatial heterogeneity of primary production the resolution of field-based measurements is too low to give good large-scale and annual estimates of primary production. To obtain large-scale estimates it is more appropriate to use data from remote sensing (Platt and Sathyendranath 1988) or to model primary production (Wassmann and Slagstad 1993). These approaches, however, are based on parameterizations and available field data for comparison and validation. Incubations in **paper I and II** were done *in situ* for 24 hours to get realistic values of daily primary production, and to increase the number of field data during different stages of phytoplankton blooms.

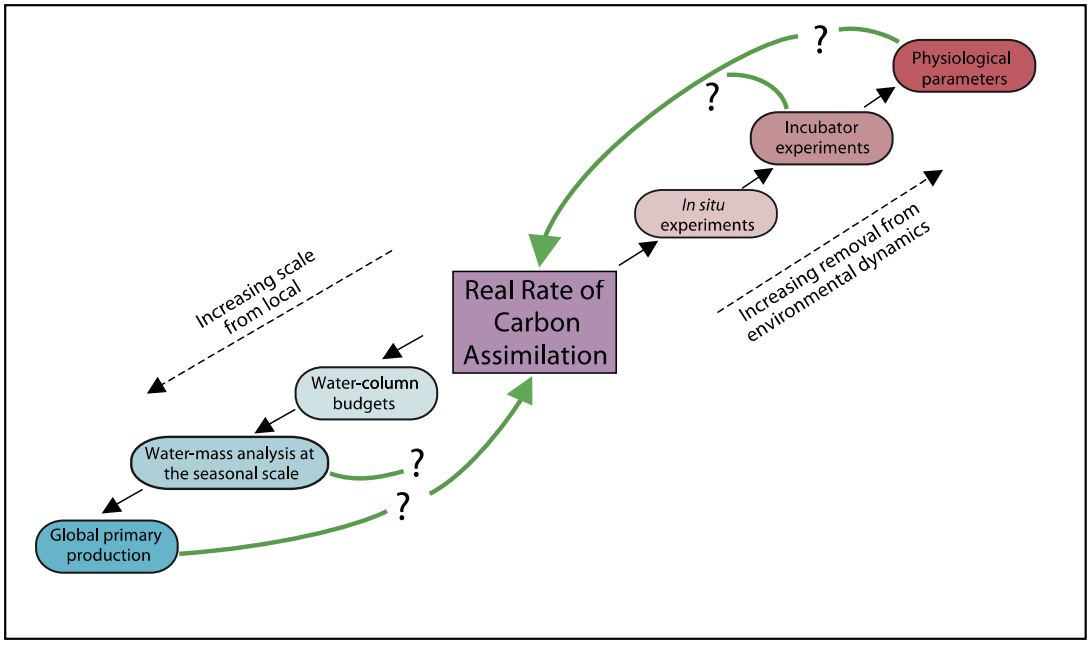


Figure 1. Schematic illustration of distance from the "Real Rate of Carbon Assimilation" for different approaches to measure primary production, adapted from Marra (2002).

Box 1. The ^{14}C-method

The ^{14}C-method was developed by Steeman-Nielsen (1952) and is probably the most widely used method in aquatic science to estimate primary production. Using the method of ^{14}C-assimilation one can quantify the rate at which inorganic carbon is converted into organic carbon cell biomass. Whether this method measures gross or net primary production is dependent on incubation time and growth rate of the phytoplankton, and the interpretation of the carbon assimilation as gross or net primary production is ambiguous (Falkowski and Raven, and references therein). For 1 hour incubation the technique is commonly assumed to indicate gross primary production while longer incubations can be seen as something between gross and net primary production.

The Danish scientist Einer Steeman-Nielsen first used the method on the 1950 "*Galathea"* expedition in the southern Atlantic and in the Indian ocean (Steeman-Nielsen 1951, 1952) and the implementation of this method lead to an increasing focus on estimations of production. Before this expedition, Steeman-Nielsen had worked with the O_2-method and was aware that this method was not sensitive enough to be used in oligotrophic oceans (Søndergaard 2002, and references therein). For many years he had discussions with the two scientists Riley from Bingham Oceanographic Laboratory and Ryther from Wood Hole Oceanographic Institution about the difference between the results of the ^{14}C-assimialtion method and their measurements done with the O_2-method and three days incubations. The discussions evolved around the high values obtained by the three-day incubations from the oligotrophic Sargasso Sea and the estimations of annual ocean primary production that Steeman-Nielsen meant should be lowered by a factor of 10. They never came to an agreement. In view of what we know today, many of the aspects in their discussion can be assigned to the temporal and spatial heterogeneity of primary production.

2.2. Phytoplankton blooms in seasonally ice-covered regions

The seasonally ice-covered regions are located between the multi-year ice and the maximal extent of the ice cover. These regions are especially exposed to climate change and the extent of the ice cover shows large inter-annual variability (Carmack et al. 2006; Carmack and Wassmann 2006). It is predicted that areas with multi-year ice will decrease in the coming decades and therefore the seasonally ice-covered regions will increase (Overland and Wang 2007; Serreze et al. 2007).

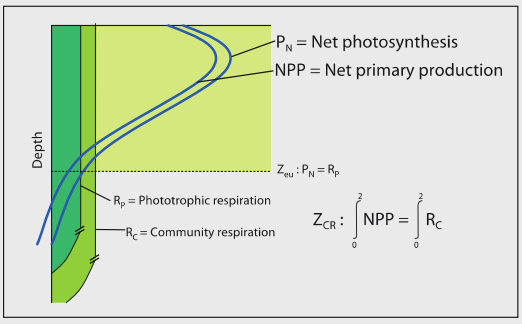
Intense phytoplankton blooms evolve along the melting and retreating ice edge due to increasing stability and irradiance in the surface (Gran 1931; Rey and Loeng 1985; Sakshaug and Skjoldal 1989). The initiation of the bloom is closely coupled to the critical depth of the water column as described in Box 2. The input of freshwater from the melting ice cover creates a strong vertical stratification with a shallow mixed surface layer at 10-50 m, where new production will be high for a short period (Dugdale and Goering 1967; Kristiansen et al. 1994; Lee et al. 2011), but where nutrients quickly are being used (Niebauer and Alexander 1985). After the depletion of nutrients in the surface mixed layer, small amounts of phytoplankton, mainly small flagellates, continue the primary production throughout the summer based on remineralized nutrients (Rey and Loeng 1985; Kristiansen et al. 1994). Ice edge blooms differ from open water blooms in that the strong stratification separates the shallow mixed layer from the deeper nutrient-rich water. In weaker stratified open water blooms, the wind-induced mixing will periodically bring up nutrients to the surface layer. This, together with a shorter productive season, results in a lower annual primary production in stratified seasonally ice-covered regions compared to open water regions (Wassmann and Slagstad 1993; Reigstad et al. 2002).

Ice edge phytoplankton blooms are ubiquitous and have been detected in many locations including the Bering Sea (Alexander and Niebauer 1981; Niebauer et al. 1995), Chukchi and Beaufort Seas (Hill et al. 2005; Sukhanova et al. 2009) Canadian Archipelago (Klein et al. 2002; Tremblay et al. 2006), Barents Sea (Rey and Loeng 1985; Hegseth and Sundfjord 2008; Degerlund and Eilertsen 2010) and the Southern Ocean (Smith and Nelson 1985). They can be very intense and short-lived. Perrette (2011) investigated ice edge blooms on a large scale using satellite data and found that ice edge blooms seldom lasted longer than 20 days, which makes them difficult to observe. After the peak of the bloom the maximum chlorophyll *a* concentrations are often observed as sub-surface

blooms close to the bottom of the mixed layer (Cullen 1982; Coon et al. 1987). At the bottom of the mixed layer nutrients are available and cells can have positive growth. Sub-surface blooms can be difficult to observe from satellites because of the depth they are located at. However, primary production here can be a substantial part of the annual primary production because the production can persist during summer (Rey and Loeng 1985; Martin et al. 2010). A quantification of size fractionated biomass and primary production in different bloom stages as well as the depth distribution is essential to estimate primary production and phytoplankton dynamic in these productive regions (**Paper I, II and III**).

Box 2. Critical depth

When Gran started to investigate the dynamics of phytoplankton biomass and production in Oslofjorden, he observed large seasonal changes. Gran and Nathanshon were pioneers in describing the connection between phytoplankton production and ocean physics (Braarud 1935). This was later validated in Norwegian fjords, the Norwegian Sea and the Bank of St. George (Braarud and Klem 1931; Riley 1942, 1946). The formalization of the concept of critical depth by Sverdrup (1953), to explain the onset of phytoplankton spring blooms, was a landmark in the history of oceanography (Platt et al. 1991). Though the original equation has some faults, it is still the backbone of todays models of primary production in the sea. Sverdrup was aware of the loss of phytoplankton through grazing and sinking but these processes were eliminated from the original equation for simplicity.



Critical depth: The depth above which integrated primary production and integrated community respiration are equal

Compensation depth: The depth at which the photosynthetic rate equals the respiration rate of phytoplankton

Euphotic zone: Above the compensation depth

2.3. Bacteria dynamics

Major advances in methods to quantify the abundance of marine bacteria were made in the late 1970s and early 1980s. Direct count assays based on epifluorescence microscopy were introduced (Hobbie et al. 1977), that allowed easy visualization and quantification of bacterial cells. Later the flow cytometry technique was implemented as a method to quantify and sort the components of the microbial community (Yentsch et al. 1983). Heterotrophic bacteria were found to be the most abundant organism in the entire biosphere. More importantly, heterotrophic bacteria dominate DOM assimilation and are suggested to consume 40-50% of primary production (Larsson and Hagström 1979; Fuhrman and Azam 1980; Larsson and Hagström 1982) and are able to out-compete all other microbes for dissolved compounds (Kirchman 2008). Bacteria also play an important role in remineralization of nutrients (Kirchman 2000).

Bacterial numbers are remarkably constant in pelagic marine environments. The numbers seldom vary with more than a factor of 10 over both time and space, suggesting that the production and loss rates are closely linked. During the productive period accumulations of dissolved organic carbon (DOC) are observed (Sugimura and Suzuki 1988; Carlson et al. 1994) and many theories have been presented on why heterotrophic bacteria are not able to utilize this increasing substrate concentration. Thingstad et al. (1997) suggested that the competition for nutrients between phytoplankton and bacteria keep the growth rate of bacteria low and that predation by heterotrophic flagellates and viral infections keep the abundance low. This is supported by others who suggest that viral lyses (Bergh et al. 1989; Proctor and Fuhrman 1990; Sandaa et al. 2009) and predation from heterotrophic flagellates regulate the stock of bacteria (McManus and Fuhrman 1988; Pace 1988; Longnecker et al. 2010).

Within any bacteria community there will be a broad range of cell-specific physiological stages, ranging from dead to highly active cells (Gasol et al. 1999; del Giorgio and Gasol 2008), and only a fraction of the cells within a community is responsible for bacterial biomass production (Cottrell and Kirchman 2003; Smith and del Giorgio 2003). Measurements of production are very often related to total cell abundances, giving growth rates and turnover rates that represent the average for the whole community. Bacteria abundance do not vary much, but growth rates range over at least three to four orders of magnitude, indicating large changes in cell specific activity (del

Giorgio and Gasol 2008). The fast growing cells are probably responsible for much of the carbon turnover even when present at low cell abundances, and del Giorgio and Gasol (2008) hypothesize that the slow growing bacteria cells play a role in stabilizing the function of the microbial food web. To better understand the changes in growth rates in natural environments between seasons and regions it is important to study the bacteria at a single-cell level to reveal the actual fraction responsible for the biomass production measured. This will give insights into the dynamics of bacteria and the influence they have on the turnover of carbon and remineralization of nutrients.

Until quite recently nearly all approaches have been limited to address bacteria as a homogeneous assemblage (Ducklow 2000). Over the last decades however, the composition and diversity of microbial assemblages have been extensively studied by 16S rRNA gene cloning and sequencing, community fingerprinting, hybridizations with oligo- or polynucleotide probes and by a combination of these approaches (Pernthaler and Amann 2005). The many new results have revealed a functional group that is far from homogeneous (Figure 2).

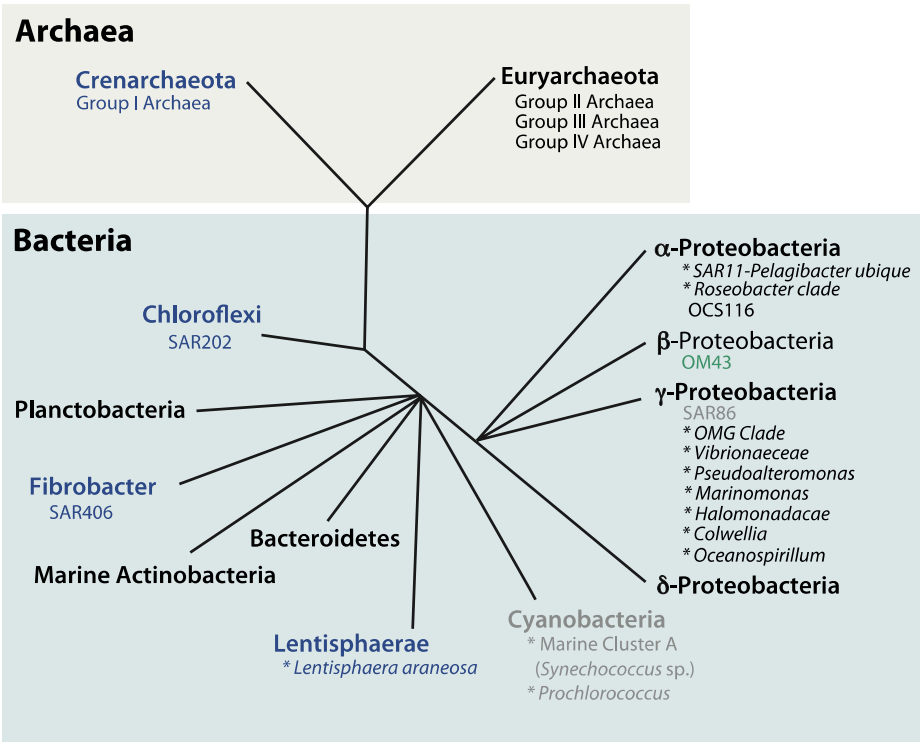


Figure 2. Schematic illustration of the phylogeny of the major plankton clades. Black letters indicate microbial groups that seem to be ubiquitous in seawater. Grey indicates groups found in the photic zone. Blue indicates groups confined to the mesopelagic and surface waters during polar winters. Green indicates microbial groups associated with coastal ocean ecosystems. Taxon names marked with asterisks represent groups for which cultured isolates are available. From Giovannoni and Stingl (2005).

Many of the marine microbial groups were first identified by sequencing rRNA genes cloned from seawater (Giovannoni et al. 1990; Fuhrman et al. 1992, 1993), and many still remain uncultured today. Giovannoni and Stingl (2005) made a schematic illustration of the phylogeny of the relatively few clades that dominate the genes recovered from seawater (Figure 2). Most of the major clades have cosmopolitan distributions. But patterns for some of the groups have been found, for example the Archaea group I (*Crenarchaeota*) and Cyanobacteria. Archaea group I is found to be most abundant in the mesopelagic and close to detection limit in the surface water of the North Pacific (Karner et al. 2001; Kirchman et al. 2007). In contrast to temperate systems, Archaea are also found to be abundant in surface waters during winter in polar oceans (Delong et al. 1994; Alonso-Sáez et al. 2008). Cyanobacteria are obligate phototrophs and only found in the photic zone of the ocean. This group is generally poorly represented in arctic seas (Booth and Horner 1997; Mostajir et al. 2001; Sherr et al. 2003), and mainly in connection with freshwater or atlantic water (Not et al. 2005; Waleron et al. 2007). Many of the clades contain different sub-clades which have been suggested to be ecotypes (Field et al. 1997). For example the SAR11 clade, belonging to the *Alphaproteobacteria*, has been found to contain three different ecotypes. An IB sub-clade that occurs throughout the water column in spring, giving space to the more specialized surface sub-clade IA group and the deep sub-clade II when the water column get thermally stratified during summer (Field et al. 1997; Carlson et al. 2009). The *Rosebacter* clade, another sub-clade of the *Alphaproteobacteria*, has been found to be very active in assimilating several molecular DOM components and having a high fraction of active cells even at low substrate concentrations (Alonso and Pernthaler 2006a, b). This clade has been suggested to act as an "ecological generalist" based on increasing data showing that this clade maintain constant productivity under various environmental conditions, This is due to their nutritional versatility in the use of organic matter (Moran et al. 2004; Buchan et al. 2005; Mou et al. 2007; Tada et al. 2011). The ecotype concept continues to expand with the recognition that many microbial groups can be subdivided according to their distribution in the water column (Giovannoni and Stingl 2005).

An important first step towards understanding the roles of various bacteria in the ocean is to determine the numbers and relative abundance of different bacterial groups (Giovannoni and Rappé 2000). Results from clone libraries most often indicate that the most abundant groups of bacteria belong to the *Alphaproteobacteria* (Giovannoni and Rappé 2000). The limited data

collected using direct counts with fluorescence *in situ* hybridization (FISH) however, suggests that bacteria in the *Cytophage*-like (Bacteroidetes) group dominate marine bacterioplankton communities (Glockner et al. 1999; Simon et al. 1999; Cottrell and Kirchman 2000a; **Paper IV**). To fully reveal the dynamics between different groups of bacteria we need to combine abundance estimates with activity or production measurements. Combining species identification methods (for example FISH) with methods of tracking assimilation of radiolabeled organic compounds, species specific activity can be investigated. Information on the proposed different roles of *Alphaproteobacteria* and *Cytophage*-like bacteria in carbon turnover has evolved from combining FISH with microautoradiography (micro-FISH) and is on of the starting points of linking the structure of natural microbial communities with their functions. In that perspective, an important start is to identify seasonal and spatial variability linked to environmental conditions (**Paper IV**).

3. Aims and objectives

The overall aim of the current research was to investigate primary production and small autotrophic and heterotrophic cells in arctic marine ecosystems, and their influence on bacteria community structure and activity.

The specific objectives were to:

1. Investigate the spring bloom dynamic in an arctic fjord with focus on the onset of the bloom and the development of phytoplankton production.

2. Quantify the *in situ* primary production during different stages of ice edge blooms in the marginal ice zone and to clarify how important small cells are to primary production during ice edge blooms.

3. Investigate the distribution of autotrophic and heterotrophic microbial biomass across the Arctic Ocean.

4. Investigate the seasonal changes in heterotrophic bacteria community structure and single cell activity in relation to phytoplankton DOM from winter to late summer.

4. Sampling strategy and study sites

To answer the objectives, field campaigns have been performed in combination with incubations in the laboratory. This PhD has combined scientific ideas with the available funding and logistic possibilities in the Arctic (Figure 3).

4.1. Sampling strategy

Paper I

To investigate the spring bloom dynamic in the Kongsfjorden, a field campaign was carried out during April and May in 2002. Samples were collected from R/V *Lance* twice in April and from a small boat twice a week in May. It was difficult to sample from a small boat and perform *in situ* incubations during the transition period between ice-covered waters and open waters. To overcome the work load we had to compromise between time and depth resolution and samples were only taken regularly down to 20 meters. Primary production was measured *in situ* down to 10 meters. The results are weakened by this but we argue that the time resolution was more important than the depth resolution to describe the development of the spring bloom in an under-sampled area.

Paper II

This paper is based on work done during the multidisciplinary project CABANERA (Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climate change). Three field campaigns were carried out in the marginal ice zone in the northern Barents Sea during May-July in the years of 2003-2005. In this study, different stages of spring blooms were encountered spatially. Chlorophyll *a* and primary production measurements were size-fractionated in a total fraction and > 10µm to investigate the influence of small cells. The depth resolution of the sampling was largely improved compared to the work in **paper I**, and at all stations primary production was measured at eight depths down to 60 meter. In addition, incubations for primary production were performed *in situ* for 24 hours.

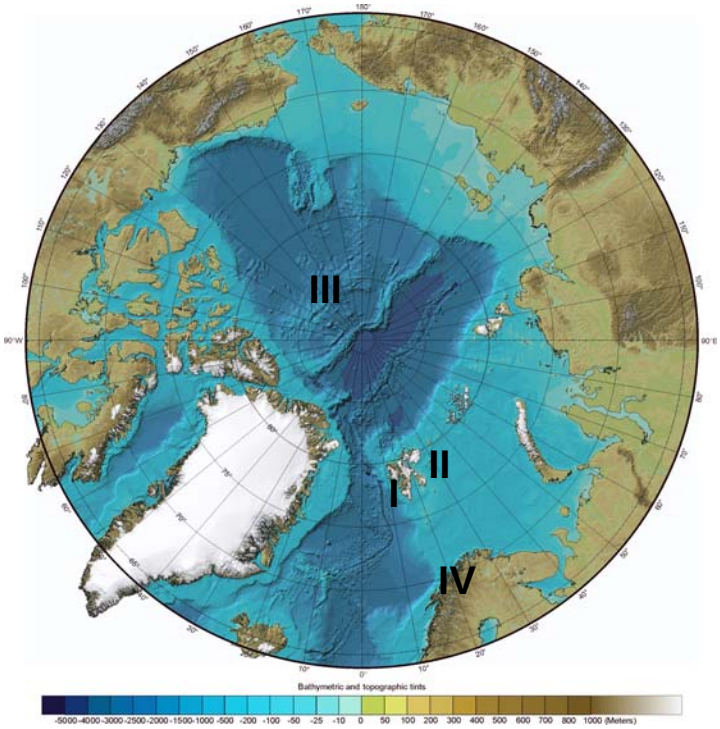


Figure 3. Map of the Arctic Ocean, with the shelf areas in light blue and the deep regions (>500 m depth) in dark blue. Roman numbers indicate the different works included in this theses. Picture adapted from IBCAO, 2003.

Paper III

The work performed in **paper III** was carried out onboard the Swedish icebreaker *Oden* during an expedition across the Arctic Ocean in August and September 2005. The original idea was to measure the levels of bacteria and primary production in the Arctic Ocean. Because of unforeseen restrictions of unnatural concentrations of radioactive isotopes on board the ship, plans had to be changed. The focus then became to identify the distribution of microbial autotrophic and heterotrophic abundance across the Arctic Ocean from the Pacific to the Atlantic region. Sampling was performed during late summer situations when day length decreased.

Paper IV

In **paper IV** the scientific focus was concentrated on heterotrophic bacteria, one of the sinks of phytoplankton DOM. This work was done using different molecular genetic methods. Using fluorescence *in situ* hybridization (FISH), different genetic groups of prokaryotes were quantified by epifluorescence microscopy. FISH combined with microautoradiography (micro-FISH) were

used to quantify which groups assimilated different low molecular DOM substrates. Analyses were performed in the laboratory of Professor David Kirchman at the University of Delaware, USA. A seasonal study of the development of bacteria community structure and activity from winter through summer was performed in the cold high latitude Balsfjorden. The fjord of Balsfjorden was chosen as the study site because of the need for easy access from the University of Tromsø to be able to sample regularly. Sampling was concentrated at one location and samples were taken from surface water (10-15 meters depth).

4.2. Study sites

Kongsfjorden

Kongsfjorden is a glacial fjord, situated on the west coast of Spitsbergen in the Svalbard archipelago. The fjord has no sill and is strongly influenced by exchange of water across the fjord-shelf boundary (Svendsen et al. 2002; Willis et al. 2006). Usually, cold arctic water dominates Kongsfjorden throughout the winter due to an external density front isolating the fjord from the warmer atlantic water. During summer, the fjord usually experiences an abrupt shift from cold to warm water mass signature, as an influx of warm atlantic water flows in from the shelf (Svendsen et al. 2002; Cottier et al. 2005). The extent of the ice cover, timing of freeze-up, melting and break-up of the ice cover, show high interannual variations (Svendsen et al. 2002).

The northern Barents Sea

The Barents Sea is characterized by a relatively shallow shelf and a complex hydrography (Loeng 1991; Loeng et al. 1997). It is divided in a northern and a southern region by a meandering polar front, which separates the relatively warm atlantic water (3-6 ºC) in the south-west from the cold arctic water (<0 ºC) in the north-east. This results in a permanently ice-free southern region, and a seasonally and interannually variable ice cover in the north and east. The ice can cover up to 90% of the surface area of the Barents Sea during cold winters, but no multi-year ice is produced here (Vinje and Kvambekk 1991). When the ice starts to melt, a strong pycnocline develops at 15-35 meter depth, and typically an ice edge bloom develops along the retreating ice edge.

The Arctic Ocean

The Arctic Ocean is a deep ocean, characterized by strong upper-ocean stratification. It is divided into two major deep basins, the Eurasian Basin and the Amerasian Basin (often called "Canada Basin"), by the major deep-sea Lomonosov Ridge, which stretch between the continental margin of northern Greenland to the Laptev Sea-shelf, off the New Siberian Islands (Jakobsson et al. 2004). Large input of freshwater creates a low-density surface layer (0-50 meter) whith seasonal circulation. During winter, brine produced by ice formation destabilize the water column. During summer, the water column is re-stabilized by melting ice and freshwater runoff creating a fresh surface layer. An intermediate layer of atlantic origin separates the surface layer from the deep ocean and prevents exchange of nutrient-rich water to the surface. This results in decreased surface nutrient concentrations compared to concentrations in pacific and atlantic water masses. The Arctic Ocean Basin used to be covered by multi-year ice, but over the past decades an increasing part of the Arctic Ocean Basin and the shelves have become seasonally ice-free (Serreze et al. 2007).

Balsfjorden

Balsfjorden is located 30 kilometres south of Tromsø, in northern Norway. Balsfjorden is a cold fjord with winter temperatures 1-3 ºC and (Eilertsen et al. 1981), partly due to convection of cooled surface water in winter. The fjord is long and narrow and has a shallow sill at 30 meters depth, also limiting exchange with the warmer coastal water. The sampling station was located in the outer part of Balsfjorden which is ice-free year round. Balsfjorden has been extensively studied for several decades, is easily accessible from Tromsø, and with a lot of background data available.

5. Summary of results and discussion

5.1. Spring bloom dynamics in Kongsfjorden

The marine ecosystem in Kongsfjorden has been extensively studied the last 10-20 years due to the infrastructure and scientific facilities in Ny-Ålesund. Research results of primary production and lower trophic levels are still scarce and especially data from winter and spring is lacking. Spring is often a logistic challenge due to the transition mode between ice-covered open waters, making sampling from snow scooter or small boat difficult. The research performed in Kongsfjorden (**paper I**) combines information on the onset of the spring bloom and primary production during the spring bloom period.

Onset of the spring bloom

In 2002 the spring phytoplankton bloom started around 18 April. This was when the ice broke up, the water column stabilized, and increased light became available for phytoplankton growth (Figure 4A-C). The onset of the bloom was identified based on the increase in biogenic silica in the period of 15-18 April (Figure 4F) and the weak stabilization established in the top 30 meters (Figure 4C). Chlorophyll *a* was not measured successively on 15 April, but biogenic silica can be used as an estimate for diatom biomass since it quantifies the amount of dissolved silica which is built into diatom frustules. Since melting of ice and run-off from land usually do not start until June/July at these latitudes (Svendsen et al. 2002), no strong density stratification developed during April and May. The stabilization was not very strong (Δsigma-t < 0.1 10 meter^{-1}) and broke down several times during the sampling period. This supports the evidence that arctic and temperate spring blooms can start in slightly or not stratified waters (Townsend et al. 1992; Eilertsen 1993; Dünweber et al. 2010).

The peak of the spring bloom in Kongsfjorden varies in time and can appear from the middle-end of April to the middle of May, and the timing has been found to be closely linked to ice cover and hydrographical conditions (Leu et al. 2006; Hegseth and Tverberg 2008; Narcy et al. 2009; Rokkan Iversen and Seuthe 2010; **Paper I**). Similar variation has been observed in Disko Bay on the west coast of Greenland where the onset of the bloom also is observed to be linked to the sea ice break-up and stabilization of the water column and the peak of the bloom appears between April and May

(Madsen et al. 2001, 2008; Dünweber et al. 2010). In Young Sound on the north east coast of Greenland and in Rijpfjorden on the northern coast of Svalbard, ice cover is more pronounced, and the onset of the spring bloom is delayed until July/August (Rysgaard et al. 1999; Leu et al. 2011). In Rijpfjorden, annual variation in ice cover and influx of warm water masses have a large influence on the development of the pelagic ecosystem with increased pelagic activity in a year with warm water influx (Leu et al. 2011).

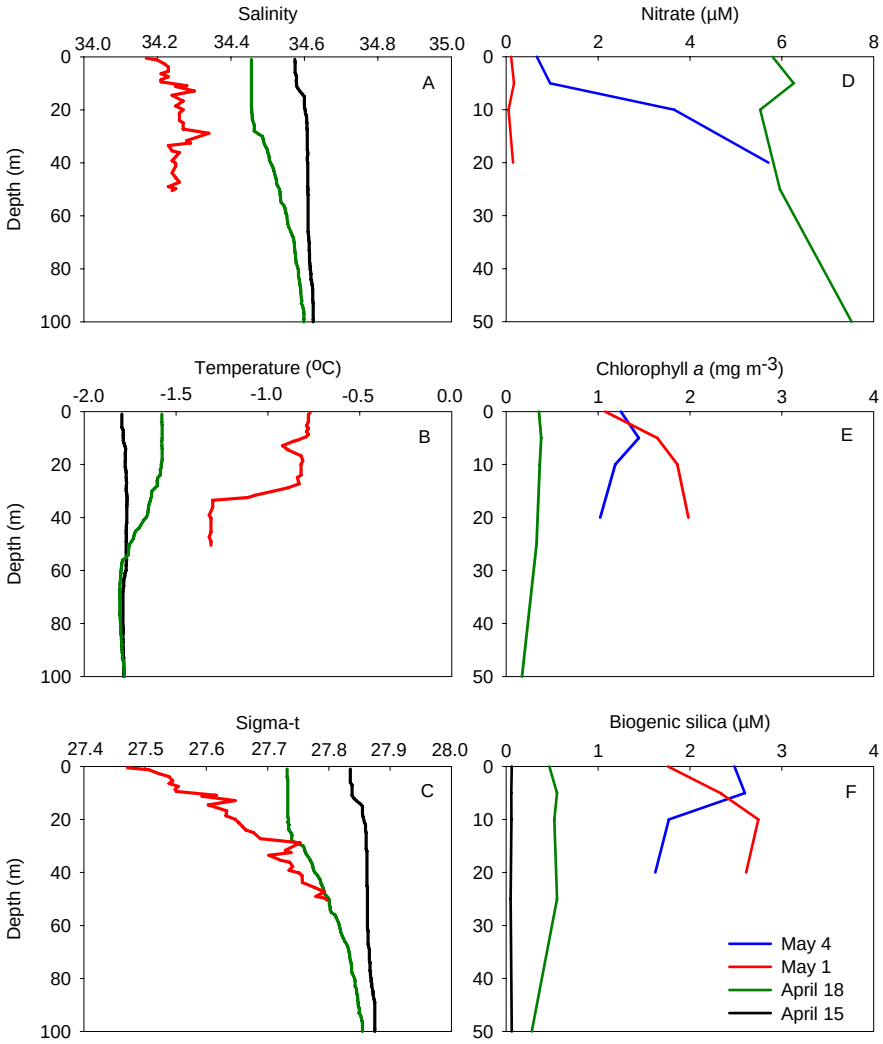


Figure 4. Depth profiles of salinity, temperature (ºC), sigma-t, nitrate (µM), chlorophyll *a* (mg m^{-3}) and biogenic silica (µM) on selected sampling dates.

Range of primary production

Primary production rates in the beginning of May ranged from 15 to 93 mg C m^{-3} d^{-1}. This is in the same range as other measurements from spring blooms in the marginal ice zone (Vernet et al. 1998; **Paper II)** and substantially higher than measurements from the spring bloom in the stratified Young Sound on the east coast of Greenland (Rysgaard et al. 1999). In Young Sound, primary production was low during the ice-covered period, but increased when the ice broke up and reached up to 12 mg C m^{-3} d^{-1} in a sub-surface bloom at 15 to 20 meters depth (Rysgaard et al. 1999). From Kongsfjorden only two primary production measurements during spring (April and May) have been published (Rokkan Iversen and Seuthe 2010). Their study was performed in 2006 when the fjord was ice-free and dominated by warmer atlantic water. In April, they encountered a very dense diatom and *Phaeocystis pouchetii*-dominated spring bloom (10 mg chl-*a* m^{-3}), distributed over the top 50 meters. Even though we measured a substantially lower biomass of phytoplankton (2 versus 10 mg chl-*a* m^{-3}), our primary production rates are in the same range as Rokkan Iversen and Seuthe (2010) measured in the surface. Because of very high accumulated biomass in April 2006 primary production was heavily reduced at 5 meters, resulting in a substantially lower integrated primary production rate than in the present study (0.4 versus 1.5-1.9 mg C m^{-2} d^{-1}) during what we assumed was a peak in the bloom. Our data could be substantially underestimated because of the weak depth resolution. The thermal stabilization of the top 30 meters of the water column on 1 May could give rise to a sub-surface bloom. Sub-surface blooms are widespread in stratified waters of the Canadian Arctic and sub-Arctic in late summer and fall (Martin et al. 2010). In **paper II,** sub-surface blooms contributed 24% to integrated primary production during spring blooms in the marginal ice zone of the northern Barents Sea, and shows that sub-surface blooms are important in stratified waters also in during spring.

In Kongsfjorden (**Paper I**) the shifts between stabilization and mixing during the spring have probably increased the primary production during the spring bloom due to inputs of nutrients from deeper water masses during the mixing events (Figure 4D). This resembles scenarios from the atlantic sector of the Barents Sea, which is also weakly stratified in spring and affected by frequent mixing events (Wassmann et al. 1999). Annual primary production and new production in the atlantic sector are therefore estimated to be higher than in the highly stratified seasonally ice-covered region of the Barents Sea (Reigstad et al. 2002).

As stated in **paper I,** strong interannual variability is observed in the timing and level of accumulation of biomass. This variation is most probably linked to variations in dominating water masses, extent of the sea ice cover, the presence of vertical stratification and the mixing depth. Weakly stratified areas are strongly affected by wind-driven mixing, and the onset of the productive period in Kongsfjorden will therefore very often by regulated by the extent of the ice cover and the wind regime. As a result, there will be higher new primary production in years with weak stratification than in years with strong stratification.

5.2. Primary production in the marginal ice zone of the northern Barents Sea

The marginal ice zone in the Barents Sea is a very dynamic system with large spatial and annual variations in ice cover, affecting biological parameters. The research performed in the CABANERA project (**Paper II**) is one of very few investigations where primary production has been measured *in situ* for 24 hours during early, peak and late stages of ice edge blooms, providing production rates in this highly heterogenic region. The research also addresses the importance of smaller phytoplankton cells for primary production.

Heterogeneity of phytoplankton biomass and primary production

At the 12 stations visited in the marginal ice zone we encountered different stages of ice edge blooms (Figure 5). We did not encounter any pre or post bloom stages, but different stages of ongoing blooms (**Paper II**). The integrated (0-90m) chlorophyll *a* concentrations ranged 12-588 mg chl-*a* m^{-2}, and integrated (0-60m) primary production ranged 103-1475 mg C m^{-2} d^{-1}. The lowest value was found at the northernmost station of the shelf, towards the Arctic Ocean north of Svalbard. The two highest values were found in May at station XVI northeast of Hopen Island and at station XIV north of Svalbard, on the shelf towards the Arctic Ocean, almost 2 degrees further north than the first one.

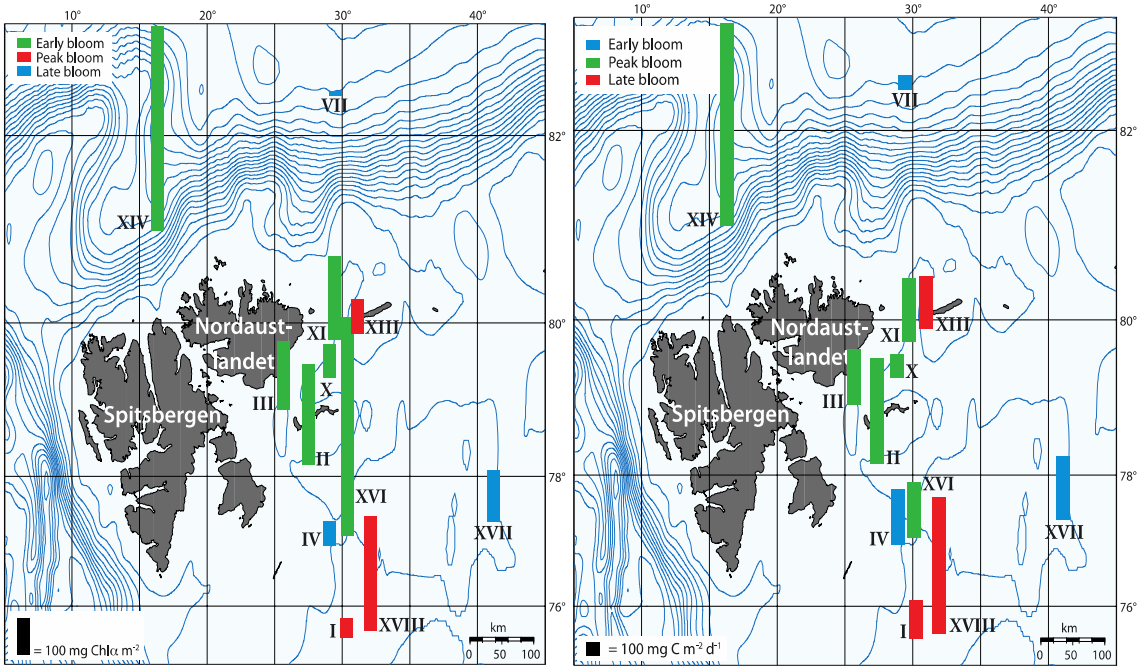


Figure 5. Stations visited during the CABANERA project 2003-2005 (**Paper II**). Columns indicate integrated levels of: chlorophyll *a* (chl-*a* m^{-2}), left panel; primary production (mg C m^{-3} d^{-1}), right panel. Colours indicate stage of bloom.

The two stations with highest integrated values of chl-*a* (stations XIV and XVI) were visited in May when spring blooms were hypothesized to be most intense (Wassmann et al. 1999). We also encountered very intense peak blooms in July (stations II, III and XI) indicating that ice edge dynamics are very complex. The field work in the CABANERA project presents only snap-shots of the system in the marginal ice zone of the northern Barents Sea, but catch the variability and illustrates that these regions are very dynamic with large spatial and temporal variations caused by the changing ice cover.

Table 1. Distribution of primary production (mg C m^{-2} d^{-1}) in the two depth intervals 0-20 m and 20-60 m and the percentage of integrated primary production (0-60 m) conducted in the sub-surface interval 20-60 m.

Stage and station number		Primary production 0-20 m	Primary production 20-60 m	% PP sub-surface
Early	IV	385	23	6
	VII	72	31	30
	XVII	425	37	8
Peak	II	322	448	58
	III	155	252	62
	X	140	30	18
	XI	335	130	28
	XIV	1395	79	5
	XVI	398	7	2
Late	I	47	230	83
	XIII (mixed)	253	130	34
	XVIII (mixed)	869	128	13
Total		4796	1525	24

In **paper I**, primary production was only measured down to 10 metres depth which weakness the results. In **paper II,** a higher depth resolution was prioritized and primary production was measured down to 60 metres. Averaged over all 12 stations visited in the marginal ice zone 24% of the primary production took place in the depth interval 20-60 meters (Table 1). Variation in the contribution from sub-surface primary production was observed between the different stages of the bloom. Station XVIII was located in open atlantic water and was characterized by a mixed water column. Primary production at this station mainly took place in the top 20 metres (87%), indicating that sub-surface primary production is less important in areas with weak vertical stratification. At station II, characterized to be in a late bloom stage, primary production mainly took place below 20 metres (83%). This underline the important contribution of sub-surface primary production to total integrated primary production, even during ongoing ice edge blooms. Though all of these data are

collected from ongoing bloom scenarios, they indicate that the deep primary production is less pronounced in the early stages of the bloom and more pronounced in the later stages when nutrients are depleted from the surface layers. An exception is station VII, which is characterized to be in early bloom stage and 30% of the primary production took place sub-surface. This station was located in the Arctic Ocean (Figure 5), it had the lowest accumulated chlorophyll *a* concentration and the 1% irradiance depth was at > 90 m (Hancke 2007). This indicates that sub-surface primary production can be very important in the central Arctic Ocean, as also suggested by Martin et al. (2010).

Importance of small cells to primary production

Of the 12 stations visited in the marginal ice zone, 10 stations were successfully size fractionated and three were characterized as early bloom, five as peak bloom and two as late bloom stages of ongoing ice edge blooms (**Paper II**). The distribution of biomass and primary production (Table 2) between the different bloom stages indicate that the early bloom stages contributes more to the summed primary production than to the summed biomass (20% versus 10%), while the peak bloom stages contribute less to primary production than to biomass. The size fractionation showed that the small (< 10 μm) cells on average over 10 stations contributed 26% to the biomass (estimated by chl-*a*) (Table 2). This support the classical picture of larger cells dominate spring bloom (Officer and Ryther 1980). Looking at the results from fractionation of primary production and the production/biomass ratio (Table 2 and Table 3), the situation is different. On average, the small cells contributed 46% to primary production and in all stages small cells had a higher production/biomass ratio. This difference in contribution to biomass and to primary production from phytoplankton present in the early bloom stages and between small and large cells could be explained by higher loss rates (most probably grazing) or by higher photosynthetic activity in the phytoplankton present in the early bloom stages and in smaller cells. The results presented here (**Paper II**) illustrates the importance of separating biomass and productivity measurements, since the biomass standing stock is a result of production and loss processes which include both grazing and vertical flux. Only looking at biomass, in this case small cells, would underestimate the importance of this size group of autotrophic cells in the food web.

Table 2. Contribution of the different bloom phases to the sum of integrated chl *a* (mg m^{-2}) and primary production (mg C m^{-2} d^{-1}) and the contribution of small (< 10 µm) cells to total biomass and primary production in the three bloom stages. Average of stations.

Stage	Chlorophyll *a*		Primary production	
	% of summed	% small cells	% of summed	% small cells
Early bloom	10	71	20	82
Peak bloom	85	19	71	31
Late bloom	5	63	9	87
Sum of all 10 stations	100	26	100	46

Table 3. Production/biomass ratio (mg C (mg chl-*a*)$^{-1}$ d^{-1}) of large cells (>10µm) and small cells (<10µm) averaged for bloom stages and averaged over for all 12 stations.

Stage	Large cells	Small cells
Early bloom	3.9	9.1
Peak bloom	3.0	8.7
Late bloom	2.1	9.6
Average ± SD	3.1 ± 1.8	8.9 ± 3.4

Small cells have traditionally not been considered quantitatively important during ice edge blooms because of the classical view that larger cells dominate. The results from **paper II** clearly shows that this is not the case. It was only during very intense blooms (stations II, XIV and XVI; Figure 6) that the large cells dominated both in terms of biomass and primary production. Even at the peak bloom stations the small cells did contribute with 31% to total primary production (Table 1). These results support the traditional picture that larger cells have an important role during the very peak of the ice edge bloom, but the results also underline that smaller cells contribute to carbon production during the peak bloom and may dominate the carbon production both before and after the short peak bloom. This contribute to the increasing understanding that small cells do play an important role in the food web, also in high productive arctic regions (Hansen et al. 1996; Lovejoy et al. 2007; Degerlund and Eilertsen 2010)

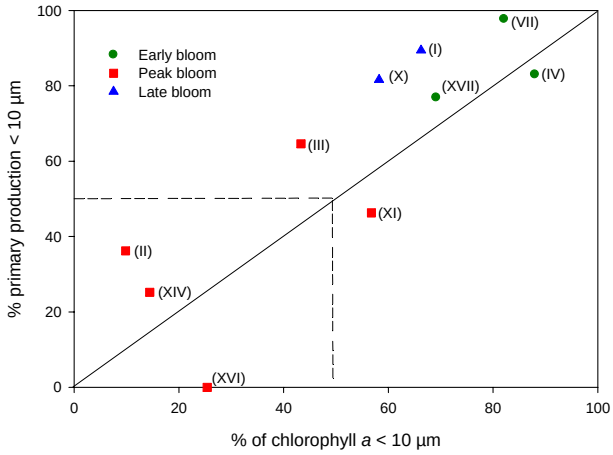


Figure 6. Scatter plot of the contribution (%) of small cells (< 10 µm) to biomass (chl-*a*) versus their contribution to primary production. Each point represents one station, and the station numbers are given in parentheses. The solid line is the 1:1 relationship and the dashed lines indicate the 50% threshold.

Whether primary production during spring blooms is produced by small cells or large cells does make a difference, because small and large cells enter the food web differently. Large cells are transferred by larger grazers to higher trophic levels while smaller cells tend to enter the microbial food web. Larger cells contribute to vertical flux to a larger extent than smaller cells, due to higher sinking rates. However, the role of smaller cells in vertical export is not well studied, but they may also contribute (Olli et al. 2001). In a pilot study by Rokkan Iversen (2011), she investigated the contribution from small cells to vertical export in the Barents Sea and found that cells < 20 µm could constitute 10-20 % of the downward carbon export.

5.3. Autotrophic and heterotrophic microbial biomass in the Arctic Ocean

During different stages of ice edge blooms in the marginal ice zone in the northern Barents Sea small cells were found to be an important component of pelagic primary producers (**Paper II**). The data from the "Beringa 2005" expedition across the Arctic Ocean, supports these findings.

During the "Beringia 2005" expedition to the Arctic Ocean (Figure 7), the abundance and biomass of bacteria, heterotrophic and autotrophic protists < 20 µm were investigated. The protists were organized into autotrophic and heterotrophic cells and the size classes of < 2 µm, 2-5 µm, 5-10 µm and 10-20 µm. The stations were organized in three groups based on physical characteristics (Table 4).

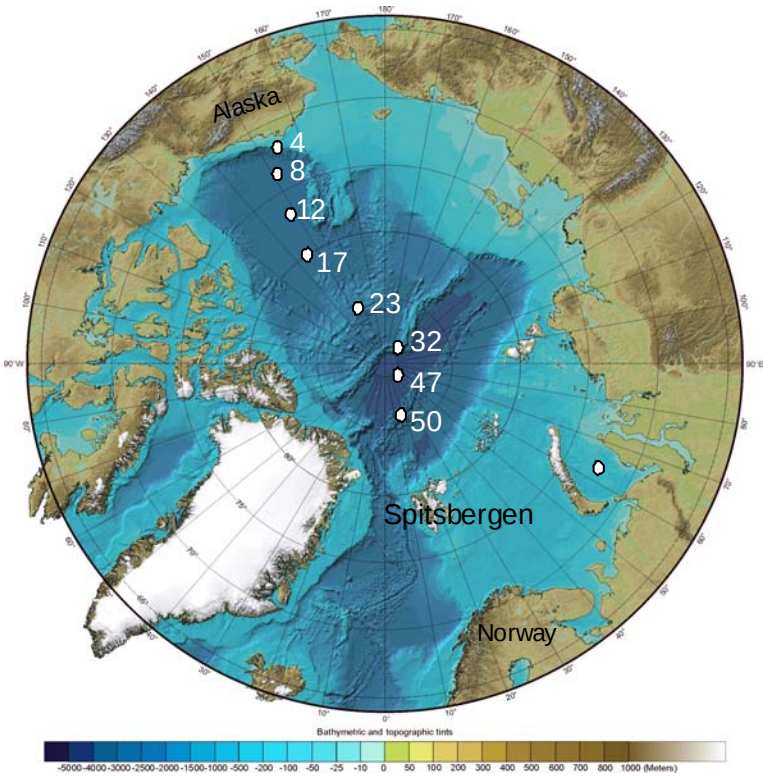


Figure 7. Map of sampling route and station numbers. Sampling started on the shelf towards the Canada Basin on 21 August and the last station was sampled on 18 September. Picture adapted from IBCAO, 2003.

Table 4. Grouping of the stations sampled during the "Beringia 2005" expedition across the Arctic Ocean, sampling date, the prevailing water masses and range of salinity and temperature (ºC) in the upper 50 metres. Station 4 was on the Alaskan shelf, station 8, 12 and 17 were in the Canada Basin (CB), station 23 was on the Alpha Ridge (AR), station 32 was on the Lomonosov Ridge (LR), station 47 was in the Amundsen Basin (AB) and station 50 was on the Gakkel Ridge (GR).

Station groups	Sampling date	Prevailing water masses	Salinity 0-50m	Temperature 0-50m (ºC)
4 (Shelf)	21.08	Pacific	29.7 - 31.6	5.2 - 7.4
8-23 (CB,AR)	23.08 - 01.09	Pacific	26.5 - 31.0	(-1.6) – (-0.2)
32-50 (LR, AB, GR)	07.09 - 18.09	Atlantic	32.2 - 33.6	(-1.7) - (-1.8)

Table 5. Average biomass (mg C m^{-3}) in the top 50 metres at the three different station groups of bacteria, autotrophic protists (< 20µm) and heterotrophic protists (<20µm). Range is given in parentheses.

Station groups	Bacteria	Autotrophic	Heterotrophic
Shelf	4.4 (2.6-5.8)	9.2 (5.7-13.7)	7.4 (5.1-10.4)
Canada Basin	1.9 (1.3-3.7)	3.2 (1.0-8.0)	2.9 (1.0-5.1)
Central AO	0.8 (0.5-1.9)	2.2 (0.7-4.2)	3.5 (0.5-6.8)

Table 6. Average abundance in the top 50 metres of bacteria and protists in the different size categories. Range is given in parentheses.

Station groups	Bacteria (10^5 cells ml^{-1})	Protists (cells ml^{-1})			
		< 2 µm	2-5 µm	5-10 µm	10-20 µm
Shelf	2.2 (1.3-2.9)	29306 (18641-40584)	707 (594-849)	77 (52-140)	30 (13-41)
Canada Basin	0.9 (0.6-1.9)	11915 (3920-24744)	203 (69-498)	20 (7-42)	11 (3-27)
Central AO	0.4 (0.2-0.9)	10242 (2045-19812)	260 (41-586)	24 (9-47)	6 (1-16)

The highest microbial biomass was found on the Alaskan shelf and decreased towards the central Arctic Ocean (Table 5). On the Alaskan shelf, the biomass of autotrophic protists was slightly higher than that of heterotrophic protists. This station had only approximately 50% ice cover (compared to the rest that had 76-91%), and the highest concentrations of chlorophyll *a* were found here (0.3-0.8 mg chl-*a* m^{-3}, in the top 50 metres). If the biomass of bacteria is included, the heterotrophic biomass was higher than the autotrophic biomass at all stations (Table 5). The microbial community was dominated by cells < 2 µm - 98% of the protist abundances were in this size category (Table 6). The total dominance of the smallest cells was less pronounced when abundance was converted to carbon, then 59% of the total biomass was from cells < 2 µm.

Very few data on picoplankton abundance has been published from the central parts of the Arctic Ocean. To my knowledge only the study of (Booth and Horner 1997) including a transect from the Chukchi Sea to the Canada Basin and into the Makarov Basin, and **paper III** give abundances of picoplankton from the more central parts of the Arctic Ocean. Other studies have investigated picoplankton abundances in shelf regions in the Canadian Arctic (Robineau et al. 1999; Mostajir et al. 2001; Waleron et al. 2007; Terrado et al. 2008; Vaqué et al. 2008; Tremblay et al. 2009), the Fram Strait during early spring (Seuthe et al. 2011), Kongsfjorden in Svalbard (Wang et al. 2009; Rokkan Iversen and Seuthe 2010) and in the Greenland, Norwegian and Barents Seas (Not et al. 2005). There is a large range of picoplankton abundances in the different studies (0-46000 cells ml $^{-1}$) and our data falls within this range. Work by Tremblay et al. (2009) done in the Beaufort Sea and Baffin Bay in August and September 2005, showed that picoeukaryote cells dominated the community. They did not separate autotrophic and heterotrophic cells, but fractionated chlorophyll *a* and concluded that small cells did not dominate autotrophic biomass. This corresponds well with the distribution we found within the autotrophic community, where 47% of the biomass was constituted by picoplankton (< 2 μm).

Bacteria abundances were generally low (Table 6). The shelf values (1.3-2.9 10^5 cells ml^{-1}) were in the same range as previously reported from arctic regions (Thingstad and Martinussen 1991; Sherr and Sherr 2003; Sherr et al. 2003; Vaqué et al. 2008; Rokkan Iversen and Seuthe 2010; Seuthe et al. 2011) but lower in the central parts (0.2-0.9 10^5 cells ml^{-1}). The very low abundance of bacteria in the central Arctic Ocean in our study, compared to the shelf and the Canada Basin, could be explained by the low autotrophic biomass (especially that of the picoplankton) and the increase in heterotrophic biomass (especially in the 2-10 μm size fractions). The autotrophic picoplankton is suggested to relief the bacteria community of heavy grazing pressure from small heterotrophic flagellates (Anderson and Rivkin 2001), which are suggested to be the most important bacterivores in arctic systems (Vaqué et al. 2008). The low abundance of bacteria can, however, also have been caused by low bacteria growth rates due to substrate limitation. More work are needed on bacteria dynamics in the central Arctic Ocean to reveal if the bacteria actually have reduced growth rates here, or if predation regulates the biomass as suggested in other regions.

The role of picoplankton in arctic marine ecosystems has received a lot of attention the last decades and many studies have illustrated that small cells do play an important role in the microbial food web, both as predators on bacteria, but also as primary producers. Autotrophic picoplankton abundances have increased, while abundances of autotrophic nanoplankton have decreased in the Arctic Ocean over a period when nitrate concentrations have decreased (Li et al. 2009). Li et al. (2009) suggest that an increase in the abundance of small cells may be a common response to global warming and thus affect the ecosystem's carbon flux.

5.4. Bacteria community structure and activity

In the central Arctic Ocean very low abundance of bacteria were found (**Paper III**) along with very low concentrations of chlorophyll *a*. In the literature, it is being discussed how substrate and predation regulate the abundance of bacteria and to what level bacteria abundance alone add to the information of bacteria dynamics and bacteria's role in food webs (Malmstrom et al. 2007; Thingstad et al. 2008; Longnecker et al. 2010). In the seasonal study in Balsfjorden (**Paper IV**), focus was put on abundance, together with species composition and activity on the single-cell level.

Seasonal variations in bacteria abundance and activity

Bacteria abundance was low during winter, increased after the phytoplankton spring bloom and stayed high during July and August, before decreasing again in September, ranging 0.3-2.2 10^6 cells ml^{-1} (Figure 8). The abundance only increased with a factor of 10 from winter to summer, while the concentration of chlorophyll *a* increased with a factor of 100. The increase in bacteria abundance can be attributed coupled to increased substrate availability, caused by the high phytoplankton and heterotrophic activity during and after the spring bloom, as discussed by Møller et al. (2003).

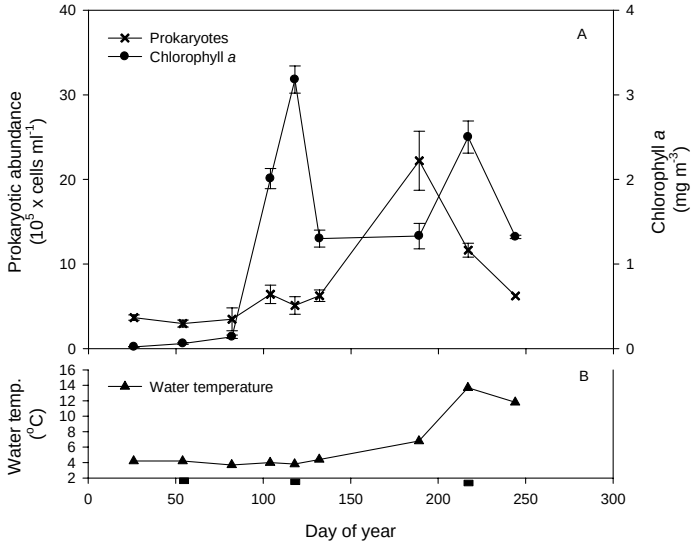


Figure 8. Seasonal development in A) bacteria abundance (10^5 cells ml^{-1}) and chlorophyll *a* (mg m^{-3}) and B) water temperature (ºC). Squares along the x-axis, indicate dates chosen to represent winter, spring and summer.

The number of cells active in DOM assimilation also increased from winter to summer (Figure 9), although this increase (three fold) was not as high as the increase in abundance (10-fold). This is consistent with general observations of the seasonal succession of bacterial community production (Fuhrman and Hagström 2008). The high number of active cells in spring and summer underline the important role bacteria play for the turnover of DOM and nutrients during and after the spring phytoplankton bloom.

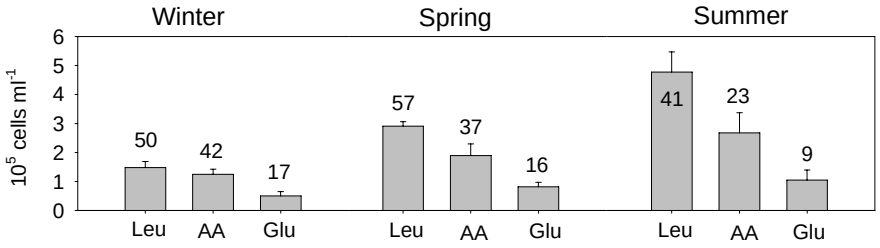


Figure 9. Amount of bacteria (cells ml^{-1}) active in substrate assimilation in winter, spring and summer. Number at the columns indicates the fraction (%) of prokaryotic cells active in assimilating substrate.

The fact that only a fraction of the bacteria community is active in carbon turnover at a given time has received increasing attention (Smith and del Giorgio 2003; del Giorgio and Gasol 2008). In Balsfjorden, the fraction of cells active in leucine assimilation did not vary much between the three seasons (41-57%). The most interesting finding, however, is that the lowest fraction was found during summer when the system is suggested to be highly productive, and the highest fraction was found during spring (Figure 9). A review of results from microaudio-radiography in natural communities shows that on average 30% of the cells are active in substrate uptake, but variability is high even within the same type of systems (Smith and del Giorgio 2003). The low fraction of active cells observed during summer in Balsfjorden can be explained by a high grazing pressure from picoflagellates and nanoflagellates on the actively growing cells. It is previously shown that heterotrophic flagellates can selectively graze on larger and more active bacteria (Sherr et al. 1992; del Giorgio et al. 1996; Gonzalez 1996). The results from Balsfjorden support the hypothesis that predation may be a strong regulating factor for bacteria abundance, and predation can also play an important role in shaping the community structure.

Species specific seasonal changes in DOM assimilation

To investigate the species dynamics within the bacteria community a genetic approach was used to identify changes in the most abundant groups (*Alphaproteobacteria*, *Gammaproteobacteria* and *cytophage*-like bacteria or bacteroidetes) and sub-groups (*Roseobacter* and SAR 11). *Alphaproteobacteria* and *Cytophage*-like bacteria dominated the abundance, as also found in Arctic waters (Elifantz et al. 2007; Vila-Costa et al. 2008; Kirchman et al. 2010) and in Antarctic waters (Straza et al. 2010). No clear pattern of seasonal succession was evident for the abundance of the three main groups of bacteria in Balsfjorden (**Paper IV**). Looking at the two sub-clades of *Alphaproteobacteria*, the SAR 11 and *Roseobacter*, it became clear that these two clades experienced large differences in abundances. This illustrates that these two groups are probably functionally very different. However, as abundance is determined by both growth and mortality, changes in bacterial abundance do not always indicate changes in growth.

The contribution from the three main groups to the uptake of DOM was well correlated (R^2 = 0.95, $p < 0.01$) with the abundance (Figure 10), and indicated that the abundance to a large extent determined the groups contribution to assimilation of DOM. However, the *Alphaproteobacteria* group always contributed more to activity than expected by their abundance, probably explained by higher predation pressure than other groups.

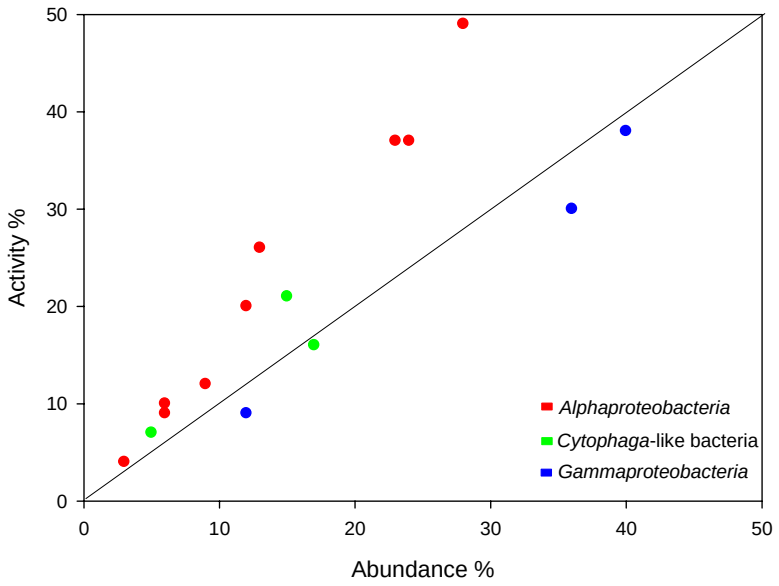


Figure 10. Percentage contribution to biomass and activity for the three main groups investigated in this study.

Generally, the *Roseobacter* clade had high fractions of active cells assimilating the different types of DOM. From the fraction of active cells within this clade one would expect a very high abundance, but the abundances were relatively low. This group has been found to have larger cell size than for example *Cytophage*-like bacteria, and therefore they are more exposed to predation (Gonzalez 1996). They have also been found to be very active in assimilating many different substrates, even at low concentrations (Alonso and Pernthaler 2006a). This corresponds well with our results, which show that even though this clade is not very abundant it probably plays an important role in the turnover of DOM and other elements.

6. Conclusions

The present doctoral study has provided new knowledge on primary production dynamics, the importance of small autotrophic and heterotrophic cells in arctic marine ecosystems and the activity of bacterial communities associated with the seasonal changes in algal biomass.

1. The onset of the spring bloom in Kongsfjorden was found to be closely linked to the hydrographical conditions and the sea ice break-up. The peak of the bloom in fjords on the west coast of Svalbard will probably occur between the middle of April and the middle of May. Primary production in Kongsfjorden remained high after the peak of the bloom because of mixing with nutrient-rich deep water masses. This means that in weakly stratified systems, high primary production will be able to persist for a long time due to mixing with nutrient-rich water masses.
2. Phytoplankton biomass and primary production were found to be highly heterogeneously distributed in the seasonally ice-covered regions of the Barents Sea. Different stages of the ice edge bloom were found spatially distributed in the marginal ice zone on the same temporal scale, following the large variations in ice cover. The most productive phytoplankton blooms occurred in May and were categorized as peak blooms. But no clear patterns of primary production were found for the different stages of the bloom or relative to latitude.
3. Primary production during ice edge blooms in the marginal ice zone of the northern Barents Sea ranged 103-1475 mg C m^{-2} d^{-1}, which is within ranges found in other seasonally ice-covered arctic shelf regions. A relatively large part (24%) of the primary production during ice edge blooms was performed at sub-surface depths (> 20 meters). Primary production in sub-surface maximum is often not sampled and can lead to underestimation of the primary production.
4. The contribution of small cells to primary production (46%) during ice edge blooms was larger than expected. Production to biomass ratios clearly indicated that small cells were either exposed to heavy grazing or they were more efficient primary producers than the larger cells. At as much as seven out of 10 stations small cells dominated chlorophyll *a* concentrations or primary production rates, which supports the increasing evidence that arctic food webs not only are dominated by large cells. The substantial contribution of

small cells to primary production found during ice edge blooms in the Barents Sea has implications for the energy transfer through the food web, with a large part of the energy entering the microbial food web.

5. Picoeukaryotes were numerically the most important protist in the Arctic Ocean. Even though the abundance decreased from the Alaskan shelf towards the less studied central part, the abundances in the central Arctic Ocean was still in the high range of what has been reported from other Arctic regions. The fraction of heterotrophic cells was highest (72%) in the central part of the Arctic Ocean, which probably increased the grazing pressure on the bacteria community, indicated by the very low bacteria abundances in this part of the ocean (0.2-0.9 10^5 cells ml^{-1}). Whether the very low bacteria abundance in the Canada Basin and the central part of the Arctic Ocean is caused by low growth rates or high grazing pressure will need further studies before we can fully understand the role that the microbial food web play in the Arctic Ocean.
6. A substantially higher number of bacteria in Balsfjorden was active in substrate assimilation in summer than in winter, which illustrates the important role heterotrophic bacteria play for the turnover of carbon and other essential elements during the season when nutrients are depleted. However, the lowest active fraction of cells was recorded in summer. Bacteria in the *Roseobacter* clade were very active in substrate assimilation, but were numerically low. This leads to the conclusion that heterotrophic flagellates selectively graze on active cells and play an important role in shaping the structure of the bacteria community both in regard to species composition and in fraction activite.

7. Future perspectives

Predicting future changes in arctic marine ecosystems is challenging since the Arctic in general, and the Arctic Ocean in particular, are among to the least investigated regions of the world (Wassmann 2006). Future changes in the Arctic are predicted to be diverse and complex and include; decrease in ice cover, increased wind-induced upwelling in open water shelves, decrease in salinity in surface layers, stronger stratification in the central Arctic Ocean and increase in DOM. These changes will, for sure, affect the marine ecosystem - but to what extent is still largely unknown. The observed decrease in ice cover will lead to increased levels of irradiance to the ocean surface. Tremblay and Gagnon (2009) proposed that primary production in seasonally ice-covered waters is regulated by nitrogen and increased light will not alter the annual primary production in these areas. But, increased light could affect the timing of the blooming events, probably the species composition, and the possibility to utilize nutrients in the lower eutrophic zone. In open water shelf areas, wind-induced upwelling, recorded in 2007 and 2008, brought nutrients up into the euphotic zone and lead to a 2-6 fold increase in production of ice algae, phytoplankton and benthos (Tremblay et al. 2011). The strong stratification caused by increased freshwater input to the central Arctic Ocean will probably prevent winter mixing with nutrient rich water, resulting in decreasing concentrations of nitrogen in the surface layer, and will also prevent any large acceleration of primary production. Decreased concentrations of nitrate has already led to measurable changes in the community composition of phytoplankton in the Arctic Ocean (Li et al. 2009), with increased importance of small cells (< 2 μm). Increasing amounts of DOM, together with increasing temperature, suggest an increase in prokaryotic production and respiration. However, the regulation of bacteria growth by substrate and temperature are still largely unknown, and the regulating mechanisms seem to be very complex (Kirchman et al. 2009b).

A lot of effort is already put into developing models that can predict the effects of the future climate changes. These models are important for us to be able to capture changes and differences on large scales. Still, it is very important to continue to collect empirical data to compare and validate model results. As for now, basic empirical data from the entire Arctic Ocean is needed (Slagstad et al. 2011). Increased data on marine ecosystems have been obtained from the Arctic shelves during the last decade or two, but are to a large extent based on biomass estimates. One

of the challenges for the future is to measure production and to understand processes and regulating mechanisms. For the central Arctic Ocean, even basic data on biomass is missing and all possible data sets from this region would add the knowledge on this remote ecosystem, and its divers.

Molecular biological methods have developed into powerful tools to identify and study aquatic microorganisms independently of successful cultivation. So far, the novel molecular approaches have focused mainly on range of diversity and evolutionary relatedness of different groups. We also need to develop this further. Unexpressed genes and unsynthesized proteins are future potentials, but we need to know about microbial activity and processes linked to genes to understand the role of microbes in various biogeochemical processes.

For a long time, prokaryotes have been considered a “black box”. Using molecular approaches, we now know that prokaryotes consist of highly heterogenic groups. Often, prokaryotes are still grouped together in one box in models describing energy or element fluxes. To fully understand the role of prokaryotes in biogeochemical cycles, or to be able to understand/predict future changes, we need to stop consider prokaryotes as organisms that fit in one box. More work is needed at single-cell levels to understand the complex reasons for the changes that today are observed on community level.

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Paper I

Paper II

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Paper IV

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