UNIVERSITY OF TROMSØ UIT

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Planktonic food webs in the Arctic Ocean:

Structure and function in contrasting seasons and physical settings across Fram Strait

Lena Seuthe

A dissertation for the degree of
Philosophiae Doctor

December 2011

Planktonic food webs in the Arctic Ocean:

structure and function in contrasting seasons and physical settings across Fram Strait

Lena Seuthe

Department of Arctic and Marine Biology
Faculty of Bioscience, Fisheries and Economics
University of Tromsø

Thesis submitted in partial fulfilment of the requirements for the
Doctor Philosophia degree

December 2011

Defence at the Faculty of Biosciences, Fisheries and Economics, University of Tromsø
December 8, 2011

Leader of the committee:	Professor Svein Kristiansen
	Department of Arctic and Marine Biology, University of Tromsø
First opponent:	Professor Tron Frede Thingstad
	University of Bergen, Norway
Second opponent:	Dr. Dolors Vaqué
	Institut de Ciències del Mar, Spain

When we try to pick out anything by itself,
we find it hitched to everything else in the universe.
John Muir (1911)

Acknowledgments

Many people have contributed to this thesis in one way or the other and they all deserve a great thanks. Some persons I wish to thank in particular. First of all, I wish to express my sincere gratitude to my supervisors, Paul Wassmann and Marit Reigstad. Paul has been my scientific mentor since my master thesis. Paul's busy schedule led to little contact between us at times, but I always could count on his fast and constructive comments on manuscripts no matter where in the world he was. Thanks, Paul, for your constant trust and belief in me, leaving me the liberty to find my own way slightly aside from "vertical export". More than anyone else, Marit has contributed to this thesis by her great scientific insight and human wisdom. Thank you, Marit, for your never-ending enthusiasm, practical and mental support, and making me laugh when things were at their darkest. You have been the most wonderful and inspiring person to work together with!

This work would not exist in its current form, was it not for the small "megalomania" of my fellow combatant, Kriss Rokkan Iversen, which resulted in many sleepless nights, but most of all in one of few Arctic seasonal studies. A great thanks to Kriss and the third cloverleaf, Fanny Narcy, for many unforgettable days and nights in Ny Ålesund. The "sedimentation group" and the ARCTOS network have been my scientific home for the last eight years, and I wish to thank all members for the open and friendly atmosphere which has made work so enjoyable. Special thanks to Christian Wexels Riser, Camilla Svensen, and Tobias Tamelander, whose readiness to discuss various aspects of ecology has been of great help and inspiration. Thanks are due to all my co-authors, Kriss Rokkan Iversen, Fanny Narcy, Camilla Svensen, Birte Töpper, Raquel Vaquer-Sunyer, Runar Thyrhaug, Anna Pasternak, Yulia Vasilyeva, and Edmond Hansen for their thoughtful comments on manuscripts and figures. I am indebted to Einar M. Nilssen and Raul Primicerio for their repeated help with statistical problems.

I am very grateful for the good time with and support by the crews on RV Jan Mayen, RV Lance, and KV Svalbard, making fieldwork to highlights of my working life. Special thanks to John-Terje Eilertsen, Kristen Fossan, and Tor Ivan Karlsen for technical assistant in the field. Fieldwork would not have been the same without all my great colleagues, with whom I had the honour to spent so much time filtering water, freezing on deck, and watching polar bears – thanks to you all! On land, work would not have been the same without all the coffee and lunch breaks with my fellow students, giving small daily refuges from Exel-sheets and uncompleted manuscripts. Thanks, Helene, Matias, Elisabeth, Louise, Clara, and Tobias for all these hours pondering about the small and large questions in life. During the last days of my PhD, Lisa Bjørnsdatter Helgason and Helene Hodal have given me much practical and mental support, for which I am deeply thankful. Malin Daase has been my hairdresser, psychologist, and graphic designer for the last ten years, and she alone deserves the credit for the nice colourful figures in the synthesis of the present work. The last days of my PhD would have been unthinkable without your all-embracing help, Malin. Thank you so much for your friendship!

Last but not least, I wish to express my deepest gratitude to my family for their constant support: My parents, for their sincere interest in and respect for my work. Edmond and our wonderful daughter, Maja, for filling my life with love and laughter.

Tromsø, 2. November 2011
Lena Seuthe

Abstract

This thesis investigates the structure and function of planktonic food webs at two sites between Greenland and the Svalbard Archipelago, covering a coastal ecosystem influenced by Atlantic water masses (Kongsfjorden, 78º N) and a more oceanic system off the East Greenlandic shelf, influenced by the outflow of Arctic water and sea ice from the Arctic Ocean (northwest Fram Strait, 75 - 80º N). In Kongsfjorden, a seasonal study was conducted with sampling at six occasions between March and December 2006. Logistical constrains prohibited a similar extensive seasonal investigation in the ice-covered waters of northwest Fram Strait. Sampling fell into the onset (April-May 2008) and end (September 2006/2007) of the productive season. All four studies investigated the stocks of pico- to micro-sized autotrophs and heterotrophs, i.e. heterotrophic bacteria, proto- and metazooplankton. Production rates of autotrophs and heterotrophic bacteria were measured in Kongsfjorden. Ratios of heterotrophic and autotrophic biomass (H:A) and of specific bacterial and primary production (μ_{Bac}:μ_{Phyto}) allowed to asses the overall structure and function of the investigated planktonic food webs and to compare them to published data from other Arctic regions. The emerging picture provides three distinct food web modes, where mode A is characterized by H:A < 1 and μ_{Bac}:$\mu_{\mathrm{Phyto}} > 1$, new production, and large-celled phytoplankton. Mode B and C are characterized by dominance of heterotrophs (H:A > 1), more regenerated production, and small-celled phytoplankton. The difference between mode B and C is a difference in the specific production ratio, with μ_{Bac}:μ_{Phyto} smaller and larger 1, respectively. According to this scheme, Arctic plankton communities appear to prevail under mode B and C most of the year. In Kongsfjorden, e.g. five of the six months sampled fell under mode B and C, with mode C being typical for light-limited winter communities. From own and literature data, it is suggested that the food web mode controlling physical factors are the amount of incident photosynthetically active radiation (PAR), ice cover, nutrient concentration, and water column stability. Due to an approximately latitudinal change in these physical settings, the relative prevalence of the three food web modes changes from the marginal seas to the central Arctic Ocean, with mode A most likely being absent from the highest latitude waters. In general, Arctic plankton communities appear to sustain on average a 3-fold higher H:A biomass ratio for a given phytoplankton stock than the world's coastal oceans, which may mainly be due to extensive import of long-lived copepods from sub-Arctic European seas through advection. It is argued that the large stock of heterotrophs plays a crucial role in structuring Arctic plankton communities, with the potential to prohibit phytoplankton bloom formation (mode A) through extensive grazing.

Table of contents

List of papers

This thesis is based on the following papers which are referred to by their Roman numbers:

I Rokkan Iversen K, Seuthe L (2011) Seasonal microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): I. Heterotrophic bacteria, picoplankton and nanoflagellates. Polar Biology 34:731–749. doi: 10.1007/s00300-010-0929-2

II Seuthe L, Rokkan Iversen K, Narcy F (2011) Microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): II. Ciliates and dinoflagellates. Polar Biology 34:751–766. doi:10.1007/s00300-010-0930-9

III Seuthe L, Töpper B, Reigstad M, Thyrhaug R, Vaquer-Sunyer R (2011) Microbial communities and processes in ice-covered Arctic waters of the northwestern Fram Strait (75 – 80ºN) during the vernal pre-bloom phase. Aquatic Microbial Ecology 64:253-266. doi:10.3354/ame01525

IV Svensen C, Seuthe L, Vasilyeva Y, Pasternak A, Hansen E (in press) Zooplankton communities across Fram Strait in autumn: are small copepods and protozooplankton important? Progress in Oceanography (2011). doi:10.1016/j.pocean.2011.08.001

1. Preface

I remember watching the stars as a child, holding my breath in deep excitement and respect for this seemingly infinite number of twinkling lights. Despite my parents' repeated assertion that the number of stars was all but endless, alone the view of the milky way has evoked the same deep feeling of an incomprehensible quantity ever since. It was not before my time at university that I learned that not only was there an estimate for how many stars there are in our universe (10^{21}; van Dokkum & Conroy 2010), but that the number of bacteria inhabiting our world's oceans is estimated to be 10 million times higher (10^{28}; Whitman et al. 1998). No wonder that I became curious. In nature, organisms that numerous must be keystones species in the food webs they are part of.

This thesis does not focus on bacteria exclusively, but includes also microbial plankton organisms that are several orders of magnitude larger (see Box 1). Yet, this work is dedicated to those parts of the marine food web closely linked to bacteria. The motivation for this thesis is anchored in a persistent fascination for brain-blowing large numbers and an enthrallment for how small things (nanoscale) can impact the structure and function of entire ecosystems.

2. Introduction

2.1 Marine planktonic food webs: the basic functional modes

Bacterial biomass largely exceeds the joint biomass of fish and mammals in the World Ocean (Pomeroy et al. 2007), suggesting that bacteria play a vital role in marine food webs. Indeed, bacteria can be placed at the base of marine food webs together with phytoplankton, i.e. the main primary producers in the sea. Marine heterotrophic bacteria are, however, part of the secondary production as they utilize dissolve organic carbon (DOC), which is ultimately derived from the photosynthetic conversion of inorganic into organic carbon. While photosynthesis leads to the formation of particulate organic carbon, it also includes a variable fraction of extracellular organic carbon (Mague et al. 1980, Gosselin et al. 1997, Vernet et al. 1998), which is concentrated in the matrix around small-celled organisms, aggregates, and faecal pellets, or dilutes in the sea (Azam & Malfatti 2007). Further, organic carbon is added to the dissolved pool by processes such as viral cell lysis (Bratbak et al. 1992, Suttle 2005),

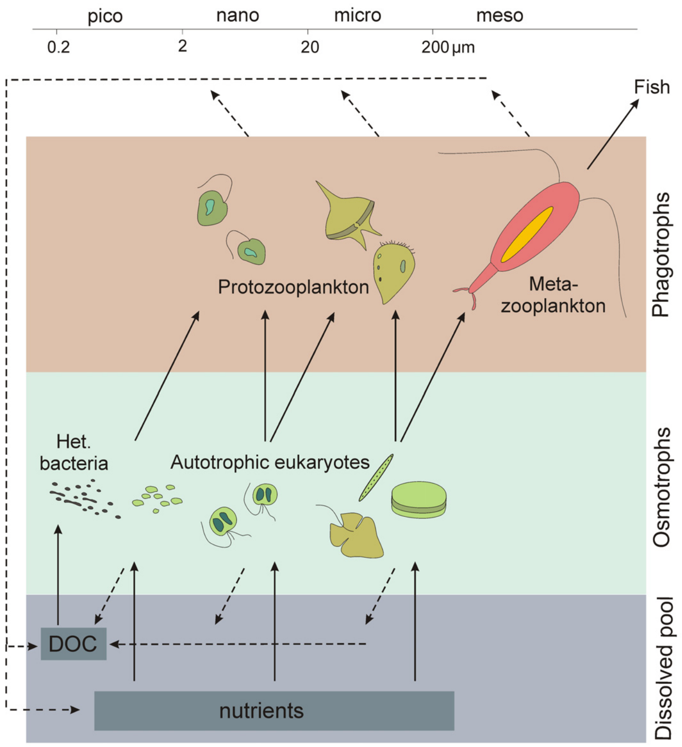

Fig. 1: Conceptual diagram of the planktonic food web, indicating the main functional groups of organisms, grouped according to size and modes of nutrition and energy acquisition (see Box 1). Basic trophic interaction between the different organism groups are indicated by black arrows, as well as the potential recycling of organic carbon and nutrients by broken arrows. Figure modified from Fenchel (1987).

excretion and sloppy feeding by phagotrophs (Roy et al. 1989, Nagata & Kirchman 1991, Møller 2007). The dependence of bacteria on DOC as well as inorganic nutrients (Zweifel et al. 1993, Rivkin & Anderson 1997, Sala et al. 2002) links them tightly to the dynamics and production of phytoplankton (Cole et al. 1988, Ducklow & Carlson 1992, Ducklow 1999). This circumstance is reflected by a remarkably constant relationship between bacterial and primary production in the World Ocean, averaging about 0.15 to 0.2 (Cole et al. 1988, Ducklow et al. 1999). The ratio between bacterial and phytoplankton biomass ranges, on the other hand, by an order of magnitude (Ducklow 1999), indicating that stocks expand until removal processes cap them, i.e. engulfment by predators (Fenchel 1982, Sanders et al. 1992, Vaqué et al. 1994, Karayanni et al. 2008) or cell lysis due to viral infection (Suttle 2005).

Heterotrophic nanoflagellates are the prime consumers of bacteria (Fenchel 1982, Sanders et al. 1992, Vaqué et al. 1994) and are a major trophic link between picoplankton (Box 1) and larger protozoan (unicellular) and metazoan (multicellular) predators. Among the larger protozoan predators, heterotrophic ciliates and dinoflagellates are predominating in most

Box 1 Classification of plankton

Planktonic organisms can be classified in many different ways, e.g. according to:

1. Size

Cell size is relatively easy to determine by traditional microscopy, at the same time as it affects metabolic rates and ecological functions. It is therefore widely used to divide planktonic organisms into logarithmic size classes (Sieburth et al. 1978) of ***mesoplankton*** (2000 – 200 µm), ***microplankton*** (200 – 20 µm), ***nanoplankton*** (20 – 2 µm) and ***picoplankton*** (2 – 0.2 µm), as depicted in Fig. 1.

A general trend appears to be that smaller organisms have i) higher specific affinity for nutrients due to a high surface area per unit volume (Jumars et al. 1993), ii) higher growth rate under nutrient or light limitation (Banse 1982, Thingstad & Sakshaug 1990), iii) decreased sinking rates (Smayda 1970), but iii) increased vulnerability to density control by grazing, since the numerical response time of grazers decreases with size (Kiørboe 1993). Most planktonic predators display size-selectivity and have a rather constant predator-prey size ration (Hansen et al. 1994).

2. Mode of energy acquisition

Organisms can acquire metabolic energy in two basic ways, i.e. by either heterotrophy or autotrophy. ***Heterotrophs*** consume particulate or dissolved organic matter to supply energy for synthesis of cellular components. ***Autotrophs***, on the other hand, gain energy from the fixation of inorganic carbon, for example by photo- or chemosynthesis.

Autotrophs and heterotrophs are found among unicellular and multicellular eukaryotes, as well as among prokaryotes, such as bacteria. A large number of protists are ***mixotrophic*** (Stoecker et al. 1989), i.e. combining both auto- and heterotrophy. In the present work, all organisms containing chloroplasts are classified as (photo-) autotrophs, although a large fraction of them may combine photosynthesis (i.e. conversion of inorganic into organic carbon by using light as energy source) with consumption of organic matter.

3. Modes of nutrition

Organisms can take up nutrition by engulfment of other organisms, called ***phagotrophy***, or by diffusion of dissolved organic or inorganic nutrients over the cell surface, i.e. ***osmotrophy***. By this classification, both heterotrophic bacteria and autotrophic phytoplankton are osmotrophs. As the surface area-to-volume ratio increases with decreasing size, smaller osmotrophs are generally the better competitors for a shared limiting substrate. Both, bacteria as well as phytoplankton need inorganic nutrients for growth and may be in competition for those in many ecological settings in the sea (Currie & Kalff 1984, Bratbak & Thingstad 1985).

marine ecosystems (Pierce & Turner 1992, Sherr & Sherr 2007), preying not only on nanoflagellates, but on a large variety of organisms of all sizes, down to pico-sized particles (Hansen et al. 1994). Consequently, ciliates and dinoflagellates are not only predators on nanoflagellates, but partly compete with them for the same source of food. Coexistence of competitive and predator-prey relationships is also encountered between ciliates, dinoflagellates and larger metazoan predators, such as copepods. Depending on the copepod species and the ecosystems' trophic state, copepods graze not only on larger phytoplankton, such as diatoms, but prey upon protozooplankton, i.e. heterotrophic nanoflagellates, ciliates, and dinoflagellates (Stoecker & Capuzzo 1990, Kleppel et al. 1991, Levinsen et al. 2000b, Calbet & Saiz 2005). Predation by copepods on protozooplanton can generate trophic cascades within the microbial plankton community, profoundly shaping composition and rates of lower trophic levels down to primary producers and bacteria (Pace et al. 1999, Zöllner et al. 2009). Thus, a multitude of trophic interactions coexist in the sea, hampering the study of carbon and nutrient flow from the dissolved pool to metazoans, i.e. higher trophic levels. To cope with this complexity, simplified models of planktonic food chains have been developed (e.g. Fig. 1).

The simplest of these theoretical planktonic food chains places large phytoplankton, such as diatoms at the base of the chain. Diatoms are grazed upon by copepods, which in turn are prey for fish (depicted at the right hand side of Fig. 1). The counterpart to this "classical" model was described by Azam et al. (1983) as "microbial loop". In this model bacteria form the basis of the food chain, utilizing DOC of phytoplankton origin (depicted at the left hand side of Fig. 1). The term "loop" was chosen because the bacterial based food chain requires an increased number of trophic level for photosynthetically fixed energy to reach copepods and fish. Each trophic interaction leads to loss of about 10 – 20% energy due to respiration processes (Ryther 1969). Most of the originally induced energy is thus respired before reaching higher trophic levels. In this process, carbon and nutrients are released to the dissolved pool, returning them to their source and thus closing the "loop".

In nature, the *classical* and *microbial* food chains do not only coexist beside each other, but interweave in a multitude of different ways to one food web. Nevertheless, various biotic and abiotic factors lead to the modulation of planktonic food webs of more *classical* or *microbial* character (Legendre & Rassoulzadegan 1995). In general, differences in food web structure can be found between coastal and open-ocean ecosystems (Ryther 1969, Cushing 1989, Legendre & Rassoulzadegan 1995, Gasol et al. 1997). While autotrophs (i.e. phytoplankton) contribute more to total plankton biomass in coastal seas, heterotrophs (i.e. heterotrophic bacteria, proto- and metazooplankton) dominate in open oceans (Legendre & Rassoulzadegan 1995, Gasol et al. 1997). Metazooplankton, and especially copepods, dominate the heterotrophic biomass in coastal waters, while the composition of heterotrophs appears more

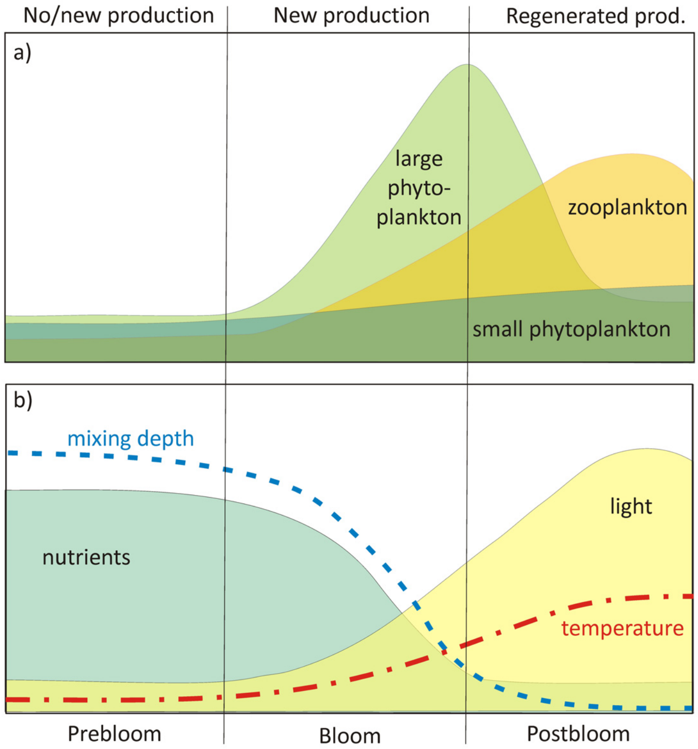

Fig. 2: Development of important a) biotic and b) abiotic factors from the prebloom to postbloom phase of a theoretical high-latitude system, modified from Berreville et al. 2008

equally partitioned between bacteria and the bulk of proto- and metazooplankton in the open sea (Gasol et al. 1997). This indicates that a greater proportion of photosynthetically fixed energy flows through *microbial* food webs under stratified oligotrophic conditions, whilst being more directly channelled to metazoan plankton and fish in more eutrophic waters (Cushing 1989, Uye et al. 1999). The dominance of copepods in turn, leads to a strong predation pressure on, and subsequent suppression of protozooplankton stocks in coastal areas (Ratkova et al. 1998, Levinsen & Nielsen 2002), generating a food web of more *classical* character.

A crucial abiotic factor, generating the described differences between coastal and open-ocean systems, is the concentration and supply of inorganic nutrients (Legendre & Rassoulzadegan 1995, Duarte et al. 2000), with coastal systems being generally more eutrophic than the open sea. The more eutrophic nature of coastal areas leads at least temporarily to the build-up of larger phytoplankton stocks than in open seas (Valiela 1995). Plankton communities in open-ocean sustain, however, on average a 10-fold higher heterotrophic biomass for a given autotrophic biomass than coastal planktonic systems (Gasol et al. 1997). This is caused by the higher phytoplankton growth rates occurring in oligotrophic systems (Goldman et al. 1979,

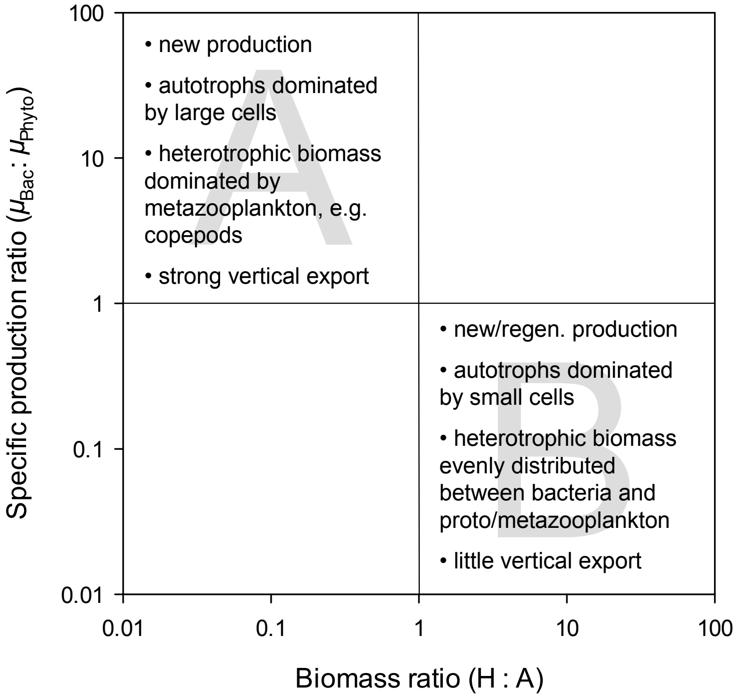

Fig. 3: Theoretical classification of the two main modes of planktonic food webs, determined by the specific production ratio of bacteria versus phytoplankton (μ_{Bac}:μ_{Phyto}) and the biomass ratio of heterotrophs (H = heterotrophic bacteria, proto- and metazooplankton) and autotrophs (A).

Laws et al. 1984), fuelled through the efficient recycling of nutrients by the heterotrophic *microbial* community (Azam et al. 1983). In contrast, the build up of large phytoplankton stocks and direct transfer to metazooplankton leads to the loss of a larger fraction of autotrophic biomass (i.e. nutrients) to deeper water layers and the benthos in coastal areas (Wassmann 1990, Baines et al. 1994). This results, in turn, in larger seasonal changes in structure and functioning of coastal plankton communities compared to open-ocean systems (Cushing 1989).

The seasonal change in plankton structure in high- and mid-latitude coastal areas consists primarily of a shift from a nitrate-based *new production* to an ammonium-based *regenerated production* (Dugdale & Goering 1967, Eppley & Peterson 1979), regulated by the plankton communities' capacity for nutrient regeneration. In general, *new production* occurs after the replenishment of inorganic nutrients in the euphotic zone from deeper water layers through mixing events, advection or upwelling (Fig. 2). Storms during autumn and winter can erode water column stratification and amend surface waters with nutrients. Subsequently, *new production* and large stocks of phytoplankton, dominated by large cells such as diatoms, are recurrently encountered in coastal seas during spring (Ryther 1969, Cushing 1989). The vernal bloom is initiated by the increase in photosynthetically active radiation (PAR), and in some areas also by the shallowing of the mixing depth (Sverdrup 1952, Platt et al. 1991). The build-up of a large autotrophic biomass and often the presence of a food web of *classical* character, results in the depletion of essential nutrients in the surface waters (Valiela 1995). The subsequent resource-control of autotrophs changes the balance between competing species and groups of organisms, leading to a restructuring of the food web to one of more pronounced *microbial* character. Production becomes thus sustained by the microbes' nutrient regeneration (Azam et al. 1983), often associated with rises in water temperature and shallowing of the surface mixed layer (Cushing 1989, Kiørboe 1993).

In summary, planktonic food webs shift between two main patterns, as depicted in Fig. 3 as mode A and B. Mode A reflects a more classical plankton community generated by new production with an autotrophic biomass dominating over that of heterotrophs (H:A < 1). Concomitantly, bacteria exert a higher specific production rate than the autotrophs ($\mu_{Bac}:\mu_{Phyto} > 1$)*. In mode B, heterotrophs dominate planktonic biomass (H:A > 1), sustained by fast-growing autotrophs* ($\mu_{Bac}:\mu_{Phyto} < 1$)*, which in turn are fuelled by the efficient recycling of nutrients by the microbes.*

2.2 Specificities of Arctic marine ecosystems

Arctic seas are distinct from other marine ecosystems in a number of ways, such as extreme seasonal changes in solar radiation and sea ice cover. Sea ice affects plankton communities twofold, by limiting penetration of PAR to the water column and strongly stratifying the water column due to freshwater release in connection with sea ice melt in summer. The strong water column stratification efficiently impedes the replenishment of nutrients to the upper mixed layer. Thus, strong water column stratification and shorter seasonal photoperiod results in lower annual primary production in ice-covered high-latitude systems, compared to lower latitude open water regions (Wassmann & Slagstad 1993, Reigstad et al. 2002, Sakshaug 2004).

While sea ice impinges the overall productivity in Arctic seas, sea ice melt in spring/summer initiates intense blooms of phytoplankton along the ice edge, often dominated by diatoms (Sakshaug & Skjoldal 1989). These blooms (mode A) are highly transient due to the fast depletion of nutrients in the fresh surface layer, lasting seldom longer than 20 days (Perrette et al. 2011). They are, however, crucial for pelagic secondary production (Ringuette et al. 2002, Leu et al. 2011), and may generate up to 65% of the annual primary production in productive seas like the Barents Sea (Sakshaug 2004). Hence, substantial vertical export of biogenic matter out of the euphotic zone may be connected to these blooms, thus fuelling much of the benthic production in Arctic marginal shelf seas (Piepenburg et al. 1997, Reigstad et al. 2008).

Pomeroy and Deibel (1986) postulated that temperature-inhibited bacterial production allowed for the development of these extensive phytoplankton blooms in perennially cold seas, since only little of the photosynthetically produced material might be subjected to bacterial degradation. In later years, several studies (e.g. Thingstad & Martinussen 1991, Rivkin et al. 1996, Wheeler et al. 1996, Rich et al. 1997, Yager et al. 2001) have casted doubt on the Pomeroy hypothesis and on whether bacterial growth is inhibited by low temperatures (Box 2). In fact, bacterial growth rates similar to those at lower latitudes have been reported from Arctic seas in summer (Rivkin et al. 1996, Anderson & Rivkin 2001). During winter, bacterial production is low (Sherr & Sherr 2003, Garneau et al. 2008) most likely due to the lack of labile DOC production through phytoplankton (Thingstad 2009).

Among the many unresolved questions is how organisms, not only bacteria, survive months without larger food supply (Paffenhöfer et al. 2007). The presence of virtually all major prokaryotic and eukaryotic lineages in Arctic waters (Lovejoy et al. 2006, Bluhm et al. 2011, Lovejoy & Potvin 2011) demonstrates, however, the successful adaptation of organisms not only to low temperatures, but also to the extreme seasonality in food supply.

Organisms have adapted differently to the long periods of food scarcity of polar seas. Among protists, mixotrophy is common (Stoecker et al. 1989, Putt 1990), although information on the extent and seasonal variation in mixotrophy is unknown from Arctic areas (but see Levinsen et al. 2000a). The best investigated adaptation to the pulsed Arctic food regime is that of larger copepods of the genus *Calanus*. These copepods synthesize large amounts of wax esters and fatty acids during the periods of elevated food supply (Lee et al. 2006). These internally sequestered lipids allow the copepods to survive the winter non-feeding at depth, and some can even fuel their reproduction based upon their internal lipid reserves (Conover & Huntley 1991, Falk-Petersen et al. 2009). The result of this strategy is twofold. It allows these

Box 2 Possible effects of low water temperatures

Temperature influences all biochemical reaction rates, and subsequently the metabolism of all organisms, from prokaryotes to unicellular and multicellular eukaryotes (Gillooly et al. 2001). Nearly all rates of biological activity increase exponentially with temperature. Many biological rates double or triple over a temperature increase of 10º C (e.g. Hansen et al. 1997). It is thus only consequent that the impact of low water temperatures on planktonic communities in polar waters has repeatedly been an issue of debate. Especially the formation of extensive phytoplankton blooms in cold waters have lead to hypothesis that growth rates of phytoplankton and heterotrophs might be affected differently by temperature (Pomeroy & Deibel 1986, Rose & Caron 2007).

For heterotrophic bacteria, the discussion on whether temperature is limiting their production has been ongoing since the article by Pomeroy and Deibel (1986). Yet, no consensus is reached, except for the notion that it might not be temperature per se which is limiting bacterial production in polar seas, but rather some combination of temperature with other factors, such as e.g. low concentrations of labile DOC (Pomeroy & Wiebe 1986, Thingstad & Martinussen 1991, Nedwell 1999, Middelboe & Lundsgaard 2003, but see Kirchman et al. 2005, Kirchman et al. 2009). Others argue that the low bacterial production often observed in polar waters may be the result of low standing stocks, despite relatively high bacterial growth rates (Billen & Becquevort 1991, Rivkin 1991, Rivkin et al. 1996). High rates of bacterivory (Laurion et al. 1995, Anderson & Rivkin 2001, Duarte 2005) and viral lysis (Wells & Deming 2006, Payet & Suttle 2008) have been argued to be responsible for the low bacterial stocks. Hence, some authors disagree with the notion that heterotrophic bacteria and the microbial food web connected to them are of less importance in the cycling of carbon in polar waters than elsewhere (Rivkin et al. 1996, Wheeler et al. 1996, Rich et al. 1997, Yager et al. 2001).

For protists, Rose and Caron (2007) suggested that the growth of heterotrophs were more severely hampered by decreasing temperatures than that of phototrophic protists. They speculate that the difference could be due to different temperature-dependence of catabolic and anabolic processes. The authors themselves appreciate, however, that data on growth rates of heterotrophs at temperatures <5º C are scarce. It thus remains the focus of future work to support or reject the ideas put forward by Rose and Caron (2007).

The observed and expected climatic changes in polar regions have stimulated various experimental investigations of how increased water temperatures may alter polar microbial communities (for review see Sarmento et al. 2010). The results suggest that increased water temperatures will not affect different rates equally, and may profoundly alter food web structure and function.

The present work does not want to negate the effects low water temperature may have on organisms, and subsequently food web structure and function, but does not discuss this issue further in detail.

copepods to time reproduction so that their offspring can take full advantage of the vernal peak in autotrophic biomass and their copepodites to grow and mature through more than one productive season (Falk-Petersen et al. 2009).

The longevity of *Calanus* allows for long-range transportation of these heterotrophs with ocean circulation through the Arctic Ocean and adjacent seas (Mumm 1993, Kosobokova & Hirche 2000, Carmack & Wassmann 2006). The Atlantic species *C. finmarchicus*, for example, is encountered in the central Arctic Ocean (Mumm 1993, Thibault et al. 1999, Kosobokova & Hirche 2000), where it most probably does not reproduce (Kosobokova & Hirche 2000, Slagstad et al. 2011). Kosobokova and Hirche (2000) argue that the Arctic Ocean hosts both an autochthonous and allochthonous metazooplankton community, with the autochthonous biomass being low.

The Arctic marine ecosystem differs from those at lower latitudes due to the extreme seasonality in light, sea ice cover, and strong haline water column stratification, resulting in variable timing of the spring bloom and a generally shorter productive season. The presence of virtually all major prokaryotic and eukaryotic lineages in Arctic waters suggests the successful adaptation of organisms to low water temperatures and strong seasonality in food supply. Arctic metazooplankton composition and biomass appear highly allochthonous.

3. Aims and objectives

The aim of this thesis is it to describe some of the above depicted trophic dynamics through the simultaneous description of stocks and rates of heterotrophic bacteria, phototrophic and heterotrophic protists, as well as copepods in two regions of the European Arctic and at different times of the year. The great heterogeneity of the physical environment in the western part of the European Arctic, namely Fram Strait, called for comparative studies in contrasting (i.e. coastal versus open-sea), but adjacent ecosystems, dominated by Atlantic versus Arctic water masses, respectively. Towards the end the perspective is widened, addressing the pelagic food web structure and function in the entire Arctic Ocean, based on own and literature data.

The specific objectives were:

1. To describe the structure and function of the planktonic food web in a high-latitude coastal ecosystem over the course of a year (**Paper I, II**)
2. To compare the planktonic food web structure of a high-latitude coastal ecosystem with that of an adjacent open-sea ecosystem (**Paper I, II, III, IV**)
3. To identify regulatory mechanisms shaping planktonic food web structure (**Paper I, II, III, IV**)
4. To discuss whether high-latitude planktonic food webs are substantially different from those encountered at lower latitudes (**Paper I, II, III, IV**)

4. Fram Strait – the study area

Fram Strait, situated between northeast Greenland and the Svalbard Archipelago, is the only deep gateway between the Arctic Ocean and sub-Arctic seas. It is a place of extensive water mass exchange with the North Atlantic (Fig. 4). Two opposing current systems characterise the hydrographic and dynamical regime in Fram Strait (Schlichtholz & Houssais 2002, Schauer & Beszczynska-Möller 2009). The West Spitsbergen Current (WSC), a continuation of the North Atlantic Current, is flowing northwards along the shelf slope of West

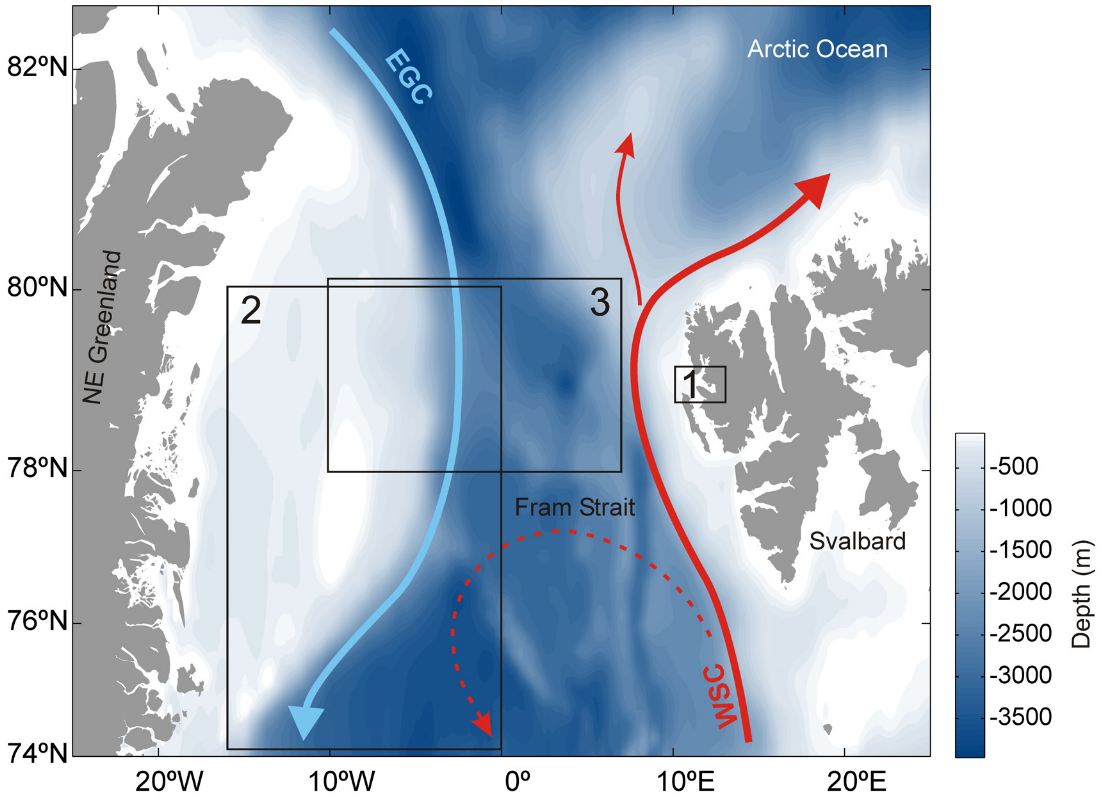

Fig. 4: Overview of the study area between northeast Greenland and the Svalbard Archipleago. The main current systems are indicated, with the West Spitsbergen Current (WSC, red arrows) transporting warm, saline water of Atlantic origin into the Arctic Ocean, while the East Greenland Current (EGC, blue arrow) exports sea ice and cold, fresh water of Arctic origin southwards. Recirculation of Atlantic water occurs between the EGC and WSC (broken red arrow). The sampling areas are indicated by boxes. Box 1: Paper I & II, box 2: Paper III, box 3: Paper IV.

Spitsbergen, transporting warm and saline Atlantic Water (AW; >2ºC and salinity >34.91) into the Arctic Ocean. To the west, the East Greenland Current (EGC; 1º and >6ºW) exports cold Arctic Water (ArW; <0ºC and salinity <34.7) in the upper layers from the Arctic Ocean southwards along the East Greenland shelf slope (Gascard et al. 1988, Schlichtholz & Houssais 2002). Between these two main currents, a complex transitional zone is found where AW from the east recirculates west and southwards, and mix with water masses of Arctic origin to the west (Gascard et al. 1988, Schauer & Beszczynska-Möller 2009). The stratification of the EGC and subduction of AW under ArW at and near the EGC front, results in strong vertical stability opposing the supply of nutrients to the surface mixed layer from below.

Sea ice conditions and position of the ice edge in Fram Strait are mainly determined by dominating wind fields and heat fluxes from the sea (Germe et al. 2011). The latter results in

Table 1 Comparison of surface water mass characteristics of eastern and western Fram Strait. Concentration of dissolved organic carbon (DOC) and nutrients are given in µM. Nutrient concentration are those reported from winter in the surface layer. Total annual primary production is based on model simulations (mg C m^{-2} y^{-1}).

	Western Fram Strait	**Eastern Fram Strait**
Water origin	Central Arctic	North Atlantic
Water mass	Polar Water (PW) [1]	Atlantic Water (AW) [1]
Temperature	<0 ºC[1]	>2 ºC[1]
Salinity	<34.7[1]	>34.91[1]
DOC	75.8 ± 10.2[2]	58.2 ± 4.9[2]
Nitrate	<8[3]	10 - 12[4]
Phosphate	≤0.5[3]	0.75[4]
Silicate	6 - 7[5]	4.5[4]
Primary production (total)	20 - 60[6]	100 - 140[6]
Primary production (new)	13 - 32[7]	55 - 100[7]
Sea ice type	first-year and multi-year	first-year
Sea ice extent	perennial	seasonal

[1] Schlichtholz and Houssais 2002; [2] Amon & Benner. 2003; [3] Paper III; [4] Reigstad et al. 2002; [5] unpublished data M. Reigstad; [6] Reigstad et al. 2011; [7] Sakshaug (2004)

much lower sea ice concentrations on the Atlantic influenced eastern side of the strait over the course of a year. Here, heat flux from the AW prevents local ice formation during winter and enhances melting of advected sea ice from the north. In the west, on the contrary, the EGC exports large quantities of Arctic sea ice (Gascard et al. 1988, Vinje et al. 1998). Historically, thick and old multiyear ice dominated the Arctic pack ice that is exported through Fram Strait, but the thinning of the Arctic sea ice is reflected by the increasing contribution of younger and hence thinner ice (Maslanik et al. 2011). Minimum sea ice extent in the western Fram Strait coincides with the annual ice minimum in the Arctic in September. Primary producers may therefore experience ice-induced PAR limitations during most of the year in the western part of Fram Strait. Thus, highly different production regimes exist at similar latitudes across Fram Strait (Wassmann et al. 2010, Reigstad et al. 2011).

Model simulations suggest an annual primary productivity of 100 to 140 g C m^{-2} y^{-1} in the waters influenced by AW in the east (Reigstad et al. 2011). Total annual primary productivity decreases sharply towards the west to about 20 to 60 g C m^{-2} y^{-1} on the northeast Greenland shelf (Reigstad et al. 2011). Beside light limitation due to ice cover, low concentrations of nitrate in the ArW (<8 µM; Table 1) may limit the overall phytoplankton production in the west (Lara et al. 1994). Owing the heterogeneity of the pack ice, interannual variations in primary production are much larger in the west than in the aestival ice-free east (Wassmann et al. 2010).

The hydrographic differences across Fram Strait make it an ideal place to study ecosystems with contrasting water temperatures, ice conditions, and biogeochemical characteristics, such as concentrations of nutrients and dissolved organic carbon (Table 1). In the present work, financial and logistic restrictions prohibited an entirely ship-based field program for sampling the different open-sea hydrographical regions in Fram Strait on a seasonal scale. The seasonal investigation of the planktonic food web was thus conducted in Kongsfjorden, with the support of the scientific land base in Ny Ålesund (Paper I & II).

Kongsfjorden, situated at the west coast of Spitsbergen (largest island of the Svalbard Archipelago), is facing the Fram Strait to the west and has been argued to be part of the eastern Fram Strait system (Hop et al. 2006). The absence of a sill and presence of a cross-shelf trench allows water mass exchange across the ocean-shelf-fjord boundary, resulting in frequent advection of warm AW from the WSC into the fjord (Svendsen et al. 2002, Cottier et al. 2005). The extent and frequency of advection events varies between years. They have been shown to heavily impact the floral (Hodal et al. in press) and faunal (Basedow et al. 2004, Willis et al. 2006, Willis et al. 2008, Walkusz et al. 2009) plankton community. In late January to early March (Cottier et al. 2007) and mid-May and mid-July 2006 (F. Cottier pers. comm.), an extensive inflow of AW was recorded by an oceanographic mooring in the outer basin of the fjord. Local processes led, however, to the modification of these advected water masses inside the fjord. Strong winds led to intense cooling and mixing of the water column in March, resulting in a homogenous water column of 0.6 ± 0.1ºC and salinity of 34.7 ± 0.2 (Paper I & II). From the time of the snow-melt (May/ June) and onwards, the fjord was influenced by freshwater run-off from glaciers and land, resulting in a shallow stratified water column with surface water salinities of 33.8 ± 0.9. Consequently, local processes (atmospheric cooling, freshwater run-off) and mixing with other water masses within the fjord (Svendsen et al. 2002), result in a very different hydrographical regime than off the shelf.

In summary, the studies on plankton food web structure derive from two different Arctic marine environments. The seasonal study, presented in Paper I and II, is from a high-latitude, ice-free Atlantic influenced coastal system, while the work presented in Paper III and IV is from the Arctic influenced, ice-covered waters of northwest Fram Strait.

5. Results and discussion

5.1 Kongsfjorden: Seasonal changes in planktonic food web structure and function in a high-latitude coastal ecosystem

The structure and function of a high-latitude coastal planktonic food web was investigated in Kongsfjorden (Paper I & II) at six occasions over the course of one year (2006), covering a pre-bloom (March), phytoplankton bloom (April), post-bloom (May), as well as summer (July), autumn (September) and winter (December) situation. Stocks and rates of autotrophs (i.e. biomass of pico-, nano- and micro-autotrophs, as well as total primary production) and heterotrophs (i.e. biomass of heterotrophic bacteria, proto- and metazooplankton, as well as bacterial production) were measured from six depths (1, 5, 10, 15, 25 and 50 m) at one station in the mid section of the fjord. Consequently, neither a high temporal nor spatial resolution was obtained, but all efforts were directed to sampling as many planktonic groups as possible simultaneously, allowing a discussion regarding the planktonic food web as a whole. The result of Paper I & II are summarized in Fig. 5 and Fig. 6.

Example of a mode A planktonic food web

According to the specific production and biomass ratios of autotrophs and heterotrophs, the high-latitude coastal planktonic food web in Kongsfjorden had a more pronounced *microbial* character during most parts of the year (mode B; Fig. 5a; Paper I, II). Only in April, when a dense bloom of phytoplankton was encountered the food web was classified as mode A (Fig. 5a and Fig. 6 upper right panel). The large autotrophic biomass was the result of the seasonal increase in irradiance at concomitantly high concentrations of inorganic nutrients (Paper I), and a low stock of metazoan grazers (Paper II). The latter most probably lead to low grazing pressure on both protozooplankton as well as large phytoplankton. While the increasing stock of protozooplankton may have impeded bloom formation of small phytoplankton, the growth of large phytoplankton was most likely neither controlled by protozoan nor metazoan grazers, thus allowing the bloom formation of large-sized phytoplankton, such as diatoms and autotrophic dinoflagellates (Paper II).

A special feature of the phytoplankton bloom encountered in April was the prodigious abundance of the prymnesiophyte *Phaeocystis pouchetii* (Paper I). *Phaeocystis* is polymorphic, with its life cycle including solitary flagellated cells of 3 to 8 µm size, as well as

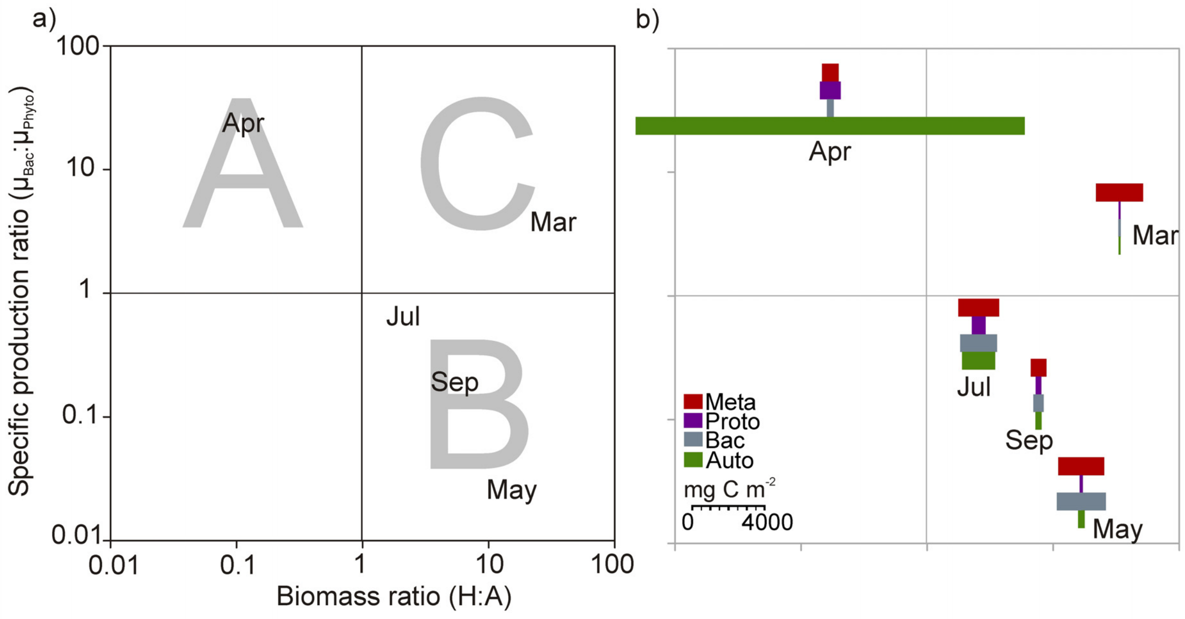

Fig. 5a,b: The planktonic food webs in Kongsfjorden for the different months sampled (Paper I & II), according to a) the specific production ratio of bacteria and phytoplankton (μ_{Bac}:μ_{Phyto}) and the biomass ratio of heterotrophs (H = heterotrophic bacteria, proto- and metazooplankton) and autotrophs (A), as well as b) biomass distribution of autotrophs (Auto), bacteria (Bac), protozooplankton (Proto) and metazooplankton (Meta).

gelatinous colonies of non-flagellated cells, reaching diameters of up to 2 cm (Verity et al. 1988, Rousseau et al. 1994). In Kongsfjorden in April, *Phaeocystis* was present in both solitary as well as colonial forms (pers. obs.). Blooms of the colonial form are recurrent in boreal and Arctic waters (Degerlund & Eilertsen 2010), and have also been reported from warm water areas (Schoemann et al. 2005 and references therein). The mechanisms causing these extensive blooms are still under debate. It might be that *Phaeocystis* escapes grazer control by colony-formation, at least when metazoan grazers are largely absent, as protozoans may not be efficient grazers on the large gelatinous colonies (Nejstgaard et al. 2007 and references therein). Thus, gaps in grazing control on phytoplankton may have lead to the formation of the high autotrophic biomass (Riegman et al. 1993, Irigoien et al. 2005) encountered in Kongsfjorden in April.

The phytoplankton bloom was most likely at its peak or the beginning of senescence, as suggested by the low specific autotrophic growth ($\mu_{Phyto} = 0.02$ d^{-1}). The long generation time of the phytoplankton population was most likely due to the onset of resource limitation for some species, as well as self-shading for large parts of the phytoplankton stock (concentration of Chl *a* remained high with 9 to 10 µg Chl *a* l^{-1} down to 50 m, while primary production dropped markedly below 5 to 10 m depths). Bacteria, on the other hand, thrived with high specific growth rates ($\mu_{Bac} = 0.45$ d^{-1}), most probably utilizing high concentrations of labile DOC from the senescing autotrophs and carbohydrate-releasing *Phaeocystis* (Thingstad & Martinussen 1991, Verity et al. 1991, Janse et al. 1999). This facilitated the build-up of a large bacterial stock as encountered in the post-bloom situation in May, resulting in a very different plankton biomass distribution than in April (Fig. 5b).

Three examples of mode B planktonic food webs

Example 1: While plankton biomass was distributed according to a regular upward pointing biomass pyramid with a broad autotrophic base in April, the biomass pyramid became inverted in May (Fig. 5b), as the concentration of essential nutrients became more limiting (N:P = 1.7) and primary production most probably largely based on *regenerated* nutrients (Paper I). Under these conditions (mode B; Fig. 6 middle left panel), bacterial biomass was as large as that of total zooplankton (proto- and metazooplankton), resulting in a biomass ratio (H:A = 15) similarly high to that found in winter. Metazoans dominated total zooplankton, and meroplankton, copepod nauplii, and small copepodids contributed >50% to the total metazooplankton biomass (Paper II), as often encountered in coastal and shelf waters at this time of the year (Turner et al. 2001, Pasternak et al. 2008).

The high contribution of meroplankton and copepod nauplii suggested that the extensive phytoplankton bloom in April had not only fuelled reproduction of holoplankton, but also that of benthic animals, most likely due to an efficient pelagic-benthic coupling as result of the high autotrophic biomass (Wassmann & Reigstad 2011). Vertical export and most probably substantial grazing by an increased metazoan community, lead to a reduction of phytoplankton and protozooplankton biomass in May compared to April by a factor of 60 and 7, respectively (Paper I and II, respectively). The potential top-down control of the phytoplankton in May was illustrated by a very high population growth rate ($\mu_{Phyto} = 1.2$ d^{-1}). In contrast, the large biomass of bacteria experienced most likely a weak substrate limitation as indicated by i) the low specific growth of the population ($\mu_{Bac} = 0.03$ d^{-1}), ii) a good linear correlation of log-transformed bacterial biomass and log-transformed bacterial production ($y_{Log\ BB} = 1.787 + 0.236x_{Log\ BP}$; $r^2 = 0.906$; $p < 0.05$) according to Ducklow (1992), as well as iii) low bactivorous biomass (heterotrophic nanoflagellates, the main predators on bacteria, contributed only 8 % to the already low total protozooplankton biomass). The data do not

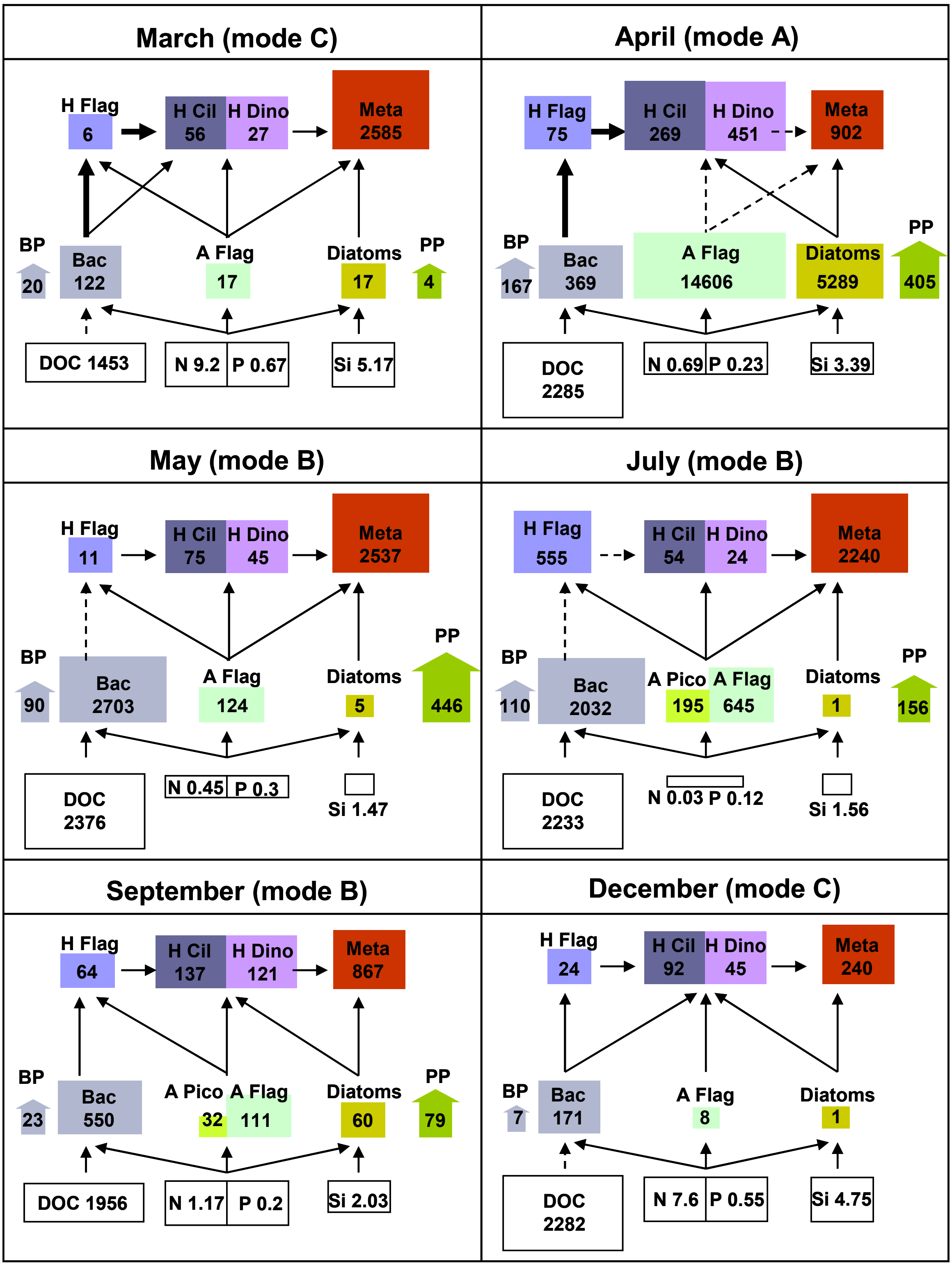

Fig. 6: Simplified food web structure of the plankton communities in Kongsfjorden based on the findings of Paper I & II. Numbers in the boxes are integrated biomass (mg C m^{-2}) and the thick grey and green arrow are bacterial and primary production (mg C m^{-2} d^{-1}), respectively. Nutrient concentrations (N: nitrate, P: phosphate, Si: silicate) are given in µM. Concentrations of dissolved organic carbon (DOC) in µg l^{-1}. The black arrows indicate possible ways of interaction between different food web compartments, with the thickness of the arrows suggesting main trophic interactions, as discussed in the text under 5.1. Note that the size of the biomass boxes and production arrows are not scaled to the real numbers but are a qualitative visualisation only.

allow for a conclusion on whether bacterial growth was limited by carbon or nutrients. However, in a field study and subsequent modelling exercise, Møller and Nielsen (2000) and Thingstad et al. (2002) demonstrated that bacteria experienced carbon limited growth under conditions similar to those encountered in Kongsfjorden in May, i.e. high joint biomass of copepods and heterotrophic dinoflagellates keeping autotrophic biomass low and nutrient regeneration high.

Example 2: In summer (July), the water column became strongly stratified due to fresh-water run-off from land and the biomass distribution became more squared (H:A closer 1; Fig. 5a,b). Despite the already low concentration of essential nutrients in May, autotrophic biomass increased by a factor of 5 in July (Fig. 6 middle right panel), depleting nutrient concentration further to a N:P ratio of 0.3 (Paper I). Pico- and nano-sized autotrophs dominated the phytoplankton stock, as typical for stratified oligotrophic conditions (Thingstad & Sakshaug 1990, Agawin et al. 2000). The small phytoplankton may have been in direct competition for inorganic nutrients with bacteria, due to the generally increasing affinity for nutrients with decreasing size. The low growth (μ_{Bac} = 0.05 d^{-1}) and large stock of the bacterial community suggested that bacteria i) were substrate limited either by DOC or inorganic nutrients, and ii) experienced little predation, despite heterotrophic nanoflagellates dominating with 87% the increased stock of protozooplankton. It can be speculated that nano-sized protozooplankton grazed on the faster growing pico- and nano-autotrophs instead for bacteria. The larger protozooplankton, such as heterotrophic ciliates and dinoflagelates, experienced most likely strong predation by the large stock of metazooplankton at a time when >70% of autotrophs were <10 µm, and consequently largely unavailable for the biomass dominating calanoid copepods (Frost 1972, Hansen et al. 1994). It thus appears that a complex and tight food web structure prevailed in July, with predation by metazooplankton on large protozooplankton (i.e. heterotrophic ciliates and dinoflagellates) most probably cascading via heterotrophic nanoflagellates down to pico- and nano-sized autotrophs as suggested by the inverse size of predator and prey stocks.

Example 3: A similar complex food web was encountered in September (Fig. 6 lower left panel). Despite erosion of the shallow water column stratification and replenishment of nutrients to the surface layer (N:P = 6.2), primary production was only half of that measured in July (Paper I), reflecting the shorter day length and lower solar angle in September. Small autotrophs continued to dominate the phytoplankton community (85% of chlorophyll *a* was

<10 µm, Paper I), but diatoms increased in abundance (Paper II), most probably fuelled by the increased nutrient concentrations and subsequently *new production*. The elevated diatom biomass was mirrored by increased abundance of heterotrophic dinoflagellates, known to graze on large phytoplankton (Hansen 1991, Sherr & Sherr 2007). Together with ciliates, heterotrophic dinoflagellates constituted 80% of the total protozooplankton biomass (Paper II). The increased biomass of large protozoans was most likely possible due to decreased abundance of metazooplankton, as well as diatoms constituting an alternative food source for large calanoid copepods, thus relieving the grazing pressure on protozooplankton (Ratkova et al. 1998, Levinsen & Nielsen 2002).

Two examples of mode C planktonic food webs

The encountered planktonic food webs in March and December were not described by either mode A nor B. Heterotrophs dominated the food web both in terms of biomass (H:A >> 1) as well as specific production (μ_{Bac}:$\mu_{\mathrm{Phyto}} > 1$); a situation referred to as mode C hereafter (Fig. 5a). Under this scenario (Fig. 6 upper left and lower right panel), bacterial production appeared uncoupled from that of autotrophs, most likely fuelled by semi-labile DOC remaining from the previous productive season (Thingstad et al. 1997, Sintes et al. 2010). Bacterial growth could therefore have been limited by the quality of DOC (Thingstad 2009), but was with 0.2 d^{-1} not exceptionally low. This may have been due to the large substrate variety bacteria are able to process during winter (Sala et al. 2008). At the same time, the bacterial community experienced most probably strong grazing pressure from a ravenous protozooplankton community, as suggested by the disconnection of bacterial biomass and production (Ducklow 1992).

The temporal decoupling of primary and secondary production, as depicted by mode C, is intuitive in December, when primary production was negligible due to the complete absence of sunlight. In March, however, the sun had returned to Kongsfjorden, with daylight lengths of about 12 hours per day. The depth of the euphotic zone was estimated to approximately 40 m at noon (E. Nøst Hegset pers. comm.). Autotrophic production appeared nevertheless restricted by PAR, as indicated by the low primary production measured (4 mg C m^{-2} d^{-1}) at wintry high concentrations of essential nutrients (N:P = 13.5, Paper I). This may have had two reasons. Firstly, solar elevation is low at 78° N in March, leading to sun rays hitting the sea surface at a very low angle which in turn results in relatively low quantities of solar energy per square metre (Sakshaug 2004). Secondly, very strong winds prevailed during the sampling period in March, which may have dispersed autotrophs repeatedly below the eutrophic zone in the unstratified water column. The very high H:A biomass ratio in March was mainly explained by the large stock of metazooplankton, which most likely had been advected into the fjord (Willis et al. 2006, Willis et al. 2008) in conjunction with a major inflow of AW just prior to sampling (Cottier et al. 2007).

Regulatory mechanism determining food web structure in Kongsfjorden

The observed shifts in food web structure and functions in Kongsfjord followed largely the theoretical models depicted in Fig. 2 and Fig. 3. The prebloom (mode C) occurred in cold, unstratified waters replenished by nutrients, but primary production was still limited by PAR. A vernal phytoplankton bloom (mode A) developed after the spring equinox when light was no longer limiting, lowering the concentration of mineral nutrients within the euphotic zone. Different from the conceptual model in Fig. 2, the bloom developed in cold and unstratified waters, as also seen in boreal waters (Townsend et al. 1992, Eilertsen 1993). First during the prebloom/summer phase (mode B), water temperatures rose and a strong pycnocline developed. Concentration of mineral nutrients decreased continuously, until replenished through limited erosion of the pycnocline in autumn. The elevated concentrations of mineral nutrients resulted, however, neither in elevated autotrophic production nor a mode A food web as hypnotized by Fig. 3, most likely due to decreasing day length in September.

Beside abiotic factors, the discussion above points to the crucial role of phagotrophs (i.e. proto- and metazooplankton) in structuring the food web (e.g. Riegman et al. 1993, Verity & Smetacek 1996). This was nicely illustrated by the formation of a extensive bloom of diatoms and *Phaeocystis* most likely due to a miss-match with their metazoan grazers in time and space. A miss-match between the vernal biomass increase of phytoplankton and metazooplankton (Paper II) has been suggested previously in Kongsfjorden (Willis et al. 2006), due to the dependence of metazooplankton biomass on advective processes, as also seen in other coastal systems (Aksnes et al. 1989, Reigstad 2000).

In conclusion, Paper I and II demonstrate that the planktonic food web in the coastal ecosystem of Kongsfjorden was dominated by heterotrophs (H:A > 1) during most of the year (mode B and C). Autotrophic biomass exceeded that of heterotrophs only in spring (mode A). The data suggest that the food web structure is not only a result of abiotic factors, such as light and nutrients, but heavily dependent on the abundance and size-structure of phagotrophs (i.e. protozooplankton versus metazooplankton). Further, advection of long-lived heterotrophs (i.e. copepods) as well as reproduction of benthic fauna may lead to a strong modulation of coastal planktonic food webs.

5.2 Western Fram Strait: Does an adjacent oceanic ecosystem differ from that encountered in Kongsfjorden?

Logistical constrains prohibited a similar extensive seasonal investigation of the plankton community in the ice-covered Arctic waters of northwestern Fram Strait as in Kongsfjorden. Sampling fell into the onset and end of the productive season, in April/May and September, respectively. In April/May (2008), a total of six stations were sampled between 75 and 80º N within the outflow area of ARW (Paper III). Stocks and rates of autotrophs (i.e. biomass of pico-, nano- and micro-autotrophs, as well as total primary production) and heterotrophs (i.e. biomass of heterotrophic bacteria, proto- and metazooplankton, as well as bacterial production) were measured from six depths (5, 10, 20, 30, 40 and 60 m). In September of two successive years (2006 and 2007), a total of eight stations were sampled between 78 and 80º N, of which five were situated in the outflow area of ArW and three further east in the central Fram Strait dominated by AW (Paper IV). The field work focused on adequate sampling of small copepods and neither measurements of bacterial biomass nor primary and bacterial production were conducted. Thus, only stocks of autotrophs (i.e. biomass of pico-, nano- and micro-autotrophs) and some heterotrophs (i.e. proto- and metazooplankton) were measured from five depths (10, 20, 30, 40 and 60 m).

Prebloom in ice-covered waters – a mode B food web

Differently from Kongsfjorden, northwest Fram Strait is perpetually covered by varying amounts of drift ice, exported from the central Arctic Ocean. This has profound effects on the

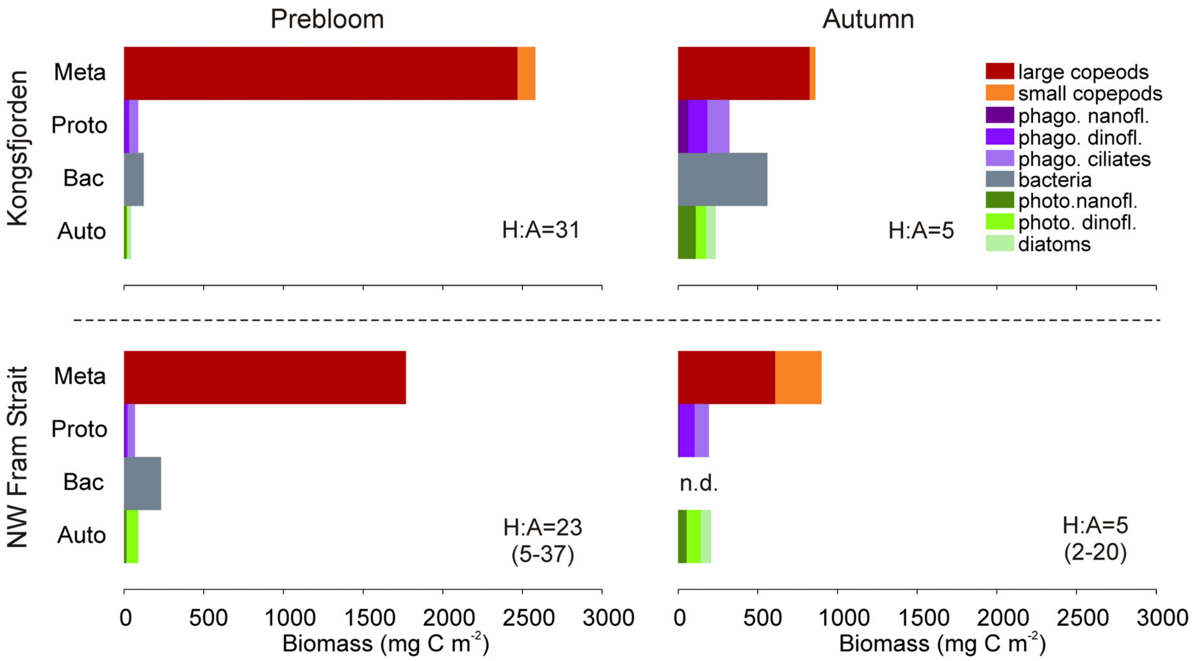

Fig. 7: Comparison of biomass distribution between autotrophs (Auto; split into phototrophic nanoflagellates, dinoflagellates, diatoms), heterotrophic bacteria (Bac), protozooplankton (Proto; split into phagotrophic nanoflagellates, dinoflagellates, ciliates), and metazooplankton (Meta; split into large and small copepods) in Kongsfjorden (upper row) and northwest Fram Strait (lower row) during prebloom (left column) and autumn (right column), based on Paper I-IV. The data from northwest Fram Strait are average biomasses of six prebloom stations (Paper III) and five autumn stations influenced by ArW (Paper IV). The biomass ratio of heterotrophs and autotrophs (H:A) is given in numbers. Note that the prebloom food webs were described in Kongsfjorden and northwest Fram Strait in March and April/May, respectively, suggesting an delay in the onset of the productive season in ice-covered waters.

onset, duration, and intensity of the productive season (Sakshaug 2004, Reigstad et al. 2011). Hence, the planktonic food web in northwest Fram Strait still prevailed in a prebloom situation in April-May (Paper III), when the open water ecosystem in Kongsfjorden was already at termination of an extensive phytoplankton bloom (mode A) and shift towards a microbial postbloom community (mode B; Paper I & II). The prebloom food web encountered in northwest Fram Strait in spring, thus resembled in terms of biomass distribution more the prebloom community described from Kongsfjorden in March (Fig. 7 upper and lower left panel), with heterotrophic biomass exceeding that of autotrophs by a factor of 5 to 37 (compared to a H:A of 31 in Kongsfjorden in March).

A major difference between the planktonic prebloom communities in Kongsfjorden and northwest Fram Strait appears to have been the way carbon was cycled, and subsequently the metabolic balance of the plankton community as a whole. Unfortunately, clear evidence for this assertion can not be provided due to problems with the rate measurements for both bacteria as well as phytoplankton in northwest Fram Strait in spring. Problems with the ^{14}C isotope for primary production as well as too short incubation times for determination of bacterial production, in conjunction with overall very low rates, hampered the detection of production rates. However, concomitant plankton community oxygen measurements in northwest Fram Strait indicated positive net community production (Paper III, Vaquer-Sunyer et al. submitted for publication). This suggested that production of phytoplankton exceeded that of bacteria, which is in contrast to Kongsfjorden in March. There bacterial production had exceeded that of phytoplankton by a factor of five (Paper I), most likely keeping the planktonic system in a net heterotrophic state.

Possible reasons for this difference between the two prebloom communities may have been different degrees in i) light-limitation of phytoplankton, ii) DOC-limitation of bacterioplankton, and/ or iii) grazing pressure on the autotrophic and bacterial communities. In Paper III it is argued that the bacterioplankton in Fram Strait was released from grazing pressure due to the presence of fast-growing pico-autotrophs but experienced substrate limitations, as seen also in other Arctic prebloom communities (Vaqué et al. 2008). In Kongsfjorden, on the other hand, light appeared to have limited phytoplankton production and the grazing pressure of the phagotrophic community may have been more directed towards the bacterioplankton (Paper I and discussion under 5.1). Consequently, the functioning of the two planktonic prebloom communities appeared profoundly different, despite similar biomass distribution (Fig. 7). This functional difference is reflected by the food webs' modes, as the prebloom community in Kongsfjorden was of mode C (Fig. 5a), while the positive net community production measured in northwest Fram Strait suggested that the encountered planktonic food webs were of mode B (H:A > 1 and $\mu_{\mathrm{Bac}}:\mu_{\mathrm{Phyto}} < 1$).

Autumn – the planktonic food web as **Calanus** *descents to depth*

The large calanoid copepods of the genus *Calanus* often dominate Arctic metazooplankton in terms of biomass during the productive season, but leave the surface layer in late summer to overwinter at depth (Falk-Petersen et al. 2009 and references therein). The descent of *Calanus* has been suggested to lead to a restructuring of the food web in the photic zone, with increased biomasses of protozooplankton and small copepods (Hansen et al. 1999, Levinsen & Nielsen 2002, Madsen et al. 2008). This notion is partly supported by a small collection of biomass data of protozooplankton and *Calanus* from Arctic literature (Fig. 8), suggesting that

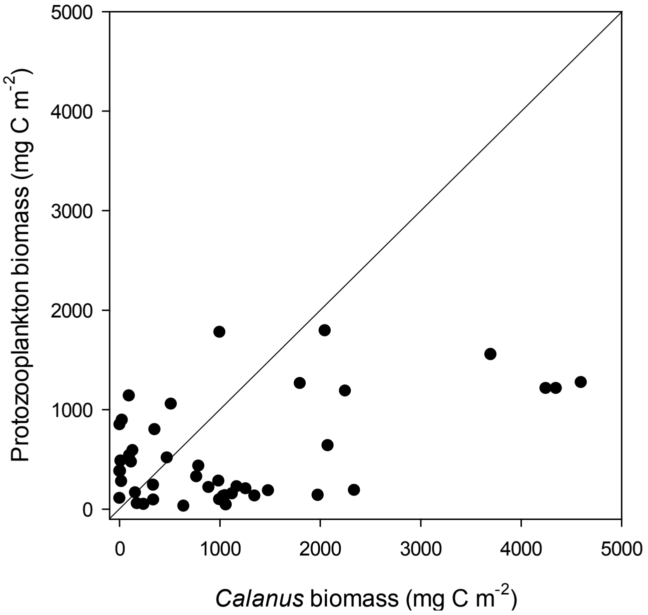

Fig. 8: Protozooplankton biomass (mg C m^{-2}) in relation to that of *Calanus* spp. as described from Kongsfjorden (Paper II), northwestern Fram Strait (Paper IV) and in literature from other Arctic areas (see Appendix).

protozooplankton biomass exceed that of *Calanus* as the biomass of the calanoids decreases below approximately 500 mg C m^{-2}.

In the plankton community in Fram Strait in September (Paper IV), *Calanus* was encountered at relatively low numbers in the upper 200 m of the water column and the total biomass of protozoopankton and small copepds (i.e. copepods < 1 mm, such as *Oithona* spp., *Oncaea*, *Microcalanus*, hapacticoids) exceeded the biomass of *Calanus* at most stations (Paper IV). *Calanus* biomass was also reduced in Kongsfjorden in September (Paper II). But unlike in Fram Strait, in Kongsfjorden the biomass of protozooplankton and small copepods did not exceed that of the large calanoids. While the stocks of protozooplankton was by a factor of 1.7 higer in Fram Strait than in Kongsfjorden, small copepods biomass in Kongsfjorden was 8 times lower than that recorded from Fram Strait (Fig. 7 upper and lower right panel). The relatively low biomass of small copepods in Kongsfjorden in September may well have been the result of inadequate sampling with a WP-2 net of 90 µm mesh size, as suggested by a comparative sampling of small copepods with net and Go-Flo bottles in Fram Strait (Paper IV). For *Oithona* spp. for example, sampling by bottles increased the biomass estimates of this species by a factor of up to 6 compared to WP-2 nets with 90 µm mesh size (Paper IV). It is thus likely that small copepods contributed more to total zooplankton biomass in Kongsfjorden than reported in Paper II.

Small copepods, such as e.g. *Oithona* spp., are known to preferentially prey on moving organisms, such as ciliates and flagellates (Drits & Semenova 1984, Svensen & Kiørboe 2000). Small copepods are thus important predators on protozooplankton (Turner 2004), and their abundance may explain why protozooplankton biomass does not increase more at times when *Calanus* is less abundance in the surface layer (Fig. 8). In Fram Strait in September, *Oithona* nauplii were found at high abundances (30×10^3 to 21×10^5 ind m^{-2}) and their grazing calculated to range from 0.2 to 772 mg C m^{-2} d^{-1} (Paper IV). Assuming a similar productivity of ciliates and dinoflagellates as in Kongsfjorden in September (76 mg C m^{-2} d^{-1}, Paper II), *Oithona* nauplii alone may have preyed 0.3 to 1000% of the protozoan production in Fram Strait. Hence, the absence of *Calanus* spp. may not always result in a strong relieve in grazing pressure on protozooplankton. This notion is supported by the observations in Kongsfjorden (Paper II), where the highest biomass of protozooplankton was encountered as low abundance of *Calanus* coincided with high autotrophic biomass in April, offering alternative prey items for small copepods and their nauplii, thus relieving the grazing pressure on the protozoan stock.

In summary, the prebloom food webs in northwest Fram Strait (Paper III) appeared similar to that encountered in Kongsfjorden in March in terms of biomass partitioning. In their function and food web mode, however, the two prebloom systems appeared profoundly different, with the prebloom system in northwest Fram Strait being net autotrophic and of food web mode B, compared to a food web of mode C in Kongsfjorden. Low abundance of Calanus *spp. alone seem not to result in largely increased protozooplankton biomass, most likely due to predation pressure from small copepods, such as* Oithona *spp. and their nauplii (Paper IV).*

5.3 Regulatory mechanisms shaping Arctic planktonic food webs

The heterogeneous nature of high-latitude seas (Carmack & Wassmann 2006) makes it difficult to compare or even extrapolate the findings on a planktonic food web from one area to the entire Arctic. The plotting of biomass and production ratios allows, however, to reassess the overall validity of the food web modes (A - C) observed in Kongsfjorden (Paper I & II) and northwest Fram Strait (Paper III & IV) for other parts of the Arctic, and deduce some common abiotic or biotic factors regulating planktonic food web structure and function in the Arctic.

Complete datasets on biomass and production of the entire range of autotrophic and heterotrophic plankton organisms are scares from the Arctic regions. Only 16 studies from Arctic marine systems were found, which had investigated simultaneously most of the autotrophic and heterotrophic plankton groups (see Appendix). Unfortunately, station-specific biomass and/or production data could only be retrieved from 10 of these studies. This set of data stems from as different Arctic regions as the central Arctic Ocean, heavily ice-covered coastal systems (Franklin Bay, NE Greenland), and more productive shelf/coastal areas (Barents Sea, Disko Bay, Kongsfjorden). All studies were conducted during some part of the productive season (March to September).

The data compilation demonstrates that planktonic food webs of mode A, B, and C are found throughout the Arctic Ocean (Fig. 9). Of the 54 data points, 46% fall under mode B, 30% under mode C and only 24% under mode A. This distribution suggests that food webs of mode B dominate throughout most of the productive season, while food webs of mode A are transient and therefore less frequently sampled.

The data falling under mode A in Fig. 9a stem from very divergent Arctic areas, such as relatively open waters of the Chukchi Sea (Wheeler et al. 1996, Gosselin et al. 1997, Rich et al. 1997, Sherr et al. 1997), the marginal ice zone in the Barents Sea (Reigstad et al. 2011 and references therein), a northeast Greenlandic fjord after ice break-up (Nielsen et al. 2007), and the ice-free Kongsfjorden (Paper I & II). Nutrient concentrations and water column stability differed greatly between the regions, with e.g. a shallow mixing depth and nitrate concentrations >4.5 µM in the Chukchi Sea (Gosselin et al. 1997), versus an unstratified water column and nitrate concentrations <1 µM in Kongsfjorden (Paper I). This suggests that the described mode A food webs ranged from early to late phytoplankton bloom stages, as indicated by the different degrees of nutrient depletion, and were taking place in water columns of different stratification. Most of the data show a dominance of large phytoplankton cells, as e.g. centric diatoms dominated the phytoplankton biomass with 61 to 98% in the Chukchi Sea (Gosselin et al. 1997) and 62 to 74% in Young Sound (Rysgaard & Nielsen 2006). The dominance of diatoms is, however, not denotative for mode A food webs, as demonstrated by the substantial contribution of *Phaeocystis pouchettii* to the autotrophic

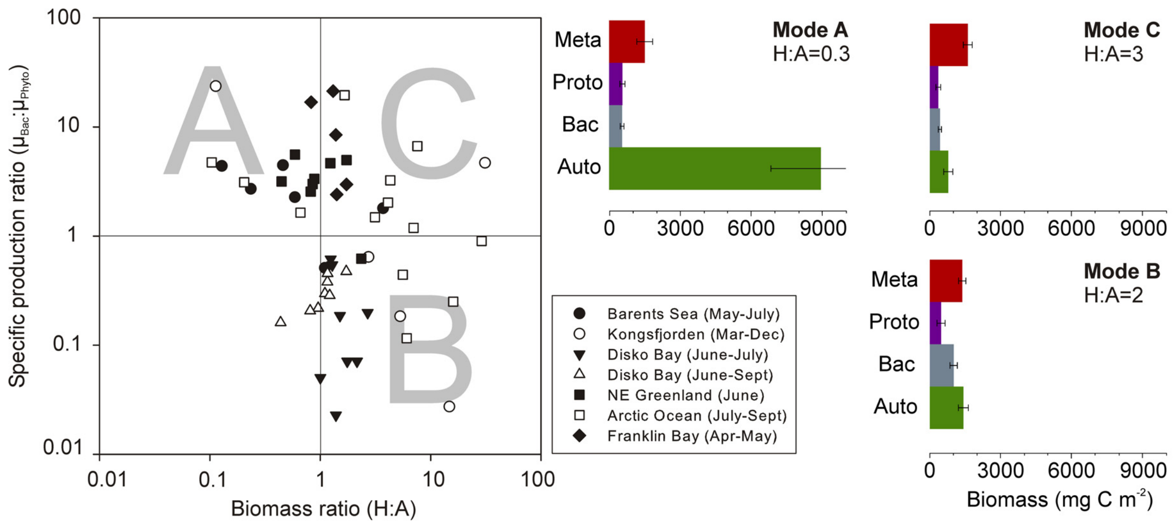

Fig. 9: Comparison of own and published data, plotted as specific production ratio of bacteria and phytoplankton (μ_{Bac}:μ_{Phyto}) and the biomass ratio of heterotrophs and autotrophs (H:A). On the right side, the biomass distribution between phytoplankton (Auto), bacteria (Bac), protozooplankton (Proto), and metazooplankton (Meta) is given for mode A – C, based on the data presented on the left side. See Appendix for data sources.

biomass in Kongsfjorden in April (Paper I). In its colonial form *Phaeocystis* may, however, act as large celled phytoplankton. Thus, large phytoplankton appear characteristic for mode A, and diatoms are certainly more common in mode A phytoplankton communities than for those of mode B and C.

Nevertheless, diatoms have been described to dominate autotrophic biomass also in mode B food webs, as under a vernal bloom (Nielsen & Hansen 1995) and summer subsurface bloom near the pycnocline (Nielsen & Hansen 1999) in Disko Bay. Similarly, diatoms became important contributors to phytoplankton biomass in Kongsfjorden in September (Paper I & II). Generally, however, phytoplankton appears to be dominated by small flagellates and autotrophic picoeukaryotes during mode B, as e.g. reported from the central Arctic Ocean (Gosselin et al. 1997, Sherr et al. 2003, Olli et al. 2007), Kongsfjorden (Paper I), the northwestern Fram Strait in spring (Paper III), and as also reported from the White and Barents Sea (Wassmann et al. 2005). While nutrient concentrations vary greatly between the stations classified as mode B (nitrate 0.03 to 7 µM), shallow mixing depths appear to be a common physical setting for food webs of mode B, as water column stratification was described by all studies reviewed here (Nielsen & Hansen 1995, Gosselin et al. 1997, Nielsen & Hansen 1999, Paper I & II). Increasing surface water temperature may be another abiotic factor characteristic for mode B food webs (Nielsen & Hansen 1995, 1999, Paper I & II), but was not associated to this mode everywhere (Gosselin et al. 1997).

The third scenario, food webs of mode C, seems to appear wherever autotrophic production is limited by PAR, as under the heavy ice cover in the central Arctic Ocean (Wheeler et al. 1996, Gosselin et al. 1997, Rich et al. 1997, Sherr et al. 1997) and Franklin Bay (Vaqué et al. 2008) or in open waters during the polar night, as discussed above for Kongsfjorden (see 5.1). Under the land-fast ice in Franklin Bay, growth of low-light adapted autotrophic pico- and nanoeukaryotes led to a continuously decreasing H:A biomass ratio from January (H:A of 6.5 ± 4.8) to May (H:A of 1.5 ± 0.02; Vaqué et al. 2008), underpinning PAR as driving factor for Arctic food webs of mode C, as also demonstrated experimentally (Terrado et al. 2008, Estrada et al. 2009). An interesting question is whether mode C food webs will shift into mode A or B when sufficient PAR is supplied. While the vernal increase in autotrophic production is traditionally thought to result in high phytoplankton biomass and mode A food webs, this is not compulsory as demonstrated by the data from Disko Bay after ice break-up (Nielsen & Hansen 1995), most probably due to the presence of a large phagotrophic community at the onset of the productive season. Similar scenarios have been described from as different high-latitude marine systems, such as the Amundsen Gulf (Forest et al. in press) and the north Norwegian shelf (Ratkova et al. 1998, Verity et al. 1999).

The reviewed data on Arctic planktonic food webs suggest that mode B prevails throughout most of the productive season (March to September), while dominance of autotrophic biomass and mode A food webs appears less frequent. Mode A food webs are encountered in water columns of different stability, while mode B food webs seem to be connected to stratification and partly increased surface water temperature. Light is the limiting factor for production in mode C food webs. Predation appears to have profound structuring effects and has the potential to prohibit the formation of mode A food webs, despite the presence of favourable abiotic conditions.

5.4 Geographic distribution and duration of planktonic food web modes in the Arctic

The reviewed data on Arctic planktonic food web structure (Fig. 9) suggest that the duration of the different food web modes (A – C) varies throughout the Arctic. Determination of the exact duration and geographical distribution is not possible based on the data reviewed here. Since the mode of planktonic food webs appears strongly determined by physical factors (i.e.

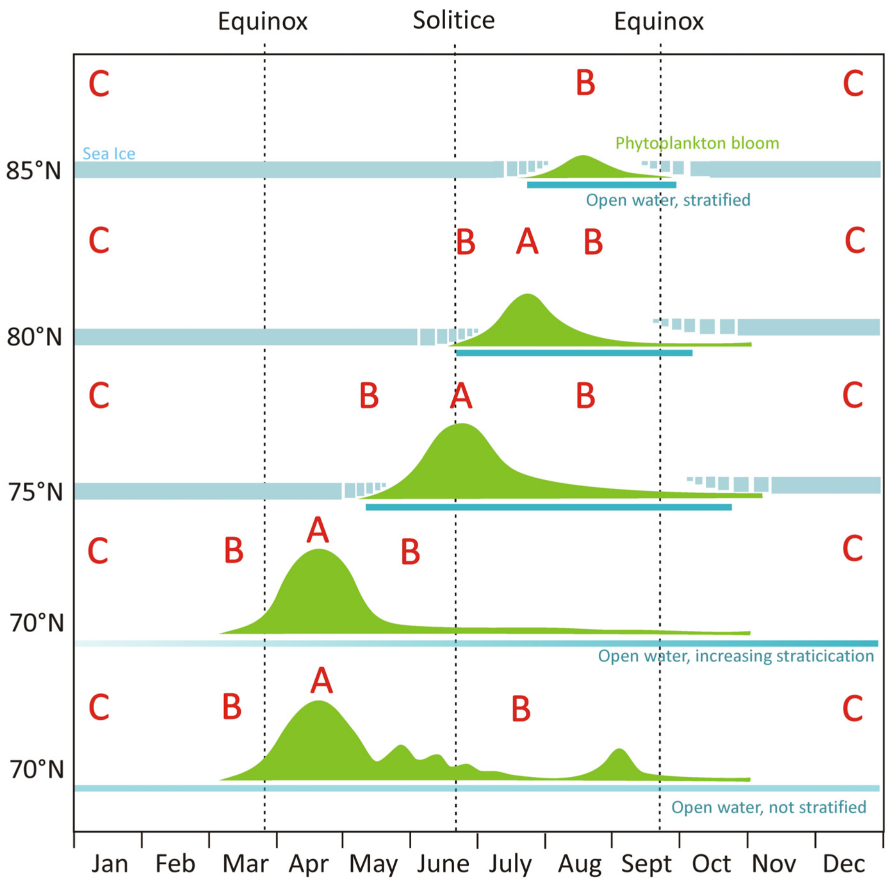

Fig. 10: Conceptual overview of the duration of the three ecosystem modes (A – C) in the European Arctic along a latitudinal gradient. Modified from Leu et al. (2011) and Wassmann & Reigstad (2011).

seasonal photoperiod, sea ice cover, and water column stability) a general trend may, however, be deduced from our knowledge on large-scale physical settings in the Arctic.

Mode C planktonic food webs

Photosynthetically active radiation is insufficient for primary production between 4 and 6 months at 70ºN and 90ºN, respectively. It can thus be speculated that Arctic planktonic food webs prevail in mode C for up to half a year (Fig. 10). The presence of sea ice may limit planktonic production also after the seasonal return of the sun and keep food webs in mode C. This circumstance is nicely illustrated by the studies from Franklin Bay (70ºN, Vaqué et al. 2008), northwest Fram Strait (75-80ºN, Paper III), and Kongsfjorden (78ºN, Paper I & II) in April/May. While the planktonic community was determining an extensive phytoplankton bloom (mode A) in the open-waters of Kongsfjorden, a mode C food web prevailed under the closed ice-cover in Franklin Bay, at the same time as a prebloom mode B community was encountered under the drift ice in northwest Fram Strait. Consequently, sea ice strongly modifies the time food webs prevail under mode C regionally.

Mode A planktonic food webs

A regression of log-transformed H:A biomass ratios versus log-transformed volumetric autotroph biomass of the reviewed data of Arctic planktonic food webs (see Appendix) indicates that mode A food webs occur at an autotroph biomass of ≥39 µg C l^{-1} ($Y_{H:A}$= -0.6551 X_A + 1.0442, r^2 = 0.7034), which equals an average chlorophyll concentration of about 1.6 µg Chl *a* l^{-1} within the euphotic zone (assuming an chlorophyll *a* to carbon conversion factor of 0.04; Sakshaug et al. (2009)). Chlorophyll concentrations of that order of magnitude are observed in spring along the ice edge, where the ice melt leads to water column stratification and favourable phytoplankton growth conditions (Gran 1931, Sakshaug & Skjoldal 1989). The ice melt can start as early as March in the Atlantic-influenced Arctic domain and span until early September at high latitudes, with most of the melting taking place from June onwards (Perrette et al. 2011). Thus, mode A food webs may occur progressively later in the season towards the North (Fig. 10), as observed by remote sensing (Perrette et al. 2011). The limited information available from the highest latitudes suggests that phytoplankton concentrations of ≥1.6 µg Chl *a* l^{-1} are rare (Gosselin et al. 1997, Sherr et al. 2003, Olli et al. 2007), and extensive blooms do not occur near the Pole. This is most likely due to very short and dynamic opening in the ice-pack (Sakshaug 2004) and the presence of a large ravenous phagotrophic community (Olli et al. 2007).

The duration a planktonic food web prevails under mode A depends largely on i) the concentration of winter accumulated nitrate, which is low in large parts of the Arctic Ocean, ii) the water column stability, which determines the degree of nutrient replenishment to the euphotic zone, but also on iii) the grazing rate of the phagotrophic community. Phytoplankton blooms along the ice edge last locally seldom longer than 20 days (Perrette et al. 2011). Wherever nutrients are replenished to the surface mixed layer through e.g. topographic steering, wind-induced mixing or up-welling, additional phytoplankton blooms may be encountered (Wassmann et al. 2006). This can, for example, be the case along the northern Arctic Ocean shelf breaks, given the absence of sea ice (Carmack & Chapman 2003, Tremblay et al. 2011). In strongly stratified regions, phytoplankton accumulation is also found at the nutricline in summer (Martin et al. 2010).

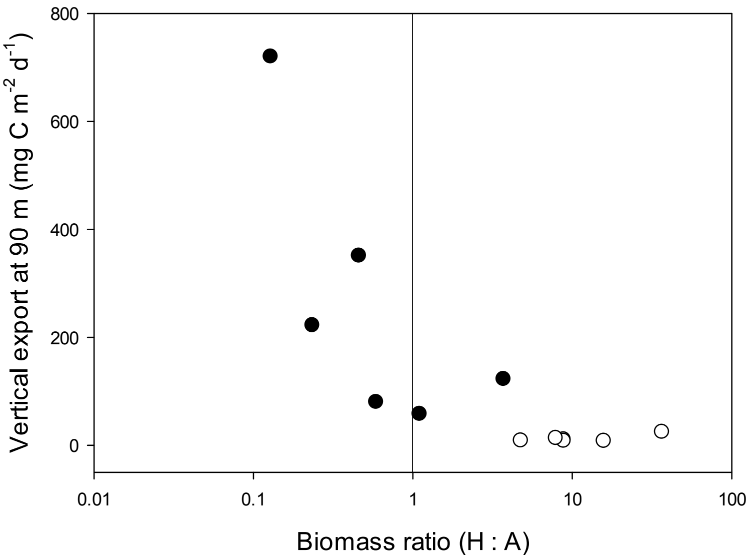

Fig 11: Vertical flux of carbon (mg C m^{-2} d^{-1}) at 90 m depth in relation to the biomass ratio of suspended heterotrophs and autotrophs (H:A) in the overlying water layer. See Appendix for data sources.

Mode B planktonic food webs

Planktonic food webs of mode B are encountered during the prebloom (e.g. Paper III) as well as postbloom phase (Fig. 5, Paper I & II), i.e. within the period in which surface irradiance can penetrate into the water column either due to snow or ice melt. Assuming that the planktonic food web only experiences an ice edge phytoplankton bloom (mode A) of 20 days duration (Perrette et al. 2011) and the ice retreat allows a productive season of 70 to 200 days (Sakshaug 2004), Arctic systems will prevail under mode B for 70 to 90% of the productive season. Even though mode B food webs may be less dominant in some areas with a weaker stratified water column (e.g. southern Barents Sea and Bering Sea), the example illustrates that food webs of more microbial character (mode B and C) dominate throughout most of the year in Arctic seas, while food webs of autotrophic dominance (mode A) are rather sporadic and highly transient events in space and time.

High vertical export of organic matter from the upper water column to the benthos is associated with planktonic food webs under mode A (Fig. 11), as observed in the Barents Sea in spring (Reigstad et al. 2011 and references therein). Ecosystems under mode B and C, on the other hand, are characterized by high retention of organic material in the upper mixed layer, as demonstrated by the extremely low vertical export rates in northwest Fram Strait during the vernal pre-bloom phase, and close to the North Pole even in summer (Olli et al. 2007). The latitudinal shift in the relative duration of the different food web modes (Fig. 10) explains why rich benthic populations are found towards the margins of the Arctic (e.g. in the Barents Sea and Bering/Chukchi Sea).

A latitudinal gradient appears to exist in the relative prevalence of different food web modes (A - C) in the Arctic. These are partly controlled by light, sea ice, and water column stability, but also by the presence of heterotrophs. It is suggested that the frequency of planktonic food webs of mode A decreases with increasing latitude and water column stratification. Throughout the Arctic, food webs of mode B and C may prevail throughout most of the year, only interrupted by sporadic events of phytoplankton accumulation in late spring and summer (mode A).

5.5 Arctic plankton biomass distribution: similarities with coastal or open ocean communities?

The biomass distribution of plankton communities was reviewed for marine environments by Gasol et al. (1997). The authors found plankton communities of oligotrophic, oceanic regions to sustain on average a 10-times higher H:A biomass ratio for a given stock of phytoplankton than coastal, as depicted by the grey lines in Fig. 12. Thus, systems of different productivity seem to support dissimilar heterotrophic biomasses.

Productivity varies greatly between different areas in the Arctic. The average annual primary production per unit area in the Barents Sea, for example, is with 90 g C m^{-2} y^{-1} close to the global average of 110 g C m^{-2} y^{-1} (Sakshaug et al. 2009). The Central Arctic Ocean, on the other hand, has with about 10 to 20 g C m^{-2} y^{-1} (Sakshaug 2004) by far the lowest annual primary production anywhere in the ocean. Despite this large heterogeneity in productivity, the H:A biomass ratios of plankton communities from different Arctic regions fall onto one line in relation to autotrophic biomass ($Y_{H:A} = -0.643X_A + 2.0698$, $r^2 = 0.6456$, Fig. 12). This relationship suggests that Arctic plankton communities maintain on average a 3-fold higher H:A biomass ratio than coastal communities. For autotrophic biomass approximately ≥3000 mg C m^{-2}, Arctic planktonic food webs sustain a similar high or even higher H:A biomass ratio as open ocean food webs, while at lower phytoplankton biomasses Arctic communities appear to maintain less heterotrophs (Fig. 12). One reason for the lower H:A biomass ratio at

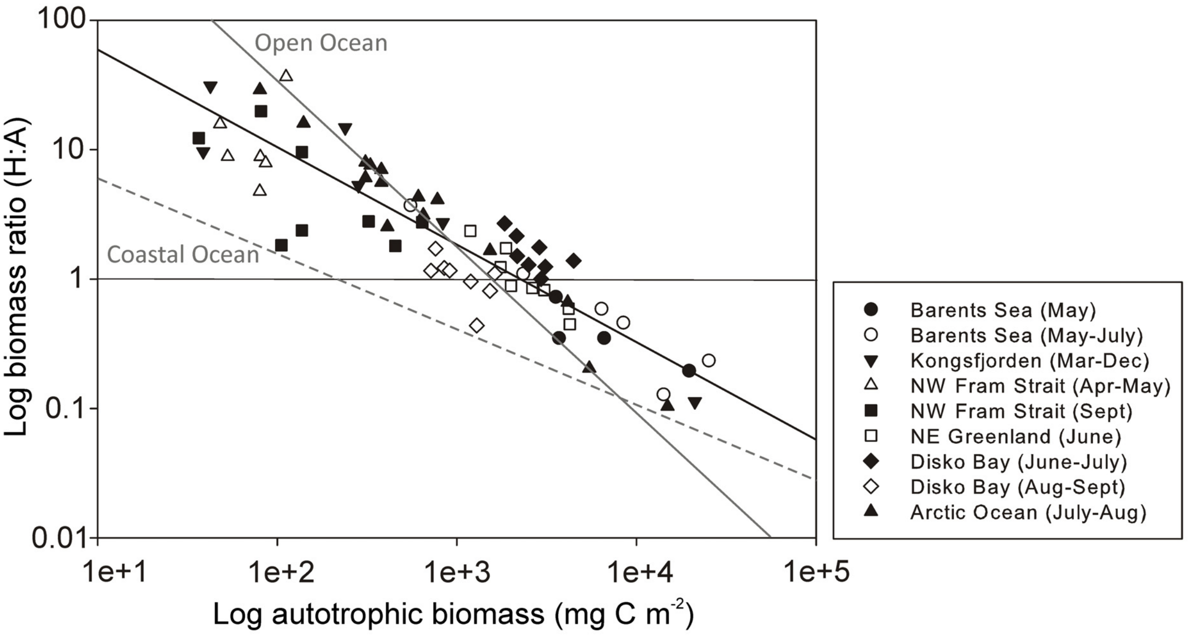

Fig. 12: Changes in the biomass ratio of heterotrophs and autotrophs (H:A) with changing autotrophic biomass (mg C m^{-2}) from different Arctic systems (see Appendix for data sources). The underlying grey lines for coastal and open ocean systems are plotted according to Gasol et al. 1997.

low autotrophic biomasses may be the dominance of mode C food webs. That is, while oceanic plankton communities can sustain a large stock of heterotrophs at the lowest phytoplankton concentrations through maintenance of high primary production through efficient nutrient recycling (Gasol et al. 1997), Arctic food webs of mode C are light-limited and can therefore only sustain a smaller fraction of heterotrophs.

While Arctic plankton communities may sustain a similar high heterotrophic stock as open ocean communities during mode A and B, they resemble coastal communities in the biomass partitioning between the different functional groups of heterotrophs, with metazooplankton dominating total heterotrophic biomass (Fig. 9, Table 2). A large fraction of the metazooplankton encountered in especially the European Arctic may, however, not be of authochthonus production, but allochthonously advected into the Arctic by ocean currents, as discussed under 2.2 of the introduction. At no times, bacteria seem to contribute equally much to total heterotrophic biomass in Arctic seas as reported from oceanic plankton communities (Table 2).

Arctic bacterial biomass is on average 23% of that of phytoplankton (Table 3), but the fraction varies greatly with food web mode, with as little as 6% or as much as 71% of

Table 2: Mean (± standard error) biomass of heterotrophs (H), as well as relative biomasses of metazooplankton (M), protozooplankton (P), and bacterioplankton (B) compared to total heterotrophic biomass. The data for coastal and open oceans are according to Gasol et al. (1997), while the information on Arctic plankton communities (mode A – C) is based on the data presented in Fig. 9.

	World-wide		**Arctic-wide**			
	Coastal Ocean	Open Ocean	Mode A	Mode B	Mode C	All modes
H	1535±196	2521±479	2622±352	2858±380	2399±220	2689±217
M/H	0.56	0.34	0.57	0.48	0.67	0.54
P/H	0.16	0.20	0.22	0.17	0.15	0.18
B/H	0.28	0.46	0.21	0.35	0.18	0.28

phytoplankton under mode A and B, respectively. This demonstrates that Arctic plankton communities may at times sustain as much bacterial biomass relative to that of phytoplankton as some open ocean communities (e.g. equatorial Pacific), but at all times profoundly less than the warm water plankton communities in the Arabian Sea and the waters around Hawaii and Bermuda (Table 3). In general, polar seas appear to maintain a relative low and constant bacterial stock (Table 3, Kirchman et al. 2009), despite temporally high rates of growth (Rivkin et al. 1996, Anderson & Rivkin 2001). This results in a mean bacterial production much lower in Arctic seas than elsewhere, comparable only to that reported from the Ross Sea and sub-north Pacific (Table 3). Relative to primary production, Arctic bacterial production is

Table 3: Phytoplankton and bacterioplankton properties, such as biomass (mg C m^{-2}), production (mg C m^{-2} d^{-1}), and growth rates (d^{-1}), in different seas. The table was adopted from Ducklow (1999) and expanded by data from the review by Gasol et al. (1997) for coastal and open ocean, as well as calculated means for Arctic plankton communities (mode A – C), based on the data presented in Fig. 9.

	Biomass (mg C m^{-2})			**Production (mg C m^{-2} d^{-1})**			**Growth rates (d^{-1})**		
	P	B	B/P	P	B	B/P	P	B	B/P
North Atlantic	4500	1000	0.2	1083	275	0.25	0.3	0.3	1
Equat. Pacific, spring	1700	1200	0.7	1083	285	0.26	0.64	0.13	0.2
Equat. Pacific, autumn	1940	1467	0.75	1548	176	0.11	0.8	0.12	0.15
Sub north Pacific	1274	1142	0.9	629	56	0.09	0.5	0.05	0.1
Arabian	1248	1448	1.2	1165	257	0.22	0.93	0.18	0.19
Hawaii	447	1500	3.6	486	nd	nd	1.1	nd	nd
Bermuda	573	1317	2.7	465	70	0.18	0.81	0.05	0.06
Ross Sea	11450	217	0.02	1248	55	0.04	0.11	0.25	2.3
Open ocean	1966	1132	0.58	1300	nd	nd	1.0	nd	nd
Coastal ocean	2921	541	0.19	794	nd	nd	0.48	nd	nd
Arctic (mode A)	**8949**	**550**	**0.06**	**630**	**105**	**0.17**	**0.06**	**0.25**	**3.87**
Arctic (mode B)	**1419**	**1009**	**0.71**	**249**	**36**	**0.14**	**0.21**	**0.05**	**0.22**
Arctic (mode C)	**782**	**430**	**0.55**	**32**	**54**	**1.69**	**0.07**	**0.28**	**4.11**
Arctic (all modes)	**3313**	**752**	**0.23**	**302**	**59**	**0.19**	**0.13**	**0.17**	**1.28**

with 19%, however, similar to that reported from other regions of the world's oceans (Table 3, Cole et al. 1988, Ducklow 1999). Here, one should however keep in mind that disproportionally many of the reviewed data stem from the productive season (March to September) in coastal and marginal seas of the European Arctic (see Appendix). This may bias the here drawn picture of Arctic plankton communities. For example, the here included data from the central Arctic are from the Arctic Ocean Section project (e.g. Wheeler et al. 1996, Gosselin et al. 1997, Rich et al. 1997), which reported substantially higher stocks and rates of phytoplankton and bacteria than later reports (Sherr & Sherr 2003, Sherr et al. 2003, Olli et al. 2007, Hodal 2011). This circumstance urges for caution in drawing final conclusions on the structure and function of Arctic plankton communities, but calls for future work to integrate further datasets from other Arctic regions and times of the year with the ideas on Arctic planktonic food webs outlined here.

Summarizing, the here reviewed Arctic plankton communities appear to sustain a 3-fold higher H:A biomass ratio for a given phytoplankton stock than coastal plankton communities. In the biomass partitioning of heterotrophs, Arctic communities appear to resemble coastal food webs, with relatively low bacterial contribution but a predominance of metazooplankton. A large fraction of these metazoans may not be of autochthonous production, but advected into the Arctic by ocean currents. Despite relatively low stocks of bacteria, bacterial production was calculated to be with 19% of primary production similar to reports from other marine systems.

6. Arctic planktonic food webs: a conclusion

The studies on planktonic food webs in Kongsfjorden (Paper I & II) and northwest Fram Strait (Paper III & IV), together with a small review of published data from other Arctic regions (Appendix), illustrate that Arctic plankton communities are basically not distinct from those found at lower latitudes. As in other marine systems, Arctic plankton communities respond to alterations in controlling abiotic factors with changes in food web structure and function (i.e. changes in food web mode; Fig. 5, Paper I & II). The relative short seasonal photoperiod, sea ice cover, and strong haline stratification limit the productive season to an increasingly narrow time window towards the North. Arctic food webs belong therefore largely to mode B and C (Fig. 10). For Arctic seas, as for other pelagic ecosystems, it thus appears that "it is the microbial food web that tracks changes in physical and chemical processes; diatoms leave and enter the system according to their own unique biology" (from Verity & Smetacek 1996, p. 285).

Food webs of mode A, with a dominance of large-celled phytoplankton, such as diatoms, seem indeed to be only relative short-lived events of autotrophic biomass dominance and extensive vertical export of biogenic matter to depth (Fig. 11). Assuming that all new production takes place under mode A, this transient food web mode could contribution to total annual primary production as much as 65% in a productive region of the Arctic, such as the Barents Sea, and as little as <3% at the highest latitudes in the central Arctic Ocean (Sakshaug 2004). As discussed for other pelagic ecosystems (Riegman et al. 1993, Verity & Smetacek 1996), predation by the large stock of phagotrophs (i.e. protozooplankton and metazooplankton) seems to have profound effects on food web structure and function in the Arctic (Paper I - IV), and has the potential to prohibit the formation of mode A food webs, despite the presence of favourable abiotic conditions.

Arctic plankton communities appear to sustain on average a 3-fold higher heterotrophic biomass for a given phytoplankton stock than the world's coastal pelagic ecosystems (Fig. 12). This may mainly be caused by extensive import of long-lived copepods from sub-arctic European seas through advection, and not due to authochthonous secondary production (Kosobokova & Hirche 2000, Slagstad et al. 2011), as typical for open ocean plankton communities (Gasol et al. 1997). In many ways, the Arctic marine ecosystems have similarities with those found in the world's coastal oceans, due to outbursts of phytoplankton blooms (Fig. 9), as well as the large contribution of metazooplankton and small contribution of bacteria to total heterotrophic biomass (Table 2).

7. Epilogue

Based upon a few detailed investigations across Fram Strait-Kongsfjorden, and a small review of published data, the present work has adopted a "bird's eye perspective", describing planktonic food web structure and functions by reducing them to biomass and production ratios of heterotrophs and autotrophs. In addition, an old paradigm, revolving around resource acquisition and growth-limiting abiotic factors (i.e. bottom-up control) versus regulation by grazers (i.e. top-down control) was applied. Despite of their importance in structuring planktonic food webs and determining their overall function, important regulatory mechanisms, such as e.g. species composition, life history strategies, viral activity, allelophaty, and mixotrophy, to mention just some, were not even attempted to be studied or discussed. In a time when we hardly understand the complexity of Arctic ecosystems, let alone their changes, the simple description of Arctic planktonic food webs presented here reflects rather an attempt to depict some basic patterns than the reality of insurmountable details that must be the focus of future investigations.

8. References

Agawin NSR, Duarte CM, Agustí S (2000) Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. Limnol Oceanogr 45:591-600

Aksnes D, Aure J, Kaartvedt S, Magnesen T, Richard J (1989) Significance of advection for the carrying capacities of fjord populations. Mar Ecol Prog Ser 50:263-274

Amon RMW, Benner R (2003) Combined neutral sugars as indicators of the diagenetic state of dissolved organic matter in the Arctic Ocean. Deep-Sea Res I 50:151-169

Anderson MR, Rivkin RB (2001) Seasonal patterns in grazing mortality of bacterioplankton in polar oceans: a bipolar comparison. Aquat Microb Ecol 25:195-206

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257-263

Azam F, Malfatti F (2007) Microbial structuring of marine ecosystems. Nature Rev Microbiol 5:782-791

Baines SB, Pace ML, Karl DM (1994) Why does the relationship between sinking flux and planktonic production differ between lakes and oceans. Limnol Oceanogr 39:213-226

Banse K (1982) Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. Limnol Oceanogr 27:1059-1071

Basedow SL, Eiane K, Tverberg V, Spindler M (2004) Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard). Est Coast Shelf Sci 60:113-124

Berreville O, Vezina A, Thompson K, Klein B (2008) Exploratory data analysis of the interactions among physics, food web structure, and function in two Arctic polynyas. Can J Fish Aquat Sci 65:1036-1046

Billen G, Becquevort S (1991) Phytoplankton and bacteria relationship in the Antarctic marine ecosystem. Polar Res 10:245-253

Bluhm BA, Gebruk AV, Gradinger R, Hopcroft RR, Huettmann F, Kosobokova KN, Sirenko BI, Weslawski JM (2011) Arctic marine biodiversity: An update of species richness and examples of biodiversity change. Oceanography 24:232–248

Bratbak G, Heldal M, Thingstad TF, Riemann B, Haslund OH (1992) Incorporation of viruses into the budget of microbial C-tranfer - a 1st approach. Mar Ecol Prog Ser 83:273-280

Bratbak G, Thingstad TF (1985) Phytoplankton-bacteria interactions: an apparent paradox? Analysis of a model system with both competition and commensalism. Mar Ecol Prog Ser 25:23-30

Calbet A, Saiz E (2005) The ciliate-copepod link in marine ecosystems. Aquat Microb Ecol 38:157-167

Campbell RG, Sherr EB, Ashjian CJ, Plourde S, Sherr BF, Hille V, Stockwell DA (2009) Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. Deep-Sea Res II 56:1274–1289

Carmack EC, Chapman DC (2003) Wind-driven shelf/basin exchange on an Arctic shelf: the joint roles of ice cover extent and shelf-break bathymetry. Geophys Res Lett 30:1778

Carmack EC, Wassmann P (2006) Food webs and physical–biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. Prog Oceanogr 71:446-477

Cole JJ, Findlay S, Pace ML (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar Ecol Prog Ser 43:1-10

Conover RJ, Huntley M (1991) Copepods in ice-covered seas - distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. J Mar Sys 2:1-41

Cottier FR, Nilsen F, Inall M, Gerland S, Tverberg V, Svendsen H (2007) Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. Geophys Res Lett 34:L10607

Cottier FR, Tverberg V, Inall M, Svendsen H, Nilsen F, Griffiths C (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. J Geophys Res 110:C12005

Currie DJ, Kalff J (1984) Can bacteria outcompete phytoplankton for phosphorus - a chemostat test. Microb Ecol 10:205-216

Cushing D (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are weakly stratified. J Plankton Res 11:1-3

Degerlund M, Eilertsen HC (2010) Main species characteristics of phytoplankton spring blooms in NE Atlantic and Arctic Waters (68-80^o N). Estuaries Coasts 33:242-269

Drits AV, Semenova TN (1984) Experimental investigations of the feeding of *Oithona similis* Claus. Oceanology 24:755-759

Duarte C, Augusti S, Gasol JM, Vaqué D, Vazquez-Dominguez E (2000) Effect of nutrient supply on the biomass structure of planktonic communities: an experimental test on a Mediterranean coastal community. Mar Ecol Prog Ser 206:87–95

Duarte CM (2005) Experimental test of bacteria-phytoplankton coupling in the Southern Ocean. Limnol Oceanogr 50:1844-1854

Ducklow H (1992) Factors regulating bottom up control of bacterial biomass in open ocean plankton communities. Arch Hydrobiol Beih Ergeb Limnol 37:207-217

Ducklow H, Carlson C, Smith W (1999) Bacterial growth in experimental plankton assemblages and seawater cultures from the Phaeocystis antarctica bloom in the Ross Sea, Antarctica. Aquat Microb Ecol 19:215-227

Ducklow HW (1999) The bacterial component of the oceanic euphotic zone. FEMS Microbiol Ecol 30:1-10

Ducklow HW, Carlson CA (1992) Oceanic bacterial production. Adv Microb Ecol 12:113-181

Dugdale RC, Goering JJ (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol Oceanogr 12:196-206

Eilertsen HC (1993) Spring blooms and straticifaction. Nature 363:24-24

Eppley RW, Peterson BJ (1979) Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282:677-680

Estrada M, Bayer-Giraldi M, Felipe J, Marrasé C, Sala MM, Vidal M (2009) Light and nutrient effects on microbial communities collected during spring and summer in the Beaufort Sea. Aquat Microb Ecol 54:217-231

Falk-Petersen S, Mayzaud P, Kattner G, Sargent J (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5:18-39

Fenchel T (1982) Ecology of heterotrophic microflagellates. IV Quantitative occurence and importance as bacterial consumers. Mar Ecol Prog Ser 9:35-42

Fenchel T (1987) Ecology of Protozoa: the biology of free-living phagotrophic protists. Science Tech Publishers, MA

Forest A, Tremblay J-É, Gratton Y, Martin J, Gagnon J, Darnis G, Sampei M, Fortier L, Ardyna M, Gosselin M, Hattori H, Nguyen D, Maranger R, Vaqué D, Marrasé C, Pedrós-Alió C, Sallon A, Michel C, Kellogg C, Deming J, Shadwick E, Thomas H, Link H, Archambault P, Piepenburg D (in press) Biogenic carbon flows through the planktonic food web of the Amundsen Gulf (Arctic Ocean): A synthesis of field measurements and inverse modeling analyses. Prog Oceanogr. doi:10.1016/j.pocean.2011.05.002

Frost BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol Oceanogr 17:805-815

Garneau MÈ, Roy S, Lovejoy C, Gratton Y, Vincent WF (2008) Seasonal dynamics of bacterial biomass and production in a coastal arctic ecosystem: Franklin Bay, western Canadian Arctic. J Geophys Res 113:C07S91

Gascard JC, Kergomard C, Jeannin PF, Fily M (1988) Diagnostic study of the Fram Strait marginal ice-zone during summer from 1983 and 1984 marginal ice-zone experimental lagrangian observations. J Geophys Res 93:3613-3641

Gasol JM, del Giorgio PA, Duarte CM (1997) Biomass distribution in marine planktonic communities. Limnol Oceanogr 42:1353-1363

Germe A, Houssais M-N, Herbaut C, Cassou C (2011) Greenland Sea sea-ice variability over 1979-2007 and its link to the surface atmosphere. J Geophys Res doi:10.1029/2011JC006960, in press

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. Science 293:2248-2251

Goldman JC, McCarthy JJ, Peavey DG (1979) Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature 279:210-215

Gosselin M, Levasseur M, Wheeler PA, Horner R, Booths BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Res II 44:1623-1644

Gradinger R (2009) Sea-ice algae: Major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. Deep-Sea Res II 56:1201-1212

Gran (1931) On the conditions for production of plankton in the sea. Rapp P-V Reun, Cons Int Explor Mer 75:37-46

Hansen B, Björnsen P, Hansen PJ (1994) The size ratio between planktonic predators and their prey. Limnol Oceanogr 39:395-403

Hansen BW, Nielsen TG, Levinsen H (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the strtified summer situation: III. Mesozooplankton. Aquat Microb Ecol 16:233-249

Hansen PJ (1991) Quantitative importance and trophic role of heterotrophic dinoflagellates in a coastal pelagial food web. Mar Ecol Prog Ser 73:253-261

Hansen PJ, Bjørnsen PK, Hansen BW (1997) Zooplankton grazing and growth: scaling within the 2-2,000 µm body size range. Limnol Oceanogr 42:687-704

Hodal H (2011) Primary production and the relevance of small autotrophic and heterotrophic cells in arctic marine ecosystems PhD-thesis. University of Tromsø, Norway.

Hodal H, Falk-Petersen S, Hop H, Kristiansen S, Reigstad M (in press) Spring bloom dynamics in Kongsfjorden, Svalbard: nutrients, phytoplankton, protozoans and primary production. Polar Biol:doi:10.1007/s00300-00011-01053-00307

Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Prog Oceanogr 71:182-231. doi:110.1016/j.pocean.2006.1009.1007

Irigoien X, Flynn KJ, Harris LR (2005) Phytoplankton blooms: a 'loophole' in microzooplankton grazing impact? J Plank Res 27:313-321

Janse I, van Rijssel M, Ottema A, Gottschal J (1999) Microbial breakdown of *Phaeocystis* mucopolysaccarides. Limnol Oceanogr 44:1447-1457

Jumars P, Deming J, Hill P, Karp-Boss L, Dade W (1993) Physical constraints on marine osmotrophy in an optimal foraging context. Mar Microb Food Webs 7:121-161

Karayanni H, Christaki U, Van Wambeke F, Thyssen M, Denise M (2008) Heterotrophic nanoflagellate and ciliate bacterivorous activity and growth in the northeast Atlantic Ocean: a seasonal mesoscale study. Aquat Microb Ecol 51:169-181

Kiørboe T (1993) Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Adv Mar Biol 29:1-72

Kirchman D, Morán X, Ducklow H (2009) Microbial growth in the polar oceans - role of temperature and potential impact of climate change. Nature Rev Microbiol 7:451-459

Kirchman DL, Malmstrom RR, Cottrell MT (2005) Control of bacterial growth by temperature and organic matter in the Western Arctic. Deep-Sea Res II 52:3386–3395

Klein B, LeBlanc B, Mei Z-P, Beret R, Michaud J, Mundy CJ, Von Quillfeldt CH, Garneau M-È, Roy S, Gratton Y, Cochran JK, Bélanger S, Larouche P, Pakulski JD, Rivkin RB, Legendre L (2002) Phytoplankton biomass, production and potential export in the North Water. Deep-Sea Res II 49:4983-5002

Kleppel GS, Holliday DV, Pieper RE (1991) Trophic interactions between copepods and microplankton: a question about the role of diatoms. Limnol Oceanogr 36:172-178

Kosobokova KN, Hirche HJ (2000) Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. Deep-Sea Res I 47:2029-2060

Lara RJ, Kattner G, Tillmann U, Hirche H-J (1994) The North East Water polynya (Greenland Sea) II. Meachanisms of nutrient supply and influence on phytoplankton distribution. Polar Biol 14:483-490

Laurion I, Demers S, Vezina A (1995) The microbial food web associated with the ice algal assemblage: biomass and bacterivory of nanoflagellate protozoans in Resolute Passage (High Canadian Arctic). Mar Ecol Prog Ser 120:77-87

Laws EA, Redalje DG, Haas LW, Bienfang PK, Eppley RW, Harrison WG, Karl DM, Marra J (1984) High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters. Limnol Oceanogr 29:1161-1169

Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273-306

Legendre L, Rassoulzadegan F (1995) Plankton and nutrient dynamics in marine waters. Ophelia 41:153-172

Leu E, Soreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. Prog Oceanogr 90:18-32

Levinsen H, Nielsen TG (2002) The trophic role of marine pelagic ciliates and heterotrophic dinoflagellates in arctic and temperate coastal ecosystems: A cross-latitude comparison. Limnol Oceanogr 47:427-439

Levinsen H, Nielsen TG, Hansen BW (2000a) Annual succession of marine pelagic protozoans in Disko Bay, West Greenland, with emphasis on winter dynamics. Mar Ecol Prog Ser 206:119-134

Levinsen H, Turner JT, Nielsen TG, Hansen BW (2000b) On the trophic coupling between protists and copepods in Arctic marine ecosystems. Mar Ecol Prog Ser 204:65-77

Lovejoy C, Legendre L, Martineau M-J, Bâcle J, Von Quillfeldt CH (2002) Distribution of phytoplankton and other protists in the North Water. Deep-Sea Res II 49:5027-5047

Lovejoy C, Massana R, Pedrós-Alió C (2006) Diversity and distribution of marine microbial eukaryotes in the Arctic Ocean and adjacent seas. Appl Environ Microbiol 72:3085-3095

Lovejoy C, Potvin M (2011) Microbial eukaryotic distribution in a dynamic Beaufort Sea and the Arctic Ocean. J Plank Res 33:431-444

Madsen SD, Nielsen TG, Hansen BW (2008) Annual population development and production by small copepods in Disko Bay, western Greenland. Mar Biol 155:63-77

Mague TH, Friberg E, Hughes DJ, Morris I (1980) Extracellular release of carbon by mrine phytoplankton - a physiological approach. Limnol Oceanogr 25:262-279

Martin J, Tremblay J-É, Gagnon J, Tremblay G, Lapoussière A, Jose C, Poulin M, Gosselin M, Gratton Y, Michel C (2010) Prevalence, structure and properties of subsurface chlorophyll maxima in Canadian Arctic waters. Mar Ecol Prog Ser 412:69–84

Maslanik J, Stroeve J, Fowler C, Emery W (2011) Distribution and trends in Arctic sea ice age through spring 2011. Geophys Res Lett 38:L13502

Mathis JT, Bates NR, Hansell DA, Babila T (2009) Net community production in the northeastern Chukchi Sea. Deep-Sea Res II 56:1213-1222

Mei Z-P, Legendre L, Gratton Y, Tremblay J-É, LeBlanc B, Klein B, Gosselin M (2003) Phytoplankton production in the North Water Polynya: size-fractions and carbon fluxes, April to July 1998. Mar Ecol Prog Ser 256:13-27

Middelboe M, Lundsgaard C (2003) Microbial activity in the Greenland Sea: role of DOC lability, mineral nutrients and temperature. Aqua Micro Ecol 32:151-163

Møller EF (2007) Production of dissolved organic carbon by sloppy feeding in the copepods *Acartia tonsa*, *Centropages typicus*, and *Temora longicornis*. Limnol Oceanogr 52:79-84

Møller EF, Nielsen TG (2000) Plankton community structure and carbon cycling off the western coast of Greenland, with emphasis on source of DOM for the bacterial community. Aquat Microb Ecol 22:13-25

Mumm N (1993) Composition and distribution of mesozooplankton in the Nansen Basin, Arctic Ocean, during summer. Polar Biol 13:451-461

Nagata T, Kirchman DL (1991) Release of dissolved free and combined amino-acids by bacterivorous marine flagellates. Limnol Oceanogr 36:433-443

Nedwell DB (1999) Effect of low temperatures on microbial growth. lowered affinity for substrates limits growth at low temperatures. FEMS Microbiol Ecol 30:101-111

Nejstgaard JC, Tang KW, Steinke M, Dutz J, Koski M, Antajan E, Long JD (2007) Zooplankton grazing on Phaeocystis: a quantitative review and future challenges. Biogeochemistry 83:147-172

Nielsen TG, Hansen BW (1995) Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. Mar Ecol Prog Ser 125:239-257

Nielsen TG, Hansen BW (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. I. Hydrography, phytoplankton and bacterioplankton. Aquat Microb Ecol 16:205-216

Nielsen TG, Ottosen LD, Hansen BW (2007) Structure and function of the pelagic ecosystem in Young Sound, NE Greenland. In: Rysgaard S, Glud RN (eds) Carbon cycling in Arctic marine ecosystems: case study Young Sound, Vol 58. Meddr Grønland, Bioscience, p 88-107

Olli K, Wassmann P, Reigstad M, Ratkova TN, Arashkevich E, Pasternak A, Matrai PA, Knulst J, Tranvik L, Klais R, Jacobsen A (2007) The fate of production in the central Arctic Ocean – top–down regulation by zooplankton expatriates? Prog Oceanogr 72:84-113. doi:110.1016/j.pocean.2006.1008.1002

Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483-488

Paffenhöfer G, Sherr B, Sherr E (2007) From small scales to the big picture: persistence mechanisms of planktonic grazers in the oligotrophic ocean. Mar Ecol 28:243-253

Pasternak A, Arashkevich E, Reigstad M, Wassmann P, Falk-Petersen S (2008) Dividing mesozooplankton into upper and lower size groups: Applications to the grazing impact in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2245-2256

Payet JP, Suttle CA (2008) Physical and biological correlates of virus dynamics in the southern Beaufort Sea and Amundsen Gulf. J Mar Sys 74:933-945

Perrette M, Yool A, Quartly GD, Popova EE (2011) Near-ubiquity of ice-edge blooms in the Arctic. Biogeosci 8:515-524

Pesant S, Legendre L, Gosselin M, Ashjian C, Booth B, Daly K, Fortier L, Hirche HJ, Michaud J, Smith REH, Smith S, Smith WO (1998) Pathways of carbon cycling in the euphotic zone: the fate of large-sized phytoplankton in the Northeast Water Polynya. J Plank Res 20:1267-1291

Pesant S, Legendre L, Gosselin M, Bjornsen P, Fortier L, Michaud J, Nielsen TG (2000) Pathways of carbon cycling in marine surface waters: the fate of small-sized phytoplankton in the Northeast Water Polynya. J Plank Res 22:779-801

Piepenburg D, Ambrose WG, Jr., Brandt A, Renaud PE, Ahrens MJ, Jensen P (1997) Benthic community patterns reflect water column processes in the Northeast Water polynya (Greenland). J Mar Syst 10:467-482

Pierce RW, Turner JT (1992) Ecology of planktonic ciliates in marine food webs. Rev Aquat Sci 6:139-181

Platt T, Bird DF, Sathyendranath S (1991) Critical depth and marine primary production. Proc R. Soc Lond Ser B-Biol Sci 246:205-217

Pomeroy LR, Deibel D (1986) Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. Science 233:359-361

Pomeroy LR, Wiebe WJ (1986) Energetics of microbial food webs. Hydrobiologia 159:7-18

Pomeroy LR, Williams PJB, Azam F, Hobbie JE (2007) The microbial loop. Oceanography 20:28-33

Putt M (1990) Abundance, chlorophyll content and photosynthetic rates of ciliates in the Nordic Seas during summer. Deep-Sea Res 37:1713-1731

Ratkova TN, Wassmann P, Verity PG, Andreassen IJ (1998) Abundance and biomass of pico-, nano-, and microplankton on a transect across Nordvestbanken, north Norwegian shelf, in 1994. Sarsia 84:213-225

Reigstad M (2000) Plankton community and vertical flux of biogenic matter in north Norwegian fjords: regulating factors, temporal and spatial variations. PhD-thesis. University of Tromsø, Norway.

Reigstad M, Carroll J, Slagstad D, Ellingsen I, Wassmann P (2011) Intra-regional comparison of productivity, carbon flux and ecosystem composition within the northern Barents Sea. Prog Oceanogr 90:33-46

Reigstad M, Wassmann P, Wexels Riser C, Øygarden S, Rey F (2002) Variations in hydrography, nutrients and chlorophyll *a* in the marginal ice-zone and the central Barents Sea. J Mar Sys 38:9-29

Reigstad M, Wexels Riser C, Wassmann P, Ratkova TN (2008) Vertical export of particulate organic carbon: attenuation, composition and loss rates in the northern Barents Sea. Deep-Sea Res II 55:2308-2319

Rich J, Gosselin M, Sherr E, Sherr B, Kirchman DL (1997) High bacterial production, uptake and concentrations of dissolved organic matter in the Central Arctic Ocean. Deep-Sea Res II 44:1645-1663

Riegman R, Kuipers BR, Noordeloos AAM, Witte HJ (1993) Size-differential control of phytoplankton and the structure of plankton communities. Neth J Sea Res 31:255-265

Ringuette M, Fortier L, Fortier M, Runge JA, Bélanger S, Larouche P, Weslawski J-M, Kwasniewski S (2002) Advanced recruitment and accelerated population development in Arctic calanoid copepods of the North Water. Deep-Sea Res II 49:5081-5099

Rivkin RB (1991) Seasonal patterns of planktonic production in Mc Murdo Sound, Antarctica. Am. Zool. 31:5-16

Rivkin RB, Anderson MR (1997) Inorganic nutrient limitation of oceanic bacterioplankton. Limnol Oceanogr 42:730-740

Rivkin RB, Anderson MR, Lajzerowicz C (1996) Microbial processes in cold oceans. I. Relationship between temperature and bacterial growth rate. Aquat Microb Ecol 10:243-254

Rose JM, Caron DA (2007) Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. Limnol Oceanogr 52:886–895

Rousseau V, Vaulot D, Casotti R, Cariou V, Lenz J, Gunkel J, Baumann M (1994) The life cycle of *Phaeocystis* (Prymnesiophyceae): evidence and hypotheses. J Mar Sys 5:23-39

Roy S, Harris RP, Poulet SA (1989) Inefficient feeding by *Calanus helgolandicus* and *Temora longicornis* on *Coscinodiscus wailesii*: quatitative estimation using chlorophyll-type pigments and effects on dissolved free amino-acids. Mar Ecol Prog Ser 52:145-153

Rysgaard S, Nielsen TG (2006) Carbon cycling in a high-arctic marine ecosystem – Young Sound, NE Greenland. Progr Oceanogr 71:426-445

Ryther JH (1969) Photosynthesis and fish production in the sea. Science 166:72-76

Sakshaug E (2004) Primary and secondary production in the Arctic seas. In: Stein R, Macdonald R (eds) The organic carbon cycle in the Arctic Ocean. Springer, Berlin, p 57-81

Sakshaug E, Johnsen G, Kristiansen S, von Quillfeldt C, Rey F, Slagstad D, Thingstad F (2009) Phytoplankton and primary production. In: Sakshaug E, Johnsen G, Kovacs K (eds) Ecosystem Barents Sea. Tapir Academic Press, Trondheim, p 167-208

Sakshaug E, Skjoldal HR (1989) Life at the ice edge. Ambio 18:60-67

Sala MM, Peters F, Gasol JM, Pedros-Alio C, Marrase C, Vaqué D (2002) Seasonal and spatial variations in the nutrient limitation of bacterioplankton growth in the northwestern Mediterranean. Aquat Microb Ecol 27:47-56

Sala MM, Terrado R, Lovejoy C, Unrein F, Pedrós-Alió C (2008) Metabolic diversity of heterotrophic bacterioplankton over winter and spring in the coastal Arctic Ocean. Environ. Microbiol. 10:942–949

Sanders RW, Caron DA, Berninger UG (1992) Relationships between bacteria and heterotrophic nanoplankton in marine and freshwaters: an inter-ecosystem comparsion. Mar Ecol Prog Ser 86:1-14

Sarmento H, Montoya JM, Vázquez-Domínguez E, Vaqué D, Gasol JM (2010) Warming effects on marine microbial food web processes: how far can we go when it comes to predictions? Phil Trans R Soc B 365:2137-2149

Schauer U, Beszczynska-Möller A (2009) Problems with estimation and interpretation of oceanic heat transport - conceptual remarks for the case of Fram Strait in the Arctic Ocean. Ocean Sci 5:487-494

Schlichtholz P, Houssais M-N (2002) An overview of the theta-S correlations in Fram Strait based on the MIZEX 84 data. Oceanologia 44:243-272

Schoemann V, Becquevort S, Stefels J, Rousseau W, Lancelot C (2005) *Phaeocystis* blooms in the global ocean and their controlling mechanisms: a review. J Sea Res 53:43-66

Sherr BF, Sherr EB (2003) Community respiration/production and bacterial activity in the upper water column of the central Arctic Ocean. Deep-Sea Res I 50:529-542

Sherr EB, Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Mar Ecol Prog Ser 352:187-197

Sherr EB, Sherr BF, Fessenden L (1997) Heterotrophic protists in the central Arctic Ocean. Deep-Sea Res II 44:1665-1682

Sherr EB, Sherr BF, Hartz AJ (2009) Microzooplankton grazing impact in the Western Arctic Ocean. Deep-Sea Res II 56:1264-1273

Sherr EB, Sherr BF, Wheeler PA, Thompson K (2003) Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. Deep-Sea Res I 50:557-571

Sieburth JMV, Smetacek V, Lenz J (1978) Pelagic ecosystem structure: heterotrophic compartments of the plankton in relationship to plankton size fractions. Limnol Oceanogr 23:1256-1263

Sintes E, Stoderegger K, Parada V, Herndl GJ (2010) Seasonal dynamics of dissolved organic matter and microbial activity in the coastal North Sea. Aquat Microb Ecol 60:85-95

Slagstad D, Ellingsen IH, Wassmann P (2011) Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: an experimental simulation approach. Prog Oceanogr 90:117-131

Smayda TJ (1970) The suspension and sinking of phytoplankton in the sea. Oceanogr Mar Biol An Rev 8:353-414

Smith W, Jr., Gosselin M, Legendre L, Wallace D, Daly K, Kattner G (1997) New production in the Northeast Water Polynya: 1993. J Mar Sys 10:199-209

Stoecker DK, Capuzzo JM (1990) Predation on protozoa: its importance to zooplankton. J Plank Res 12:891-908

Stoecker DK, Taniguchi A, Michaels AE (1989) Abundance of autotrophic, mixotrophic and heterotrophic planktonic ciliates in shelf and slope waters. Mar Ecol Prog Ser 50:241-254

Suttle CA (2005) Viruses in the sea. Nature 437:356-361

Svendsen H, Beszczynska-Møller A, Hagen J, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther J-G, Dallmann W (2002) The physical environmant of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Res 21:133-166

Svensen C, Kiørboe T (2000) Remote prey detection in Oithona similis: hydrochemical versus chemical cues. J Plank Res 22:1155-1166

Sverdrup HU (1952) On conditions for the vernal blooming of phytoplankton. J Du Cpnseil 18:287-295

Terrado R, Lovejoy C, Massana R, Vincent WF (2008) Microbial food web responses to light and nutrients beneath the coastal Arctic Ocean sea ice during the winter–spring transition. J Mar Syst 74:964-977

Thibault D, Head EJH, Wheeler PA (1999) Mesozooplankton in the Arctic Ocean in summer. Deep-Sea Res I 46:1391-1415

Thingstad F (2009) Bacteria and other members of the microbial loop. In: Sakshaug E, Johnsen G, Kovacs K (eds) Ecosystem Barents Sea. Tapir Academic Press, Trondheim, p 235-250

Thingstad TF, Hagstrom A, Rassoulzadegan F (1997) Accumulation of degradable DOC in surface waters: Is it caused by a malfunctioning microbial loop? Limnol Oceanogr 42:398-404

Thingstad TF, Martinussen I (1991) Are bacteria active in the cold pelagic ecosystem of the Barents Sea? Polar Res 10:255-266

Thingstad TF, Nielsen TG, Hansen AS, Levinsen H (2002) Control of bacterial production in cold waters. A theoretical analysis of mechanisms relating bacterial production and zooplankton biomass in Disko Bay, Western Greenland. Mar Ecol Prog Ser 228:15-24

Thingstad TF, Sakshaug E (1990) Control of phytoplankton growth in nutrient recycling ecosystems. Theory and terminology. Mar Ecol Prog Ser 63:261-272

Townsend DW, Keller MD, Sieracki ME, Ackleson SG (1992) Spring phytoplankton blooms in the absence of vertical water column stratification. Nature 360:59-62

Tremblay JE, Belanger S, Barber DG, Asplin M, Martin J, Darnis G, Fortier L, Gratton Y, Link H, Archambault P, Sallon A, Michel C, Williams WJ, Philippe B, Gosselin M (2011) Climate forcing multiplies biological productivity in the coastal Arctic Ocean. Geophys Res Lett 38

Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. Zoological Studies 43:255-266

Turner JT, Levinsen H, Nielsen TG, Hansen BW (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. Mar Ecol Prog Ser 221:209-219

Uye S, Iwamoto N, Ueda T, Tamaki H, Nakahira K (1999) Geographical variations in the trophic structure of the plankton community along a eutrophic-mesotrophic-oligotrophic transect. Fish Oceanogr 8:227-237

Valiela I (1995) Marine ecological processes. Springer-Verlag, New York. p 686 van Dokkum PG, Conroy C (2010) A substantial population of low-mass stars in luminous elliptical galaxies. Nature 468:940-942

Vaqué D, Gasol JM, Marrase C (1994) Grazing rates on bacteria - the significance of methodology and ecological factors. Mar Ecol Prog Ser 109:263-274

Vaqué D, Guadayol Ò, Peters F, Felipe J, Angel-Ripoll L, Terrado R, Lovejoy C, Pedrós-Alió C (2008) Seasonal changes in planktonic bacterivory rates under the ice-covered coastal Arctic Ocean. Limnol Oceanogr 53:2427–2438

Vaquer-Sunyer R, Regaudie-de-Gioux A, Duarte C, Wassmann P, Reigstad M (submitted for publication) Seasonal patterns in Arctic planktonic metabolism (Fram Strait - Svalbard Islands). Limnol Oceanogr

Verity PG, Smayda TJ, Sakshaug E (1991) Photosynthesis, excretion, and growth of *Phaeocystis* colonies and solitary cells. Polar Res 10:117-128

Verity PG, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar Ecol Prog Ser 130:277-293

Verity PG, Villareal TA, Smayda TJ (1988) Ecological investigations of colonial *Phaeocystis pouchetii.* II. The role of life cycle phenomena in bloom termination. J Plank Res 10:749-766

Verity PG, Wassmann P, Ratkova TN, Andreassen IJ, Nordby E (1999) Seasonal patterns in composition and biomass of autotrophic and heterotrophic nano- and microplankton communities on the north Norwegian shelf. Sarsia 84:265-277

Vernet M, Matrai PA, Andreassen I (1998) Synthesis of particulate and extracellular carbon by phytoplankton at the marginal ice zone in the Barents Sea. J Geophys Res C 103:1023-1037

Vinje T, Nordlund N, Kvambekk A (1998) Monitoring ice thickness in Fram Strait. J Geophys Res 103:10437-10449

Walkusz W, Kwasniewski S, Falk-Petersen S, Hop H, Tverberg V, Wieczorek P, Weslawski JM (2009) Seasonal and spatial changes in the zooplankton community of Kongsfjorden, Svalbard. Polar Res 28:254-281

Wassmann P (1990) Relationship between primary and export production in the boreal coastal zone of the North Atlantic. Limnol Oceanogr 35:464-471

Wassmann P, Rat´kova TN, Reigstad M (2005) The contribution of solitary and colonial cells of *Phaeocystis pouchetii* to spring and summer blooms in the north-eastern North Atlantic. Harmful Algae 4:823-840

Wassmann P, Reigstad M (2011) Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. Oceanography 24:220–231

Wassmann P, Slagstad D (1993) Seasonal and annual dynamics of particluate carbon flux in the Barents Sea - a model approach. Polar Biol 13:363-372

Wassmann P, Slagstad D, Ellingsen I (2010) Primary production and climatic variability in the European sector of the Arctic Ocean prior to 2007: preliminary results. Polar Biol 33:1641-1650

Wassmann P, Slagstad D, Wexels Riser C, Reigstad M (2006) Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone II. Carbon flux and interannual variability. J Mar Sys 59:1-24

Wells LE, Deming JW (2006) Significance of bacterivory and viral lysis in bottom waters of Franklin Bay, Canadian Arctic, during winter. Aquat Microb Ecol 43:209-221

Wheeler PA, Gosselin M, Sher E, Thibault D, Kirchman DL, Benner R, Whitledge TE (1996) Active cycling of organic carbon in the central Arctic Ocean. Nature 380:697-699

Whitman WB, Coleman DC, Wiebe WJ (1998) Prokaryotes. The unseen majority. Preoceedings of the National Academy of Science of the United States of America 95:6,578-576,583

Willis KJ, Cottier FR, Kwamniewski S (2008) Impact of warm water advection on the winter zooplankton community in an Arctic fjord. Polar Biol 31:475-481

Willis KJ, Cottier FR, Kwasnieaski S, Wold A, Falk-Petersen S (2006) The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). J Mar Sys 61:39-54

Yager PL, Connelly TL, Mortazavi B, Wommack KE, Bano N, Bauer JE, Opsahl S, Hollibaugh JT (2001) Dynamic bacterial and viral response to an algal bloom at subzero temperatures. Limnol Oceanogr 46:790-801

Zöllner E, Hoppe HG, Sommer U, Jürgens K (2009) Effect of zooplankton-mediated trophic cascades on marine microbial food web components (bacteria, nanoflagellates, ciliates). Limnol Oceanogr 54:262-275

Zweifel UL, Norrman B, Hagstrom A (1993) Consumption of dissolved organic carbon by marine bacteria and demand for inorganic nutrients. Mar Ecol Prog Ser 101:23-32

Appendix

Biological variables gathered from different Arctic marine environments, used to calculate biomass and specific production ratios presented in Fig. 8 (8), 9a,b (9), 11 (11) and 12 (12). PP: primary production; BP: bacterial production; A: phytoplankton biomass; BB: bacterial biomass; Protozoopl.: protozooplankton; Metazoopl.: metazooplankton.

Region	Month	No.	Variable	Original unit	Depth	References
Arctic Ocean[9,12]	Jul-Sep	12	PP	mg C m^{-2} d^{-1}	0-30	Rich et al. 1997
			BP	mg C m^{-2} d^{-1}	0-30	
			PB	mg C m^{-2}	0-50	Sherr et al. 1997 and references therein
			BB	mg C m^{-2}	0-50	Sherr et al. 1997
			Protozoopl.	mg C m^{-2}	0-50	Sherr et al. 1997
			Metazoopl.	g C m^{-2}	0-100	Wheeler et al. 1996
Franklin Bay[9] (Beaufort Sea)	Apr-May	6	PP	µg C l^{-1} d^{-1}	3	unpublished data S. Brugel
			BP	µg C l^{-1} d^{-1}	3	Vaqué et al. 2007
			PB	µg C l^{-1}		
			BB	µg C l^{-1}		
			Protozoopl.	µg C l^{-1}		
Disko Bay[8,9,12]	Jun-Jul	8	PP	mg C m^{-3} d^{-1}	0-30	Nielsen & Hansen 1995
			BP	mg C m^{-3} d^{-1}		
			PB	mg C m^{-3}		
			BB	mg C m^{-3}		
			Protozoopl.	mg C m^{-3}		
			Metazoopl.	mg C m^{-3}	0-50	
Disko Bay[8,9,12]	Aug-Sep	8	PP	mg C m^{-2} d^{-1}	0-30	Nielsen & Hansen 1999
			BP	mg C m^{-2} d^{-1}		
			PB	mg C m^{-2}		
			BB	mg C m^{-2}		
			Protozoopl.	mg C m^{-3}	0-30	Hansen et al. 1999
			Metazoopl.	mg C m^{-3}		
NE Greenland[8,9,12]	June	8	PP	mg C m^{-2} d^{-1}	0-36	Nielsen et al. 2007
			BP	mg C m^{-2} d^{-1}		
			PB	mg C m^{-2}		
			BB	mg C m^{-2}		
			Protozoopl.	mg C m^{-2}		
			Metazoopl.	mg C m^{-3}		
NW Fram Strait[8,11,12]	Apr-May	6	PB	mg C m^{-2}	0-60	Paper III
			BB	mg C m^{-2}		
			Protozoopl.	mg C m^{-2}		
			Metazoopl.	mg C m^{-2}	0-100	unpublished data K. Solovyev
			Export	mg C m^{-2} d^{-1}	90	unpublished data C. Wexels Riser and M. Reigstad
NW Fram Strait[8,12]	Sep	6	PB	mg C m^{-2}	0-60	Paper IV
			Protozoopl.	mg C m^{-2}		
			Metazoopl.	mg C m^{-2}		
Kongsfjorden[8,9,12]	Mar-Dec	6	PP	mg C m^{-2} d^{-1}	0-50	Paper I & II
			BP	mg C m^{-2} d^{-1}		
			PB	mg C m^{-2}		
			BB	mg C m^{-2}		
			Protozoopl.	mg C m^{-2}		
			Metazoopl.	mg C m^{-2}		

Continuation of Appendix.

Region	Month	No.	Variable	Original unit	Depth	References
Barents Sea[8,9,11,12]	May, Jul	6	PP	mg C m^{-2} d^{-1}	0-60	Reigstad et al. 2011 and references therein
			BP	mg C m^{-2} d^{-1}		
			PB	mg C m^{-2}		
			BB	mg C m^{-2}		
			Protozoopl.	mg C m^{-2}		
			Metazoopl.	mg C m^{-2}	0-100	
			Export	mg C m^{-2} d^{-1}	90	
Barents Sea[8,12]	May	4	PB	mg C m^{-3}	0-50	Hansen et al.1996
			BB	mg C m^{-3}		
			Protozoopl.	mg C m^{-3}		
			Metazoopl.	mg C m^{-3}		

Note: Further datasets on Arctic plankton communities exist from the Arctic Ocean (Hodal 2011, Olli et al. 2007, Sherr & Sherr 2003, Sherr et al. 2003), North Water polynya (Klein et al. 2002, Lovejoy et al. 2002, Ringuette et al. 2002, Mei et al. 2003), Northeast Water polynya (Smith et al. 1997, Pesant et al. 1998, Pesant et al. 2000), and the Chukchi Sea (Campbell et al. 2009, Gradinger 2009, Kirchman et al. 2009, Mathis et al. 2009, Sherr et al. 2009, Sukhanova et al. 2009). Unfortunately, the station-specific biomass and production data from these studies could not be retrieved within the timeframe of the present work. It thus remains for future work to integrate these important and extensive datasets with the ideas on Arctic plankton communities outlined in this thesis.

Paper I

Rokkan Iversen K, Seuthe L (2011) Seasonal microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): I. Heterotrophic bacteria, picoplankton and nanoflagellates. Polar Biology 34:731–749

Paper II

Seuthe L, Rokkan Iversen K, Narcy F (2011) Microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): II. Ciliates and dinoflagellates. Polar Biology 34:751–766

Paper III

Seuthe L, Töpper B, Reigstad M, Thyrhaug R, Vaquer-Sunyer R (2011)
Microbial communities and processes in ice-covered Arctic waters
of the northwestern Fram Strait (75 – 80ºN) during the vernal
pre-bloom phase. Aquatic Microbial Ecology 64:253-266

Paper IV

Svensen C, Seuthe L, Vasilyeva Y, Pasternak A, Hansen E (in press) Zooplankton communities across Fram Strait in autumn: are small copepods and protozooplankton important? Progress in Oceanography

ISBN xxx-xx-xxxx-xxx-x