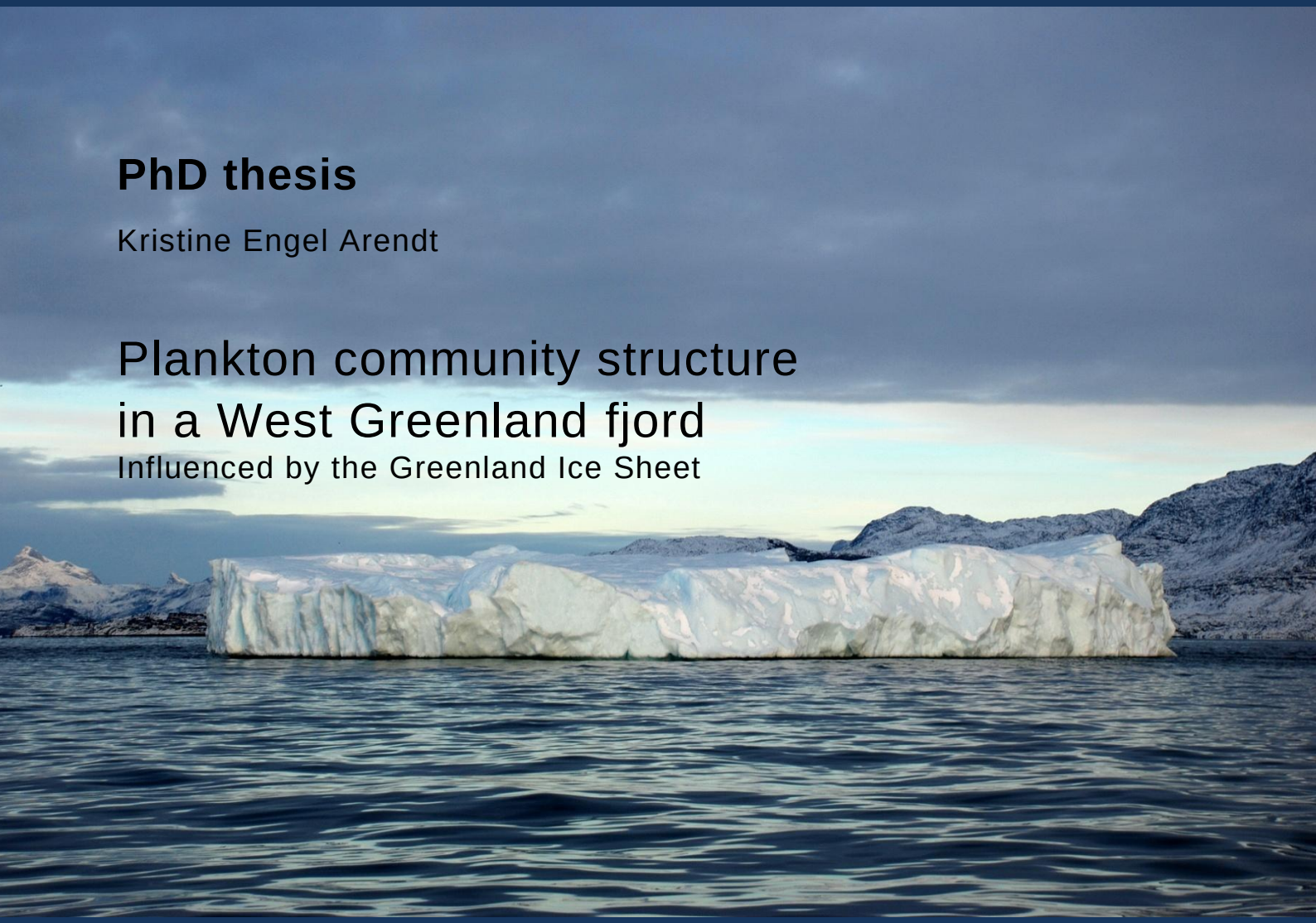
PhD thesis

Kristine Engel Arendt

Plankton community structure in a West Greenland fjord

Influenced by the Greenland Ice Sheet



FACULTY OF SCIENCE
UNIVERSITY OF COPENHAGEN

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Academic advisors: Torkel Gissel Nielsen, Søren Rysgaard and Per Juel Hansen

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Abstract: Greenlandic fjords are located at the junction between the ocean and the Greenland Ice Sheet and therefore sensitive to future climate change. However, little is known about the fjord-glacier link, and fjords are in general understudied. Furthermore, biological studies and basic ecological understanding remain very incomplete. This PhD thesis describes differences in plankton community structure in the offshore West Greenland system towards a glacial outlet fjord, and the results suggest differences in offshore and fjord systems. The abundance of small copepods is surprisingly high in the fjord and the studies contradict the traditional emphasis on large *Calanus* copepods as the main grazer on an annual basis. Instead the studies demonstrate that small copepods can be a key component in Arctic pelagic food webs. Concentrations of suspended sediments in the fjord are high. However, suspended sediments cannot solely explain the spatial distribution of plankton communities. Instead, the high primary production of the system coupled with ocean-fjord-glacier interaction is suggested as an important driver for the findings.

Keywords: Small copepods, ocean-fjord-glacier interactions, carbon cycling

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Content

1. Preface

The complexity of the marine food web and the pathways of energy transfer from one organism to another can be difficult to visualize. Mostly because the initial steps in the marine food web are dominated by organisms that are hardly visible to the human eye and it is only by using microscopes that one realizes the diversity and magnificence of the organisms who constitute primary production (phytoplankton, Fig. 1A) and those who directly utilize this production (zooplankton, see example Fig. 1B). Zooplankton organisms constitute a very important link between small and large organisms and hold a central position in the food web.

One of the first descriptions of marine ecology in Greenland and the important role of plankton in the food web were made by Otto Fabricius in 1780, who described his thoughts on the importance of plankton to what he calls "*Nordhval*" (bowhead whale):

"Food. Its nourishment is peculiar" "small marine animals" "It is strange that the tiniest animals can be sufficient food for the largest, and that this can result in such obesity. However, these are so abundant in the Greenland sea that the whale simply by opening its jaws can swallow together with the water many thousand which contain sufficient fat."

In the present, 231 years after Otto Fabricius, the understanding of marine ecology off Greenland is still a challenging subject. I have found it inspiring to take part in the exploration of the ecology of Greenlandic fjords which, in spite of their central role for the Inuit culture, still remain incompletely described. Descriptive studies with basic knowledge of species composition, biomasses and life rates of the different organisms still contribute with new knowledge. I will find it interesting to follow and hopefully take part in the exploration of the ocean-fjord-glacier interaction and the importance of small zooplankton in Arctic marine systems in the future.

"Nordhval"

"Føde. Dens Næring er særlig" "smaa Havdyr" "Det er mærkeligt nok, at de allermindste Dyr kan være tilstrækkelig Føde for de største, og at deraf kan opstaa saa stor en Fedme. Men disse er saa rigeligt i Grønlandshavet, at Hvalen blot ved at aabne Gabet kan sluge sammen med Vandet mange Tusinder, der indeholder Fedt nok." (Otto Fabricius 1780, oversat til Dansk Helms 1929)

2. Acknowledgements

This thesis is the result of my PhD study at University of Copenhagen and Greenland Climate Research Centre at Greenland Institute of Natural Resources. The project was founded by the Commission for Scientific Research in Greenland (KVUG) and Greenland Institute of Natural Resources. Much of the work has been conducted with financial and logistic support from the project ECOGREEN founded by Commission for Scientific Research in Greenland and from the MarineBasis monitoring program in Nuuk founded by Danish Agency for Science, Technology and Innovation, The Danish Energy Agency, The Danish Environmental Protection Agency and Greenland Institute of Natural Resources.

Tanks to my supervisors for scientific advice, support and for making this project possible. I owe a tremendous thanks to Torkel Gissel Nielsen for excellent supervision and support despite the long distance between Greenland and Denmark. Tanks for inviting me to work with your group at Arctic Station in Qeqertarsuaq and for inviting people to come to Nuuk to work with me. Søren Rysgaard your enthusiasm will always be a source of inspiration for me. Thanks for letting me take part in all the new initiatives in Nuuk since 2005. I am grateful to my director, Klaus Nygaard, and his administrative staff that reduced the administrative workload during the process. Also thanks to Per Juel Hansen who has been my university supervisor.

I thank everyone at Greenland Institute of Natural Resources and the Climate Centre for helping with all sort of things, but first of all for an inspiring and pleasant work environment.

Vitus, Naaja, Regine aamma Ataata, uannut pingaarnerpaasuaannassusi. Aparpassi Anaana.

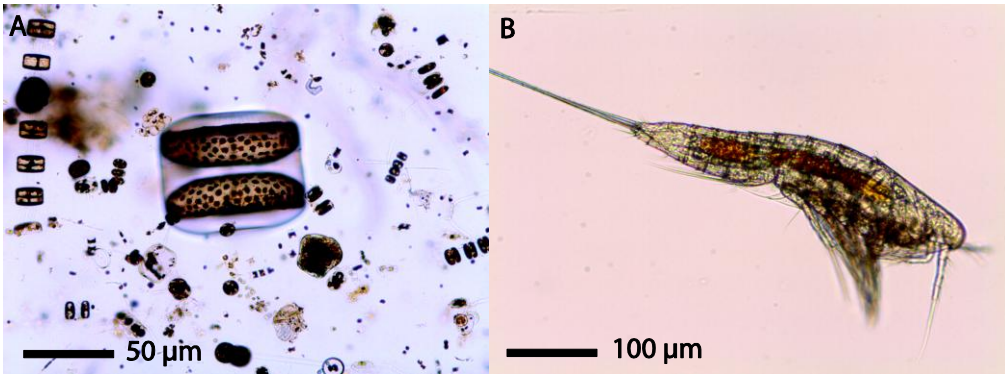

Fig. 1. Examples of A) phytoplankton and B) zooplankton; *Microsetella norvegica* often found in Godthåbsfjord. Photo K.E. Arendt.

3. Summary (in English)

Ongoing climate change in the Arctic has received a lot of attention in recent years. Knowledge about the effects on ecosystems, however, is often limited by lack of datasets and poor understanding of basic ecological processes.

Greenlandic fjords are located at the junction between the Greenland Ice Sheet and the ocean. Discharge from the Ice Sheet, runoff from surrounding land and the interaction with large scale circulation systems of the ocean makes Greenlandic fjords sensitive to future climate change and changes would probably alter the function of the fjord food web. Despite this obvious influence of climate change to fjords and there central role for the Inuit culture the fjords of Greenland are in general understudied. Biological studies of species composition, abundances, biomass and basic ecological understanding remains very incomplete.

This PhD thesis describes studies of plankton community structure and its function in West Greenland waters. The focus is laid on the differences between offshore and fjord system and describes how the pelagic food web of the fjord differs from what is in general observed in Arctic offshore areas.

The studies revealed huge differences in plankton community composition and hereby function of the food web in offshore towards fjord system. The biomass of small copepods is surprisingly high in the fjord. *Pseudocalanus* spp. dominates the inner fjord in spring and high biomasses of *Microsetella norvegica* (Fig. 1B) enhance the biomass of particular small copepods in summer. Together with high biomasses of rotifers these small zooplankton species seem to be well adapted to the fjord environment. Whereas, the larger copepods *Calanus* is found at higher biomass offshore than in the fjord. On an annual basis the outer fjord mouth is found to be dominated by the small copepod *M. norvegica* and copepod biomass peaks as late as in August. Large *Calanus* copepods are found to be an important grazer on the spring phytoplankton bloom as in other Arctic areas. Though, these studies contradict the traditional emphasis of *Calanus* as the main grazer on an annual basis. Instead the studies demonstrate that small copepods can be a key component in Arctic fjord environments on an annual basis.

Concentration of suspended sediments is high in the fjord, however, suspended sediments cannot solely explain the spatial distribution of plankton communities. Instead ocean-fjord-glacier interactions through its potential ability to prolong the productive season of the primary producers are suggested as an important driver for the findings.

4. Resumé (in Danish)

Klima forandringer i Arktis har medført megen omtale i de seneste år. Alligevel er viden om effekterne, af klima forandringer, på økosystemet ofte begrænset af mangel på data og ringe forståelse af basale økologiske processer.

Grønlandske fjorde er beliggende mellem Indlandsisen og havet. Afsmeltningen fra isen, afstrømningen fra land og samspillet med de overordnede havstrømme gør grønlandske fjorde følsomme overfor fremtidige klimaforandringer, forandringer der formentlig vil ændre funktionen af fødenettet. På trods af denne åbenbare indflydelse af klimaforandringer på fjorde, samt deres centrale rolle for Inuit kulturen, er grønlandske fjorde generelt understuderede. Biologiske studier af artssammensætning, antal, mængde samt basal økologisk forståelse er stadig meget sparsomt.

Denne PhD afhandling beskriver studier af planktonsamfundets struktur og dets funktion i det marine miljø i Vest Grønland. Fokus er lagt på forskelle i planktonsamfundene mellem havet og fjorden, og beskriver hvordan det pelagiske fødenet i fjorden er væsentligt anderledes end det der normalt opserveres i subarktiske havområder.

Studierne viser store forskelle i planktonsamfundenes sammensætning og funktion af fødenettet mellem havområdet og fjordsystemet. Mængden af små vandlopper er overraskende høj i fjorden. *Pseudocalanus* spp. dominerer i fjorden om foråret mens den lille vandloppe *Microsetella norvegica* (Fig. 1B) forøger mængden of specielt de små vandlopper om sommeren. Sammen med høje mængder af hjuldyr lader det til at små vandlopper er godt tilpasset fjordmiljøet. Derimod, er mængden af de større vandlopper *Calanus* højere i havområdet end i fjorden. På årligbasis er den ydre fjordmunding domineret af *M. norvegica* og mængden af vandlopper topper så sent som i august. De store *Calanus* vandlopper er en vigtig græsser på forårsopblomstringen, som i andre Arktiske områder. Dog er resultatet af disse studier i modstrid med den generelle opfattelse af at *Calanus* er den vigtigste græsser på årsbasis. I stedet demonstrerer studierne at små vandlopper kan være en vigtig komponent i Arktiske fjordmiljøer på årligbasis.

Koncentrationen af opløst sediment er højt i fjorden men sedimentet kan ikke alene forklare den rumlige variation i planktonsamfundne. I stedet er hav-fjord-glacier sammenspillet og dens mulige evne til at forlænge den produktive sæson af primær produktion foreslået som en vigtig faktor for observationerne.

5. Eqikkaaneq (in Greenlandic)

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Kangerluup iluani sioraaqqanik mikisuaqqanik ulikkaarpoq. Uffali imaq-kangerluk-sermeq sunniiveqatigiipput piffissaq sivittorlugu Attataasat (naasut) misissuinermi qulaani taaneqartoq.

6. Synopsis

6.1 Focus and aims

Climate models predict dramatic changes in the Arctic areas during the next decade (Kattsov and Källén 2005). Changes in the Arctic climate and sea currents would have remarkable consequences for the West Greenland marine ecosystems, and would affect the economically important fisheries and traditional hunting patterns that make up the basis of the Greenlandic society today. Acceleration of mass loss of the Greenland Ice Sheet has been observed (Velicogna and Wahr 2006, Hanna et al. 2008). In addition, precipitation has been predicted to increase during the next decade (Kattsov and Källén 2005). This would greatly increase runoff from the Ice Sheet and surrounding land to the fjords of Greenland. Enhanced runoff would greatly affect the water column structure and circulation and thereby alter the biology and ecological pathways in the fjord and coastal regions of Greenland.

Despite this obvious influence of climate change on Greenlandic fjords the fjords of Greenland are exceedingly understudied. Very little is still known about circulation patterns, freshwater runoff and the link to the Greenland Ice Sheet. Furthermore, biological studies in terms of species composition, abundances, biomass and basic ecological understanding remain very incomplete. Knowledge is simply limited by lack of seasonal data sets and therefore it is still necessary to carry out descriptive studies in Greenland.

Studies of pelagic processes in fjords of Greenland are space and restricted to studies of Jørgen Brønlund Fjord (Andersen 1977), Young Sound (Rysgaard et al. 1999, Nielsen et al. 2007), the fjord systems near Ella Island and Eskimonæs (Ussing 1938) and Scoresby Sound (Digby 1953) on the Northeast Greenland coast and Disko Fjord (Andersen 1981) and Godthåbsfjord (Smidt 1979) on the Southwest Greenland coast. In the Northeastern Greenlandic fjords annual primary production is low (Andersen 1977, Rysgaard et al. 1999) and grazed mainly by the large copepod *Calanus* during the short open water period in midsummer (Digby 1953, Rysgaard et al. 1999). In the Southwest fjords annual primary production is higher (Andersen 1981, Smidt 1979) and the grazer community in a higher extent dominated by small species (Smidt 1979).

In order to increase knowledge about climate change impacting Greenland, laboratory facilities and logistics support were built up at Greenland Institute of Natural Resources in 2005, which later led to Greenland Climate Research Centre. Since 2005, Nuup Kangerlua or Godthåbsfjord has been intensely studied. Crucial knowledge has been obtained supported by the Nuuk Ecological Research Operations which acquire data over the entire annual cycle from a fjord station near Nuuk (Rysgaard et al. 2008 – Juul-Pedersen et al. 2011). Furthermore, numerous research projects have supplied with important knowledge about hydrographic, physical (Mortensen et al. 2011) and chemical factors

(Paper I), and comprehensive contributions have been made to the understanding of benthic (Blicher et al. 2009, Blicher et al. 2010, Sejr et al. 2009, Blicher et al. 2011) and pelagic ecology (Papers I, II, III and IV, Agersted et al. 2011, Calbet et al. 2011).

The zooplankton community in the shelf and offshore region of Southwest Greenland is well documented (Pedersen and Smidt 2000, Pedersen and Rice 2002, Munk et al. 2003, Papers I and II) but the interaction between the offshore and fjord plankton communities has remained undescribed until now. Furthermore, whether or not the plankton community in the fjord represents an isolated community adapted to the microhabitat inside the fjord has not been further investigated or verified since suggested by Smidt (1979). The aim of this study was to contribute to a better understanding of pelagic processes in Arctic fjord environments. The study describes the ecology and carbon cycling of the pelagic environment in a sub-Arctic fjord, Godthåbsfjord, in order to describe the link and influence of discharge from the Greenland Ice Sheet. The focus is on the plankton community structure (Papers I, II and III), its temporal (Paper III) and spatial variability (Papers I and II), and its ecological role in different physical environments (Papers I, II and V).

In terms of plankton, copepods constitute a key trophic group, with a central role in the pelagic ecosystem. They are the dominant form of marine plankton and among the most successful animal groups in the world (Humes 1994). Copepods feed on a variety of organisms, marine snow (Dagg 1993), other particles, even those of low nutritional value (Poulet 1983, Bayliss and Syvitski 1982). They constitute a key group in the food web as they transfer energy from the phytoplankton to the higher trophic levels. The copepod community structure and species composition is largely dependent on hydrographic, physical and chemical factors and therefore changes in these parameters would affect energy flow through the entire food web. Changes of energy flow through the food web would lead to dramatic changes in ecosystem structure and function in the future. Therefore, the understanding of the processes at the base of the food web and their interaction is important knowledge for predicting the consequences of global warming.

The overall objective of my PhD project was to describe differences in plankton community structure and their efficiency in transferring energy from lower to higher trophic levels in the offshore region towards the fjord system (Papers I and II). Secondly, I wanted to describe the seasonal pattern and interannual variations in the plankton community structure of a sub-Arctic fjord (Paper III), and to gain knowledge about copepod life rates when feeding in a glacial outlet fjord high in suspended sediments (Paper IV). Finally, my co-authors and I have conducted an overall description of the carbon fate of the spring bloom in an Arctic ice covered area (Paper V), and I intend to use this paper to place the sub-Arctic fjord system in a broader Arctic perspective.

This synopsis gives a short introduction to the physical and ecological knowledge about the West Greenland marine system. Furthermore, an interpretation of the topic and results obtained during my work put into a broader ecological perspective will be given, followed by the papers that compose the core work of my PhD.

6.2 West Greenland marine system

The coastal waters off Southwest Greenland is the most productive area in Greenland and it is natural, therefore, that most of the human population is situated here (Born and Bøcher 2001). The area is important for commercial fisheries of shrimp, halibut and crab and hunting of large marine mammals that use the area as feeding grounds (Heide-Jørgensen et al. 2007a) during the productive season, and seabirds such as eiders (Merkel et al. 2002) and little auk (Stempniewicz 2001) feed here during winter.

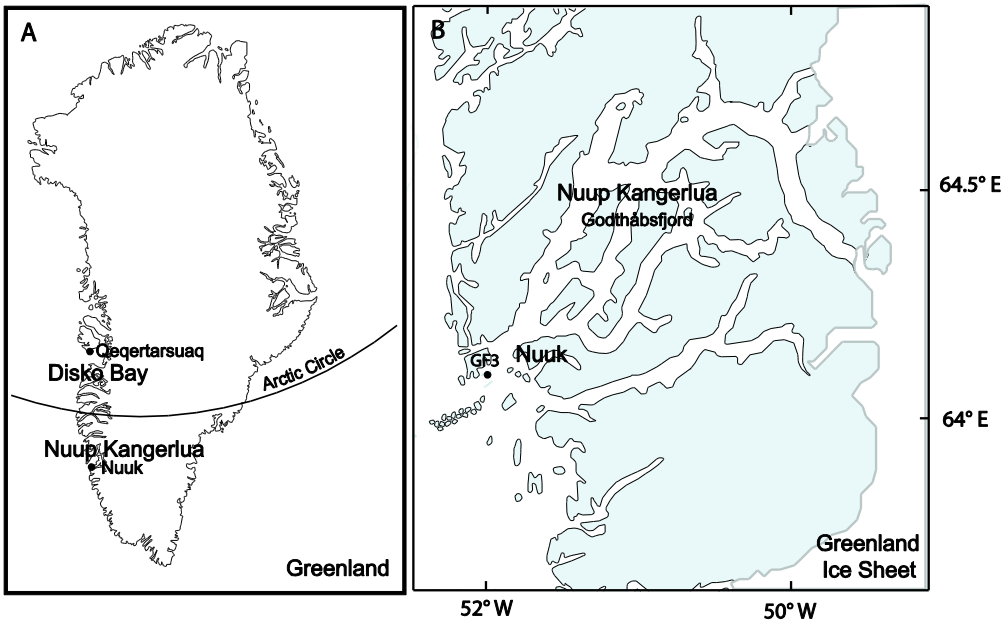

Fig. 2. A) Greenland and B) the Godthåbsfjord located at the junction between the Greenland Ice Sheet and the ocean. Nuuk and the sampling station GF3 is located at the mouth of the fjord.

The high productivity is in part a result of large-scale physical processes, particularly mixing of nutritive water masses that are brought to the photic zone and a long productive season, as the area is sparsely covered by sea ice during winter. Along the continental shelf along West Greenland lies the shallow fishing banks that are sites of hydrographic fronts (Munk et al. 2003) and mixing of water masses. The northward flowing West Greenland Current (Fig. 2A) has characteristics of both Arctic and

temperate waters as this current compounds the southward flowing East Greenland current of Arctic origin and the Irminger current with Atlantic water masses which runs toward Cape Farwell and flows south of Greenland up along the west coast (Buch et al. 2004, Sutherland and Pickart 2008).

The extent of sea ice in Baffin Bay and along the Davis Strait represents a noticeable distinction between Arctic areas further to the north and the waters of sub-Arctic Southwest Greenland that do not become covered by sea ice during winter. The West Ice spreads towards the south along with the cold southward flowing Baffin Current during autumn and expands towards Southwest Greenland (Fig. 3). The southern limit of the West ice reflects a balance of inflow of warm water from the West Greenland Current. The West ice retreats during spring when the West coast is opened up. In ice-covered areas the sea ice and its time of breakup are crucial factors influencing important biological processes (Hansen et al. 2003, Heide-Jørgensen et al. 2007b).

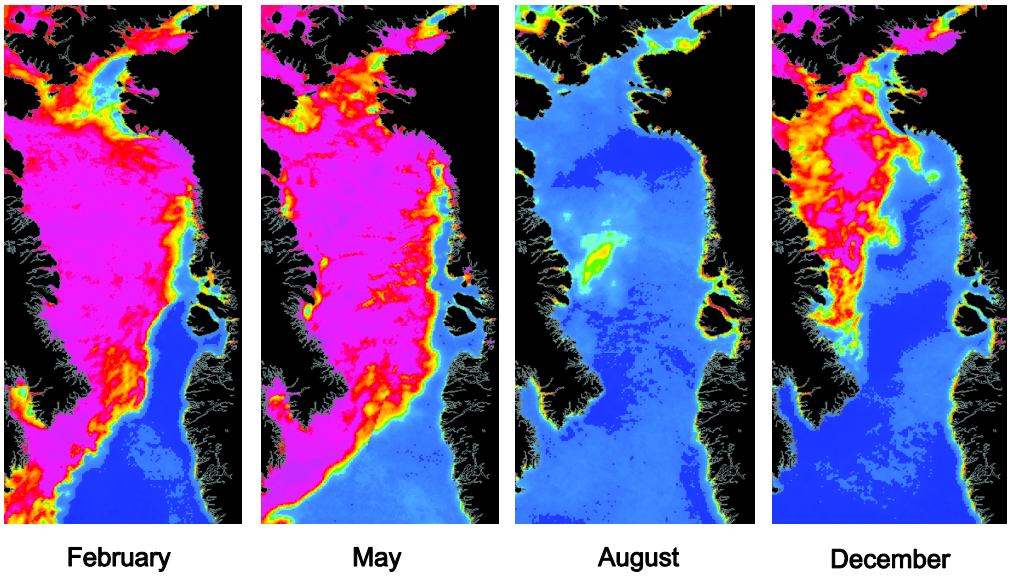

Fig. 3. Satellite images (AQUA AMSR-E) showing sea ice extent in Baffin Bay in February, May, August and December 2010. Blue represents open water and pink-yellow represent sea ice extension. Modified from Juul-Pedersen et al. (2010).

Runoff from land and the Greenland Ice Sheet meets the West Greenland Current system in the coastal region and fjords of West Greenland. The large input of freshwater enters the surface layer of the fjords unhindered where it affects the stability and depth of the mixed layer of the water column. In contrast, the warm and saline water from the West Greenland Current must pass through a complex of canyons and sills to reach the inner basins of the sill fjords (Mortensen et al. 2011).

Godthåbsfjord is one of these sill fjords where waters from the West Greenland Current come in contact with the Greenland Ice Sheet (Fig. 2).

During winter, the West Greenland Current enters the fjord as intermittent dense coastal inflows (Mortensen et al. 2011). Admission of freshwater is transported out of the fjord in a thin surface layer and a compensation current occurs beneath it, which is driven by estuarine circulation (Bendtsen et al. 2007, Mortensen et al. 2011). The circulation pattern is described in greater detail in a recent study which shows rather complex circulation patterns within the fjord (Mortensen et al. 2011). In summer and autumn when discharge from the Greenland Ice Sheet occurs, subglacial freshwater enters the fjord at depth (Motyka et al. 2003) (Fig. 4, arrow A) and hereby freshwater mixes with ambient fjord water as it flows towards the surface (Fig. 4). Due to the mixing it is denser than the freshwater runoff from land and it is therefore transported out of the fjord just below the thin freshwater surface layer (Mortensen et al. 2011) (Fig. 4). In addition, intense vertical mixing due to tidal forces at the fjord entrance mixes the upper freshwater layers downward (Fig. 4, arrow B) making the water column less dense in the outer sill region. Thus, horizontal density gradients are created which drive an in-fjord current in the upper intermediate layer. The circulation mode results in significant freshening and warming of the intermediate layer in the main fjord basin. The process progresses throughout the summer, whereas the direction of heat flux is opposite during winter, resulting in cooling and minor freshening of the intermediate layer in the main fjord basin (Mortensen et al. 2011). However, the water exchange and circulation patterns of this fjord are still not fully understood and the description of its implications for the ecological processes is now in progress.

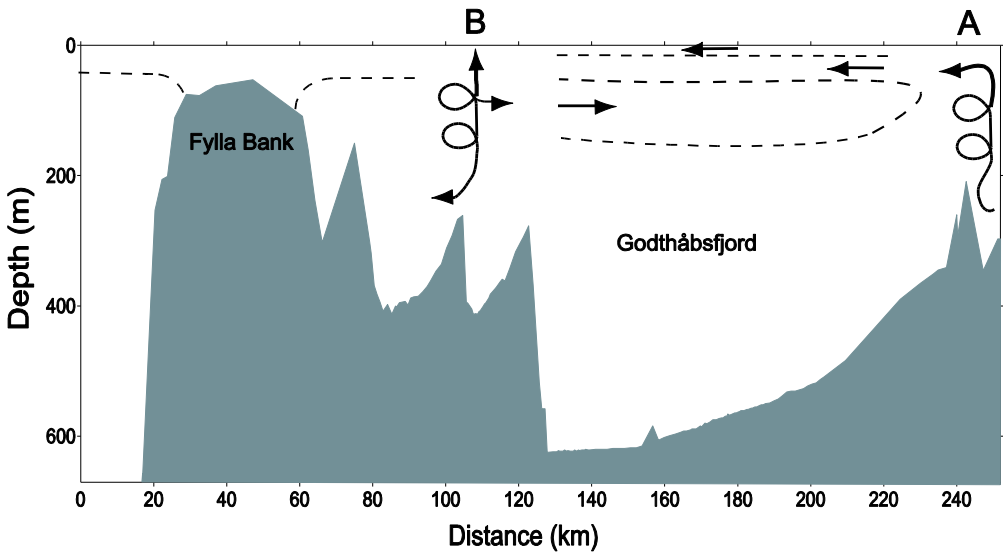

Fig. 4. Schematic drawing of the hydrographic circulation in Godthåbsfjord. A) Sub-glacial runoff and B) tidal mixing of the water column. Modified from Mortensen et al. (2011).

6.3 Mesozooplankton in pelagic processes

Zooplankton constitutes a fundamental step in the marine food web as they transfer energy from the lower trophic levels to the higher trophic levels. Photosynthesis, however, is the fundamental initial process initiating the flow of energy through the food web. Zooplankton, on the other hand, is important because they eat and are subsequently eaten by various predators (Fig. 5).

Primary producers use sunlight as an energy source for oxic photosynthesis and the organic compounds synthesized in this process make up the principal energy that flows continuously through the system. Organic matter produced by phytoplankton is therefore a universal carrier of potential energy within marine ecosystems.

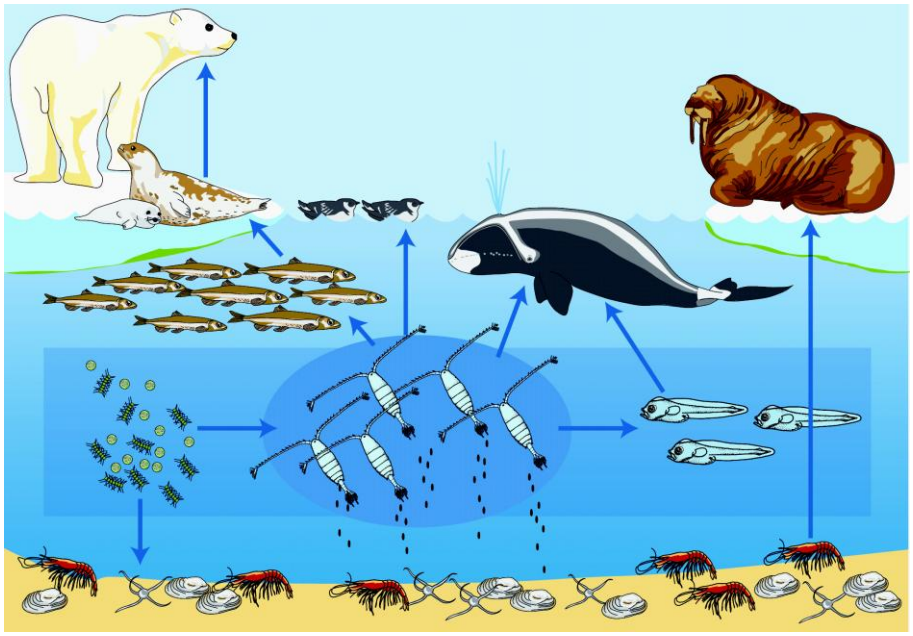

Fig. 5. Zooplankton (center) plays a crucial role in the Arctic marine food web. Schematic drawing kindly provided by B. Munter and T.G. Nielsen.

Pelagic phytoplankton are the dominant primary producers in marine ecosystems and, as they depend on sunlight, their productive period starts in spring when solar radiation increases, sea ice breaks up (Fig. 5AC) and heat and freshening by runoff and melting sea ice stabilize the water column and thus keep the phytoplankton in a nutrient rich photic layer. The bloom has a short pronounced growth peak (Fig. 6C, e.g. Disko Bay, Paper V) before it depletes the nutrients in the photic zone (Smith and Sakshaug 1990). The bloom then decreases as it becomes short in nitrate (Paper V). This happens within 2 to 3 weeks and up to 50% of the annual

primary production takes place in this short period (Sakshaug 1997). As sea ice breakup is highly variable between years, the spring peak production can vary greatly in intensity (Fig. 6AC, Andersen 1981, Levinsen and Nielsen 2002) which can result in mismatch between primary producers and its main grazers (Leu et al. 2011). In general annual primary production is found to depend on the open-water period in sea ice covered areas (Rysgaard et al. 1999).

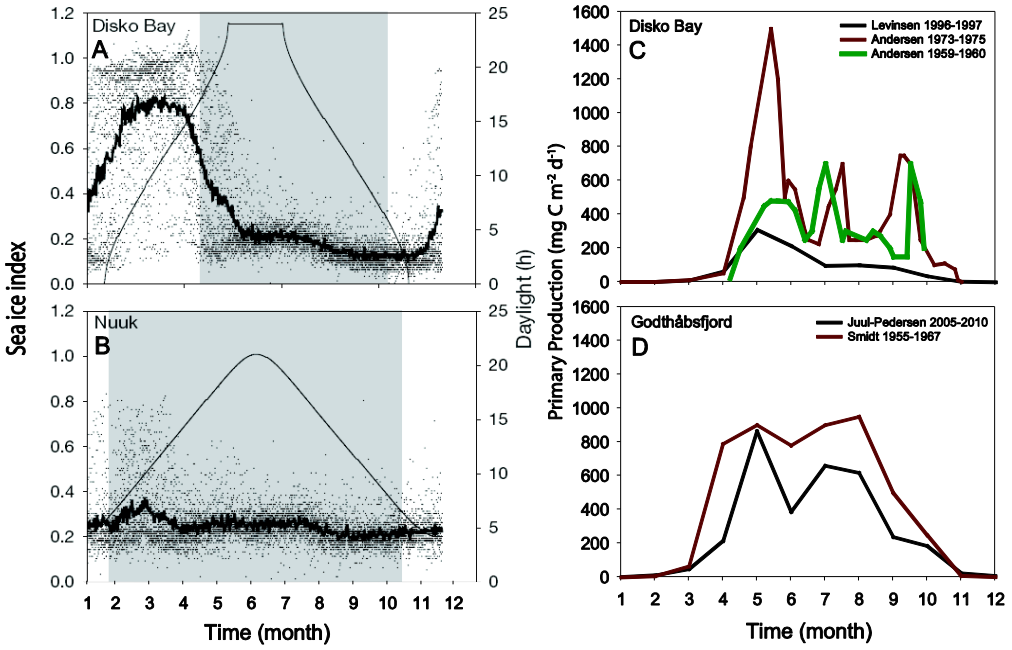

Fig. 6. Seasonal variation parameters for the Disko Bay area and Nuuk/ Godthåbsfjord area, respectively. AB) sea ice index (dots, average as thick line), daylight variation (thin line) and the open-water productive period (gray area) modified from Sejr et al. (2009). CD) Annual variation in primary production (mg C m^{-2} d^{-1}) modified from Smidt (1979), Andersen (1981), Levinsen and Nielsen (2002) and Juul-Pedersen et al. (in prep).

When nitrate is depleted and the water column stratified, further production depends on regeneration or occasional upwelling of nutrients for primary production and utilization of dissolved organic matter by bacteria that are channeled up the food web by nanoflagellates (Fenchel 1982) through the microbial food web (Azam 1983). In the summer bloom situation a larger part of the energy is channeled up through the microbial food web than in the spring bloom situation (Cushing 1989, Levinsen and Nielsen 2002). Simply lack of nitrate results in low primary productivity in the stratified summer situation (Fig. 6C) whereas the microbial food web is found well developed and active from the beginning of the spring bloom (Nielsen and Hansen 1995, Sturluson et al. 2008).

In large parts of the Arctic the spring phytoplankton bloom is grazed primarily by the large herbivore copepod genus *Calanus* (Hirche and Mumm 1992, Nielsen and Hansen 1995, Søreide et al. 2008, Paper I and

V). *Calanus* spp. abundances peak in the upper water strata in midsummer after which it descends to hibernate for the winter (Lee et al. 2006 review, Madsen et al. 2001, Swalethorp et al. 2011). Here it has to withstand a long period without food. Therefore, *Calanus* are dependent on energy storage for respiration in the unproductive Arctic winter and for that reason they accumulate high-energy lipids from phytoplankton (Lee 1975, Sargent and Henderson 1986, Falk-Pedersen et al. 2009). *Calanus* are capable of storing and concentrating lipids from phytoplankton, turning phytoplankton biomass with a content of 10-20% lipids into copepod biomass of 50-70% lipids (Falk-Pedersen et al. 2007). This capability makes them valuable prey items for higher trophic levels that vary from fish, marine birds to large marine mammals such as the bowhead whale (Fig. 5). As each trophic level in the food web respires energy and consequently loses energy, the spring bloom food web driven by large *Calanus* is highly energy efficient. This is based on the short and direct pathway from phytoplankton to mesozooplankton (Berglund et al. 2007) and subsequently the direct link between mesozooplankton and large predators (Steele 1974).

The winter dormancy of *Calanus* results in a shift in relative zooplankton composition in the surface layer from dominance of *Calanus* to dominance of small zooplankton. This can be protozooplankton (Levinsen and Nielsen 2002) and e.g. smaller species and juvenile stages of copepods (Madsen et al. 2008, Hopcroft et al. 2010, Svensen 2011). Smaller copepods seldom achieve the biomass (Møller et al. 2006, Svensen 2011) and hereby grazing values of *Calanus* (Madsen et al. 2008) even though smaller organisms have higher growth rates than those of larger organisms (Fenchel 1974, Banse 1982). Small copepods have been observed to be actively grazing and producing in summer and autumn in high latitudes (Norrbin 1996, Hansen et al. 1999) and can in general be said to be uncoupled to the spring phytoplankton bloom. They take advantage of the niche created when Calanus leaves the surface layer for hibernation and the outcome is a restructuring of the grazer community (Hansen 1999). Little is known about overwintering tactics of small copepods, although *Pseudocalanus* and *Acartia* seems to overwinter in a form of resting populations (Naess and Nilssen 1991, Norrbin 1996) that feed at lower rates during winter due to reduced metabolism at low temperatures (Norrbin 1990, Conover and Huntely 1991).

In Godthåbsfjord, the spring bloom starts in April and usually peaks during May (Fig. 5D), whereas June is characterized by lower production values (Rysgaard et al. 2008, Juul-Pedersen et al. 2011, Paper III). Subsequently, we find a very productive summer bloom period with high production rates in July and August when stratification of the water column occurs. Continuous production throughout September and October leads to an long productive season with a annual production of 95 ±12 g C m^{-2} y^{-1} (Juul-Pedersen et al. 2011). The system shows low inter annual variability compared to ice covered areas further to the North (Fig. 5CD) an observation that correspond observations in other Arctic areas with

Atlantic inflow (Reigstad et al. 2011). The highest summer bloom rates are found in July and August (Fig. 5D) coincident with the intense discharge from the Greenland Ice sheet (Paper III). The findings suggest that the high summer and autumn production is boosted by new nutrient supplies. These are brought to the photic zone by upwelling in front of the glacier driven by the mixing of sub-glacial discharge and ambient nutrient-rich fjord water (Fig. 4, arrow A) and the in-fjord current of mixed water in the upper intermediate layer (Fig. 4, arrow B). The processes behind these circulation patterns depend on the runoff from the Greenland Ice Sheet (Mortensen et al. 2011). However, the exact mechanisms and link between biological processes and hydrographic circulation patterns in the fjord are still to be described.

6.4 Offshore and fjord zooplankton communities

Two transect studies in spring (Paper I) and summer (Paper II) both revealed differences in plankton community structure when sampling with a multi releasing net (Fig. 7, MultiNet®) along a transect from the offshore West Greenland Current system in to the glacial outlet fjord Godthåbsfjord (Fig. 2).

Fig. 7. Preparing for zooplankton sampling with a MultiNet® equipped with five 50-µm nets. Photo S.H. Jónasdóttir.

In spring the offshore region had pronounced vertical mixing, with centric diatoms and *Phaeocystis* spp. dominating the phytoplankton. Chlorophyll *a* was evenly distributed and nutrients were depleted in the upper 50 m. Ciliates and heterotrophic dinoflagellates constituted equal parts of the protozooplankton biomass. The large *Calanus* species were primarily found to be associated with oceanic or coastal waters.

The water column was stratified in the fjord during spring, causing Chl *a* to be concentrated in a thin sub-surface layer. In the central parts of the fjord nutrients were depleted above the pycnocline, whereas *Thalassiosira* spp. dominated the phytoplankton assemblage close to the Ice Sheet where primary production was high and nutrients rose towards the surface. Dinoflagellates dominated the protozooplankton biomass and protozooplankton production exceeded copepod production in the fjord. In both studies, the biomass of small copepods was surprisingly high in the fjord. *Pseudocalanus* spp. dominated in spring and high biomasses of *M. norvegica* (Fig. 1B) enhanced the biomass of small copepods in summer. Together with high biomasses of rotifers these small zooplankton species seem to be well adapted to the fjord environment. The three *Calanus* species were all present in the fjord but at rather low biomasses and their distribution pattern suggests that they were connected to the populations in the offshore area.

The results of both physical/chemical factors and biological parameters suggest separation of offshore and fjord systems, where the water column structure appears to influence the distribution of the zooplankton species in the fjord. Collectively, these studies showed that *Calanus* is an important grazer in the offshore waters (Papers I and II) whereas a very different planktonic food web structures exist inside the glacial outlet fjord. Function of the pelagic food web in the fjord contradicts the traditional emphasis on large *Calanus* in Arctic waters. Here grazing impact from large copepods on standing stock phytoplankton is low (Papers I and II) whereas grazing by small copepods and protozooplankton is found to be valid (Papers I, Calbet et al. 2011). Differences in pelagic food web function between fjord and offshore system seems to be a common feature throughout the ecosystem as differences in e.g. krill biomass between fjord and offshore system has been found (Agersted et al. 2010) and Sejr et al. (2009) shows differences in abundances of macrobenthic species between fjord and offshore system.

Located at the junction between the Ice Sheet and the ocean, glacial outlet fjords are dynamic systems that are influenced by both terrestrial and marine processes. The West Greenland fjords would most likely be influenced by enhanced discharge from the Greenland Ice Sheet in the future. However, most of the existing ocean-climate models operate down to the coastal shelf spatial scale, but do not extend into glacial fjords. Therefore, understanding of the food web structure is crucial for understanding the implications of climate change, which would most likely alter the food web that makes up the fundament of the natural resources that are so important to the southwest Greenlanders.

6.5 Seasonal succession in the mesozooplankton community

To evaluate the findings of Papers I and II, which suggest establishment of offshore and fjord-system mesozooplankton communities, data provided

by the annual monitoring program Marine Basic Nuuk (Fig. 8) was used to describe the plankton community and its ecological role on an annual basis (Paper III). As the two previous studies showed surprisingly high biomasses of small copepods in the fjord we expected to find a plankton community structure unlike those generally found in Arctic areas.

Fig. 8. Sampling with a 45-µm WP2-net equipped with a flow meter at the monthly samplings at Nuuk Ecological Research Operations. Photo L. Port.

Our findings showed that *Microsetella norvegica* (Fig. 1B) is a key species in the Godthåbsfjord system as it dominates the mesoplankton community structure in terms of both abundance and biomass on an annual basis (Paper III). The knowledge obtained during the 5 years of zooplankton monitoring shows that the plankton community structure in general follows a seasonal pattern with Cirripedia nauplii dominating the biomass in the spring bloom period in April and May, *Calanus* dominating in June followed by *M. norvegica* in July to September, whereas the remaining copepod taxa were evenly distributed throughout the productive season (Fig. 9). Taking into consideration the large interannual differences in abundances of *Calanus* in spring (Paper III) our study unambiguously shows that *Calanus* only exceeds the smaller copepod taxa in June.

On an annual basis, the copepod community grazes 30 g C m^{-2}, distributed equally between *Calanus* spp. 10 g C m^{-2} y^{-1}, *M. norvegica* 11 g C m^{-2} y^{-1} and other copepods 9 g C m^{-2} y^{-1} (Paper III). We found small copepods to require more carbon than *Calanus* on an annual basis (20 g C m^{-2} y^{-1} vs. 10 g C m^{-2} y^{-1} respectively).

The traditional emphasis on large *Calanus* in Arctic marine ecosystems (Hopkins 1969, Hirche 1991) has been found to be true for offshore West Greenland waters (Munk et al. 2003, Pedersen et al. 2005, Paper I and II) and the Disko Bay area (Madsen et al. 2001, Paper V) whereas this study

area contradicts the traditional emphasis on *Calanus*. Instead, we showed that small copepods overruled *Calanus* on an annual basis in the fjord mouth area. The results obtained verify the ideas stated in Papers I and II that the fjord environment should be considered as separated from the offshore system. Furthermore, the results underline the need for annual sampling with small mesh nets in order to determine the entire mesozooplankton community in the Arctic as in any other marine system.

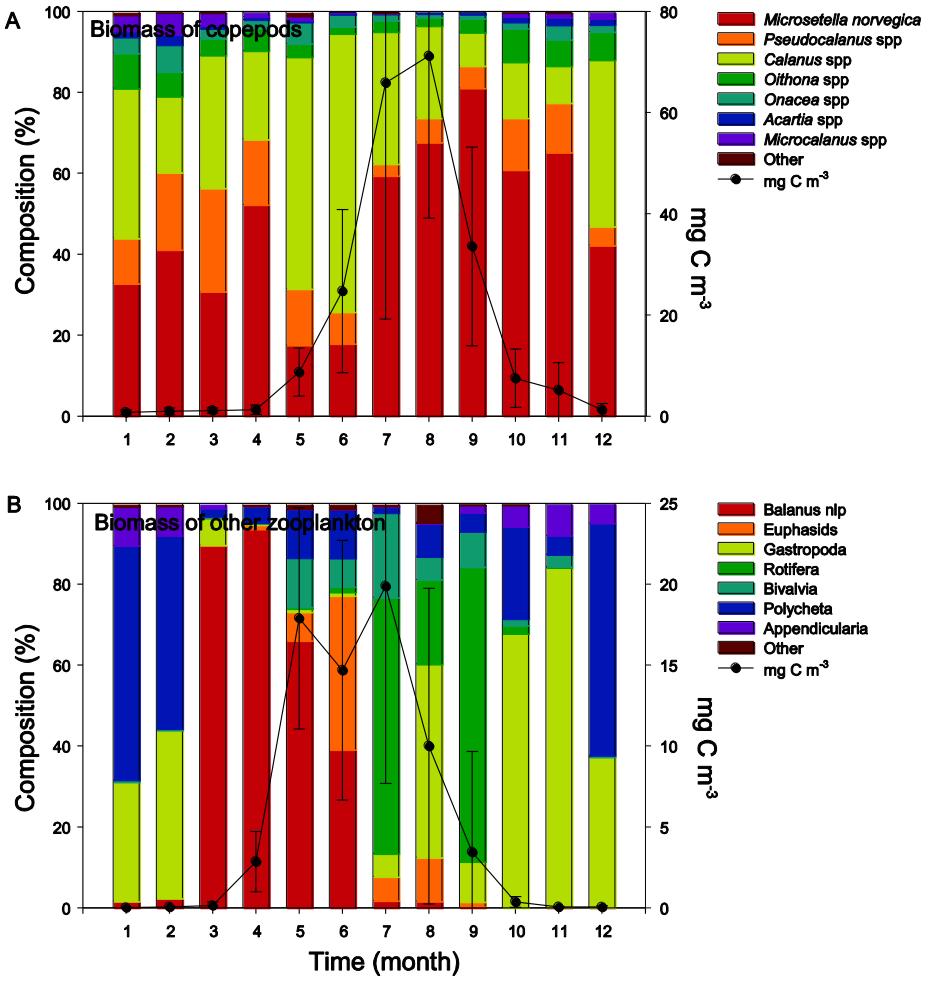

Fig. 9. Monthly average community composition (% of total biomass) of A) copepods and B) other zooplankton. Average monthly biomasses (mg C m^{-3}) ±standard deviations are presented for copepods and other zooplankton.

M. norvegica was found in extremely high numbers during summer and autumn at the fjord entrance (Papers II and III), probably due to convergence in the upper water column of the outer sill region maintained by the strong tidal mixing and special circulation system. Furthermore, circulation retains relatively warm water in an intermediate layer (Fig. 4) where suspended sediments and organic material provided by the high summer bloom in the area (Juul-Pedersen et al. in prep, Fig. 6D) could probably generate aggregates appropriate for grazing of *M. norvegica* as *M. norvegica* has been shown to graze well on particulate and attached

food sources (Koski and Kiørboe 2005, Koski et al. 2007). The long productive season in the fjord area with constant and high summer production may in general benefit populations of small copepods that, unlike *Calanus*, maintain active feeding throughout the productive season. Lipid analyses of *Pseudocalanus minutus* indicates a diatom-based diet in spring where females depend on spring phytoplankton bloom for reproduction whereas a flagellate-based diet seems to dominating the rest of the year (Lischka and Hagen 2007). *Oithona similis* seems to have a omnivorous diet during all seasons (Lischka and Hagen 2007) and spring phytoplankton bloom seems not to influence on the feeding of this species (Lischka et al. 2007).

It has been suggested that zooplankton communities dominated by small zooplankton species low in lipids could impact the upward transfer of lipids in the food web, affecting production at higher trophic levels (Falk-Pedersen et al. 2007). However, growth of young capelin has been shown to correlate well with abundances of small zooplankton (Gjøsæter et al. 2002, Pedersen et al. 2008) and small harpacticoid copepods are suggested to be suitable food for fish larvae (Cutts 2003). The youngest capelin larvae feed on a variety of small zooplankton whereas it has been found that only larvae of a certain size feed on *Calanus* copepodites (Pedersen 2008). Capelin can be present at very high biomasses in the fjords of West Greenland (Laidre et al. 2010) where they spawn, and the high biomasses and productivity of small copepod in e.g. Godthåbsfjord could sustain high-quality food for these larvae. Copepodites of *Calanus* are an important food source for cod larvae (Sundby 1990, Ellertsen 1989), though. Cod has been found to spawn in the inner fjord branch of Godhåbsfjord (Smidt 1979, Hedeholm 2010) in an area with higher abundances of *Calanus* than in the remaining fjord (Smidt 1979). Overall, capelin does not seem to be linked to the food web involving *Calanus* (Fossheim 2006, Pedersen 2008) in the same way as e.g. cod.

6.6 Feeding in a glacial outlet fjord

Glacially influenced fjords can temporarily have high concentrations of suspended particulate matter due to extensive glacial erosion of the bedrock that leads to high sediment load in the runoff (Paper IV, Domack et al. 1994, Hallet et al 1996). Most fjords in Greenland receive large amounts of meltwater with high sediment concentrations from the Greenland Ice Sheet. The runoff is extensive during summer (Mortensen et al. 2011), but plumes containing sediment can be observed by remote sensing even in winter when they are intensified by tidal re-suspension. To test if the differences in plankton community structure between offshore and fjord area could be due to species ability to cope with these high concentrations of suspended sediments, we set up an incubation experiment at the Greenland Institute of Natural Resources (Paper VI). In

order to use the results to better understand the spatial distribution of copepods in glacial marine environments.

Preliminary investigation of the in situ concentrations of suspended particulate matter in the fjord was obtained by vertical measurements of fluorescence and turbidity. The turbidity measurements were then associated with in situ concentrations of suspended matter obtained from niskin bottle water samples in order to given an overall idea of the concentrations of suspended matter along the fjord. The fjord had a natural gradient of suspended matter with very high concentrations in the innermost parts of up to more than 50 mg l^{-1} due to glacial melt water runoff. Sediment concentrations decreased towards the fjord mouth whereas fluorescence increased towards the fjord mouth.

The high concentrations of suspended matter observed in the fjord were expected to have an effect on copepod vital rates. Laboratory experiments showed that high sediment concentrations influence the capability of carbon turnover for *Calanus finmarchicus* and *Pseudocalanus* sp., whereas *Metridia longa* was more tolerant (Paper IV). Ingestion rates when feeding on a nutrition-rich diatom were low at high concentrations of sediment for *C. finmarchicus* (> 20 mg l^{-1}) and *Pseudocalanus* sp. (> 50 mg l^{-1}) while no effect was found for *M. longa*. Decrease in ingestion of diatom food didn't lead to decrease in fecal pellet production for *C. finmarchicus* which can only be explained by ingestion of sediment, which can clearly be observed in fecal pellets (Fig. 10). A decrease in ingestion of the diatom therefore led to reduction in egg production rate at high sediment concentrations for this species.

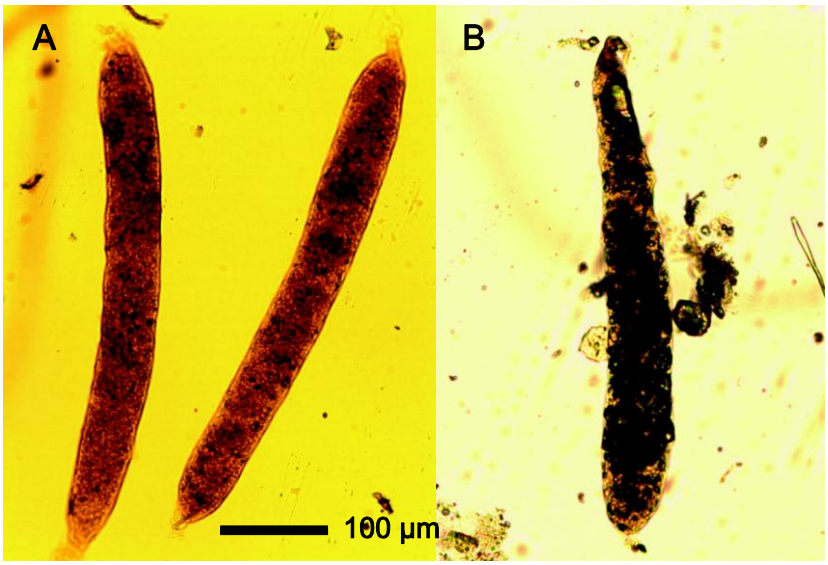

Fig. 10. Lugol fixed fecal pellets of *Calanus finmarchicus* when feeding on a diatom diet A) without suspended sediments and B) with suspended sediments. Photo K.E. Arendt.

It is worth noticing that survival of the copepod females was > 95% (4 days) for all concentrations and copepod species. This is surprisingly high and shows that these species are generally well adapted to environments with suspended sediments containing high food availability. Other studies have shown that the capability to feed efficiently may be reduced at lower food concentrations (Paffenhöfer 1972, Roman 1984). This may explain the high tolerance to suspended sediments in this study where food concentrations were high. However, effects on copepod vital rates would probably be more pronounced in the natural environment where food concentrations are often much lower. The species distribution found in the previous papers (Papers I, II and III) cannot be explained solely by the distribution of suspended sediments. However, species tolerance towards these conditions should be taken into consideration. For example both ciliates (Boenigk and Novarino 2004) and rotifers (Kirk 1991) found to feed well in high contents of suspended sediments, and since they are found in high abundances in Godthåbsfjord (Papers I, II and III), they seem to be well adapted to the fjord environment.

6.7 Fate of the spring bloom

The spring phytoplankton bloom is a key event in marine ecosystems, important for fueling secondary production. It is triggered by breakup of sea ice (see Fig. 6AC) and stabilization of the water column. The development of the spring and summer bloom was studied from February until July at a station near Qeqertarsuaq in Disco Bay at the central part of the West Greenland coast (Fig. 2A). At the time of the spring bloom peak I participated in an intense sampling campaign in April - May 2008, a work that got me involved in Paper V.

In the studied spring bloom situation in Disko Bay, peak concentrations of 24 µg Chl *a* l^{-1} were found. *Calanus* comprised 99% of the copepod biomass even when the small copepod species were taken into account (sampling with a 50 µm net). *Calanus* were present at high biomasses 10,000 mg C m^{-2} in the upper 50 m in the decaying bloom fase in the beginning of May.

Despite the fact that *Calanus* were present from the beginning of the bloom and occurred at very high biomasses in the upper layers where the bloom occurred, they only had a small grazing impact on the phytoplankton. Grazing impact was estimated by four methods and they all indicated grazing to be < 4% of the phytoplankton biomass in the decaying bloom (Table 2, Paper V). Consequently, sedimentation out of the fotic zone was high (1836 mg C m^{-2} d^{-1},) and 60% of this was due to phytoplankton biomass. Succession of the phytoplankton spring bloom was controlled by nitrogen limitation and subsequent sedimentation. From mid May until mid June Chl *a* concentrations dropped to < 4 µg Chl *a* l^{-1}, after which a summer bloom was observed to occur in mid June with Chl *a* concentrations up to 12 µg Chl *a* l^{-1} in a subsurface layer.

The results obtained in this study are in accordance with Sejr et al. (2007) for the spring bloom situation and with Juul-Pedersen et al. (2006) sampled in the post-bloom situation measured in the same area. These studies point out that the copepod community in Disko Bay are not able to control and turn over the developing spring bloom. The high vertical transport fuels relatively high biomasses of macrobenthos, although the carbon demand of the benthic community is low compared with the pelagic community (Sejr et al. 2007).

The Disko Bay transect studies in the late summer season showed differences in plankton community structure between the present study site near Qeqertarsuaq and the southern part of the bay close to the mainland near Aasiaat (see map Fig. 2) (Møller and Nielsen 2000). In the southern part, a herbivorous food chain dominated whereas a more complex food web dominated the strongly stratified area near Qeqertarsuaq which had high biomasses of plankton. In the stratified summer period, bacterial production is an important component for the pelagic production (Nielsen and Hansen 1999) whereas peaks in the primary production seem to be due to new nutrients induced by wind mixing of the upper water strata (Andersen 1981).

7. Conclusions and perspectives

Before 2005, studies of pelagic marine ecology in fjords of Southwest Greenland were restricted to studies by Andersen (1977) and Smidt (1979). The knowledge of marine ecology in Nuup Kangerlua / Godthåbsfjord has now increased remarkably sustained by the monitoring program Marine Basic Nuuk and several research projects operated by Greenland Climate Research Centre. However, the analysis of the ocean-fjord-glacier interaction in the fjords of Greenland has just begun.

In summary, the results of the present work show that there is a huge difference in plankton community structure between the offshore West Greenland Current system and the glacial outlet fjord Godthåbsfjord. The spatial variability seems to be determined by oceanic or coastal waters were the large *Calanus* species are primarily found, whereas small copepod species are important in the fjord environment. The temporal fjord study showed that small copepods such as *Pseudocalanus* spp. and especially *Microsetella norvegica*, which dominate in late summer rule the fjord mouth area on an annual basis. All together the papers suggest separation of offshore and fjord systems and collectively these studies contradict the traditional emphasis on large *Calanus* in Arctic waters and suggest instead very different planktonic food web structures inside the glacial outlet fjord relative to the offshore system.

It has been known for decades that the outer region of Godthåbsfjord is a high productive area (Smidt 1979) an outcome of a long productive season with high and relative constant production rates. Also the inner part of the fjord is due to intrusion of nutrients in front of the glacier productive. Although, the exact process behind this and the cohesion that the discharge from the Greenland Ice Sheet could be a pronounced driver behind this process is not fully described. The constant fueling of the system with new production could be a driver that influences the entire fjord ecosystem and thereby also the plankton community structure and its function. The high concentrations of suspended sediments from eroding glaciers in combination with organic material provided by the primary producers could generate aggregates appropriate for grazing by *Microsetella norvegica* and hereby sustain the surprisingly high biomass of this species. In general the long productive season may sustain small copepods that maintain actively feeding throughout the productive season.

Located at the junction between the Ice Sheet and ocean, the fjords of Greenland would be modified if climate changes alter the flow of marine-terminated outlet glaciers, land runoff as well as changes in large-scale marine circulation patterns. If we are supposed to give forecasts of what to expect in future situations it is crucial to know from what state the ecosystem will change. Therefore it is important to conduct descriptive studies and obtain a basic ecological understanding. Regarding the numerous glacial marine fjords in Greenland we only have a rough description of very few and even here much remains to be done.

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Differences in plankton community structure along the Godthåbsfjord, from the Greenland Ice Sheet to offshore waters

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Differences in plankton community structure along the Godthåbsfjord, from the Greenland Ice Sheet to offshore waters

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ABSTRACT: This study describes differences in plankton community structure and in chemical and physical gradients between the offshore West Greenland Current system and inland regions close to the Greenland Ice Sheet during the post-bloom in Godthåbsfjorden (64° N, 51° W). The offshore region had pronounced vertical mixing, with centric diatoms and *Phaeocystis* spp. dominating the phytoplankton, chlorophyll (chl) *a* (0.3 to 3.9 µg l^{-1}) was evenly distributed and nutrients were depleted in the upper 50 m. Ciliates and heterotrophic dinoflagellates constituted equal parts of the protozooplankton biomass. Copepod biomass was dominated by *Calanus* spp. Primary production, copepod production and the vertical flux were high offshore. The water column was stratified in the fjord, causing chl *a* to be concentrated in a thin sub-surface layer. Nutrients were depleted above the pycnocline, and *Thalassiosira* spp. dominated the phytoplankton assemblage close to the ice sheet. Dinoflagellates dominated the protozooplankton biomass, whereas copepod biomass was low and was dominated by *Pseudocalanus* spp. and *Metridia longa*. Primary production was low in the outer part of the fjord but considerably higher in the inner parts of the fjord. Copepod production was exceeded by protozooplankton production in the fjord. The results of both physical/chemical factors and biological parameters suggest separation of offshore and fjord systems.

KEY WORDS: West Greenland coast · Sub-Arctic fjord · Physical gradients · Plankton community structure · Primary and secondary production · Vertical flux

INTRODUCTION

West Greenland marine ecosystems present a complex interaction between the marine areas along the West Greenland banks and the numerous fjords that drain melt water from the Greenland Ice Sheet to the sea. The freshwater discharge from land creates a gradient in freshwater content from the inner parts of the fjord systems to the shelf area dominated by the relatively warm and saline West Greenland Current. The mixing of water masses of distinct origin creates a highly productive system (Smidt 1979) sustaining a rich and diverse food web. Whales (Heide-Jørgensen et al. 2007) and seals feed here during summer, and seabirds from the entire Baffin Bay find their winter habitat in this ice-free area (Merkel et al. 2002). Furthermore, the area is important for the Greenland society, in terms of commercial fishing as well as traditional and recreational fishing and hunting.

Copepods are key organisms responsible for the transfer of carbon from the primary producers and microzooplankton to higher trophic levels. In the Arctic, *Calanus* spp. play an important role because of their ability to effectively convert phytoplankton and accumulate lipids (Falk-Petersen et al. 2007). The importance of *Calanus* spp. is well documented in the shelf and offshore region of West Greenland (Pedersen & Smidt 2000, Munk et al. 2003). It has been shown

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that circulation of the north-flowing current around the West Greenland banks creates eddies that retain plankton in high biomass patches (Pedersen et al. 2005). In the shelf and offshore area, *Calanus* leave the surface water in mid-summer, after which smaller species and juvenile stages of copepods dominate the mesozooplankton biomass (Thor et al. 2005, Møller et al. 2006). Simultaneously, a significant biomass of protozooplankton builds up (Levinsen & Nielsen 2002), which, together with the small species and copepod stages, is responsible for recycling the primary production in an extended period of time. It has been shown that plankton community structure in the shelf area is dependent on depth and time (Thor et al. 2005), but the interaction between the fjords and offshore plankton communities is currently unknown. Furthermore, it is not known whether the succession dynamics of offshore plankton communities are representative of the inner fjord systems, as advection of zooplankton could determine the plankton community structure in the fjord, or whether the plankton composition represents an isolated community adapted to the microhabitat in the fjord, as suggested by Smidt (1979).

Due to global climate change, acceleration of mass loss of the Greenland Ice Sheet has been observed (Velicogna & Wahr 2006, Hanna et al. 2008). In addition, precipitation has been predicted to increase during the next decade (Kattsov & Källén 2005). Increased runoff from the ice sheet and surrounding land to the inner parts of the fjord would greatly affect the water column structure and thereby the microhabitat in the fjord and coastal regions. The enhanced admission of freshwater could potentially enhance estuarine circulation and thereby nutrient input to the inner parts of the fjord (Rysgaard et al. 2003, Bendtsen et al. 2007). Entrainment of nutrient-rich deep water into the photic zone of the inner fjord would result in increased biological productivity (Aure et al. 2007, Rysgaard & Glud 2007) and would most likely affect the energy flow through the entire food web. Furthermore, changes in the West Greenland Current are an important factor determining the characteristics of the pelagic system. A general warming has been found to occur in the central parts of Baffin Bay (Zweng & Münchow 2006) and along the West Greenland coast (Holland et al. 2008). Changes in the water mass circulation in the North Atlantic and Arctic areas are known to determine the distribution and relationship between the important *Calanus* species (Fleminger & Hulsemann 1977, Hirche 1991), but the extent to which it determines the mesozooplankton community in the West Greenland fjords remains unknown.

The coastal ecosystem is still inadequately understood, and it is not yet described how the ecosystem and its organisms adapt to the variability of climate gradients. Long-term monitoring data are lacking, and a more comprehensive understanding of the system is needed in order to make predictions of how global climate change will affect the ecosystem and its productivity. The aim of the present study was to describe how the plankton community structure and productivity and the vertical flux vary in relation to differences in the physical/chemical gradients from the offshore area and along the fjord to the Greenland Ice Sheet and to initiate a long-term monitoring program in West Greenland waters (Rysgaard et al. 2008).

MATERIALS AND METHODS

Study site and sampling. This study was conducted along a section from the inner parts of Godthåbsfjorden close to the Greenland Ice Sheet along the fjord to the offshore parts of the Fyllas Banke (Fig. 1). Samples were collected from RV 'Adolf Jensen' (Greenland Institute of Natural Resources) in the daytime (07:00 to 21:00 h) from 15 to 20 May 2006.

Vertical profiles of water temperature, salinity, density and fluorescence were obtained using a CTD (SBE 19plus, SeaCat) equipped with a Seapoint Chlorophyll Fluorometer and a Biospherical/Licor sensor. Profiles were recorded from the surface to approximately 5 m above the bottom. Water samples were taken using a 5 l Niskin water sampler at depths of 1, 5, 10, 15, 20, 30, 50, 100, 200, 400, 600, 800 … m, with the deepest sample being collected 10 m above the bottom.

Water chemistry. Water samples (10 ml) were GF/C filtered and kept frozen (–18°C) until analyses for nutrients. Concentrations of NO_2^- + NO_3^- were measured by vanadium chloride reduction (Braman & Hendrix 1989). Phosphate and SiO_2 concentrations were analysed using standard spectrophotometric methods (Strickland & Parsons 1972, Grasshoff et al. 1983). At each station, water samples from 5, 30 and 50 m depth were taken for chlorophyll *a* (chl *a*) measurements. The samples were split into 3 subsamples of 150 ml; 2 samples were passed through 11 µm and 40 µm filters, while 1 sample remained untreated until the samples were filtered onto GF/C filters (<0.2 bar) and frozen (–18°C). Chl *a* samples were extracted in 96% ethanol for 18 h before fluorescence was measured on a fluorometer (TD-700, Turner Designs) calibrated against a pure chl *a* standard (Turner Designs). The analysis was used for calibration of the CTD fluorometer, and chl *a* concentrations were then calculated from CTD fluorescence profiles at all stations.

Phytoplankton biomass and primary production. Net phytoplankton was sampled by triplicate vertical hauls using a 20 µm plankton net (0 to 60 m), and the phytoplankton composition was identified to major

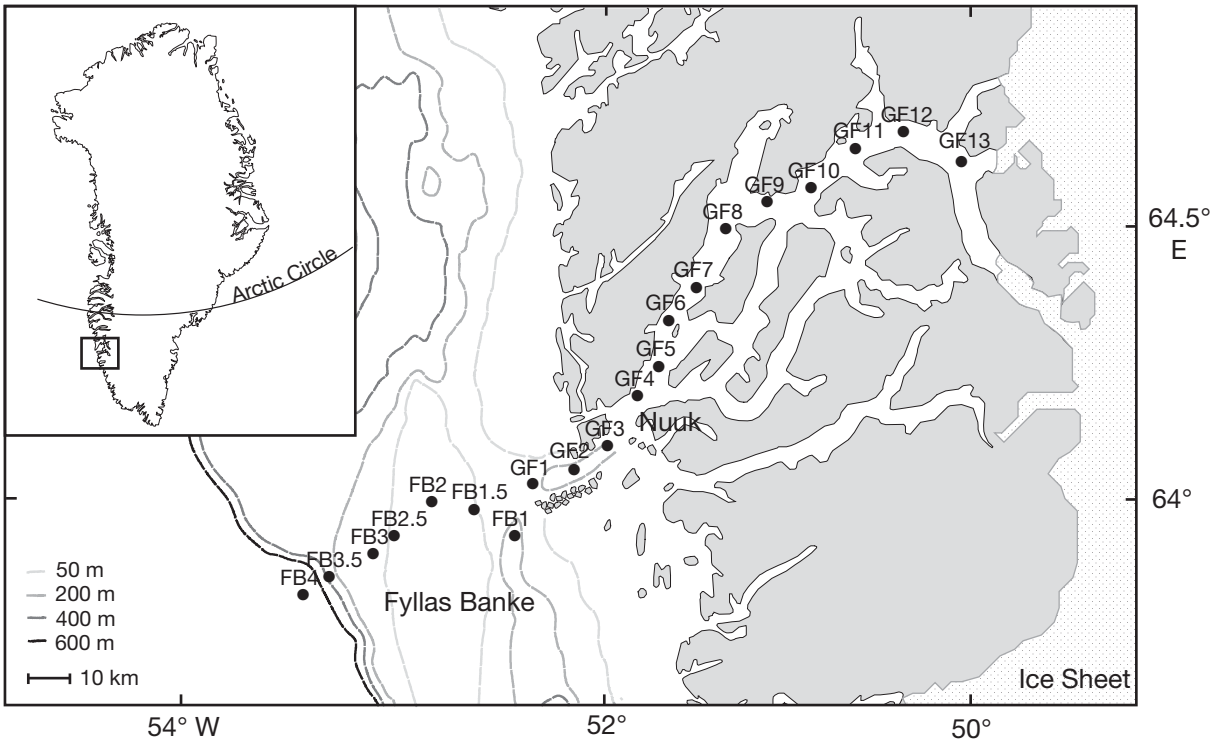

Fig. 1. Sampling locations in the Godthåbsfjord and at Fyllas Banke, West Greenland

taxonomical groups at the Arctic Agency, Poland. The phytoplankton biomass (chl *a* C) was estimated using the carbon:chl *a* ratio of 42.7 originating from Disko bay, West Greenland waters during a similar successional stage of the phytoplankton community (Juul-Pedersen et al. 2006). Primary production was measured *in situ* applying the ^{14}C incubation technique (Steeman-Nielsen 1952). Triplicate samples from 5, 10, 20, 30 and 40 m were incubated in 2 clear and 1 dark glass bottles (120 ml) containing 200 µl $H^{14}CO_3^-$ for 2 h during mid-day. After incubation, the bottles were fixed with 100 µl 5% $ZnCl_2$ and the entire content of each bottle was filtered onto GF/C filters and stored frozen in a vial. Before analysis, 100 µl 1N HCl were added to the vials. The vials were fumed for 24 h, after which PerkinElmer Ultima Gold scintillation liquid was added and the samples were counted on a PerkinElmer TriCarb 2800 TR liquid scintillation analyser. The gross primary production was calculated adding the actual dissolved inorganic carbon (DIC) values measured on a CM5012 CO_2 coulometer as described by Rysgaard & Glud (2004). Primary production was adjusted for irradiance using irradiance values for the sampling period provided by Asiaq (Greenland Survey), and integrated to 45 m depth.

Protozooplankton. Abundance, size and overall taxonomic composition of protozooplankton were determined at 3 depths; 10, 30 and 50 m. At each depth, a 500 ml water sample was fixed in acidic Lugol's solution (final concentration 1%). The samples were kept dark and cool until processing. A subsample (50 ml) was allowed to settle for 24 h before it was counted under an inverted microscope. Ciliates and heterotrophic dinoflagellates were categorised by functional group, and cell lengths and widths were measured. The carbon content was calculated using the size measurements and carbon content factors according to Menden-Deuer & Lessard (2000). Clearance of heterotrophic dinoflagellates and ciliates was calculated assuming maximum clearance according to the equations in Hansen et al. (1997) for ciliates:

$$\log(C_{max}) = 1.491 - 0.23\log(P_{vol}) \quad (1)$$

and for heterotrophic dinoflagellates:

$$\log(C_{max}) = 0.851 - 0.23\log(P_{vol}) \quad (2)$$

where C_{max} (10^5 h^{-1}) (Fenchel 1982) is maximum specific clearance and P_{vol} (µm^3) is body volume. The clearance was converted to *in situ* temperatures by the application of a Q_{10} of 2.8 (Hansen et al. 1997). Grazing was calculated from the clearance and the *in situ* chl *a* C for heterotrophic dinoflagellates and chl *a* C <11 µm for ciliates. Growth was estimated using an average gross growth efficiency of 0.33 (Hansen et al. 1997).

Mesozooplankton. Samples of large mesozooplankton were collected by vertical hauls with a MultiNet (Hydrobios) equipped with five 300 µm nets. The samples were collected at 5 depth intervals: 0–50, 50–100,

100–150, 150–200 and 200–270 m. At stations with depths <270 m, samples were collected with a 200 µm WP-2 net instead. Furthermore, samples of the small-sized mesozooplankton were collected in the upper 100 m, using a 45 µm WP-2 net. The mesozooplankton was fixed in buffered formaldehyde (4% final concentration), and identified to either species or genus and developmental stage. The prosome lengths of a minimum of 10 ind. in each copepod stage and the body lengths of a minimum of 20 nauplii were measured. Identifications and length measurements of mesozooplankton were made at the Arctic Agency, Poland. The carbon content of copepods was calculated using the length-weight regression given in the literature (*Microsetella* spp. provided by Satapoomin 1999; *Paraeucheta norvegica* by K. Tönnesson unpubl.; values for the remaining groups were summarised by Thor et al. 2005).

The egg production rate (EPR) and faecal pellet production (FPP) of *Calanus finmarchicus* and *Metridia longa* were measured. Healthy and active fertilised females of *C. finmarchicus* and *M. longa* were collected by vertical hauls from 100 to 0 m using a 200 µm WP-2 net equipped with a large non-filtering cod end. The females were immediately placed in a 525 ml polycarbonate bottle containing 50 µm prescreened surface seawater. At each station, individual females were incubated in replicates of 8 to 20 bottles and incubated in a thermo box with flow-through surface water at *in situ* temperature. After 24 h, eggs and faecal pellets (FP) were counted. Length and width of FP, the copepod prosome length and egg width were measured. Egg volumes were converted to carbon using a conversion factor of 0.14 pg C μm^{-3} (Kiørboe et al. 1985), and FP volumes were converted to carbon using a factor of 0.069 pg C μm^{-3} (Riebesell et al. 1995). Production of the copepod community (secondary production) was estimated using the total biomass of the large and small mesh nets multiplied by specific EPR measured for *C. finmarchicus*, assuming that specific EPR was equal to somatic growth of juveniles and other species (Berggreen et al. 1988). Grazing impact was not directly measured but was estimated from the EPR and FPP, assuming a gross growth efficiency of 33% (Hansen et al. 1997).

Sedimentation traps. Vertical flux was measured using 2 sediment traps, each equipped with paired cylinders (∅80 mm × 450 mm, KC Denmark). The traps were filled with GF/C filtered bottom water and deployed for 2 to 4 h at 60 m depth. After incubation, the entire contents of 2 traps were filtered onto GF/C filters. One filter was analysed for chl *a*, and 1 filter was analysed for particulate organic carbon (POC). For POC analysis, a subsample of the filter was moistened with 1M sulphurous acid (H_2SO_3), dried for 24 h at 60°C prior to analysis on an elemental analyser (SerCon ANCA GSL) in line with a mass spectrometer (SerCon Hydra 20-20). The molar C/N ratio was calculated as POC/particulate nitrogen (PN). One trap was stored cold and dark for 24 h before the settled particles were gently decanted and fixed in acidic Lugol's solution (final concentration 1%). The numbers of intact and fragmented FP were counted under an inverted light microscope, and the sizes of 30 randomly intact or fragmented FP per station were measured. The volume was estimated using the equation of a cylinder and converted to biomass as in the copepod FPP experiments.

RESULTS

Physical environment, nutrients and chlorophyll distribution

The shallow Fyllas Banke with depths of approximately 40 m functions as a barrier separating the Godthåbsfjord from the offshore regions (Fig. 1). The offshore region outside Fyllas Banke is dominated by the West Greenland Current flowing northward along the West Greenland shelf (Buch 1990), while the fjord is strongly impacted by melt water from the surrounding area and the Greenland Ice Sheet.

The north-flowing currents contain highly saline water with maximum salinity, temperature and density at a plume below 300 m (Fig. 2). These water masses follow the bathymetry, as a side branch of this highly saline water can be seen on the inside of the bank close to the fjord inlet (Fig. 2). At Fyllas Banke (Stns FB2 and FB2.5) and at the inlet of the fjord (Stns GF2 and GF3) vertical mixing takes place because of the strong tidal forces. The fjord inlet is a turbulent area, as all water transport into and out of the fjord must pass the narrow inlet. At the central and inner parts of the fjord, a low-saline water plume in the upper parts of the water column is separated from the deeper water masses by a pycnocline (Figs. 2C & 3). Despite the fact that the low-saline water originates from melting ice and snow, the low-saline water is warmer than the fjord water below due to atmospheric heating of the surface layer (Fig. 2B). At Stn GF13 close to the ice sheet, a plume of cold water (< −0.5°C) is situated at 13 m water depth (Fig. 2B). In the deeper waters of the inner parts of the fjord, water of high salinity, temperature and density is observed, originating from occasional exchange with deeper water outside the fjord (Fig. 2).

The nutrient distribution followed the water column structure with low concentrations above the pycnocline (Fig. 3). At Fyllas Banke, nutrients were depleted

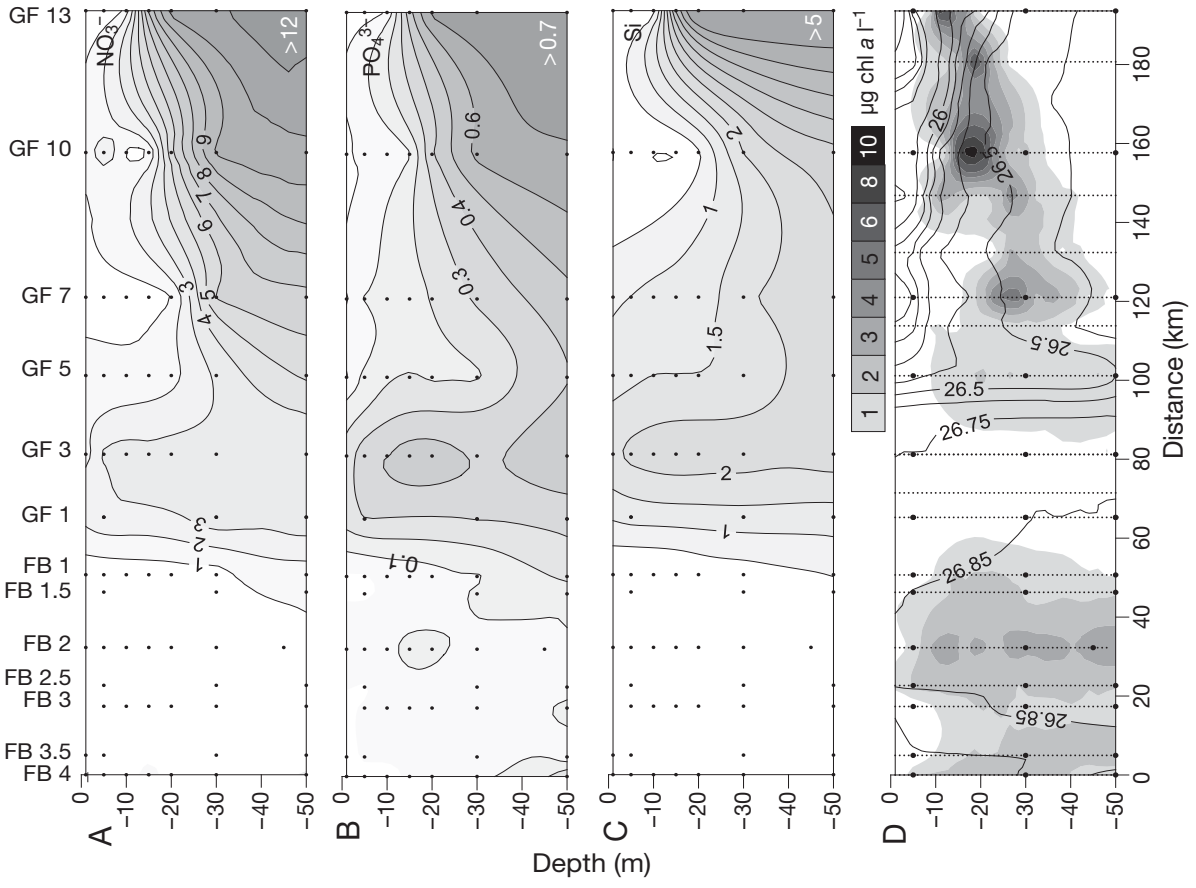

Fig. 3. Depth distribution of (A–C) nutrients (µM), and (D) density (δ, isolines) and chl *a* (µg l^{-1}, shading) in the upper 50 m. Points represent water samples, dotted lines represent fluorescence measurements

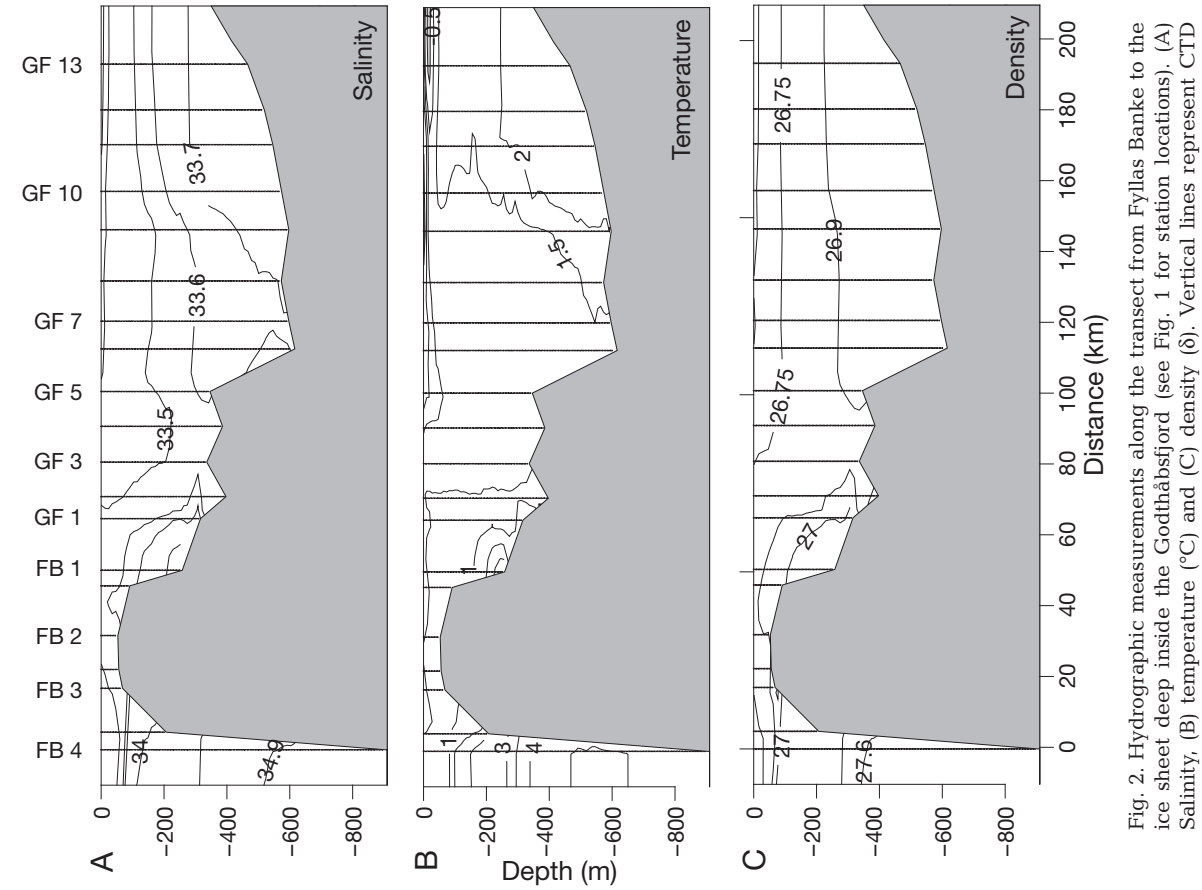

Fig. 2. Hydrographic measurements along the transect from Fyllas Banke to the ice sheet deep inside the Godthåbsfjord (see Fig. 1 for station locations). (A) Salinity, (B) temperature (°C) and (C) density (δ). Vertical lines represent CTD data points

in the upper 50 m, whereas high concentrations were found in the high-salinity waters below 300 m on the offshore parts of Fyllas Banke. Peak contents of all nutrients were observed at Stn FB4 at 600 m depth: 19.1 µM nitrate, 1.0 µM phosphate and 7.9 µM silicate. A branch of this nutrient-rich water mass occurs in the deepest parts on the inside of the bank and at the innermost stations (data not shown). At the entrance to the fjord, nutrients were quite evenly distributed in the water column due to vertical mixing, while being depleted above the pycnocline at the fjord stations (Fig. 3).

Chl *a* was quite evenly distributed in the water column at Fyllas Banke, whereas low concentrations were observed at the fjord inlet due to vertical mixing (Fig. 3D). In the central and inner parts of the fjord, chl *a* distribution followed the pycnocline and the nutrient-rich water deep at the mouth of the fjord and gradually rose to the surface as it approached the innermost stations (Fig. 3). High chl *a* concentrations (11.8 µg l^{-1} at Stn GF10) was observed in a subsurface layer at the pycnocline in these inner parts of the fjord.

Plankton community structure

The qualitative composition of the net phytoplankton (>20 µm) varied along the section, with dominance of centric diatoms at the offshore stations and dominance of the colonial cells of the haptophytes *Phaeocystis* spp. at most stations on the bank and in the central parts of the fjord, while chain-forming diatoms (*Thalassiosira* spp.) dominated the station close to the Greenland Ice Sheet (Fig. 4A).

The protozooplankton community was dominated by ciliates and large (>40 µm) athecate heterotrophic dinoflagellates (*Gymnodinium* spp. and *Gyrodinium* spp.) at all stations along the transect (Fig. 4B). Large (>40 µm) ciliates constituted a greater part of the protozooplankton community on the bank, while small (<40 µm) athecate dinoflagellates were more abundant at the fjord stations (Fig. 4B). Thecate dinoflagellates constituted only a small part of the heterotrophic biomass at all stations along the section (<14% of total biomass).

The copepod community structure showed great variance along the transect (Fig. 5A,B), with dominance of the *Calanus* spp. in the offshore regions, *Pseudocalanus* spp. in the central parts of the fjord and *Metridia longa* and *Microsetella* spp. in the inner parts of the fjord.

In the offshore region, *Calanus* spp. constituted >90% of the total biomass of both the MultiNet and WP-2 net (200 and 300 µm) samples (Fig. 5A). At the stations located on the slopes of the bank, larger copepodite stages of *C. finmarchicus* and *C. hyperboreus* were dominant, whereas nauplii and the copepodite stage CI of *Calanus* spp. dominated the assemblage in the central parts of the bank. Also in the 45 µm net samples, *Calanus* spp. were the dominant group in the offshore region (Fig. 5B), although *Pseudocalanus* spp. constituted a considerable part of the total biomass (Fig. 5B). For a section from the open water to the ice sheet, along the fjord, *Calanus* spp. became gradually less abundant (Fig. 5A,B). *Pseudocalanus* spp. dominated the community in the central parts of the fjord, whereas *Metridia longa* constituted a considerable part at the station close to the ice sheet (Stn GF 13). In the 45 µm net samples, *Microsetella* spp. made up a considerable part of the total biomass and became increasingly dominant towards the ice sheet (Fig. 5B).

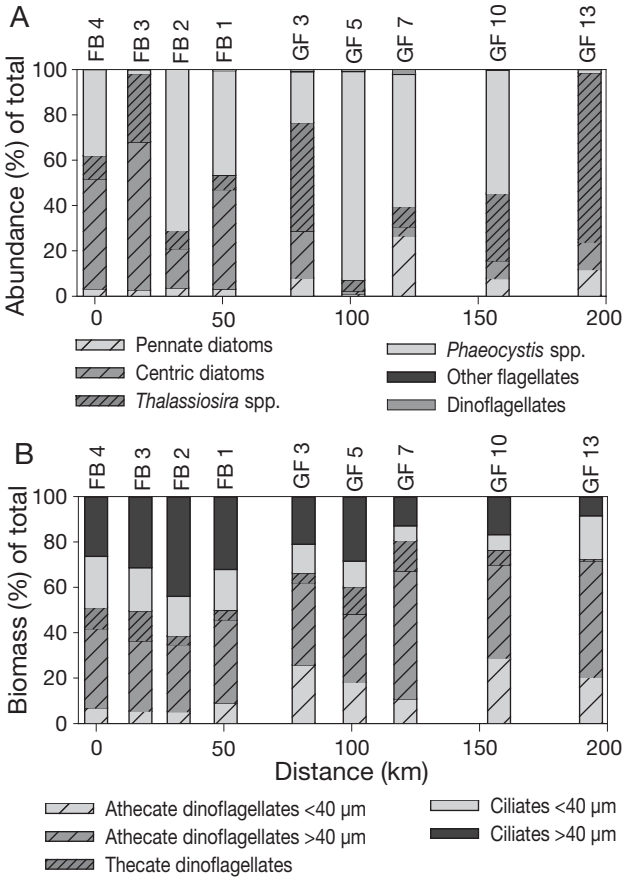

Fig. 4. (A) Net phytoplankton community composition (>20 µm), in % of abundance. (B) Community composition of heterotrophic protozooplankton, in % of total biomass. See Fig. 1 for station locations

Plankton community biomasses

At the offshore stations and the central parts of the bank, chl *a* was mainly present in the size fraction

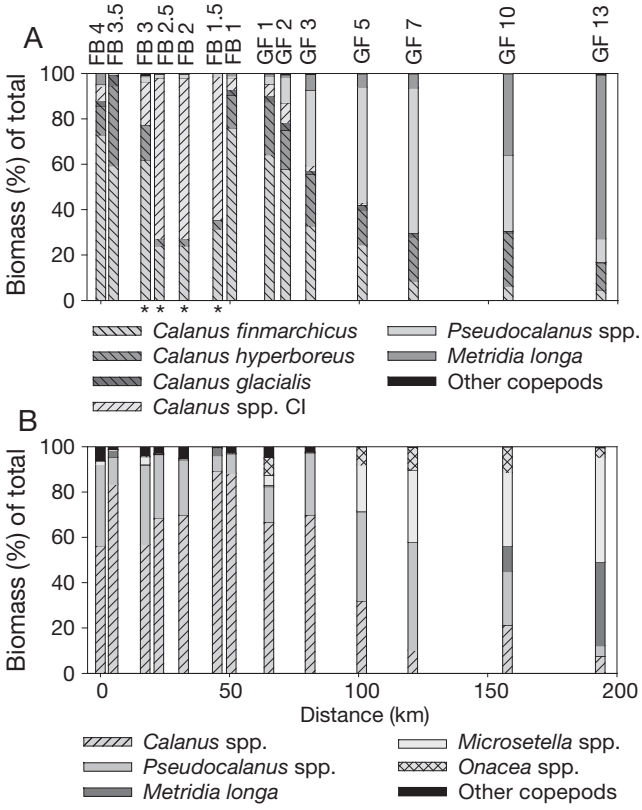

Fig. 5. Community composition of copepods, in % of total biomass in (A) 300 µm MultiNet and 200 µm WP-2 net (*) and (B) 45 µm WP-2 net. See Fig. 1 for station locations

>40 µm (Figs. 3D & 6A). However, the plankton communities of the central parts of the fjord turned out to be mainly <40 µm (Figs. 3D & 6). The highest chl *a* concentration was observed at Stn GF10, where the measured chl *a* for the size fractions <11 µm, 11–40 µm and >40 µm was 4.8, 4.6 and 2.4 µg l^{-1}, respectively. At the innermost station, chl *a* was mainly in the size fraction >40 µm (Fig. 6A) due to the dominance of chain-forming diatoms.

The integrated biomass (chl *a* converted to biomass: chl *a* C) of the primary producers in the upper 50 m was highest in the central parts of the bank (4857 mg C m^{-2}), while it declined steeply at the entrance to the fjord (833 mg C m^{-2}, Fig. 7A). In the fjord, integrated biomass varied from 1672 to 4253 mg C m^{-2}, with 2 distinct peaks in the central parts, while decreasing at the station closest to the ice sheet.

The standing stock of heterotrophic protozooplankton followed the same pattern as the primary producers (Fig. 7B). Biomasses were high offshore (817 to 1301 mg C m^{-2}) and declined to 497 mg C m^{-2} at the entrance to the fjord and increasing to 1545 mg C m^{-2} in the central parts of the fjord. Low biomasses were found at the station closest to the ice sheet (559 mg C m^{-2}).

The total biomass of the copepod community showed great variability along the transect, with 2 peaks in association with the fronts on the slopes of the bank and low biomasses on the bank itself and within the fjord (Fig. 8A,B). The 200 and 300 µm mesh nets showed 2 peaks in biomass on either side of the bank (9310 and 4671 mg C m^{-2}). Biomasses were more than an order of magnitude lower (ca. 500 mg C m^{-2}) in the central parts of the bank, at the entrance of the fjord and at the stations close to the ice sheet, while there was a small biomass peak in the central part of the fjord (1016 mg C m^{-2}). The biomass sampled with the 45 µm mesh net (0 to 100 m) generally followed the same pattern as the larger mesh nets (Fig. 8B). Biomass peaked on either side of the bank (1330 and 1655 mg C m^{-2}) but was low at all other stations. It is notable that the biomass of the 45 µm mesh net exceeded 100% of the biomass sampled with the 300 µm net at the entrance of the fjord.

Vertical distribution of the copepod biomass (data from 200 and 300 µm mesh nets) showed explicit division of the habitat of the 3 dominating species (*Calanus finmarchicus*, *Pseudocalanus* spp. and *Metridia longa*; Fig. 9). Maximum biomass of *C. finmarchicus* was found in the 50 to 100 m sample on either side of the bank (81 and 8.7 mg C m^{-3}, respectively), but species were well represented (>1 mg C m^{-3}) in the water column down to 200 m at the offshore stations and at the mouth of the fjord (Fig. 9A). *Pseudocalanus* spp., the dominating species in the central parts of the fjord, were also well represented (>1 mg C m^{-3}) down to 200 m depth but had a maximum abundance of 5.5 mg C m^{-3} in the upper 50 m (Fig. 9B). Close to the ice sheet, the dominant species *M. longa* was well represented in the water column at 50 to 150 m depth, with a maximum abundance of 2.6 mg C m^{-3} at 100 to 150 m (Fig. 9C). The biomass of *M. longa* was negatively correlated to fluorescence ($r = -0.74$, $n = 55$, $p < 0.01$) and positively correlated with temperature and depth ($r = 0.52$, $n = 55$, $p < 0.01$ and $r = 0.53$, $n = 55$, $p < 0.01$, respectively).

Plankton community production and vertical flux

In the outer parts of Fyllas Banke, primary production exceeded 1200 mg C m^{-2} d^{-1}, while it decreased in the central parts of the bank (Stn FB2; 466 mg C m^{-2} d^{-1}; Fig. 10A). Along the fjord, primary production increased towards the stations close to the ice sheet where very high primary production rates were found (1739 mg C m^{-2} d^{-1}).

Secondary production of the protozooplankton also varied considerably along the transect (Fig. 10 B). Protozooplankton production in the offshore region was

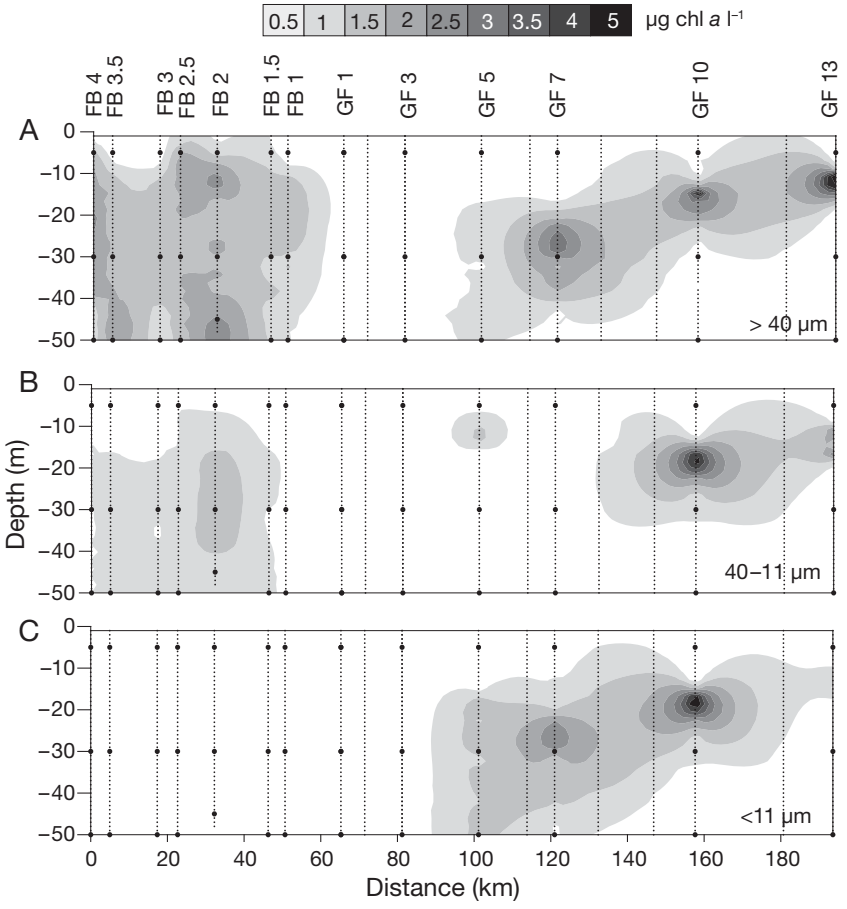

Fig. 6. Fractionated chl *a* (µg l^{-1}) for cells (A) >40 µm, (B) 11–40 µm and (C) <11 µm. Points represent water samples, dotted lines represent fluorescence measurements. See Fig. 1 for station locations

estimated to between 33 and 66 mg C m^{-2} d^{-1}, with the lowest production at the entrance to the fjord, while production increased inside the fjord (Fig. 10B).

The EPR of *Calanus finmarchicus* was high close to and on Fyllas Banke (19 to 27 eggs $female^{-1}$ d^{-1}, Fig. 11A) and, at the same stations, high rates of FPP were measured (33 to 38 FP $female^{-1}$ d^{-1}). The EPR and FPP declined at the entrance to the fjord, while it increased in the central parts of the fjord, but decreased at the station closest to the ice sheet. The EPR and FPP of *Metridia longa* were only measured at the innermost fjord stations. EPR was between 1.5 and 7.8 $female^{-1}$ d^{-1} and FPP between 4.5 and 7.8 fem^{-1} d^{-1} (Fig. 11A).

There was a significant correlation between specific egg production rate (SEP) and specific faecal pellet production (SPP; Table 1), with a median FP volume of 3.3×10^6 $\mu m^3 \pm 0.08 \times 10^6$, n = 593. SPP was significantly correlated with total biomass of chl *a* (mg chl *a* m^{-2}) and in the 11 to 40 µm size spectrum, whereas a significant correlation was not found for SEP (Table 1). Due to the significant correlation between SPP and chl *a* in the 11 to 40 µm size spectrum, which is assumed to be the major food source for *Calanus finmarchicus*, the grazing rate of the copepod community was based on the SPP of *C. finmarchicus.*

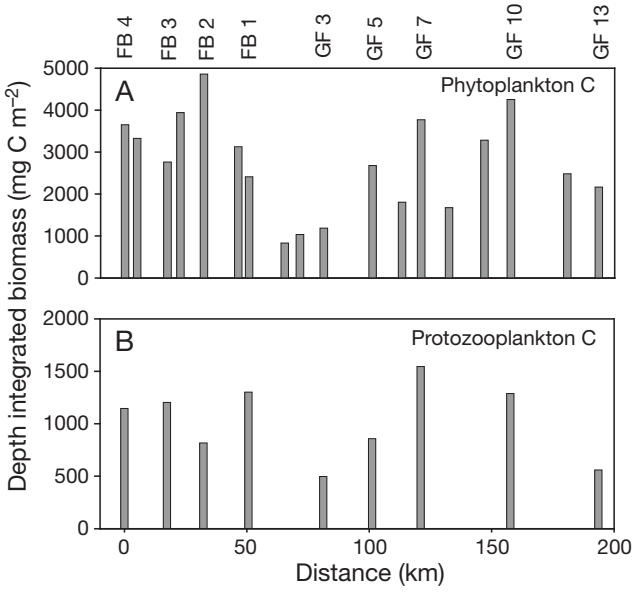

Fig. 7. Depth integrated biomass (0–50 m, mg C m^{-2}) of (A) phytoplankton and (B) heterotrophic protozooplankton. See Fig. 1 for station locations

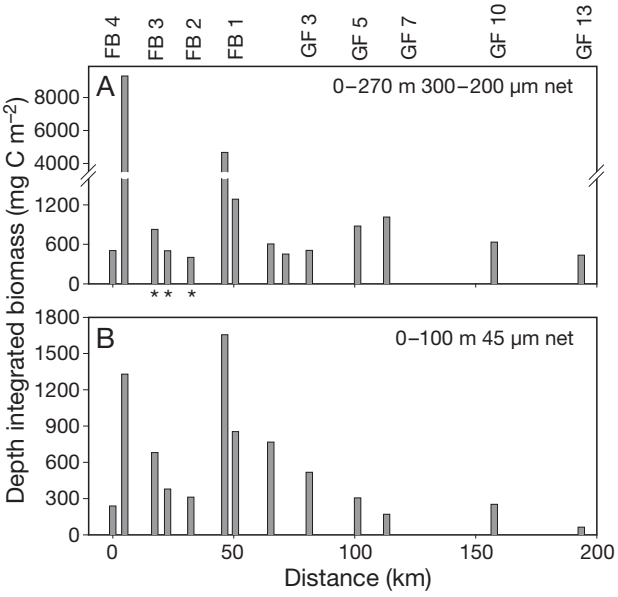

Fig. 8. Depth integrated biomass of copepods (mg C m^{-2}) sampled with (A) 300 µm MultiNet and 200 µm WP-2 net (*) and (B) 45 µm WP-2 net. See Fig. 1 for station locations

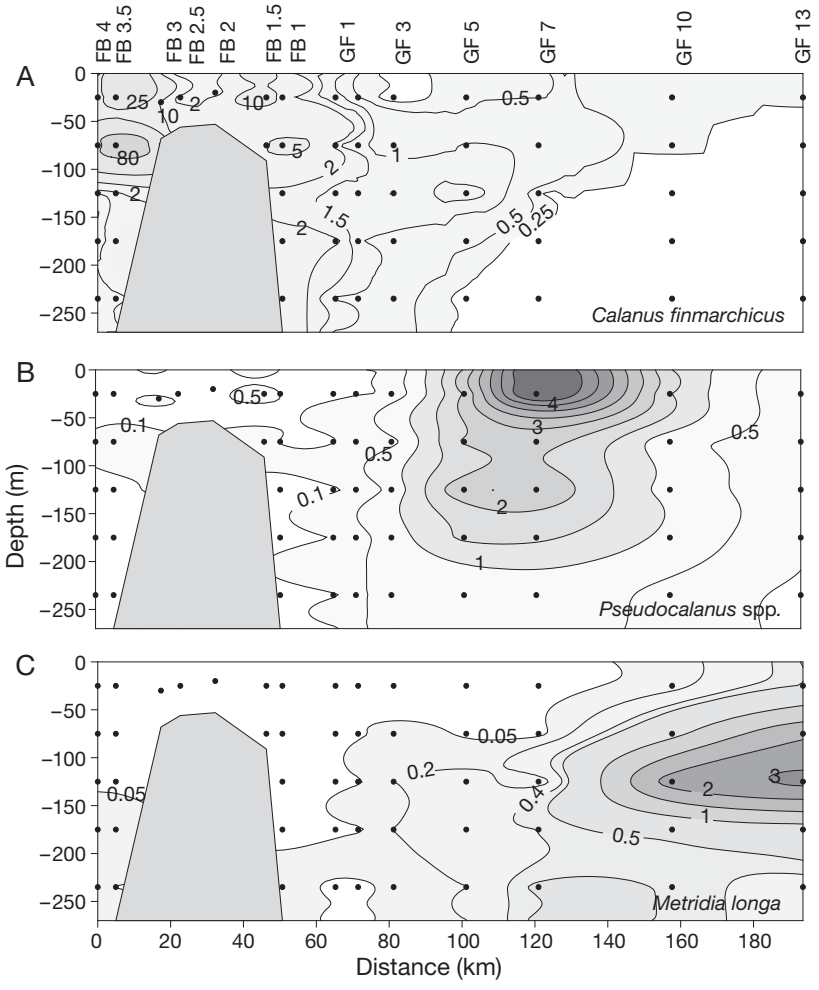

Fig. 9. (A) *Calanus finmarchicus*, (B) *Pseudocalanus* spp. and (C) *Metridia longa*. Distribution of copepod biomass (mg C m^{-3}) along the transect sampled with the 300 µm MultiNet and 200 µm WP-2 net. Dots represent sample intervals. See Fig. 1 for sampling locations

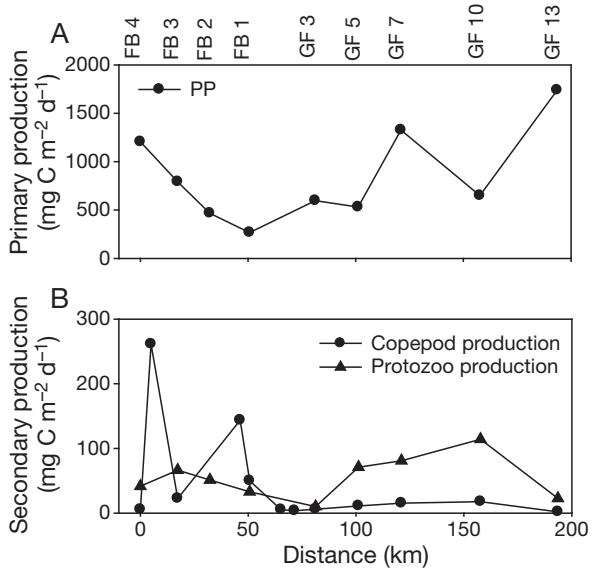

Fig. 10. (A) Primary production (PP) in the upper 50 m (mg C m^{-2} d^{-1}), and (B) secondary production (mg C m^{-2} d^{-1}) of copepods (0–270 m) and protozooplankton (protozoo) (0–50 m). See Fig. 1 for sampling locations

Copepod production closely followed the distribution of copepod biomass, with 2 very high peaks in production in the offshore region, whereas the production was notably lower at the remaining stations (Fig. 10B). On either side of the bank, very high copepod productions were observed (299 and 194 mg C m^{-2} d^{-1}), while production at the remaining offshore stations varied between 8 and 41 mg C m^{-2} d^{-1}. In the fjord, production was generally low, being highest at the central station (up to 25 mg C m^{-2} d^{-1}) and lowest close to the ice sheet (2 mg C m^{-2} d^{-1}). There was no significant correlation between secondary production and the biomass of chl *a* ($r = 0.15$, $n = 10$). The general pattern of EPR and estimated secondary copepod production is corroborated by the abundance of copepod eggs and nauplii in the 45 µm mesh net (Fig. 11B).

Vertical fluxes from the photic zone were high in the offshore region, and lower at the fjord stations (Fig. 12). Measured POC, entering the trap in the outer parts of Fyllas Banke, was >1594 mg m^{-2} d^{-1} and of that, >721 was due to phytoplankton carbon, according to the measured chl *a*. In the central parts of the bank, a high amount of chl *a* (1261 mg C m^{-2} d^{-1}) was measured in the trap. In the fjord, the vertical fluxes were lower between 658 and 1165 mg POC m^{-2} d^{-1}, and between 140 and 766 mg C m^{-2} d^{-1} was due to chl *a* (Fig. 12). The flux of FPC shows some similarities with the FP community production, with the highest flux at station GF10 in the inner fjord (Fig. 12).

DISCUSSION

The present study showed a steep gradient in physical, chemical and biological conditions from the offshore regions along the Godthåbsfjord to the Greenland Ice Sheet. This gradient was strongly reflected in the plankton community structure. The strong physical/chemical gradient might induce these large changes in the plankton community composition. The geographi-

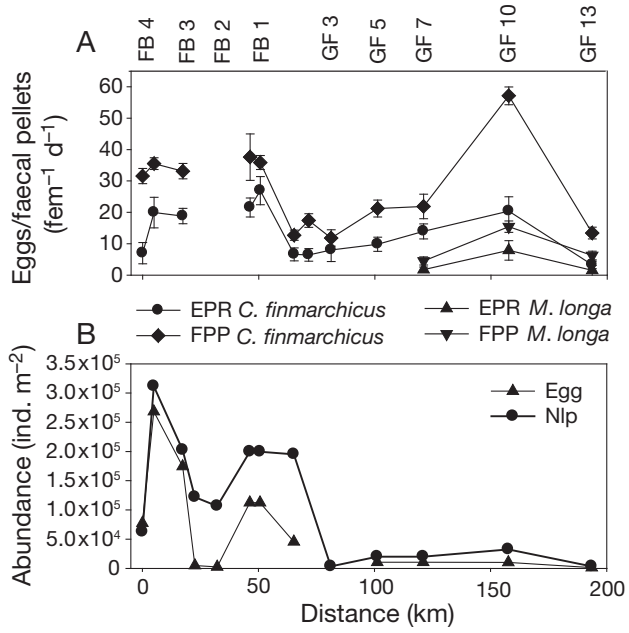

Fig. 11. *Calanus finmarchicus* and *Metridia longa*. Differences in (A) egg production rate (EPR) and faecal pellet production (FPP; female^{-1} d^{-1}) and (B) abundance (ind. m^{-2}) of copepod eggs (Egg) and nauplii (Nlp) sampled with the 45 µm WP-2 net along the transect. See Fig. 1 for sampling locations

cal distribution of zooplankton has been confirmed by investigations at other times of the year (Rysgaard et al. 2008 and K. Arendt pers. obs.) and is furthermore in accordance with observations by Smidt (1979). Therefore, the differences in copepod community structure cannot be explained by differences in succession stage along the section.

The study showed a general shift in physical/chemical factors and water column structure at the entrance to the fjord (Figs. 2 & 3). Likewise, there is a general shift in the species composition (Figs. 4, 5, & 9) and biomasses (Figs. 7 & 8) of the plankton communities at the entrance to the fjord. Therefore, it is reasonable to split up the study area into 2 systems, viz. the offshore region and the fjord. An overview of the carbon budget for the upper 50 m in the 2 systems is shown in Fig. 13.

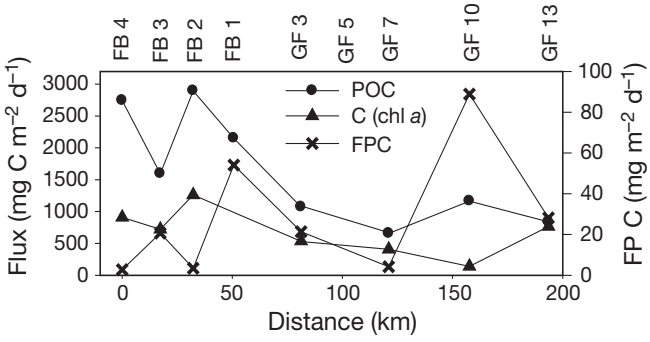

Fig. 12. Differences in flux of particulate organic carbon (POC), C (chl *a*) and faecal pellet (FP) C (mg m^{-2} d^{-1}) in the upper 60 m. See Fig. 1 for sampling locations

Table 1. Correlation coefficients (r) in linear regression between specific egg production (SEP), specific pellet production (SPP), and chl *a* measurements (mg m^{-2}). Significance of the correlation is given by an asterisk: * $p < 0.05$, ** $p < 0.01$

	SEP r (n = 12)	SPP r (n = 12)
SEP	–	0.60*
Chl *a* total	0.46	0.69*
Chl *a* <11 µm	0.00	0.15
Chl *a* 11–40 µm	0.47	0.92**

Mean biomass and production rate for the primary producers and the mean biomass and carbon turnover by the protozooplankton are roughly in the same range in the offshore region and the fjord system (Fig. 13). In contrast, the vertical flux was twice as high in the offshore region than in the fjord (Fig. 13), indicating a transport to the area as more material is lost than produced. Furthermore, there is a large difference in the copepod biomass and their carbon turnover in the offshore region and the fjord system (Fig. 13). Our data indicate that the differences in copepod community structure and biomass are determined by the hydrographic conditions. The offshore region is strongly influenced by the Atlantic inflow, resulting in dominance of the true Atlantic species *Calanus finmarchicus*, whereas the fjord was strongly influenced by glacial runoff and therefore had a unique species composition with much lower biomasses. Two high peaks of copepod biomass were observed in association with the fronts on both sides of Fyllas Banke. These copepods were productive, resulting in large numbers of *Calanus* spp. copepodites in the central parts of the bank. In the offshore region, copepods were able to turn over 213 ± 80 mg C m^{-2} d^{-1} (ca. 33%) of the primary production, which exceeds the carbon turnover by protozooplankton of 144 ± 22 mg C m^{-2} d^{-1} (Fig. 13A).

In the fjord, copepod biomasses were remarkably low, which has been found to be the case most of the year (Rysgaard et al. 2008). The dominating copepod species were *Pseudocalanus* spp., *Metridia longa* and *Microsetella* spp. The low biomasses are due to the low abundance of *Calanus* spp., and the copepod community was able to turn over only 3% of the primary production (Fig. 13B). Grazing by protozooplankton is approximately the same as in the offshore region (179 ± 58 mg C m^{-2} d^{-1}) and by far exceeds the copepod grazing (24 ± 13 mg C m^{-2} d^{-1}; Fig. 13B). Thus, protozooplankton is important for the carbon turnover of the primary production in the fjord, in accordance with other studies that have shown that protozooplankton are ubiquitous in arctic regions (Levinsen & Nielsen 2002, Verity et al. 2002, Møller et al. 2006).

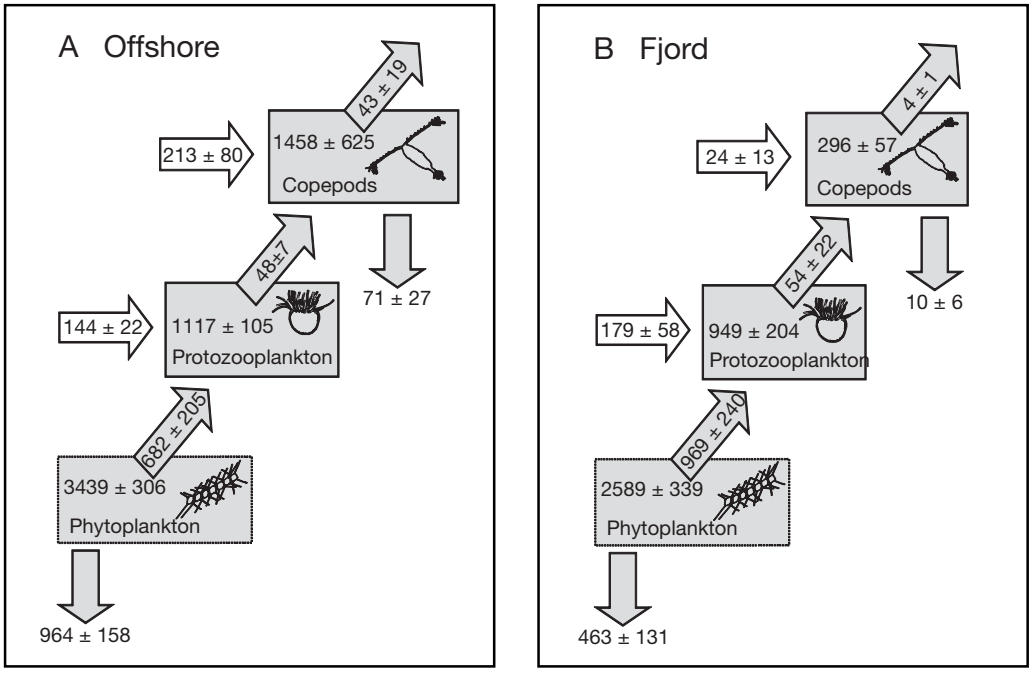

Fig. 13. Carbon flow budgets for the upper 50 m in (A) the offshore region and (B) the fjord as integrated mean ± SE. Numbers in boxes show average biomass (mg C m^{-2}), numbers in arrows entering and leaving the boxes represent ingestion and production (mg C m^{-2} d^{-1}), and vertical arrows leaving the boxes represent vertical flux (mg chl C m^{-2} d^{-1})

At Stn GF13, 3 glacial fronts that lie within a distance of 3 km (Fig. 1) strongly influence the plankton community. We suggest that these conditions determine the unique species composition of the copepod community. Primary production was high at this station due to nutrient-rich upwelling in front of the glacier (Fig. 3).

It should be taken into consideration that the production and grazing rates of the copepod community in the fjord were estimated on the basis of production rates of *Calanus finmarchicus.* The production rates of this species were probably not representative of the copepod species dominating the fjord stations, as the growth and fecundity rates of different species can vary significantly (Hirst & Bunker 2003). Therefore, production was estimated according to Hirst & Bunker (2003) (Table 2, all data) using *in situ* temperatures and chl *a*. The results of the 3 methods used to determine the production rate are shown in Table 2. The estimated production rate falls remarkably close to the measured production on the basis of SEP and SPP in the offshore area. However, the estimated production rates were higher than the production measured on the basis of SEP and SPP in the fjord. The results indicate that the dominating copepods in the fjord (*Pseudocalanus* spp., *Metridia longa* and *Microsetella* sp.) have different life strategies than *C. finmarchicus* and that the measured production of this species probably underestimates the production of other species. The flux rates from the traps, which were deployed for only a short time, were extrapolated to daily rates, and it should be taken into consideration that dual migration and feeding rhythm of the grazers could have an influence on the dual flux.

Table 2. Production (mg C m^{-2} d^{-1}) of the copepod community in the upper 50 m, measured as specific egg production (SEP) and specific pellet production (SPP) assuming a gross growth efficiency of 33 % (Hansen et al. 1997) and estimated according to Hirst & Bunker (2003)

Station	Production based on SEP	Production based on SPP	Estimated production
Offshore			
FB4	2.1	12.0	13.8
FB3.5	56.4	130.8	70.2
FB3	31.7	64.6	43.7
FB2.5	20.1	33.3	35.2
FB2	26.8	16.2	33.0
FB1.5	152.7	202.0	130.0
FB1	23.7	26.9	26.1
Average ± SE	43.3 ± 19.3	70.9 ± 26.5	50.3 ± 14.8
Fjord			
GF1	4.3	4.6	14.6
GF2	0.4	0.8	3.0
GF3	3.3	3.9	11.4
GF5	3.8	4.9	17.3
GF7	7.4	6.2	27.8
GF10	8.0	33.6	20.0
GF13	0.5	1.4	8.1
Average ± SE	4.6 ± 1.4	10.0 ± 6.0	14.6 ± 3.1

The overall species composition and biomass distribution are in accordance with other high-latitude fjords (Hop et al. 2002). It has been suggested that zooplankton in glacier-influenced fjords suffers direct mortality from the glacial outflow (Hop et al. 2002). High concentration of silt could presumably be fatal for the suspension-feeding copepods (e.g. *Calanus* spp.), while the omnivorous feeding strategy of *Metridia longa* would probably remain unaffected. Differences in numerous physical/chemical factors create microhabitats that affect the distribution of copepods due to their species-specific responses to environmental factors.

Potential climate change effects on plankton community structure

Rapid changes in the environmental conditions have occurred over the last decade in both offshore waters and fjord regions. The fjord must receive increased amounts of melt water as the Greenland Ice Sheet is losing mass (Velicogna & Wahr 2006), including the glaciers in the inner parts of Godthåbsfjorden (Rignot & Kanagaratnam 2006). Models have shown that increased runoff from land would not change the thickness of the mixed layer above the pycnocline in the fjord, although it is expected to intensify the estuarine circulation and bring more nutrient-rich water from the shelf into the fjord (Bendtsen et al. 2007). Enhanced estuarine circulation would enhance new production and could expand the area with high primary production, which at present is located in the inner part of the fjord close to the ice sheet. An expanded area with very high primary productivity would probably lead to a significant rise in the vertical flux, which would fuel the benthic community in an extended portion of the fjord.

In the offshore region, temperature has increased both in coastal West Greenland waters (Holland et al. 2008) and in the entire Baffin Bay (Zweng & Münchow 2006). The increase in temperature could lead to decreasing peak phytoplankton biomass, decreasing mean cell size and a shift towards reduced dominance of diatoms (Sommer & Lengfellner 2008). In the present study, a significant relationship was found between SPP and standing stock of chl *a* in the 11 to 40 µm size spectrum, indicating that *Calanus finmarchicus* finds its prey items mainly in this size spectrum, which is in accordance with other studies showing that this is the optimum cell size range for particles taken by *Calanus* (Frost 1972, Berggreen et al. 1988, Levinsen et al. 2000) and that the species is primarily herbivorous (Marshall & Orr 1955, Meyer-Harms et al. 1999). The SPP was correlated with the SEP, indicating close coupling between ingestion and secondary production. A shift towards smaller cell size of primary producers would enhance the role played by protozooplankton in the carbon turnover and thus lead to losses in energy transfer to copepods (Sommer & Lengfellner 2008). This situation seems to be present in the central fjord region where small cells represent a considerable part of the phytoplankton assemblage (Fig. 6), and protozooplankton accounts for 33% of the turnover of the primary production (Fig. 13B). A temperature rise would furthermore accelerate the physiological rates of both autotrophic and heterotrophic organisms (Hirst & Bunker 2003), and more nutrients would be recycled in the pelagic due to an increased proportion of the carbon being assimilated by the microbial community (Rivkin & Legendre 2001). Changes in both runoff from land and Atlantic inflow are expected to occur in the future (Kattsov & Källén 2005), and we have shown that the changes might have a strong influence on carbon cycling in West Greenlandic waters.

The strength and heat capacity of Atlantic inflow together with the runoff from the ice sheet determine the physical gradients and thereby the geographical distribution of the plankton community structure, which is shown clearly in the present study. However, the exact mechanisms determining the copepod community distribution and their specific adaptations to physical/chemical gradients are still unknown. Further studies of species-specific adaptation would provide key knowledge to determine the geographical distribution of the plankton communities in the future.

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Metazooplankton community structure, feeding rate estimates, and hydrography in a meltwater-influenced Greenlandic fjord

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ABSTRACT: In order to assess the potential responses of Greenland's coastal ecosystems to future climate change, we studied the hydrography and distribution of metazooplankton, along a transect from the slope waters beyond Fyllas Banke to the inner part of Godthåbsfjord, West Greenland, in July and August 2008, and estimated feeding rates for some of the larger species groups. Within the 4 regional domains that were covered in the study (continental slope, continental shelf, outer sill region, and main fjord basin), salty coastal water and glacial runoff mixed to various extents, and 7 water masses with specific characteristics were identified. The common large copepod species were *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, and *Metridia longa*. Small copepod genera included *Microsetella*, *Pseudocalanus*, and *Oithona*, while rotifers and gastropods (primarily pteropods) were also found in high abundance. Species could be linked to the specific water masses, e.g. *Calanus* spp. were primarily associated with oceanic or coastal waters, whereas *M. longa*, *Microsetella* sp., *Pseudocalanus* sp., and rotifers were mostly found inside the fjord. The combined biomass of the large zooplankton species (5.5×10^3 mg C m^{-2}) was less than that of the small species (6.8×10^3 mg C m^{-2}) averaged across all sampled stations along the transect. Estimated *in situ* grazing rates for the large copepod species were <10% of their maximum rates, indicating food limitation. The major predatory zooplankton groups, *Pareuchaeta norvegica* and chaetognaths, had estimated predation effects of <1% d^{-1} on the prey community. The dominance of small zooplankton species within the fjord contradicts the traditional emphasis on large, lipid-rich zooplankton species in the arctic seas, and suggests that the planktonic food web structure inside the glacial fjord was different from that of the system outside.

KEY WORDS: Glacial fjord · Greenland · Climate change · Copepod · Grazing · Predation · Food web

INTRODUCTION

Glacial fjords and coastal waters off western Greenland are very productive, contributing 95% of Greenland's fisheries exports. They are also important feeding grounds for marine mammals (Born et al. 2003, Aquarone 2004) and wintering habitats for seabirds (Merkel et al. 2002, Boertmann et al. 2004). Commercial and recreational fishing, hunting, and related industries are essential to the economy of the local communities. Located at the junction between land ice and sea, glacial fjords are dynamic systems that are under the influences of both terrestrial and marine processes. The functioning of the food web within the

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fjords is ultimately tied to the abundance, composition, and feeding activities of the plankton community. Climate models predict that, while the warming of surface waters will be gradual, even mild warming in glacial fjords may tip the delicate ice/water balance and lead to drastic increases in freshwater discharge into the fjords over a short period of time (Rysgaard et al. 2003, Willis et al. 2006). For example, between 1995 and 2003, an increase of 0.4°C in the autumn air temperature in Young Sound (northeastern Greenland) led to a 46% increase in thawing degree days and a 12% increase in thawing days (Mernild et al. 2007). More frequent breaching of ice-dammed lakes would also discharge an increasing amount of freshwater along the western Greenland coast (Krawczynski et al. 2009). It is this delicate balance that makes the plankton communities within glacial fjords particularly vulnerable to global warming.

Godthåbsfjord is located in the vicinity of Nuuk, the capital city of Greenland, just below the Arctic Circle. The fjord extends inward to the edge of the Greenland Ice Sheet, covering 2013 km^2 with a mean depth of 260 m (Mortensen et al. 2011). A systematic monitoring program was initiated here in August 2005 by the Greenland Institute of Natural Resources. Sampling at a single station at the mouth of the fjord from 2005 to the present indicated that the metazooplankton community is dominated by small genera such as *Microsetella*, *Oithona*, and *Oncaea* (Rysgaard et al. 2008, Juul-Pedersen et al. 2010). A section along the fjord sampled in late spring (May 2006) showed that the biomass of small copepods was important in the middle to inner parts of the fjord, contributing ≥50% of the total copepod biomass (Arendt et al. 2010). High abundances of small copepods were also found in Disko Bay (Madsen et al. 2008), Young Sound (Nielsen et al. 2007), as well as in some other arctic fjords (e.g. Walkusz et al. 2003). Collectively, these studies contradict the traditional emphasis on large *Calanus* and *Metridia* species in arctic seas (e.g. Hopkins 1969, Hirche 1991, Thibault et al. 1999, Ashjian et al. 2003) and suggest very different planktonic food web structures inside the fjords relative to shelf-sea areas. A study of the hydrography within Godthåbsfjord has recently been published (Mortensen et al. 2011), providing important information for properly understanding the distribution, production, and community structure of metazooplankton, as well as their potential response to future climate change.

The present paper is a part of a multidisciplinary intensive field study in Godthåbsfjord in the summer of 2008 aimed at understanding the food web and biogeochemistry of the fjord. Here we report the hydrography, and the community structure and feeding rate estimates of the large metazooplankton, at stations along a transect from the coastal waters to the inner part of the fjord.

MATERIALS AND METHODS

Hydrography and chlorophyll *a*. The study was conducted in July and August 2008. The vessel RV 'Dana' (National Institute of Aquatic Resources, DTU Aqua) followed a transect of 20 stations that extended from the continental slope off Fyllas Banke to the inner part of Godthåbsfjord, which is in contact with several tidal outlet glaciers (Fig. 1). Due to logistical constraints, zooplankton sampling and experiments were done at selected stations (see below). Vertical profiles of water temperature, salinity, density, and fluorescence were obtained using a CTD (SBE 911 plus CTD from Sea-Bird Electronics) equipped with a Seapoint chlorophyll *a* fluorometer and a Biospherical/Licor sensor. Profiles were recorded from the surface to approximately 5 m above the bottom.

Water samples were taken from 5 depths within the upper 150 to 200 m at each station using 5 l Niskin bottles on a rosette. Aliquots were filtered onto GF/F filters (250 to 500 ml) for total chlorophyll (chl *a*) and were size fractionated by Nitex screens for <10 µm and <50 µm chl *a* (500 to 1000 ml). Chl *a* samples were extracted in 96% ethanol for 18 h before fluorescence was measured on a fluorometer (TD-700, Turner Designs) calibrated against a pure chl *a* standard (Turner Designs). The discrete chlorophyll measurements were used to calibrate the CTD fluorometer, and chl *a* concentrations were then calculated for each station from CTD fluorescence profiles. Hydrographic data were used to identify the different water masses within the fjord following the analysis of Mortensen et al. (2011).

Zooplankton species composition and abundances. Zooplankton were collected from 4 to 9 strata, depending on the total depth, at 19 of the 20 stations using both a large (MIDI) and a small (MINI) Multinet (HydroBios). The large Multinet was equipped with 300 µm mesh nets, with a 0.25 m^2 opening area, and could reach down to 1000 m. Volumes filtered through the large Multinet were measured by flow meters. The small Multinet was equipped with 50 µm mesh nets, with a 0.125 m^2 opening area, and was deployed to a maximum depth of 300 m. Because a flow meter was not available on the 50 µm nets, filtered volumes were calculated as towed depths multiplied by net opening area, and the resulting zooplankton concentrations should be considered conservative because of potential net clogging. Upon retrieval, the nets were backflushed with seawater, and the cod end contents were emptied into sample jars and preserved in 4% buffered formaldehyde.

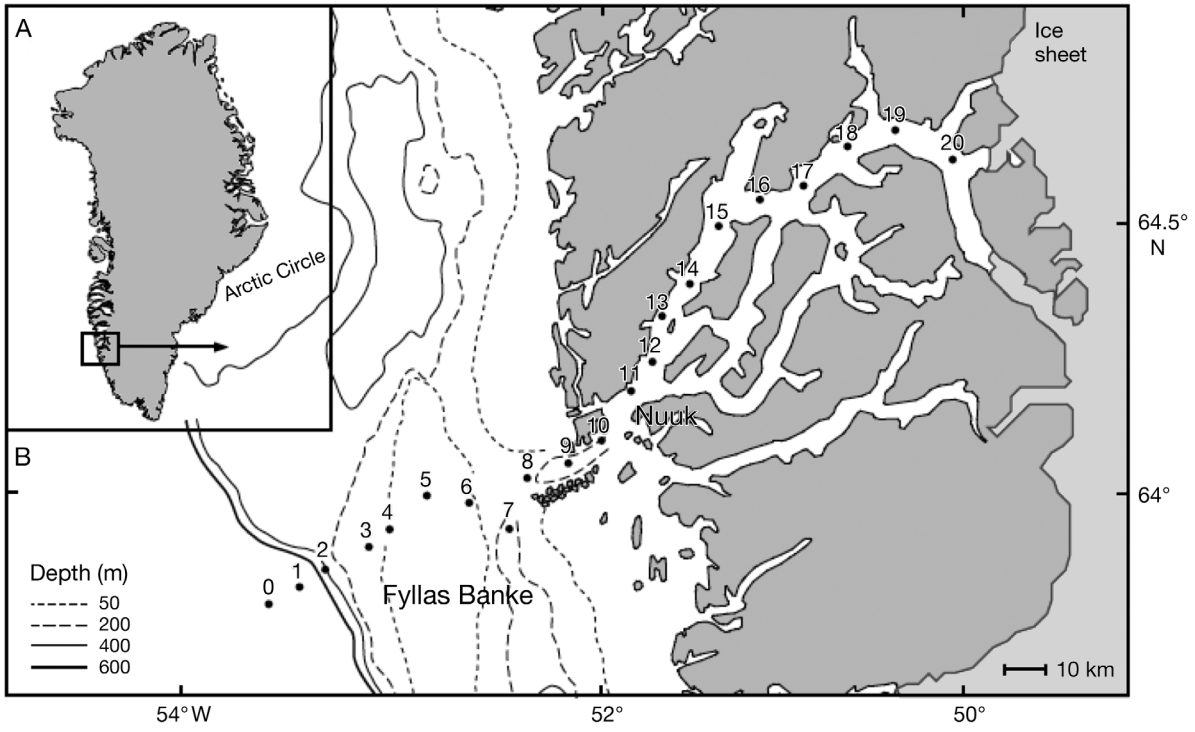

Fig. 1. Station positions along Godthåbsfjord in southwestern Greenland

Preserved zooplankton samples were processed at the Arctic Agency, Poland, for species identification and enumeration. For each sample, copepod species were identified according to developmental stages and sex, while gastropods (mainly pteropods) were grouped by size. For all identified groups, body lengths of up to 10 random individuals within each group were measured and then converted to body carbon content based on published algorithms (Table 1).

Large copepod grazing rates. Grazing by large copepods was calculated from fecal pellet production (Juul-Pedersen et al. unpubl. data) measured in short-term incubations at noon and midnight at the 7 stations, which were sampled during the day and at night. Copepods were collected from the upper 60 m using a 200 µm WP-2 net with a non-filtering cod end. On deck, a subsample from the cod end was immediately rinsed on a 400 µm sieve submerged in running seawater. Subsamples were then distributed into 4 cylinders (40 cm height × 8 cm inner diameter), each equipped with a 400 µm meshed bottom and filled with 1.8 l of 10 µm prescreened surface water. When surface water salinity was <30, water from subsurface depths was used. The procedure from the sampling of copepods to the start of the incubations took <5 min. The few pellets present at the beginning of the incubation were recorded. The copepods were incubated for 1 h in a thermo-box at surface water temperature in the dark. At the end of the incubation, 2 samples were collected from each incubation, 1 containing the copepods on the mesh and 1 containing the fecal pellets that had fallen though the mesh. The few pellets caught on the mesh were added to the others. These samples were preserved in 2% Lugol's solution, counted, and sized. The initial pellet counts were subtracted from the final counts. Fecal pellet volume was calculated assuming a cylindrical shape and converted to carbon based on a conversion factor of 0.43 ng C µm^{-3} (Swalethorp et al. 2011). Copepod biomass was calculated based on length–weight regressions for *Calanus finmarchicus* and *C. glacialis* combined (Table 1). To estimate ingestion, an assimilation efficiency of 0.68 was assumed (Conover 1966). To estimate *in situ* grazing rates, the rates obtained from the experiments were adjusted to temperatures at the depths where the copepods resided, using a Q_{10} of 2.8 (Hansen et al. 1997). The grazing rate of the large copepods in the upper 60 m was calculated by multiplying the specific rates for each depth by the total biomass of the dominant copepod species >400 µm in size, i.e. *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*, and *Pseudocalanus* sp. *In situ* grazing rates were compared with size-specific maximum grazing rates according to Hansen et al. (1997); the differences should indicate whether the copepods were food limited. The size-specific maximum grazing rate was calculated from the

Table 1. Algorithms used to convert body length (L, µm) to body carbon content (µg C ind.$^{-1}$)

Taxon	Developmental stage	Equation	Reference
Calanus finmarchicus	Nauplius[a]	µg C ind.$^{-1}$ = 4.168e-6 × L(µm)$^{2.03}$ (low resource) µg C ind.$^{-1}$ = 4.29e-6 × L(µm)$^{2.05}$ (high resource)	Hygum et al. (2000)
	Copepodite[a]	µg C ind.$^{-1}$ = 2.101e-8 × L(µm)$^{2.88}$ (low resource) µg C ind.$^{-1}$ = 2.037e-10 × L(µm)$^{3.52}$ (high resource)	
Calanus glacialis	Copepodite	Same equations as for *C. finmarchicus*	Hygum et al. (2000)
Calanus hyperboreus	Copepodite	µg C ind.$^{-1}$ = 9.47e-11 × L(µm)$^{3.3899}$	Hirche & Mumm (1992)
Metridia longa	Copepodite	µg C ind.$^{-1}$ = 5.39e-9 × L(µm)$^{3.0167}$	Hirche & Mumm (1992)
Oithona sp.	Nauplius	µg C ind.$^{-1}$ = 5.545e-8 × L(µm)$^{2.71}$	Sabatini & Kiørboe (1994)
	Copepodite	µg C ind.$^{-1}$ = 9.467e-7 × L(µm)$^{2.16}$	
Pseudocalanus sp.	Nauplius	Same equations as for *C. finmarchicus*	Hygum et al. (2000)
	Copepodite	µg C ind.$^{-1}$ = 6.21e-11 × L(µm)$^{3.745}$	Cohen & Lough (1981)
Microsetella sp.	Nauplius	Same equations as for *Oithona* sp.	Sabatini & Kiørboe (1994)
	Copepodite	µg C ind.$^{-1}$ = 4.14e-4 × L(µm)$^{1.15}$	Satapoomin (1999)
Oncaea sp.	Copepodite	µg C ind.$^{-1}$ = 2.51e-8 × L(µm)$^{2.90}$	Satapoomin (1999)
Gastropod larvae		µg C ind.$^{-1}$ = 2.31e-5 × L(µm)$^{2.05}$	Hansen & Ockelmann (1991)
Rotifera[b]		0.101 µg C ind.$^{-1}$	Øie et al. (1997)
Pareuchaeta sp.	Nauplius and copepodite	µg C ind.$^{-1}$ = 3.96e-9 × L(µm)$^{3.01}$	Tönnesson et al. (2006)
	Adult	µg C ind.$^{-1}$ = 1.15e-23 × L(µm)$^{6.92}$	
Chaetognatha		µg C ind.$^{-1}$ = 9.17e-12 × L(µm)$^{3.13}$	Conway & Robins (1991)

[a]Carbon content was estimated as the average for low and high resource conditions
[b]Species and body length were not measured. Funch & Sørensen (2001) reported 16 species of saline water rotifers in Disko Bay, Greenland, and measured the size of 6 of them, which averaged 154.3 µm. According to Øie et al. (1997), *Brachionus plicatilis* is 200 µm long, with 0.17 µg C ind.$^{-1}$. Conservatively assuming that rotifer body carbon scales to squared body length, we estimated that saline rotifers in Greenland have a carbon content of 0.101 µg C ind.$^{-1}$

average size of the 5 dominant copepod species mentioned earlier at each station. Based on the copepod's body size, the food particle size most accessible to the copepods would be >10 µm (Berggreen et al. 1988, Hansen et al. 1997). Therefore, grazing effect on the phytoplankton was calculated based on total chl *a* and chl *a* > 10 µm, assuming a carbon-to-chlorophyll ratio of 47 (Møller et al. 2006).

Feeding rates of predatory zooplankton species. *In situ* feeding rates were estimated for 2 major predatory zooplankton groups in the fjord: *Pareuchaeta norvegica* and chaetognaths (*Sagitta* spp. and *Eukrohina* sp.). Animals were collected from the upper 150 m using WP-2 nets (mesh size: 90 and 200 µm) with non-filtering cod ends. Water for incubation was screened through 60 µm mesh to remove prey.

Gut content of *Pareuchaeta norvegica* was estimated from fecal pellet production based on a linear relationship between food intake and the number of pellets produced (Yen 1987, 1991, Tiselius et al. 1997, Olsen et al. 2000), assuming that each pellet represented 1 small copepod prey (Tiselius et al. 1997). Fecal pellet production experiments were done at 7 stations, 2 of which included day and night time measurements. Within 1 h after collection, individual *P. norvegica* females or copepodites were transferred into a 50 ml plastic centrifuge tube filled with pre-screened water from 5 m and incubated in darkness at 5°C for ca. 60 h to ensure complete gut evacuation. At the end of the incubation, the content was gently poured through a 90 µm sieve to collect the copepods and fecal pellets, and the number of fecal pellets was counted. To obtain feeding rate, a separate gut evacuation rate measurement was done at Stn 1 and applied to all fecal pellet production data. To measure gut evacuation rate, 15 females were gently transferred to a cylinder (25 cm height × 10 cm inner diameter; n = 4) with a 1000 µm meshed bottom. The cylinder was lowered into a 2 l bucket filled with pre-screened water from the upper 50 m and incubated in the dark at 5°C for 80 h. Every 30 to 120 min the cylinder was moved to a new bucket, and fecal pellets that had fallen through the meshed bottom were counted. The gut evacuation rate was determined by regression of the number of pellets produced remaining in the gut against time. The daily feeding rate (FR) of *P. norvegica* was then calculated as:

$$FR = (NP \times 24) / DT$$

where NP is the number of prey per hour (assuming 1 pellet = 1 prey) and DT is the digestion time (h) and is equal to the reciprocal of the gut evacuation rate.

The gut contents of chaetognaths (*Sagitta elegans*, *S. maxima*, and *Eukrohnia hamata*) were analyzed at 12 stations, 5 of which were sampled both day and night. The number of chaetognaths used for gut content analysis ranged from 86 to 354 per staion; samples with <20 chaetognaths were not used. Each chaetognath was dissected and examined for remains of ingested prey. The position of prey in the gut was noted according to Øresland (1987), and the number of prey per chaetognath was determined. Individuals containing prey only in the anterior one-third of the gut might represent cod-end feeding, and were therefore not included in the analysis (Øresland 1987, Baier & Purcell 1997). Prey were identified to species and stage, and their lengths were measured. Mandible plates of ingested copepods were converted to prey size according to Karlson & Båmstedt (1994) and Saito & Kiørboe (2001). If the remains did not allow for species identification, the prey copepod was recorded as unidentified. Ingested appendicularians were detected by their fecal pellets, and 3 pellets were assumed to originate from 1 individual (López-Urrutia & Acuña 1999). Ingested chaetognaths were recognized by their grasping spines. Feeding rates were calculated in the same way as for *Pareuchaeta norvegica*, whereby the digestion time was estimated from *in situ* temperature according to Ohman (1986). Digestion time was not adjusted by a factor of 2 (Feigenbaum 1991), since prey in the anterior gut were not included in our analysis.

RESULTS

Hydrographic conditions and water masses

A distinct warm surface water mass was observed on the west side of Fyllas Banke, which coincided with a dense patch of chl *a* (Fig. 2). Over Fyllas Banke, salinity and density profiles were similar and showed little vertical structure, and the chl *a* concentration was lower (Fig. 2). There was distinct thermal stratification over the bank, but strong mixing was observed near the mid-point of the transect (~100 km), as indicated by the depression of the isopleths for salinity, density, and chl *a* (Fig. 2). A very sharp but shallow density gradient driven by differences in temperature and salinity was present in the inner part of the fjord (Fig. 2). A distinctly warm and saline water mass was present at depth in the inner fjord, and elevated chl *a* concentrations also extended to the deeper part of the water column (Fig. 2).

In a recent detailed hydrographic study, Mortensen et al. (2011) identified 4 regional domains in the study area: continental slope, continental shelf, outer sill region, and main fjord basin. Following the analysis by Mortensen et al. (2011), we identified the different water masses from our hydrographic data (Fig.

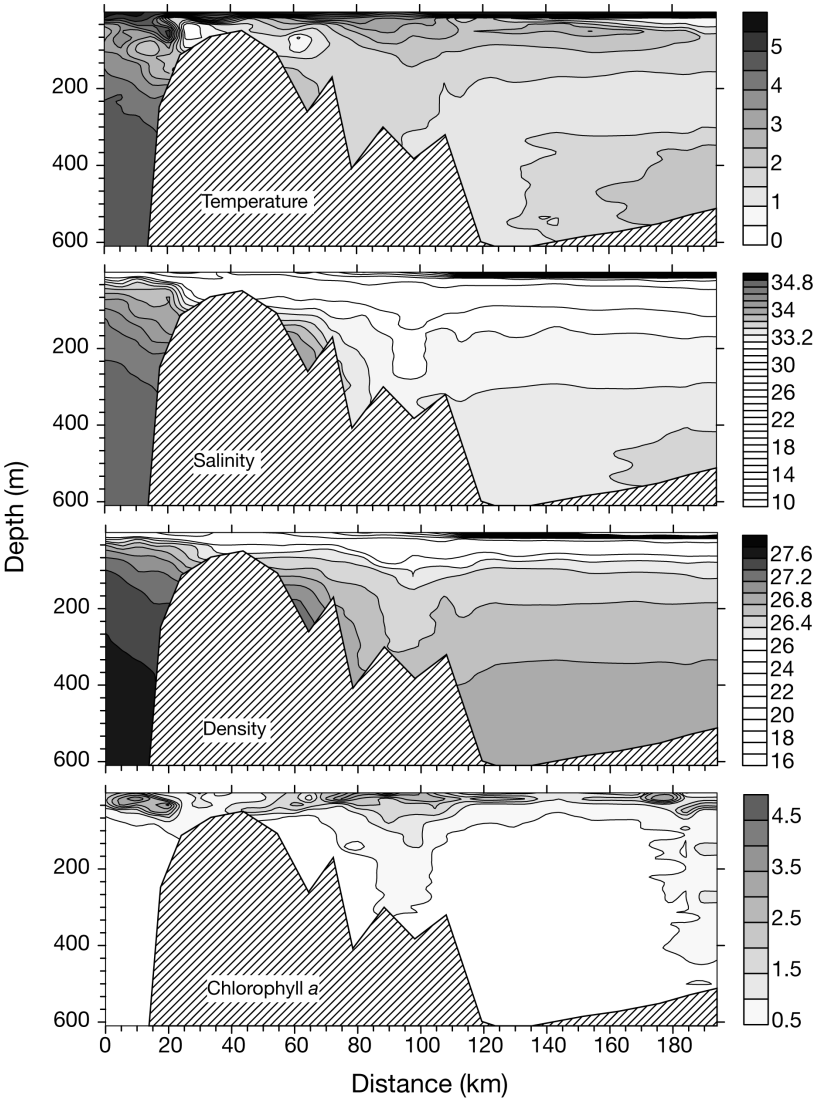

Fig. 2. Contour plots of water temperature (°C), salinity, density (σ_T; kg m^{-3}) and chlorophyll *a* (mg m^{-3}) along the transect. Distances were measured from Station 0. Note the different contour line scales for different panels. Hatched area in each panel represents bottom topography

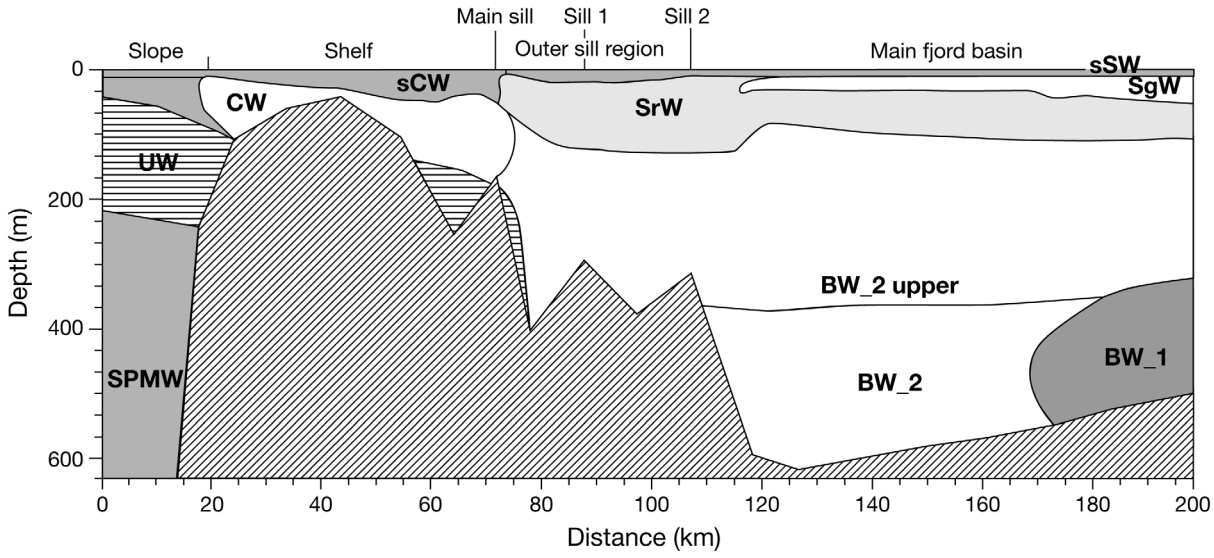

Fig. 3. Schematic drawing of water mass distribution in Godthåbsfjord in July and August 2008. Four domains were identified: slope, shelf, outer sill region, and main fjord basin. SPMW: subpolar mode water; CW: coastal water; UW: mixture of SPMW and CW; sCW: summer coastal water; SrW: sill region water; sSW: summer surface water; SgW: subglacial water; BW: basin water (further divided into inflow events 1 and 2, and upper layer). Hatched area = bottom topography

3). Subpolar mode water (SPMW) was formed by winter convection in the subpolar North Atlantic. Its temperature and salinity signatures near Nuuk were ca. 5°C and 35, respectively, but they were variable, and its core (defined by its potential temperature maximum) was at 500 m. Coastal water (CW) was observed in a wedge above the SPMW in areas close to the coast of Greenland. It had its origin in the Arctic Ocean and was modified locally as it traveled along the eastern and western coasts of Greenland. We observed a frontal zone at the shelf/slope, where CW met Labrador Sea surface water. A distinctive thin surface water layer referred to as summer coastal water (sCW) had developed over the summer, characterized by relatively high temperatures and slightly lower salinities. The water mass found in a depth range of from 100 to 200 m over the slope was made up of a mixture of SPMW and CW near the main sill of the fjord. In the outer sill region, the coastal water masses met the water masses from the fjord. This is an area influenced by strong tidal mixing, as evident from our hydrographic measurements (Fig. 2). In the main fjord basin, 4 identified water masses were found: summer surface water (sSW), subglacial water (SgW), sill region water (SrW), and basin water (BW). sSW was formed from freshwater runoff to the surface layer during summer, and was subsequently heated by solar insolation and mixing with the underlying waters. SgW was formed by subglacial freshwater discharge from tidal outlet glaciers (freshwater which enters the fjord at depth) and subsequent mixing with ambient waters (SrW and BW described in this section; Mortensen et al. 2011). SgW was found in a depth range of from 6 to 45 m in the inner parts of the fjord, and was characterized by low temperatures of 1°C and salinities of from 30 to 32. SrW was formed by mixing of water masses in the outer sill region (sSW, sCW, SgW, CW, SPMW, and BW). The vertical extent of SrW was ca. 100 m in the outer sill region domain, and decreased slightly toward the inner part of the fjord. The deepest water mass (BW) filled the main basin of the fjord, and was a mixture of inflowing CW and SPMW. The main inflow of deep water masses into the fjord takes place during the winter and spring months (Mortensen et al. 2011). In our study we distinguished 2 different types of BW, which were derived from 2 different inflow events. The water from the first event (BW_1) was warmer and more saline than that from the second (BW_2), apparently because it contained a higher fraction of SPMW.

Zooplankton composition and biomass

Diverse communities of copepods plus several other zooplankton groups were present along the transect; the overall zooplankton taxa observed at more than one station were: (1) copepods (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*, *Microsetella* sp., *Pseudocalanus* sp., *Oithona* sp., *Oncaea* sp., *Microcalanus* sp., *Acartia* sp., *Paracalanus* sp., *Temora* sp., *Centropages* sp., *Pareuchaeta* sp., *Rhincalanus* sp., *Spinocalanus* sp., *Pleu-*

romamma sp., Scolecithricidae [family], Heterohabdidae [family], Aetideidae [family], Harpacticoid [order]); (2) amphipods (Gammaridae [family], Hyperiidae [family]); (3) cladocerans (*Podon* sp., *Evadne* sp.); (4) chaetognaths (*Sagitta elegans*, *S. maxima*, *Eukrohnia hamata*); (5) Arctic krill (*Thysanoessa inermis*, *T. rashii*); (6) rotifers; (7) isopods; (8) bryozoans; (9) siphonophores; (10) Foraminifera; (11) Echinodermata; (12) tintinnid ciliates; (13) ctenophores; (14) gastropods (mainly pteropods); (15) polychaetes; (16) cirripeds; (17) bivalves; (18) appendicularians.

The 300 µm mesh Multinet captured primarily large zooplankton species, among which *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, and *Metridia longa* comprised most of the biomass. A comparison of *C. finmarchicus* biomass, as estimated from the 50 and 300 µm net samples, showed no significant difference (Pearson's correlation coefficient = 0.763; n = 153; $p < 0.01$). High *C. finmarchicus* biomass was found within the upper 200 m in the waters on both sides of Fyllas Banke (Fig. 4). *C. glacialis* was concentrated within the upper 200 m over the sill and just inside the fjord (Fig. 4). *C. hyperboreus* was found mainly over the sill and in the inner fjord below 500 m (Fig. 4). Unlike the *Calanus* species, *M. longa* was concentrated in the inner part of the fjord within the upper 200 m (Fig. 4).

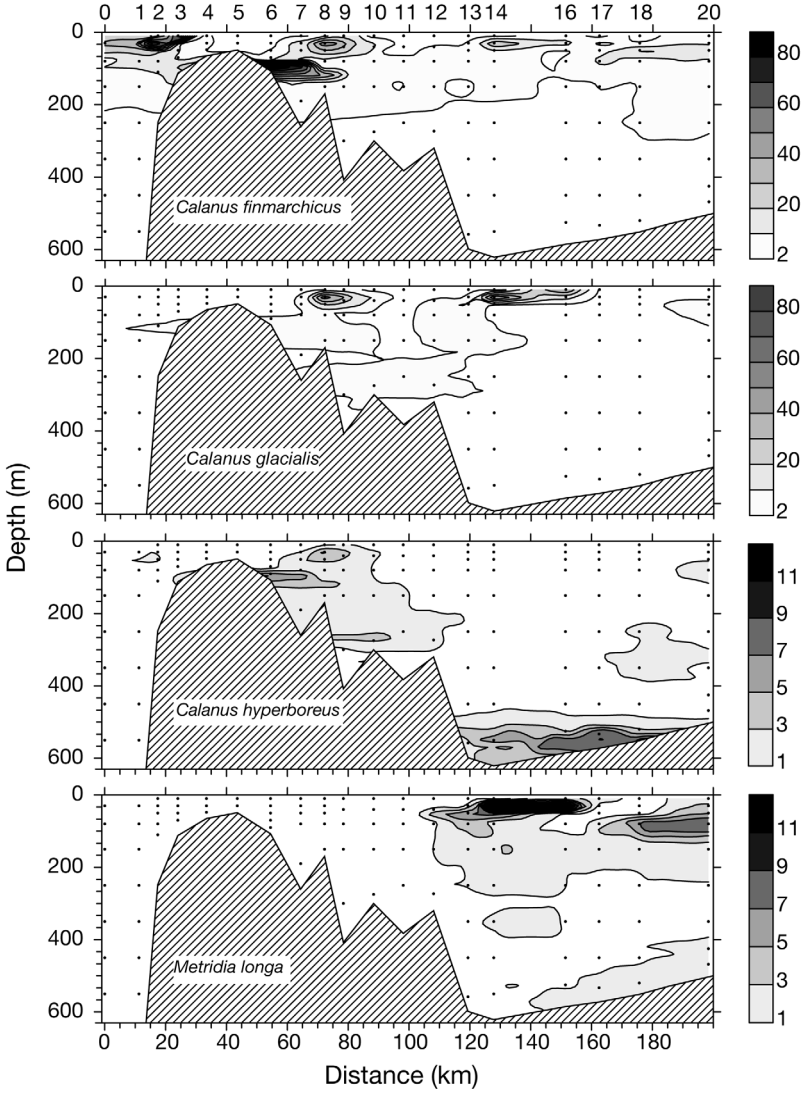

Fig. 4. Contour plots of biomass (mg C m^{-3}) of the dominant large zooplankton species from the 300 µm Multinet samples along the transect. Dots are midpoints of sampling intervals. Numbers on top are stations. Note the different contour line scales for different panels. For stations with >1 sampling time, the daily averages are shown. Hatched area = bottom topography

The small Multinet (50 µm mesh) captured a vast variety of small zooplankton species, mainly in the upper 100 m that were undersampled or missing from the large Multinet samples (300 µm mesh). Among them the numerically dominant groups were rotifers, *Microsetella* sp., *Pseudocalanus* sp., *Oithona* sp., and gastropods (mainly pteropods). A very high concentration of rotifer biomass was present over the sill, with a smaller patch just over Fyllas Banke (Fig. 5). *Microsetella* sp. was mainly concentrated in the outer sill region of the fjord, whereas *Pseudocalanus* sp. was found near the surface west of Fyllas Banke and within the fjord (Fig. 5). *Oithona* sp. did not show any distinct horizontal zonation (Fig. 5). The biomass of gastropods was high within the upper 100 m west of the bank, with additional smaller patches inside the fjord (Fig. 5).

To better compare the distributions of different zooplankton species along the fjord, we calculated the integrated biomass throughout the sampled water column for each group (Fig. 6). Among the 3 *Calanus* species, the biomass of *C. finmarchicus* > *C. glacialis* > *C. hyperboreus*. The *Metridia longa* biomass was low, comparable to that of *C. hyperboreus*. Among the small zooplankton species, rotifer biomass was the highest and exceeded that of the sum of all 3 *Calanus* species at certain stations. *Microsetella* sp. had the next highest biomass followed by gastropods, *Pseudocalanus* sp., and *Oithona* sp.

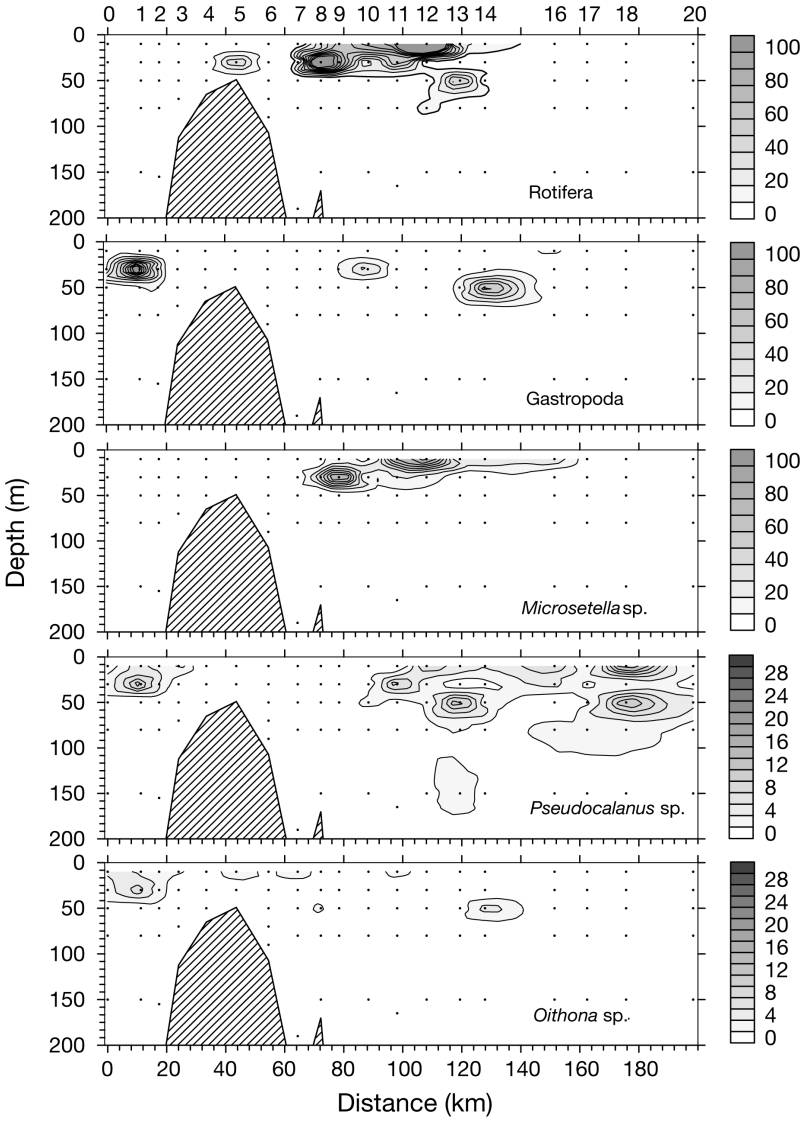

Fig. 5. Contour plots of biomass (mg C m^{-3}) of the dominant small zooplankton species from the 50 µm Multinet samples along the transect. Dots are mid-points of sampling intervals. Numbers on top are stations. Tows were limited to the upper 300 m. For stations with >1 sampling time, the daily averages are shown. Hatched area = bottom topography

Copepod grazing

Estimated grazing by the 5 calanoid copepod species (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*, and *Pseudocalanus* sp.) was highest over Fyllas Banke (~30 mg C m^{-2} d^{-1}), while it was generally lower in the fjord, except at Stn 14, where there was high grazing at night (Fig. 7A). This was the result of a combination of both high grazing rates and high copepod biomass. In the fjord (Stns 10 to 20), however, the phytoplankton biomass was much higher, and the grazing effects of the large copepods on total phytoplankton (Fig. 7B) and phytoplankton >10 µm (Fig. 7C) were both very low (<0.5% standing stock d^{-1} except for Stn 14).

Compared with the estimated maximum grazing potential (Hansen et al. 1997), the *in situ* grazing effect of the large copepods calculated from fecal pellet production was low, never exceeding 10%, with most values at ~5%, of maximum ingestion (Fig. 7D).

Predatory zooplankton species and their prey consumption

Two major groups of predatory zooplankton were found along the transect: the carnivorous copepod (*Pareuchaeta norvegica*) and chaetognaths (*Sagitta elegans*, *S. maxima*, and *Eukrohnia hamata*) (Fig. 8). In our study region, *P. norvegica* was most abundant around Fyllas Banke and less abundant toward the inner part of the fjord. The abundance of *P. norvegica* ranged between 0 and 10.4 ind. m^{-3}, with peak biomass recorded in the 20 to 60 m layer at night at Stn 9 (2.05 mg C m^{-3}). *P. norvegica* showed strong night time upward migration at Stns 1 and 2 beyond the bank (data not shown). The proportion of females and older juveniles (Stage C5) decreased toward the inner part of the fjord. Small, dense patches of *P. norvegica* were observed in the middle section of the fjord, which appeared to overlap the distributions of *Calanus* spp., rotifers, and *Microsetella* sp.

In the fecal pellet production experiments, *Pareuchaeta norvegica* copepodites (Stages C4 and C5) produced 2.8 to 4.5 pellets ind.$^{-1}$. Females produced fewer pellets, ranging from 1.4 to 1.6 pellets ind.$^{-1}$. At stations where day–night sampling was carried out, there was no clear difference in number of pellets egested between night and day. Mortality of *P. norvegica* during the fecal pellet production experiments was low (1%, n = 190). Examination of a sample of egested pellets (n = 50) showed remains of copepod mandibles or other parts of appendages. The measured gut evacuation rate was –0.049 h^{-1}, and the corresponding digestion time was 20.5 h. Estimated feeding rates were from 1.7 to 1.9 prey d^{-1} for females and from 3.3 to 5.4 prey d^{-1} for copepodites (Fig. 9).

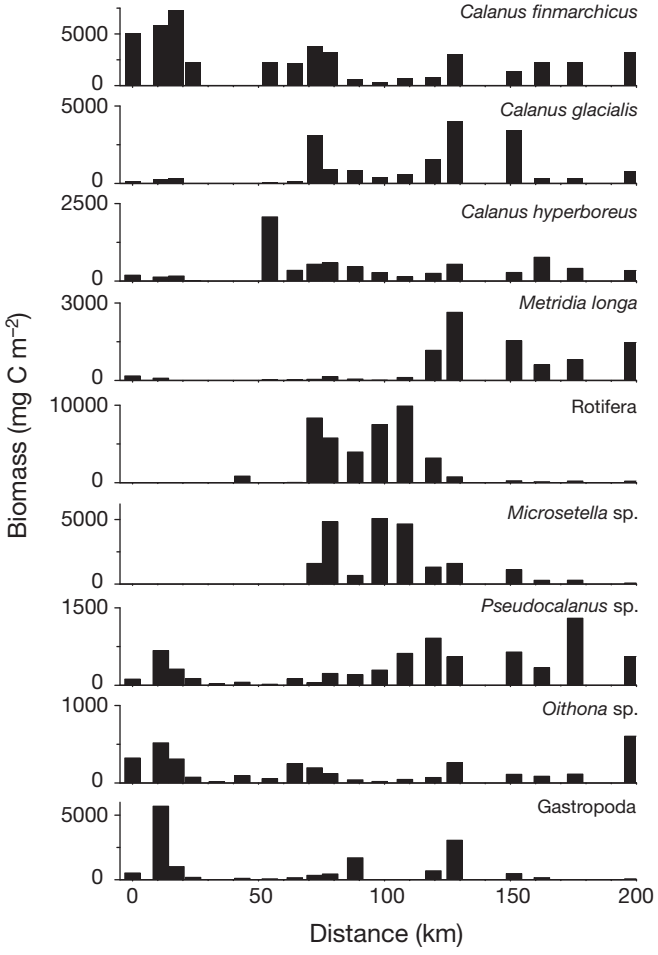

Fig. 6. Zooplankton biomass integrated throughout the sampled water column. Note the different scales on *y*-axes. For stations with >1 sampling time, the daily averages are shown

Chaetognaths were rare on the shelf, but *Sagitta elegans* was abundant within the upper 100 m in the middle to inner section of the fjord (Fig. 8). The peak abundance of *S. elegans* was 95 ind. m^{-3} in the 20 to 40 m layer at night at Stn 14. The 2 other chaetognath species, *S. maxima* and *Eukrohnia hamata*, were most abundant beyond the bank (Stns 1 and 2) and in the deep outer parts of the fjord (Stns 9 and 10). The guts of 215 out of a total of 770 *E. hamata* examined contained prey, including copepods and appendicularians. Of the 153 *S. maxima* examined, 31 contained prey, which included *Calanus* copepodites and larger prey such as *Pareuchaeta norvegica*. Of the 1869 *S. elegans* examined, 598 contained prey. *Pseudocalanus*, *Oithona* and *Metridia* copepodites were the dominant prey for *S. elegans*. *S. elegans* also consumed large numbers of appendicularians. The average number of prey per chaetognath (NPC) varied between 0.15 and 0.48 among the stations (Fig. 10).

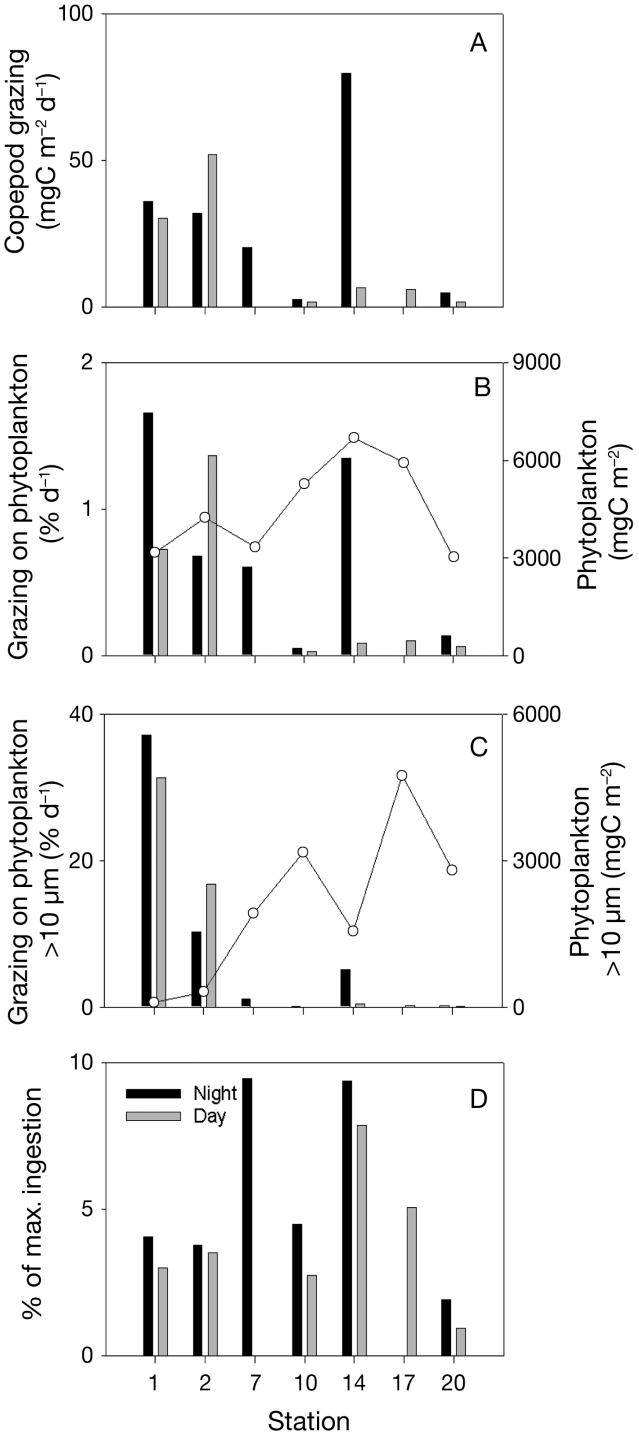

Fig. 7. Combined grazing by the 5 dominant copepod species >400 µm: *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*, and *Pseudocalanus* sp. at noon and midnight. (A) Community grazing in the upper 60 m, (B) phytoplankton biomass (line) and grazing impact as percent standing stock per day by copepods (bars), (C) phytoplankton biomass >10 µm (line) and the grazing impact as percent standing stock per day by copepods (bars), and (D) day and night *in situ* grazing as percent potential maximum grazing calculated from size-specific maximum grazing rates (Hansen et al. 1997)

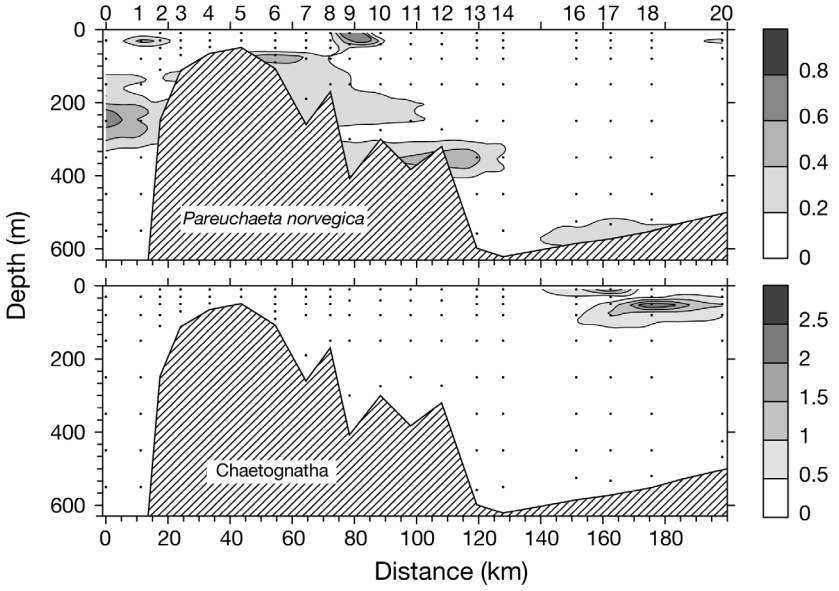

Fig. 8. *Pareuchaeta norvegica*, Chaetognatha. Contour plots of biomass (mg C m^{-3}) of 2 major predatory zooplankton groups in the fjord from the 300 µm Multinet samples. Dots are mid-points of sampling intervals. Numbers on top are stations. For stations with >1 sampling time, the daily averages are shown. For *P. norvegica*, the total biomasses of all developmental stages are plotted. Hatched area = bottom topography

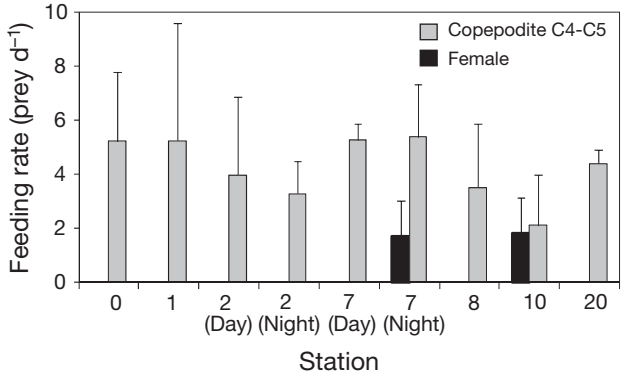

Fig. 9. *Pareuchaeta norvegica*. Feeding rates at different stations. Means + SD

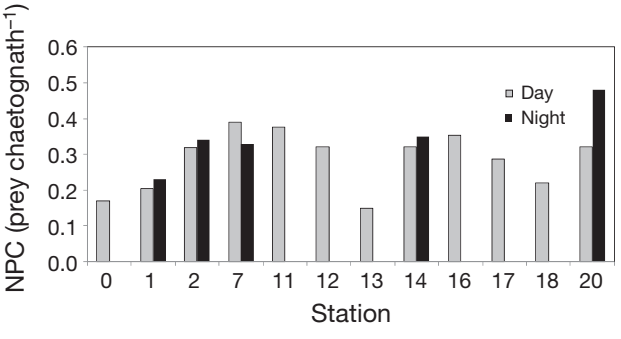

Fig. 10. Chaetognatha. Number of prey per chaetognath (NPC) at different stations. The chaetognaths included were *Sagitta elegans*, *S. maxima*, and *Eukrohnia hamata*

Predation effect by predatory zooplankton

The predatory effect of *Pareuchaeta norvegica* was calculated for Stns 1 and 2, where high abundances of this species were observed. The feeding rate by *P. norvegica* C4 and C5 copepodites (Fig. 9), expressed as prey per day, was taken to represent the feeding rate of all copepodites (Stages C1 to C5). Predation effect was then calculated based on feeding rates (Fig. 9), *P. norvegica* abundance (Fig. 8), and prey abundance (data not shown), and was expressed as the percent of copepod abundance ingested per day at each station. The predation effect of *P. norvegica* was 0.4% standing stock d^{-1} at Stn 1 (0 to 60 m) and 0.2% standing stock d^{-1} at Stn 2 (0 to 60 m). The highest predation effect was recorded in the 200 to 300 m depth range during the day at Stn 1 (0.6% standing stock d^{-1}).

The predation effect of chaetognaths was only calculated for the dominant species, *Sagitta elegans*. Despite its high abundance in the middle to inner part of the fjord, its predation effect on the copepod standing stock was low (0.4% d^{-1} at Stn 14 and 0.2% d^{-1} at Stn 20). A comparison of prey abundance and gut content of *S. elegans*, however, showed that prey were not eaten in proportion to their abundance such that the predation effect was stronger on *Pseudocalanus* sp., with *S. elegans* consuming 2.4% d^{-1} of *Pseudocalanus* sp. standing stock at Stn 14 (20 to 40 m) and 1.6% d^{-1} at Stn 20 (0 to 20 m).

DISCUSSION

Hydrography and zooplankton community structure

The water column structure appeared to influence the distribution of the zooplankton species along the fjord. *Calanus finmarchicus* was associated primarily with the shallow water masses above the slope and on the shelf. Both *C. glacialis* and *C. hyperboreus* were present in the inner shelf and outer sill regions associated with surface water masses, as well as with deeper water masses. *C. hyperboreus* biomass was conspicuously more concentrated near the bottom of the main basin. These distribution patterns suggest that the 3 populations were more connected with populations

outside of the fjord via SPMW, CW, or BW. *Metridia longa* was mainly associated with surface water and, to a lesser extent, with deep water, within the basin. This implies that the *M. longa* population is more restricted to the fjord, and its life history is probably more influenced by freshwater runoff and mixing within the fjord.

Biomass levels of the small zooplankton species in Godthåbsfjord were surprisingly high. *Microsetella* sp. and *Oithona* sp. have been observed elsewhere on the southwestern Greenland shelf, but in low abundances (Pedersen et al. 2005), although our finding of high biomass for *Microsetella* sp. and *Pseudocalanus* sp. within the fjord is consistent with the observations of Arendt et al. (2010). *Microsetella* sp. was concentrated in the upper water column within the outer sill region, where strong vertical mixing was also observed. *Microsetella* sp. is known to colonize and feed on particle surfaces (Koski et al. 2005), and the strong mixing may help maintain particles, hence particle-colonizing *Microsetella* sp., within the water column. The observation of very high rotifer biomass in the outer sill region and above Fyllas Banke is unprecedented. The ability of rotifers to reproduce asexually may allow them to quickly exploit spring phytoplankton production (Hernroth 1983), and their populations also tend to exhibit rapid boom-and-bust cycles (Hernroth 1983, Dolan & Gallegos 1992), resulting in patchy distributions in time and space. The distribution patterns for rotifers, *Microsetella* sp., and *Pseudocalanus* sp. in relation to water masses suggest that these populations were endemic to the fjord. The lack of distinct zonal patterns for *Oithona* sp. and gastropods (mainly pteropods) may reflect the broad ranges of acceptable environmental conditions for these groups and/or the presence of multiple populations.

The average biomass over all sampled stations was 5.5×10^3 mg C m^{-2} for the large zooplankton species combined (from the 300 µm nets) and 6.8×10^3 mg C m^{-2} for the small zooplankton species combined (from the 50 µm nets). Hence, sampling using only large-mesh-sized nets would have greatly underestimated the total zooplankton community diversity and biomass in Godthåbsfjord. The ecological roles of many of these small zooplankton species that dominate within the fjord remain unknown. Due to their small size, they likely consume small phytoplankton and micro-zooplankton (Møller et al. 2006) or live in association with particle aggregates, and they, in turn, may become prey for larger zooplankton and larval fish (Simonsen et al. 2006). In addition, the smaller species may numerically respond faster to environmental changes than larger species, which have longer and more complex life cycles. Given the fact that the biomass of small zooplankton species was comparable with or even exceeded that of the large zooplankton species at some stations, and that small species tend to have higher growth rates (Hansen et al. 1997), these small zooplankton likely contribute substantial and yet unquantified biological production to the system (Madsen et al. 2008).

Zooplankton feeding

The low estimated copepod grazing rates (Fig. 7) relative to the expected maximum grazing rates suggest that the copepods (>400 µm) might have been food limited. This may be particularly true at offshore stations, where phytoplankton biomass in the size range most accessible to the copepods (>10 µm; Berggreen et al. 1988, Hansen et al. 1997) was low and grazing impact was high. Within the fjord, a significant fraction of the phytoplankton was of the genus *Phaeocystis* (Arendt et al. 2010), which is usually not grazed very effectively by suspension-feeding copepods (Nejstgaard et al. 2007). In addition, the low copepod biomass within the fjord also contributed to the low grazing effect. Overall, direct trophic linkage between phytoplankton and the large copepods appeared weak along the transect.

The estimated predation rates of *Pareuchaeta norvegica* were in agreement with other measurements in the field (Tönnesson et al. 2006) and in the laboratory (Olsen et al. 2000). The estimated predation impact of *P. norvegica* was low (<1% d^{-1}), suggesting that its top-down effect on the copepod community was weak. The overall predation impact by chaetognaths also seemed low, but was consistent with previous reports (Kimmerer 1984, Drits & Utkina 1988, Stuart & Verheye 1991). However, chaetognaths appeared to select for *Pseudocalanus* sp. and might have had a greater impact on this species than on others. Because our calculations relied on gut content analysis, however, predation impact would have been underestimated if these predatory species ingested prey, such as rotifers, that do not have preservable body parts.

Climate change and the planktonic food web in Godthåbsfjord

The Greenland Ice Sheet continues to be affected by global warming (Krabill et al. 2000, Chen et al. 2006, Hanna et al. 2008), and recent data suggest that melting has intensified along the coast, especially in southwestern Greenland (Krabill et al. 2000, 2004, Johannessen et al. 2005, Rignot et al. 2010). The very different zooplankton species compositions between the fjord and the slope-shelf region suggest that the

respective planktonic food webs will respond to climate change differently.

The East Greenland Current flows south from the high arctic along the east coast and meets with the Irminger Current derived from the North Atlantic Current. Both currents contribute to the formation of the West Greenland Current that flows north along the west coast (Buch et al. 2004). High abundances of *Calanus* spp. have been observed beyond the shelf off the coast of SW Greenland (Head et al. 2000, 2003). Additional *Calanus* populations are also present within the Irminger Current, off the southeast coast of Greenland (Astthorsson & Gislason 2003, Heath et al. 2008). These remote populations could be connected to the *Calanus* populations in Godthåbsfjord and buffer them against fluctuations due to local climate change. To test this hypothesis, there is a clear need to investigate the population genetic variation of the *Calanus* populations to discern the extent of connection between Godthåbsfjord and the neighboring regions (Bucklin et al. 2000).

Most of the existing ocean-climate models operate down to the coastal shelf spatial scale, but do not extend into glacial fjords. Understanding the biological oceanography (i.e. the interaction between hydrography and the planktonic food web structure of glacial fjords) will be crucial for predicting climate change impacts on these delicate sea/ice junctures and on the resident populations that rely on their natural resources. Here we have described the hydrographic structure of Godthåbsfjord, along with the community structure, grazing, and predation among its metazooplankton. Increased ice melting will intensify freshwater intrusion into the fjord, which may, in turn, have a negative influence on oceanic or coastal zooplankton species, but favor resident self-sustaining species. In particular, the increasing dominance of rotifers and other small zooplankton species in the outer sill and main fjord basin regions might yield a trophic structure with an added level. Because the phytoplankton composition is expected to shift toward one with a smaller cell size (Sommer & Lengfellner 2008), this could lead to a closer coupling between primary production and grazing by microzooplankton. However, a shift towards a community dominated by small and less lipid-rich zooplankton species could also greatly impact the transfer of lipid and essential fatty acids up the food chain, affecting production at higher trophic levels (Falk-Petersen et al. 2007).

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Seasonal patterns in mesozooplankton community structure in a sub-Arctic pelagic system – the dominance of *Microsetella norvegica*

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Seasonal patterns in mesozooplankton community structure in a sub-Arctic fjord system - the dominance of *Microsetella norvegica*

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ABSTRACT

The present study represents one of only few multiyear zooplankton monitoring programs with year-around sampling covering the entire seasonal cycle in a sub-Arctic fjord. We show that *Microsetella norvegica* is a key species dominating the mesozooplankton community on an annual basis. The studied area showed weak water column stability due to strong tidal mixing and the spring phytoplankton bloom is dispersed over the upper 100 m during April whereas a pycnocline keeps the summer blooms in the upper 50 m from July to September. A total of 56 zooplankton groups were identified. The seasonal succession follows a seasonal pattern where Cirripedia nauplii dominates the assemblage in the spring bloom period April and May, *Calanus* spp. dominates in June followed by *M. norvegica* July to September in both terms of abundance and biomass. *M. norvegica* is found to be very abundant (max observations; 408.125 ±161.387 nauplii, 91.995 ±6.864 copepodites m^{-3}) and makes up 68% of the total copepod biomass that peaks in August (71 ±10 mg C m^{-3}). Grazing estimates shows that the genus *Calanus* request less carbon on an annual basis than the assemblage of other copepods (10 g C m^{-2} y^{-1} to 20 g C m^{-2} y^{-1} respectively).

INTRODUCTION

The large herbivorous genus *Calanus* are considered to be the primary herbivores in Arctic pelagic ecosystems, often linked to high phytoplankton biomass during the spring phytoplankton bloom. *Calanus* is an important prey item for many species of fish, birds and whales as they build up large lipid reserves, which are an important component of the energy transfer up through the Arctic marine food web (Falk-Pedersen et al. 2007).

The sub-Arctic waters off West Greenland is dominated by the West Greenland Current which consist of a mixture of local waters, Arctic waters from the East Greenland Current and Atlantic water from the Irminger Current. Therefore the dominating mesozooplankton group in these waters, *Calanus*, consists of a mix of the true Arctic species *Calanus glacialis* and *C. hyperboreus* and the Atlantic species *C. finmarchicus* (Pedersen et al. 2005, Arendt et al. 2010). *Calanus* spp. abundances peak in the upper water strata in midsummer where after it descends to hibernation for the winter (Madsen 2001, Lee 2006).

It has been shown that smaller copepod species plays a central role after *Calanus* has left the upper water strata in summer (e.g. Jespersen 1934, Hansen et al. 1999, Madsen et al. 2008, Svensen 2011). Small copepods may contribute through different food strategies in the food web such as omnivory and phagotrophy (Thor et al. 2005), and they can potentially contribute significantly to secondary production, as their growth rates are generally higher than those of larger organism (Fenchel 1974, Banse 1982). However, the role of the smaller copepod taxa in the Arctic are still not well understood.

The fact that there exist Arctic areas where *Calanus* are not the dominating zooplankton on an annual basis can easily be overlooked. Weather this is due to lack of annual sampling programs that describes the entire seasonal cycle or if this is related to sampling procedures using too course nets (Dugas and Koslow 1984, Hopcroft et al. 2005, Svensen 2011) is not clear. Nielsen and Andersen (2002) found that sampling with 200 µm WP2 net largely underestimated the total copepod biomass compared to samples from Niskin bottles (concentrated on a 45µm mesh sieve) in a Norwegian fjord, here especially nauplii of smaller copepod taxa such as *Microsetella norvegica* and *Oithona* spp. were underestimated.

As early as in 1934, it was reported (Jespersen 1934) that the genus "*Harpacticus*" were found to be very abundant in surface waters of a Greenlandic fjord, and Smidt (1979) reported that the harpacticoid *M. norvegica* was very abundant in the coastal region of the sub-Arctic fjord Nuup Kangerlua (Godthåbsfjord, West Greenland). Recent transect studies have shown pronounced

differences in plankton community structure from offshore regions towards the inner part of the Godhåbsfjord system. In spring, Arendt et al. (2010) found *C. finmarchicus* to dominate the offshore region whereas the plankton community within the fjord was different, a pattern that was corroborated in a summer study by Tang et al. (2011). These findings suggest separation of offshore and fjord systems, where especially the fjord mouth has very low *Calanus* biomass.

The aim of the present study is to describe annual and interannual variations in plankton community structure at the entrance of the sub-Arctic Godthåbsfjord, to provide futher details of the suggestion that small copepod species can overrule *Calanus* in coastal areas of the sub-Arctic region (Smidt, 1979, Arendt et al. 2010 and Tang et al. 2011). Our study gives a better insight into the hypothesis that biomass of small copepods can contribute on equal terms with larger species on an annual basis. In addition, the study represents one of only few multi-year zooplankton monitoring programs with year-around sampling covering the entire seasonal cycle. It describes the entire copepod community and other zooplankton groups using a small-mesh net (i.e. 45 μm). The presented work is part of the marine subprogram of Nuuk Ecological Research Operations which together with the marine monitoring in Zackenberg Ecological Research Operations in Northeast Greenland is managed by Greenland Climate Research Centre and the complete dataset of the monitoring program is described in annual reports (http://www.natur.gl).

MATERIALS AND METHODS

Study site and sampling. From October 2005 to December 2010, a total of 57 samplings were conducted at station GF3 (64°07N 51°53W – 350 m) on a monthly interval. Stn. GF3 is located at the entrance to Godthåbsfjord (Fig. 1) near Nuuk, the capital of Greenland, just below the Arctic Circle (64˚N). Samples were collected around noon, although previous investigations showed no differences due to tidal cycle. The Godthåbsfjord covers a surface area of 2013 km^2 (average depth of c. 250 m) with several sills around the entrance of the fjord (Mortensen et al. 2011).

Vertical profiles of water temperature, salinity, density and fluorescence were obtained using a CTD profiler (SBE 19plus, SeaCat) equipped with a Seapoint Chlorophyll *a* (Chl *a*) Fluorometer and a Biospherical/Licor sensor. CTD profiles were recorded from the surface to approximately 300 m. Water samples were collected using a 5-liter Niskin water sampler at depths of 1, 5, 10, 15, 20, 30, 50, 100 m. At each depth 50 – 2000 ml water were taken for Chl *a* measurements. Samples were

filtered onto GF/C filters (≤ 0.3 bar) and immediately extracted in 10 ml 96% ethanol for 18 hours before fluorescence was measured on a fluorometer (TD-700, Turner Designs, California, USA) calibrated against a pure Chl *a* standard (Turner Designs). Information on hydrographic conditions can be found in Mortensen et al. (2011), whereas water chemistry and primary production are reported by Juul-Pedersen et al. (*in prep*).

Mesozooplankton. Zooplankton was sampled at triplicate hauls using a 45 µm WP2 net (0 - 100 m) fitted with a flowmeter. The mesozooplankton was fixed in buffered formaldehyde (4% final concentration). Preserved zooplankton samples were processed at the Arctic Agency, Poland, for species identification and enumeration using a stereomicroscope. Species were counted from a volumetric subsample. Identification of copepods were made to species or when not possible to highest taxonomical level, whereas other zooplankton were identified to phylum and when possible to species. For each sample, copepod species were identified according to developmental stages and sex; while other zooplankton groups were grouped by size. For all identified groups, body lengths of up to 10 random individuals within each group were measured. Out of the 57 sampling campaigns only one net-sample were omitted (June 2010), whereas on four occasions samples were not collected in triplicate hauls. The total data set represents a sum of 161 processed samples.

The carbon content of all zooplankton groups was calculated using length-weight regression when found in the literature or from estimations of dry weight to carbon (Table 1). The carbon content of *Microsetella norvegica* was measured by first transfer individuals without ambient water onto a GF/F filter where prosome length (TL, µm) was measured. Hereafter, 18-25 individuals of each size groups were transferred to a pre-combusted GF/F filter and dried for 24 h at 60°C prior to analysis on an elemental analyzer (SerCon ANCA GSL) in line with a mass spectrometer (SerCon Hydra 20-20). Values of TL and weight (W, µg C) were log transformed before the regression line was plotted, in accordance with Satapoomin (1999). The length carbon relationship was expressed as:

$$1) \quad \ln(W) = 1.7843 \ln(TL) - 11.1366 \ (R^2 = 0.4004)$$

Production of the copepod community (secondary production) was calculated following the regression model of Hirst and Bunker (2003) (Table 2), using average *in situ* temperatures (°C) and average Chl *a* concentrations (µg Chl *a* l^{-1}; 0 – 100 m) and integrated copepod biomasses (mg C m^{-2}; 0 – 100 m). Grazing impact was then estimated assuming a gross growth efficiency of 33 % (Hansen et al. 1997). Cirripedia nauplii (nlp) were assumed to have a similar growth rates as

copepod nlp and therefore grazing and production was estimated using the same method as for copepods.

RESULTS

Water column structure and chlorophyll *a*. During winter, the water column at station GF3 is well mixed due to tidal mixing and low freshwater runoff from land (Fig. 2). From July to September/October increased freshwater runoff to the fjord forms a pycnocline in the upper 40 m strong enough to withstand the tidal mixing. Above this pycnocline seasonal minimum salinities and maximum temperatures (Fig. 2A, B) are recorded. During autumn/winter the runoff decreases and the salinity of the surface water increases. Maximum salinities are recorded between February and May. The spring bloom initiates in late April and peaks in early May before the stratification of the water column builds up (Fig. 2C). The bloom is dispersed over the upper 100 m due to the strong tidal mixing at the sills and the Chl *a* concentrations at the station GF3 is rarely > 5 µg Chl *a* l^{-1} (Fig. 2C). The spring bloom is followed by post and summer blooms in the upper 50 m as the pycnocline builds up.

Zooplankton community structure. A total of 56 groups (phylum to species) were identified in the 161 net samples, including 15 species of copepods plus unidentified Harpacticoida, Cyclopoida, copepod eggs and copepod nauplii (nlp) (Fig. 3: arranged into nlp of *Microsetella norvegica* and of other copepods). Aside from copepods, 9 groups of Crustaceans were identified, 5 groups of cnidarians and ctenophores, gastropod and bivalve larvae and pelagic pteropods (primarily C*lione limacina* and *Limacina* sp.) among addition groups (Fig. 3) where of rotifers make up the lower size range of organisms comprised in this study.

Abundance copepods. *M. norvegica* dominated the copepod community (Fig. 4A). During 7 months out of a year it makes up > 50 % of the total abundance. However, abundances are low in January – April (< 2000 ± 916 ind m^{-3}) where *M. norvegica* make up 32 - 49 % of the total abundance, *Calanus* spp. constitute 9 - 24 % were as *Pseudocalanus* spp., *Oithona* spp., *Onacea* spp. and *Microcalanus* spp. together make up a considerably part 35 – 59 % of the total community assemblage. In May abundances increases due to higher abundances of *Calanus* spp. and *Pseudocalanus* spp. (fig. 4A). May is the only month throughout the year when *Calanus* spp. is the

dominating genus, in average 37 % of total abundance (Fig. 4A). From June the abundance of *M. norvegica* increases rapidly and peaks in July with in average 159.000 ± 56.000 ind m^{-3}. Due to the massive abundance of *M. norvegica* it constitutes 95 – 86 % of total abundance in July – September, respectively, whereas the contribution of *Calanus* spp. decreases to < 0.1 % in the same period. In October *M. norvegica* numbers decreases relatively more than the abundances of *Pseudocalanus* spp., *Oithona* spp., *Oncaea* spp. and *Microcalanus* spp. and these species therefore make up an increasing part of the total community structure (36 – 39 %). The relative contribution of *Calanus* spp. remain low (< 2 %) throughout the rest of the year (i.e. October - December, Fig. 4A).

Interannual variations in copepods. Calanoid nlp show the first peak in spring of all the studied groups (Fig. 5A), although peak abundances vary by more than one month between years. In 2006, 2008 and 2010 Calanoid nlp were found to peak in May, whereas they peaked a month later in June 2007. The time when nlp reside in the upper 100 m is relatively short as their abundance decreases by mid July in all years. *Calanus* spp. is the first copepodites to peak in spring, coinciding with or just after the peak in nlp (Fig. 6A). The peak in copepodites varies by a month between years. The earliest increasing abundances in mid-April and peaked in mid-May during 2010, whereas rising abundances and peak occur a month later in 2007 and 2008. No defined spring peak is observed in 2006 and 2009. Copepodites of *Calanus* spp. usually withdraw by July though it was delayed in 2007 (Fig. 6A). *Pseudocalanus* spp. peaked in June during 2006-07 and was delayed until July in 2008 (Fig. 6B). *Acartia* spp. and *Onacea* spp. also peakes during May – July showing a similar one month inter-annual variation (Fig. 6C, D). *Pseudocalanus* spp., *Acartia* spp. and *Onacea* spp. are abundant throughout summer and autumn until they decent in November (Fig. 6B, C, D). It is noteworthy, that abundances of all three species are lower in 2010 than in the previous years.

Nauplii of *M. norvegica* is the most numerous group, with highest abundances in July 2007 of 408.000 ±161.000 ind m^{-3} (Fig. 5). Peak abundance occurred in July or as late as August in 2009, approximately two months later than the peak abundance of Calanoid nlp (Fig 5A, B). Copepodites of *M. norvegica* and *Oithona* spp. are the species that peaks latest in the season although interannual variations for both species occur (Fig. 6E, F). In 2006 – 2009 peak abundance of *M. norvegica* occurred in August and even later in 2007, whereas the peak was observed a month earlier in July 2010 (Fig. 6E). *Oithona* spp. peaked in July of 2007 whereas the peak took place a month later in

2007 and 2009 (Fig. 6F). Abundances were lower in 2006 and 2010 than in the remaining years. Both *M. norvegica* and *Oithons* spp. withdraw from the upper water column sampled in October. *Microcalanus* spp. does not have a defined peak abundance or time of withdrawal during the year. The abundances vary over the year, some years showing decreasing numbers during summer as seen in 2006 and 2010 (Fig. 6G).

Abundance of other zooplankton. The community structure of other zooplankton than copepods showes considerable variations over between seasons (Fig 4B). In the first two months of the year polychaetes and appendicularians constitutes up to 88% of the total assrmblage whereas increasing abundances of Cirripedia nlp up to 87% is seen in March and April. Peak abundances of Cirripedia nlp occur in May (4.370 ±2.810) together with bivalve larvae (9.750 ±4.210) (Fig. 4B). In midsummer, an increase in rotifers builds up to a peak in July 73.900 ±14.690 ind m^{-3}. Rotifers are the dominating group until October, after which they show a pronounced decrease in abundance. In November and December gastropod, bivalve and polychaete larvae dominate (Fig. 4B).
Interannual variations are observed in Cirripedia nlp and for the later development stage cypris (Fig. 5C, D). Cirripedia nlp peaks in late-April to early-May where after the development from nlp to cypris occurs. The peak in cypris occurred early mid-May in 2010 whereas the highest abundance was found a month later in 2006-2009 (Fig. 5D). Cirripedia cypris withdraw from the upper 100 m in mid July.

Biomass of copepods. In total *M. norvegica, Pseudocalanus* spp., and *Calanus* spp. makes up 81 – 96 % of the total copepod biomass throughout the year. The biomass is dominated by *M. norvegica* and only temporarily exceeded by *Calanus* spp. in May and June **(**Fig. 7A). Biomasses of *Calanus* spp. are very low from January to April < 1.5 mg C m^{-3} where after an increase up to 17 ±19 mg C m^{-3} is seen in May and June (Fig. 7A). During summer, the increase in copepod biomass is due to higher biomasses in *M. norvegica*. The copepod biomass peaks in August with 71 ± 49 mg C m^{-3}. During autumn, total biomasses is reduced for all copepod species due to a drop from September. Nevertheless, *M. norvegica* remain the dominating species throughout the year.

Biomass of other zooplankton. The non copepod groups shows increasing biomasses from March to May due to higher numbers of Cirripedia nlp (Fig. 7B). During these months Cirripedia makes up 66 – 94 % of the total biomass. Hereafter, Cirripedia biomass decreases, whereas the euphasid

biomass show a short increase before the rotifer biomass takes over in July. Rotifers makes up 63 % of the biomass peak in July. From August, biomasses of rotifers decrease and here after they disappear from the upper 100 m in October. Gastropods, polychaetes and appendicularians makes up the main biomass throughout winter until February.

Grazing. On an annual basis the copepod community grazes 30 g C m^{-2}, equally distributed between *Calanus* spp. 10 g C m^{-2} y^{-1}, *M. norvegica* 11 g C m^{-2} y^{-1} and other copepods 9 g C m^{-2} y^{-1}. During the bloom situation in May the grazing of the copepod community is exceeded by the grazing of Cirripedia nlp which demands 146 ± 50 mg C m^{-2} d^{-1} (Fig. 8), whereas *Calanus* spp. demand is 81 ±104 mg C m^{-2} d^{-1} in June when their grazing is highest. In July and August the grazing of *M. norvegica* peaks with 132 ± 97 and 98 ± 31 mg C m^{-2} d^{-1} respectively (Fig. 8). The remaining group of copepods demands c. 45 mg C m^{-2} d^{-1} during the period May – September. *Pseudocalanus* spp. nlp dominate in spring and their copepodit stages throughout the season.
On an annual basis *Calanus* spp. graze 11% of the primary production (average annual primary production; 95 ± 12 g C m^{-2} y^{-1} from 2006-2010, obtained from Juul-Pedersen et al. 2011). The small copepods (*M. norvegica* and other groups of copepods) are able to turnover 21% of the annual primary production. In total, copepods and Cirripedia turn over approximately 39 % of the primary production on an annual basis.

DISCUSSION

Microsetella norvegica is a key species in the fjord system as it dominates the mesozooplankton community on an annual basis. The knowledge obtained during the 5 years of zooplankton monitoring shows unambiguously that *Calanus* spp. only exceeds the smaller copepod taxa in terms of biomass during May and June, when they are active in surface waters. In May, biomass and grazing rate of Cirripedia exceeds that of *Calanus* spp., thus *Calanus* spp. is only the dominating and ecologically most important mesozooplankton group in June when it graze 20% of the primary production. The estimated grazing impact for Cirripedia was in the same range as that reported by Rodhouse and Rhoden (1987) (P/B = 0.1). However, the average rates found by Turner et al. (2001) were much lower (P/B = 0.02), and therefore Cirripedia grazing could be overestimated in this study.

Previous investigations (Arendt et al. 2010, Tang et al. 2011) showed that *Calanus* spp. can be found at higher abundances at a relatively short distance from the study area with considerably higher biomasses in the offshore area and slightly higher biomasses in the main fjord basin. *Calanus* are poorly represented in the turbulent outer sill region also when the entire water column are sampled with coarser nets (Arendt et al. 2010, Tang et al. 2011) although a minor increase in biomass of the larger copepod species is observed at the sample site during night (Tang et al. 2011). On the other hand, *M. norvegica* is very numerous in the outer fjord region (Arendt et al. 2010, Tang et al. 2011). *M. norvegica* has been found to be numerous in other coastal regions (Anraku 1975, Dugas and Koslow 1984, Uye et al. 2002) and fjords (Andersen and Nielsen 2002) although, only abundances reported by Fish (1955) reports abundances in coastal waters of Nova Scotia, North West Atlantic (> 200.000 copepodites and > 400.000 nlp m^{-3}) comparable to our study.

In the outher sill region of Godthåbsfjord a convergence zone is maintained by the strong tidal mixing and special circulation system (Mortensen et al. 2011). These patterns retain water in the intermediate layer and zooplankton may hereby be trapped in a high biomass patch. A re-circulating relative warm water masses could maintain environmental conditions that favor *M. norvegica* above other copepod species. *M. norvegica* has been shown to graze well on particulate and attached food sources (Koski et al. 2005, Koski et al. 2007). The Godthåbsfjord has numerous sources of suspended sediments (Arendt et al. 2011) which together with organic material provided by the high and constant primary production during summer and autumn (Juul-Pedersen et al. 2011) could generate aggregates appropriate for grazing by *M. norvegica*. Low pCO_2 levels in the surface layer of the fjord (Rysgaard et al. in revision) suggest that a large fraction of carbon assimilated by phytoplankton is degraded at depths below the mixed surface layer, and *M. norvegica* could be an active player in this degradation.

Annual primary production at the entrance to Godthåbsfjord is high (Smidt 1979, Juul-Pedersen et al. 2011) with a long productive season from April to October due to high nutrient supplies brought to the photic zone by tidal mixing. In the main fjord basin water masses is stratified (Arendt et al. 2010, Mortensen et al. 2011) and here, growth rates increases towards the inner part of the fjord where several glacier are situated as observed by Arendt et al. (2010) due to high nutrient levels in the photic zone and in mid summer by Calbet et al. (2011) due to upwelling driven by sub-glacial freshwater discharge and mixing with deeper lying ambient water (Mortensen et al. 2011). The areas in the fjord where high summer production is found fuel the entire fjord assemblage with organic material throughout the productive season and hereby it may lead to a high activity in the

microbial food web. Small copepods like *Oithona* spp. has been suggested to take advantage of the microbial food web (Svensen et al. 2011) and in general the long productive season may sustain populations of small copepods like *M. norvegica* that maintains active feeding throughout the entire productive season (e.g. *Pseudocalanus* spp., *Acartia* spp., *Oithona* spp. and *Oncaea* spp.).

The mesozooplankton community follows a similar seasonal succession in all years, although interannual variations in numbers and timing of peak abundance occurred (Fig. 6). These variances could be due to a combination of variations in hydrographic circulation patterns and temporal variations in species succession and development caused by temperature changes. The warmest and least saline water conditions throughout the study period were observed in 2010 (Fig. 2AB). In 2010, peak abundances of both *Calanus* spp. and *M. norvegica* copepodites occurred early, compared to previous years (Fig. 6A, E). On the other hand, a tendency towards lower abundances of smaller copepod species was observed in 2010 compared to previous years (Fig 6 B, C, D, F, G). Unfortunately, sampling in June 2010 was omitted making it difficult to determine the peak abundance of both *M.norvegica* nlp and copepodites, Cirripedia cypris and others. Mesozooplankton data obtained in the 1950th and 1960th in the same area shows similar succession patterns as observed during the present study (Smidt 1979, Table 3; presented values are ind. net haul^{-1} from 0-30 m). Smidt (1979) showed a comparable peak in Cirripedia nlp in April, whereas he report a peak in copepods (mainly *M. norvegica*) during August a month later than in the present study. This difference can primarily be explained by the fact that Smidt (1979) sampled with a coarser net (120 µm) and therefore under-sampled benthos invertebrate larvae, copepod nauplii and younger copepodite stages of smaller species, compared to our study.

The species composition in the study area differs from other Arctic areas by a low biomass of *Calanus* spp. during spring months. An annual study in the Disko Bay area further north showed high biomasses (c. 80 mg C m^{-3}; Madsen et al. 2001) of *Calanus* spp. from late May and throughout June, whereas reported biomasses of smaller copepod species were rather constant throughout the season (c. 1 mg C m^{-3} in the upper 50 m; Madsen et al. 2008). In the Disko Bay area, the large *Calanus* species are the main grazers of phytoplankton ingesting approximately 38 g C m^{-2} y^{-1}, whereas the smaller copepod species graze approximately 5 g C m^{-2} y^{-1} (grazing is estimated from production data obtained from Madsen et al. 2008 (Table 2) assuming an gross growth efficiency of 33 % (Hansen et al. 1997)). In contrast we found *Calanus* to utilizing less carbon than other copepods on an annual basis (10 g C m^{-2} y^{-1} to 20 g C m^{-2} y^{-1} respectively). Copepods utilize approximately 32 % of the annual primary production (95 ±12 g C m^{-2} y^{-1}, Juul-Pedersen 2011)

which is in the same range as in the Disko Bay whereas copepods have been estimated to gain > 85% of the yearly primary production in the North East Greenlandic fjord Young Sound (Rysgaard et al. 1999) where primary production is remarkable lower (10 g C m^{-2} y^{-1}) than in the present study site.

The results obtained in this study outline the need for continuous sampling throughout the year with small mesh nets in order to determine the entire mesozooplankton community and its seasonal succession in Arctic areas as the assemblage of the small copepods/zooplankton species can overrule large species such as *Calanus* on an annual basis. In the Godthåbsfjord system, *M. norvegica* is found to be the key zooplankton species, but since little is known about the ecology and life strategy of this small harpactocoid copepod it is an interesting candidate for further study.

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TABLES

Table 1. Algorithms used to convert body length to body carbon. TL is prosome length for copepods or total length for nauplii and other zooplankton taxa. Dry Weight (DW).

Taxa		Equation (DW)	Reference (DW)	Equation (Carbon)	Reference (Carbon)
Pseudocalanus sp. & small calanoids (♀ < 1mm)				mg C = $6.12E^{-11}$ x L(µm)$^{2.7302}$	Klein Bretler et al. (1982)
Calanus hyperboreus				mg C = $1.4E^{-3}$ x L(mm)$^{3.3899}$	Hirche and Mumm (1992)
Calanus finmarchicus & *Calanus glacialis*				mg C = $4.8E^{-3}$ x L(mm)$^{3.5687}$	Madsen et al. (2001)
Pareuchaeta sp.	nlp & copepodite			mg C = $4.2E^{-3}$ x L(mm)$^{3.01}$	Tönnesson et al. (2006)
	adult			mg C = $6.6E^{-6}$ x L(mm)$^{6.92}$	
Metridia longa				mg C = $6.05E^{-3}$ x L(mm)$^{3.0167}$	Hirche and Mumm (1992)
Acartia sp.				mg C = $1.11E^{-11}$ x L(µm)$^{2.92}$	Berggreen et al. (1988)
Microcalanus sp. & *Oithona* sp.				mg C = $9.47E^{-10}$ x L(µm)$^{2.16}$	Sabatini and Kiørboe (1994)
Onceae sp.				mg C = $2.51E^{-11}$ x L(µm)$^{2.9}$	Satapoomin (1999)
Microsetella norvegica				ln(µg C) = 1.7843ln(L(µm)) + ln11.14	This study
Calanus nlp				mg C = $4.29E^{-9}$ x L(µm)$^{2.05}$	Hygum et al. (2000)
Copepod egg				mg C = $1.4E^{-10}$ x 4/3 x PI x (L(µm)/2)^3	Kiørboe et al. (1985)
Ostracoda					
Cirripedia nlp & cypris				nlp: 2.5µg C ind^{-1}, Cypris: 11µg C ind^{-1}	Rodhouse and Roden (1987)
Bivalvia	larvae			0.12 pg C µm^{-3}	Fotel et al. (1999)
Gastropod	larvae			µg C = $2.3E^{-5}$ x L(µm)$^{2.05}$	Hansen and Ockelmann (1991)
Oikopleura				log C(µg) = 3.20 x logL(µm)-8.93	Diebel (1986)
Polychaet	larvae			µg C = $1.58E^{-4}$ x L(µm)$^{1.38}$	Pedersen et al. (2010)
Chaetognath				µg C = $2.225E^{-2}$ x L(mm)$^{3.13}$	Conway and Robins (1991)
Podon		DW/L(µm) = $3.456E^{-3}$	Hay (1991)	0.22mg C mg DW^{-1}	Postel et al. (2000) (Table 4.7)
Euphausiacea nlp & larvae		logDW(mg) = 0.38 + 2.871 x logL(mm)	Lindley et al. (1999)	38.2(C(mg)) as percentage of DW	Lindley et al. (1999) (Table 4)
	juvenile	logDW(mg) = 0.283 + 2.998 x logL(mm)		38.2(C(mg)) as percentage of DW	
Ctenophora		DW(mg) = $1.94E^{-3}$ x L(mm)$^{3.05}$	Matthews and Hestad (1977)	0.03 mg C mg DW^{-1} (average)	Postel et al. (2000) (Table 4.7)

FIGURE LEGENDS

Fig. 1. (A) Greenland and (B) the Nuup Kangerlua (Godthåbsfjord) fjord system with location of the monitoring stn. GF3.

Fig. 2. Hydrographic measurements at stn. GF3 from September 2005 to December 2010. (A) salinity and (B) temperature, with minimum salinity and maximum temperatures given for the surface layer in August each year. (C) Depth distribution of Chl *a* (µg l^{-1}) for the upper 100 m. Dotted lines represents sampling days and depth of CTD casts and points represents water samples.

Fig. 3. A list of all identified groups and species in the mesozooplankton community arranged according to average abundance in all samples (n = 161). Abundances (ind m^{-3}) are on a logarithmic scale ±standard deviation.

Fig. 4. Monthly average community composition (% of total number) of (A) copepods and (B) other zooplankton. Average monthly abundance (ind m^{-3}) ± standard deviation are presented for copepods and other zooplankton.

Fig. 5. Abundances (ind m^{-3}) of (A) calanoid nlp, (B) *Microsetella norvegica* nlp, (C) Cirripedia nlp and Cirripedia cypris from 2006 – 2010.

Fig. 6. Abundances (ind m^{-3}) of the copepodite stage I – VI of (A) *Calanus* spp., (B) *Pseudocalanus* spp., (C) *Acartia* spp., (D) *Onacea* spp., (E) *Microsetella norvegica*, (F) *Oithona* spp. and (G) *Microcalanus* spp. from 2006 – 2010.

Fig. 7. Monthly average community composition (% of total biomass) of (A) copepods and (B) other zooplankton. Average monthly biomasses (mg C m^{-3}) ± standard deviations are presented for copepods and other zooplankton.

Fig. 8. Monthly average grazing rates (mg C m^{-2} d^{-1}) of Cirripedia, *Microsetella norvegica*, *Calanus* spp. and other copepods ± standard deviation.

Fig. 1.

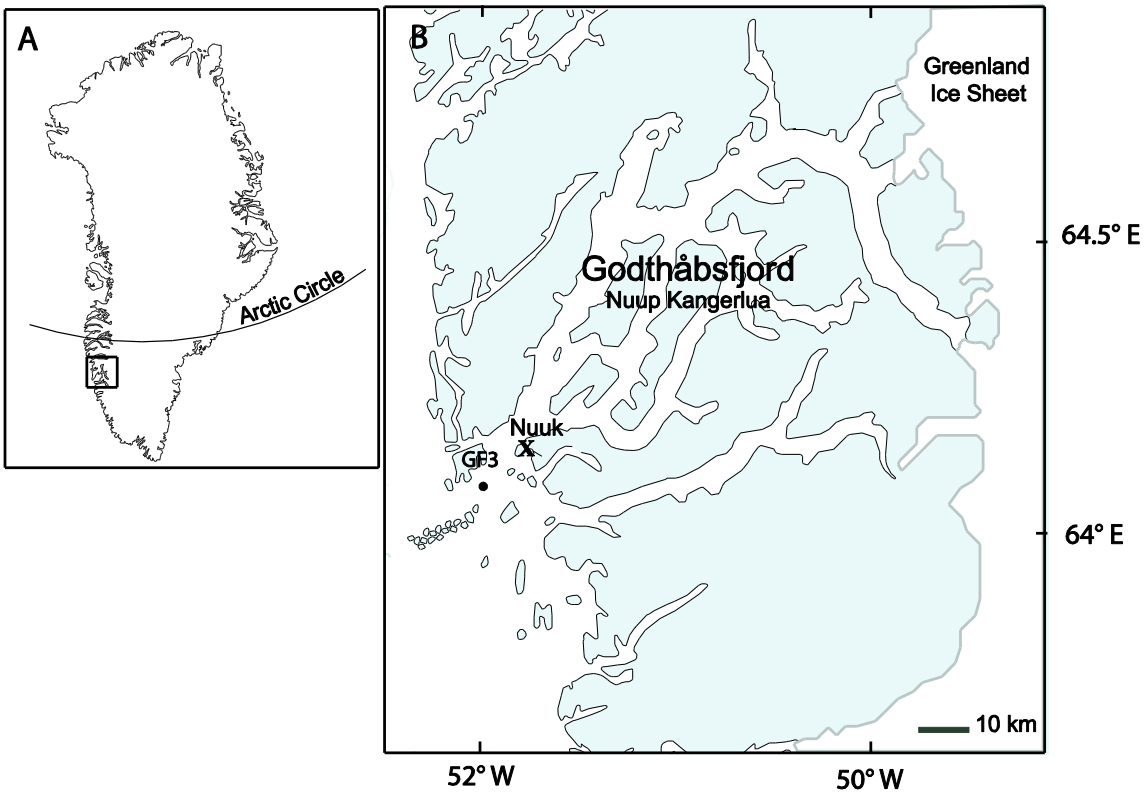

A
Arctic Circle
B
Greenland
Ice Sheet
Godthåbsfjord
Nuup Kangerlua
Nuuk
GF3
64.5° E
64° E
10 km
52° W
50° W

Fig. 2.

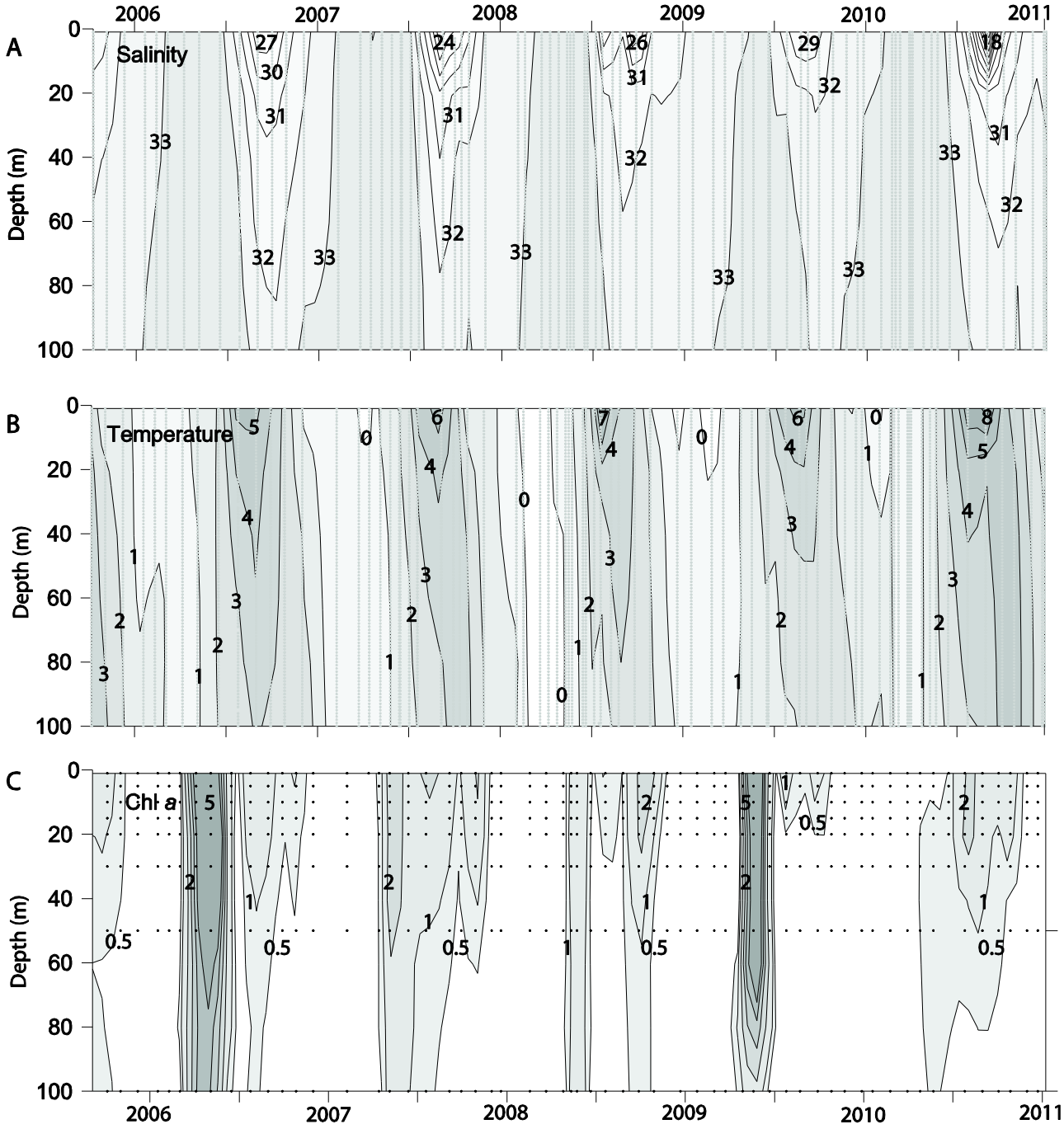

A
Salinity
B
Temperature
C
Chl a
Depth (m)
2006
2007
2008
2009
2010
2011

Fig. 3.

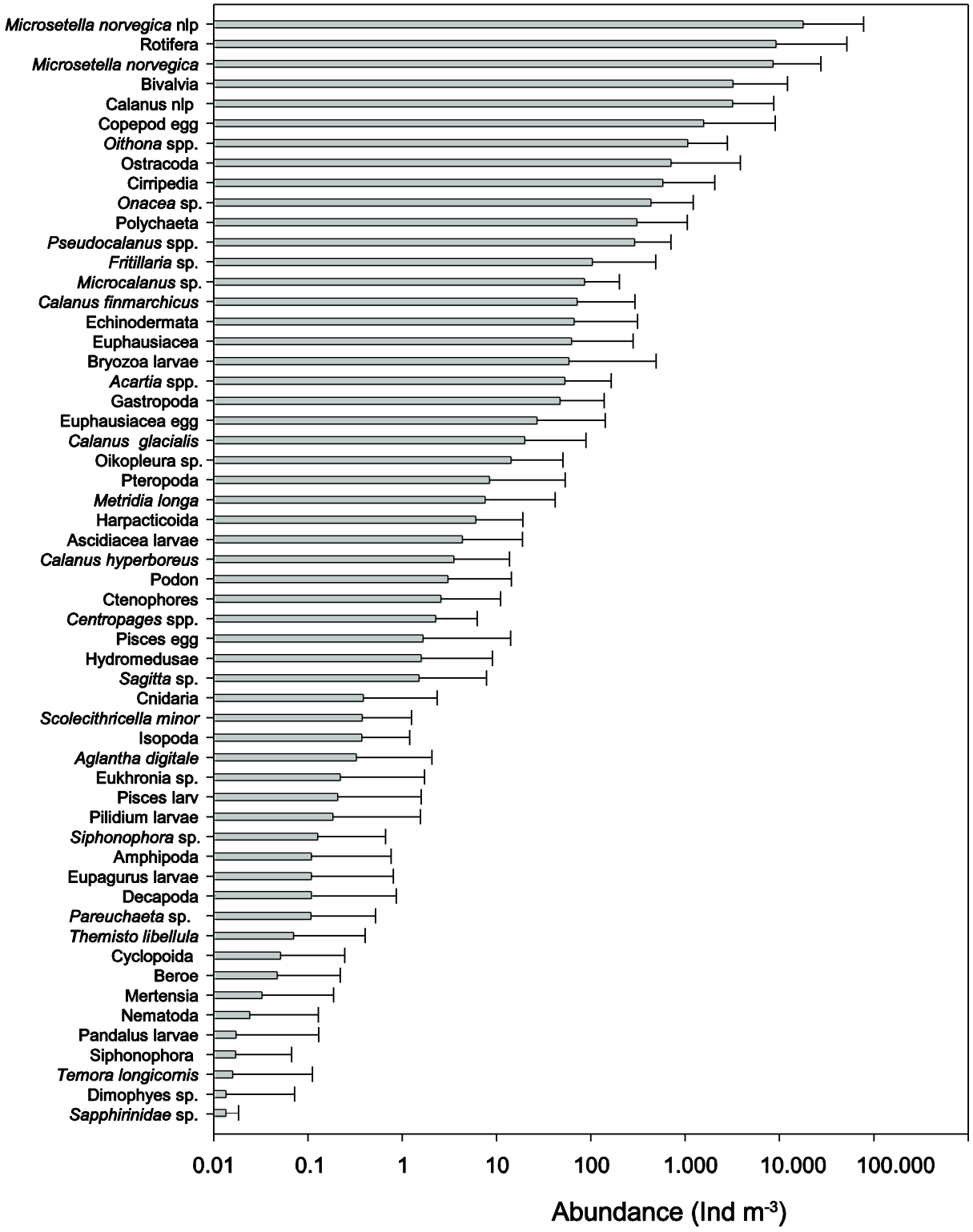

Microsetella norvegica nlp
Rotifera
Microsetella norvegica
Bivalvia
Calanus nlp
Copepod egg
Oithona spp.
Ostracoda
Cirripedia
Onacea sp.
Polychaeta
Pseudocalanus spp.
Fritillaria sp.
Microcalanus sp.
Calanus finmarchicus
Echinodermata
Euphausiacea
Bryozoa larvae
Acartia spp.
Gastropoda
Euphausiacea egg
Calanus glacialis
Oikopleura sp.
Pteropoda
Metridia longa
Harpacticoida
Ascidiacea larvae
Calanus hyperboreus
Podon
Ctenophores
Centropages spp.
Pisces egg
Hydromedusae
Sagitta sp.
Cnidaria
Scolecithricella minor
Isopoda
Aglantha digitale
Eukhronia sp.
Pisces larv
Pilidium larvae
Siphonophora sp.
Amphipoda
Eupagurus larvae
Decapoda
Pareuchaeta sp.
Themisto libellula
Cyclopoida
Beroe
Mertensia
Nematoda
Pandalus larvae
Siphonophora
Temora longicornis
Dimophyes sp.
Sapphirinidae sp.
0.01
0.1
1
10
100
1.000
10.000
100.000
Abundance (Ind m-3)

Fig. 4.

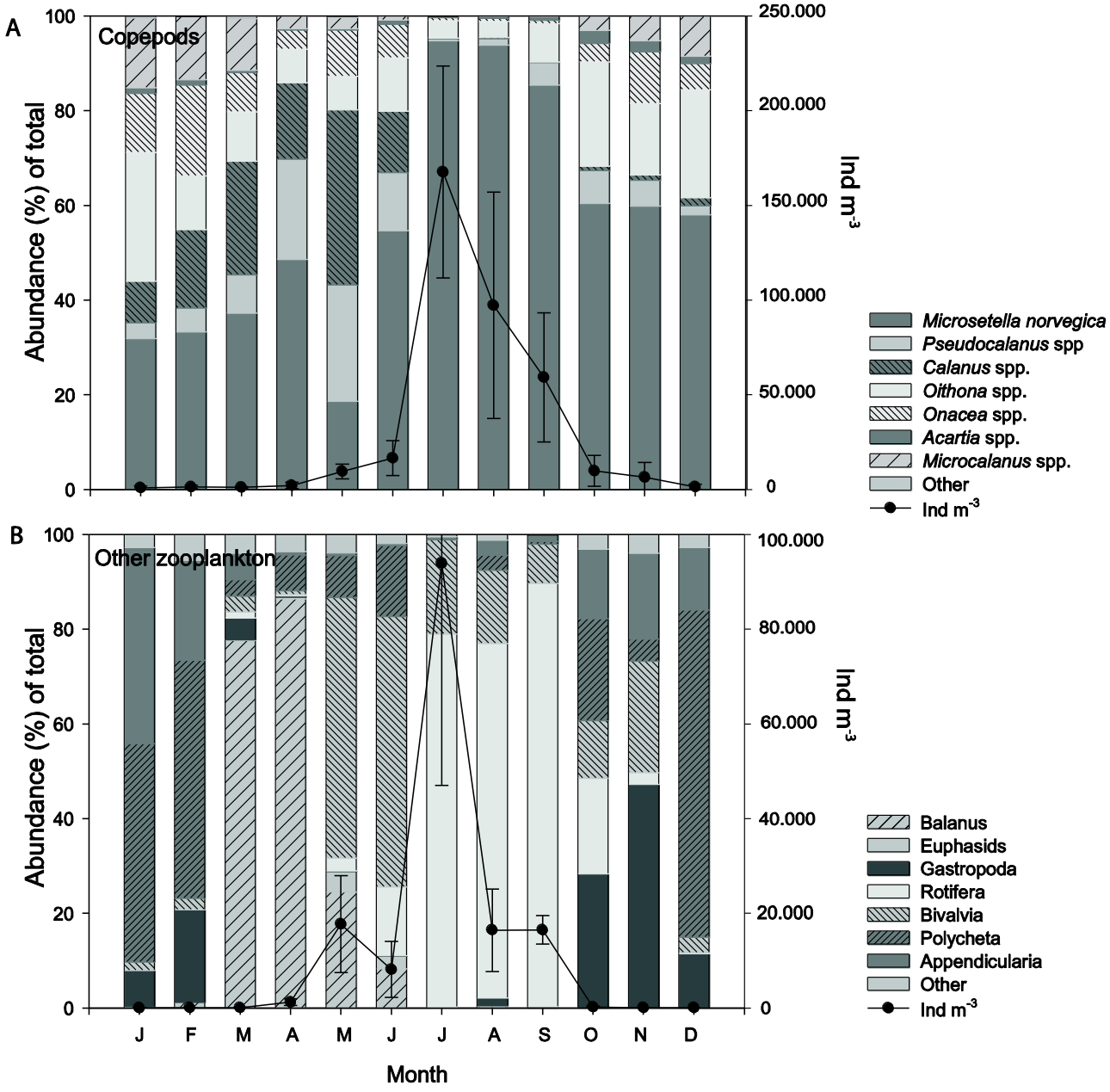

A
Copepods
Abundance (%) of total
Ind m-3
Microsetella norvegica
Pseudocalanus spp
Calanus spp.
Oithona spp.
Onacea spp.
Acartia spp.
Microcalanus spp.
Other
Ind m-3
B
Other zooplankton
Abundance (%) of total
Ind m-3
Balanus
Euphasids
Gastropoda
Rotifera
Bivalvia
Polycheta
Appendicularia
Other
Ind m-3
J F M A M J J A S O N D
Month

Fig. 5.

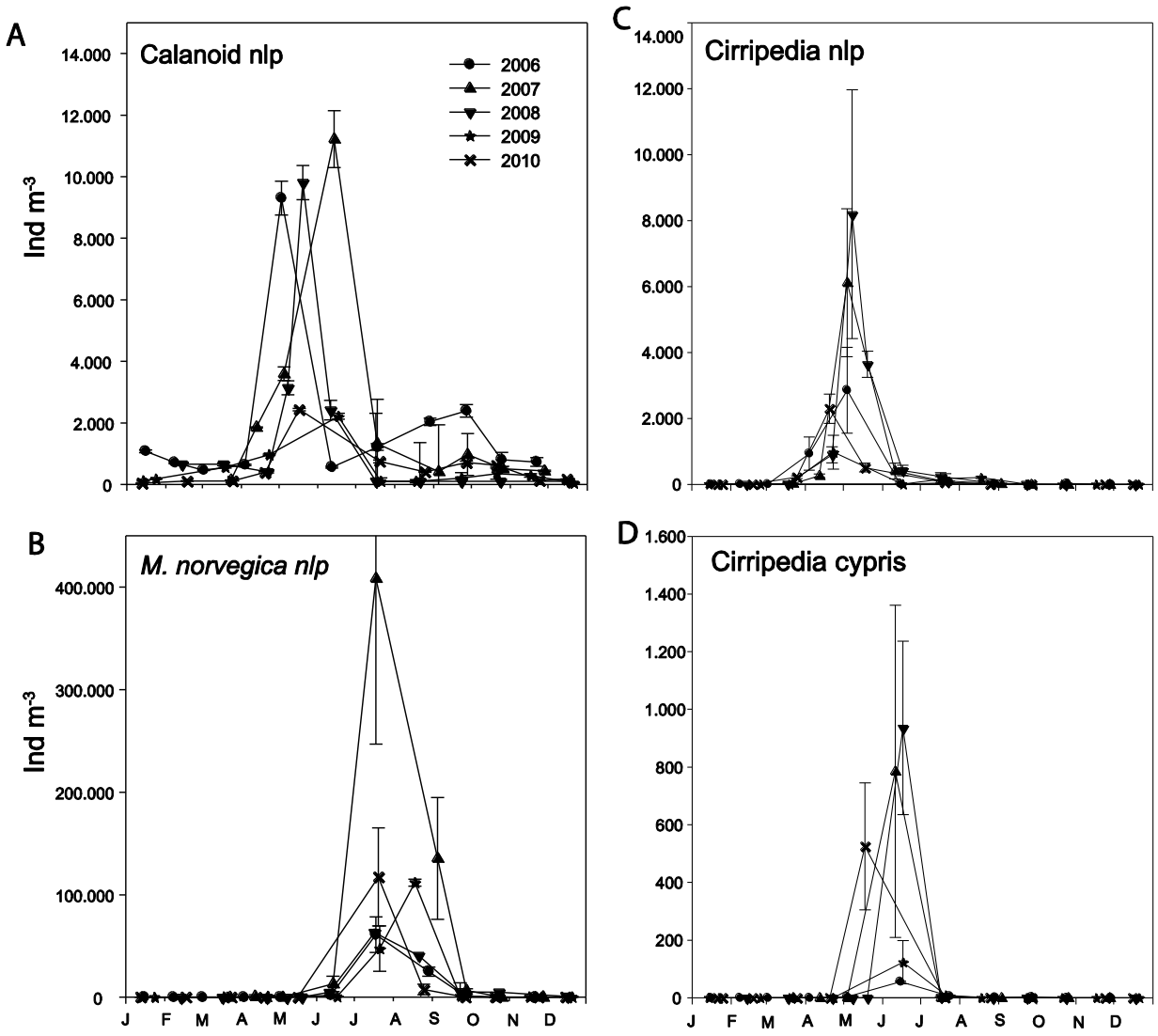

A
Calanoid nlp
2006
2007
2008
2009
2010
Ind m-3
14.000
12.000
10.000
8.000
6.000
4.000
2.000
0
C
Cirripedia nlp
B
M. norvegica nlp
400.000
300.000
200.000
100.000
D
Cirripedia cypris
1.600
1.400
1.200
1.000
800
600
400
200
J F M A M J J A S O N D

Fig. 6.

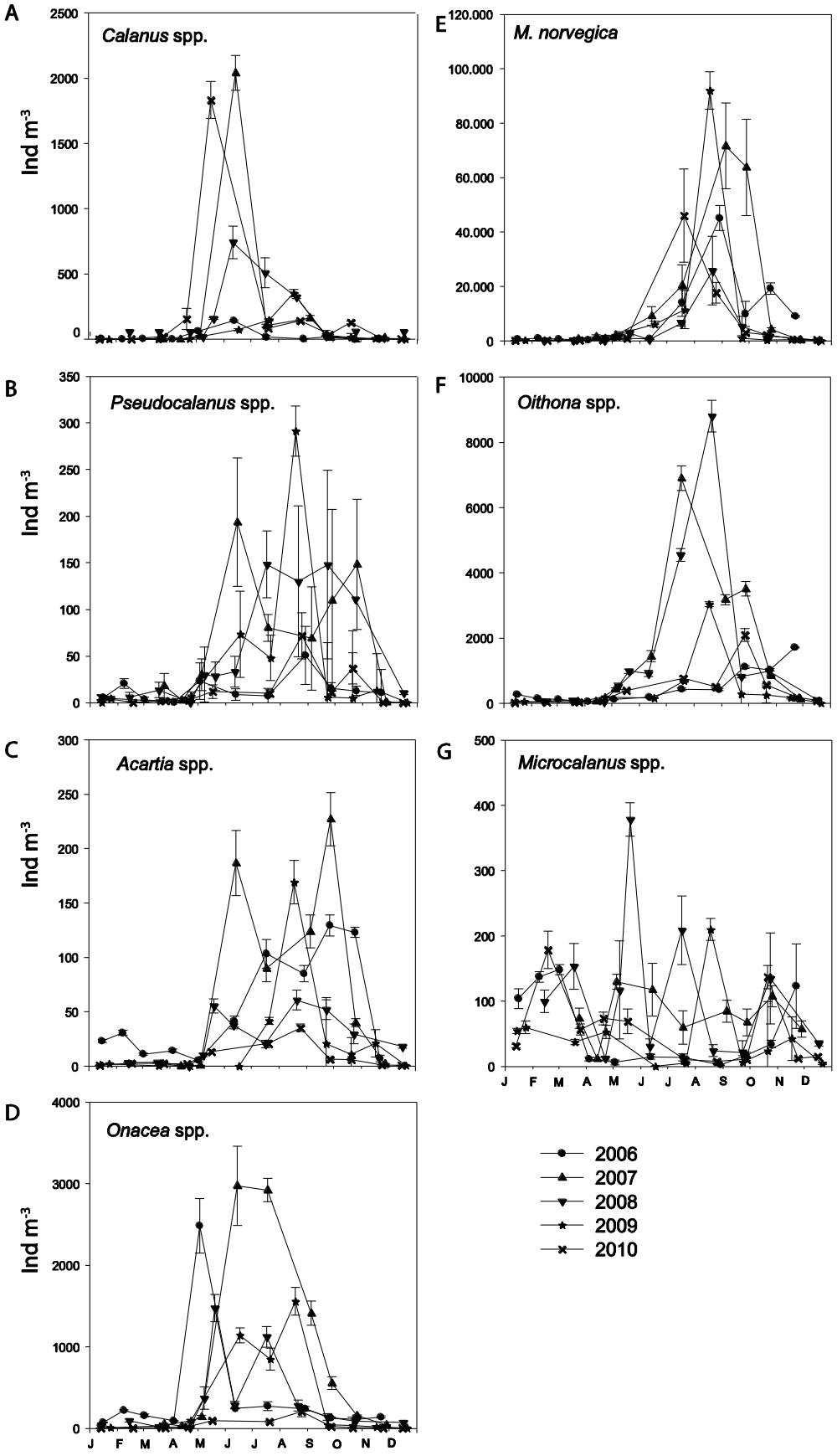

A
Calanus spp.
Ind m-3
2500
2000
1500
1000
500
0
E
M. norvegica
120.000
100.000
80.000
60.000
40.000
20.000
0
B
Pseudocalanus spp.
350
300
250
200
150
100
50
0
F
Oithona spp.
10000
8000
6000
4000
2000
0
C
Acartia spp.
300
250
200
150
100
50
0
G
Microcalanus spp.
500
400
300
200
100
0
D
Onacea spp.
4000
3000
2000
1000
0
J F M A M J J A S O N D
2006
2007
2008
2009
2010

Fig. 7.

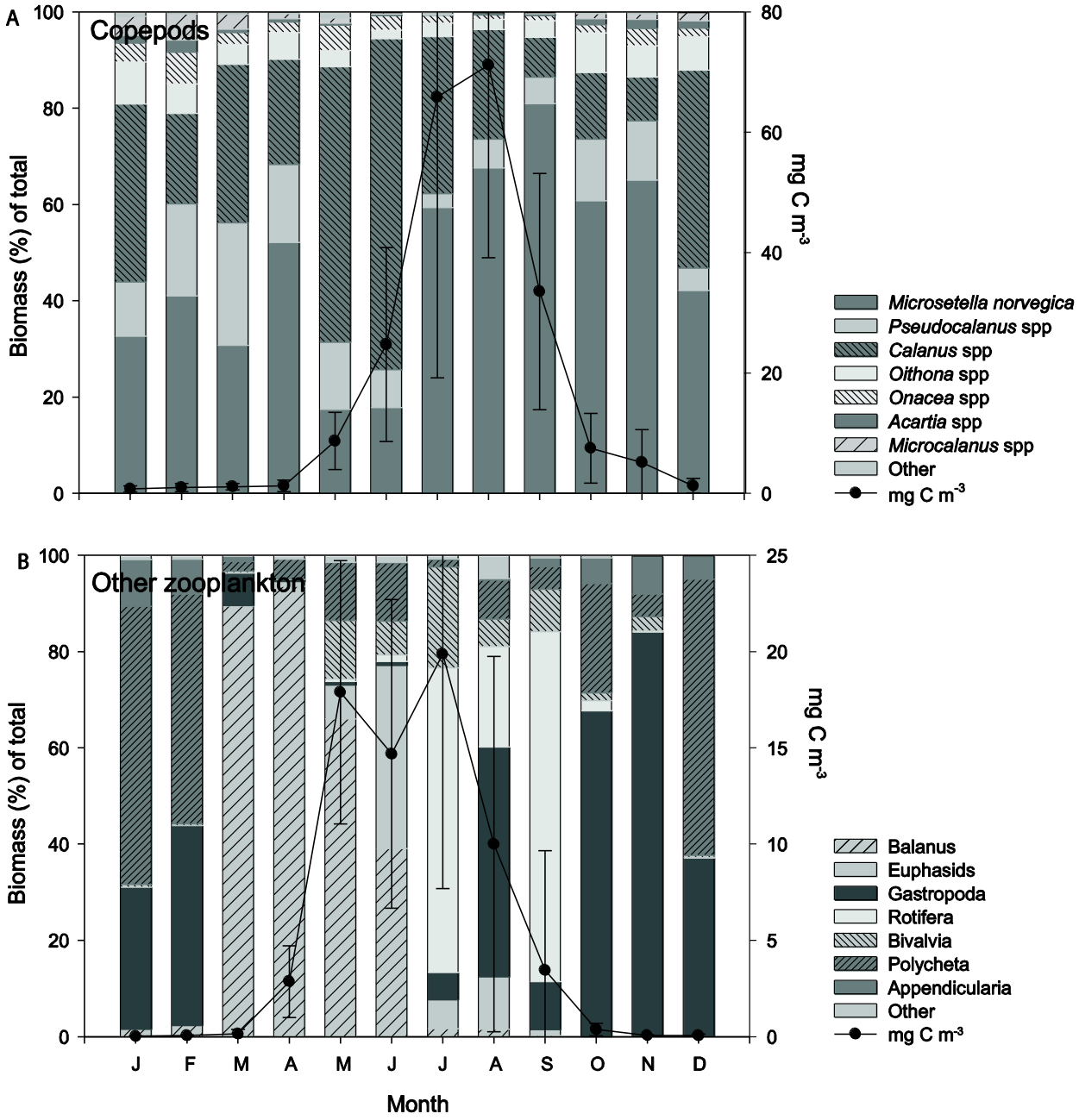
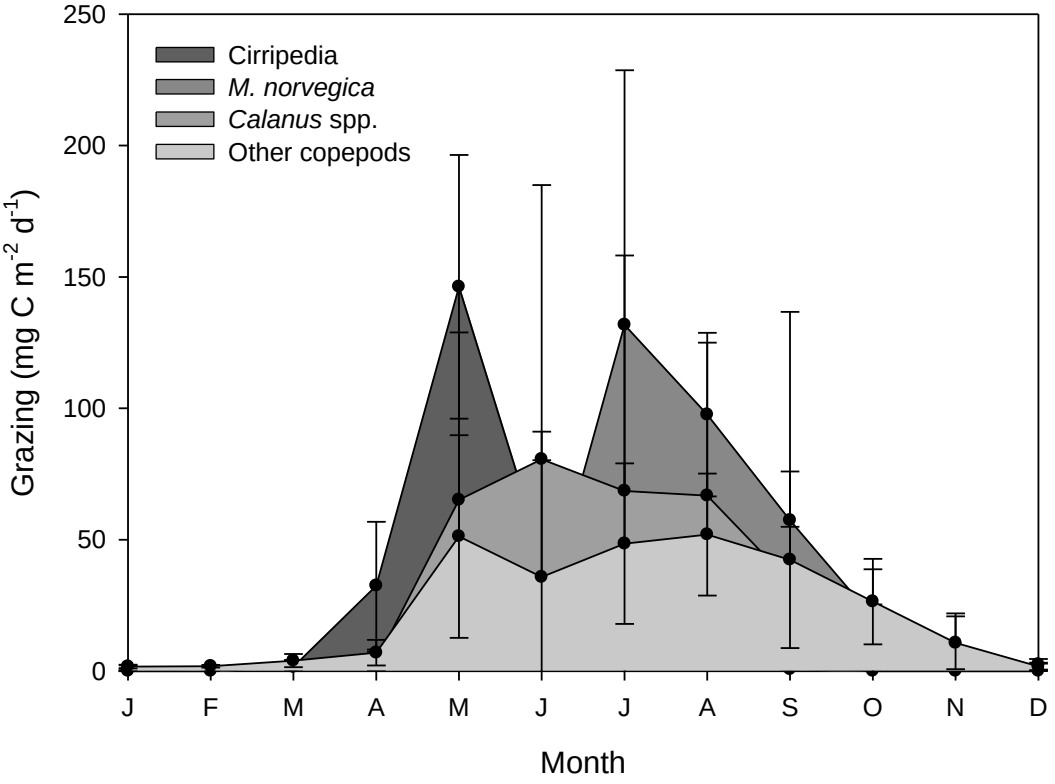

A
Copepods
Biomass (%) of total
mg C m-3
Microsetella norvegica
Pseudocalanus spp
Calanus spp
Oithona spp
Onacea spp
Acartia spp
Microcalanus spp
Other
mg C m-3
B
Other zooplankton
Biomass (%) of total
mg C m-3
Balanus
Euphasids
Gastropoda
Rotifera
Bivalvia
Polycheta
Appendicularia
Other
mg C m-3
J F M A M J J A S O N D
Month

Fig. 8.


Cirripedia
M. norvegica
Calanus spp.
Other copepods
Grazing (mg C m-2 d-1)
250
200
150
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D
Month

Effects of suspended sediment on copepod feeding in a glacial influenced sub-Arctic fjord

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Effects of suspended sediments on copepods feeding in a glacial influenced sub-Arctic fjord

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We investigated the effect of suspended sediments on the vital rates of the copepods *Calanus finmarchicus*, *Pseudocalanus* sp. and *Metridia longa* in a Greenland sub-Arctic fjord. The fjord had a gradient of suspended particulate matter (SPM) with high concentrations (>50 mg L^{-1}) in the inner fjord due to glacial melt water runoff. Laboratory experiments showed that when feeding on the diatom *Thalassiosira weissflogii* specific ingestion rates were low at high concentrations of suspended sediment for *C. finmarchicus* (>20 mg L^{-1}) and *Pseudocalanus* sp. (>50 mg L^{-1}), while no effect was found for *M. longa*. For *C. finmarchicus*, a relatively constant fecal pellet production (FPP) and fecal pellet volume suggested ingestion of sediment, which probably led to reduction in egg production rates (EPRs) at high sediment concentrations. For *Pseudocalanus* sp., FPP decreased with increasing sediment concentrations, while no effect was observed on EPR. No significant difference was observed in FPP for *M. longa* feeding on the diatom *T. weissflogii* compared to the ciliate *Strombidium sulcatum*. The study shows that high sediment concentrations influence the capability of carbon turnover in *C. finmarchicus* and *Pseudocalanus* sp., while *M. longa* appears to be more tolerant to high sediment loads. Therefore, high concentrations of SPM could potentially influence the species composition of glacially influenced fjords.

KEYWORDS: grazing; copepoda; suspended sediment; Greenland

INTRODUCTION

Coastal planktonic organisms encounter, for periods, a wide range of suspended particulate matter (SPM) due to river runoff and re-suspension of sediments. Glacially influenced marine environments can temporally have high concentrations of SPM due to extensive glacial erosion of the bedrock that leads to a high sediment load in the runoff (Domack *et al.*, 1994; Hallet *et al.*, 1996). Marine organisms inhabiting these environments are, therefore, exposed to high loads of SPM. Most fjords in Greenland receive large amounts of melt water with high sediment concentrations from the Greenland Ice Sheet. The runoff is extensive during summer (Mortensen *et al.*, 2011), but plumes containing sediment can be observed by remote sensing even in winter when they are intensified by tidal re-suspension (Rysgaard *et al.*, 2008). At present, run off and SPM

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loads are expected to increase as a result of the melting of the Greenland Ice Sheet. The melting is advancing northwards along the northwestern coast of Greenland (Kahn *et al.*, 2010). Furthermore, the fact that circulation modes within fjords link to the outlet from Greenland ice Sheet glaciers (Mortensen *et al.*, 2011) highlights the urgent need of knowledge about fjord ecology and effects from melting of the Greenland Ice Sheet.

It is well documented that marine zooplankton ingest particles of low nutritional value, even mineral particles as inferred from both grazing experiments (Poulet, 1983; Paffenhöffer and Van Sant, 1985) and fecal pellet (FP) analysis (Bayliss and Syvitski, 1982; Turner, 1984; Urban *et al.*, 1992). Although ingested, inorganic material itself provides little food for zooplankton. On the other hand, relatively little information is available on whether or not the inert particles have an effect on the absorption of nutritional compounds, feeding strategy or food accessibility. Some protozooplankton seem to be well adapted to environments with high clay loads (Boenigk and Novarino, 2004). Flagellates discriminate against clay particles, while ciliates reject larger clay particles but incorporate smaller clay particles into food vacuoles and later excrete them without any significant negative effect on feeding, growth rate or maximal abundance (Boenigk and Novarino, 2004). Metazoans such as rotifers also seem to be well adapted to clay and silt loads, whereas silt alone can significantly negatively affect the ingestion of phytoplankton by cladocerans (Kirk, 1991). For this reason, filter-feeding cladocerans are often absent from glacial lakes and the macrozooplankton community is instead dominated by raptorial feeding copepods (Koenings *et al.*, 1990). Some copepod species are able to reject non-food particles (Paffenhöfer and Van Sant, 1985) by use of chemo- or mechanoreceptors either by perception at a distance or when particles are being handled (Koehl and Strickler, 1981; Paffenhöfer, 1998; Kiørboe, 2008). Other copepod species do ingest non-food particles, such as sediments of clay and silt particles (Paffenhöfer, 1972; White and Dagg, 1989; De Troch *et al.*, 2006). Ingested clay and silt particles take up space in the gut that otherwise could be occupied by more nutritious food particles and can therefore have a negative effect on the nutritional intake of the copepod (Paffenhöfer, 1972). On the other hand, sediment particles can absorb trace metals, organics and nutrients (Brown *et al.*, 2002) and serve as a substrate for bacteria (Syvitski and Lewis, 1980) and therefore indirectly end up being a nutritional source for the copepod (Lewis and Syvitski, 1983).

Previous studies have shown horizontal zonation of copepod species along the glacially influenced Godthåbsfjord (Southwest Greenland) (Arendt *et al.*, 2010a). There, the Atlantic species *Calanus finmarchicus* is most abundant in the mouth of the fjord and particularly in the offshore region, while *Pseudocalanus* sp. is most abundant in the central region of the fjord and *Metridia longa* in the inner parts of the fjord close to the glacial terminus. *Metridia longa* generally inhabits deep waters but migrates to the surface waters daily (Daase *et al.*, 2008). *Pseudocalanus* sp. are often found in surface plumes or fronts where freshwater plumes meet oceanic water and flocculation and aggregation of organic material takes place (Brown *et al.*, 2002; Dagg *et al.*, 2004). The dominance of *Pseudocalanus* sp. and *M. longa* in the Godthåbsfjord could therefore reflect the species ability to cope with high concentrations of SPM as suspended sediment. The distribution of *C. finmarchicus* is best related to the hydrography of the water flowing into the fjord from the adjacent shelf (Pedersen and Smidt, 2000; Arendt *et al.*, 2010a). However, why *Calanus* spp. has not established itself in the fjord receiving glacial melt water runoff is unclear. Based on the observed distribution pattern in the Godthåbsfjord, we hypothesize that species tolerance to high sediment concentrations may determine the distribution of these three copepod species along the glacially influenced fjord branch. The aim of this study was to investigate the species tolerance to natural concentrations of suspended sediments, in terms of grazing rate, fecal pellet production (FPP) and egg production rate (EPR).

METHOD

The effects of suspended sediment on feeding and egg production of the three copepod species *Calanus finmarchicus*, *Pseudocalanus* sp. and *Metridia longa* were investigated at increasing concentrations of suspended sediment. The clearance rate (F), specific ingestion rate (SIR), FPP, FP volume and EPR were determined at a fixed concentration of the diatom *Thalassiosira weissflogii* (300 $\mu g\ C\ L^{-1}$) at six different concentrations of sediment suspensions. Additional experiments were performed for *M. longa* offered the ciliate *Strombidium sulcatum* as food at 40 $\mu g\ C\ L^{-1}$ at four different sediment suspensions. All laboratory work was conducted at the Greenland Institute of Natural Resources.

SPM, field

Turbidity (FTU; Formazin Turbidity Units) and fluorescence were measured in the water column along a transect in the Godthåbsfjord in August 2008 (Fig. 1) using a Sea-Bird Electronics SBE19plus SEACAT

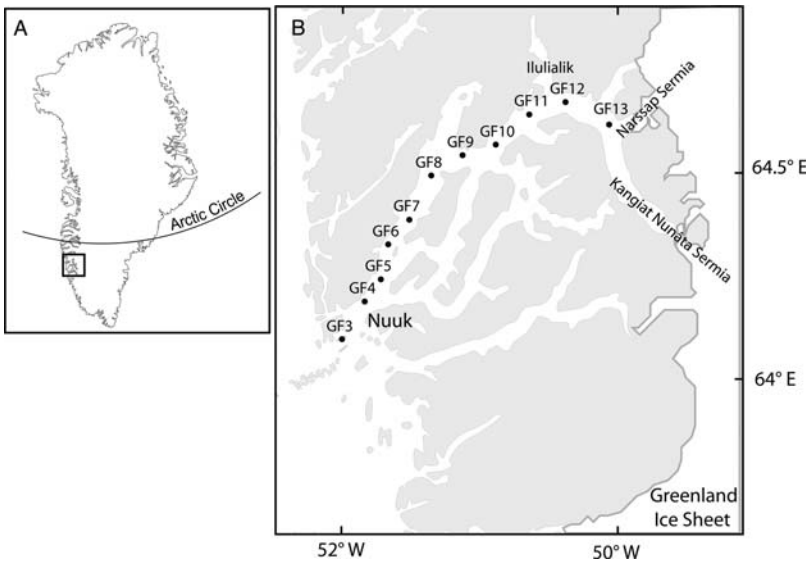


Fig. 1. (**A**) Greenland, and (**B**) the Godthåbsfjord system with station location.

Profiler CTD (conductivity, temperature and depth) equipped with a Seapoint Turbidity Meter and a Seapoint Chlorophyll Fluorometer. In January and August 2009, water was sampled near the outlet from Lake Tasersuaq (Stn GF11) and near the glacial terminus of Narssap Sermia (Stn GF13) for quantification of SPM (Figs 1 and 2A). Water samples were taken with 5 L Niskin bottles, from which 2000 mL were filtered on to pre-weighed GF/F filters. The filters were dried at 60°C for 24 h and weighed. At the same time, fjord water was sampled to determine concentration and particle size of SPM. Approximately 50 L of fjord water was sampled from both the surface plume at 1 m depth and from the subsurface plume at 100 m depth (indicated by crosses in Fig. 2A). The fjord water was allowed to settle for 2 weeks after which the supernatant was discharged. The precipitate was sieved through a 500 μm sieve to remove larger fractions and dried at 60°C for 3 days. The dry matter was then sieved through a 50 μm sieve, representing clay (grain size <2 μm) and silt (grain size 2–50 μm). Two stock solutions of natural SPM (SPM plume and SPM 100 m) were then made by suspending the dried material in demineralized water (Purelab Option, ELGA). The size frequency distribution in terms of number and volume of the stock solutions (1–50 μm) was measured with a Multisizer^{TM} Model 3 (Beckman Coulter) equipped with a 100 μm orifice.

Experimental sediment stock

In March 2009, a block of ice originating from the Greenland Ice Sheet was collected from the inner part of the Godthåbsfjord (Fig. 1) near to the outlet glacier Kangiata Nunâta Sermia (Fig. 1B). The ice block was found trapped in the sea ice and contained high amounts of sediment, so-called black ice.

The ice block was brought to the laboratory where it was melted. The solution was treated as the SPM sampled in the water column (see above). A sediment stock solution of 20 g sediment L^{-1} was made for use in the laboratory experiments. The sediment stock solution was kept cold and dark until use.

Laboratory cultures

The diatom *Thalassiosira weissflogii* and the chlorophyte *Dunaliella tertiolecta* were grown in batch cultures in the L1 medium (Scandinavian Culture Centre for Algae and Protozoa) at 15°C in natural sea water of 34. Illumination was provided by cool fluorescent lamps at 75 μE m^{-2} s^{-1} [measured using a LiCor 1411 (Li-Cor, NE, USA)] following a 12:12 h light:dark cycle. Cultures were kept in exponential growth by replacing one-third of the culture stock every day with new L1 medium. The heterotrophic ciliate *Strombidium sulcatum* was grown in batch cultures in 2 L polycarbonate bottles at 10°C in the dark and fed with *D. tertiolecta*. The carbon content of 131 pg carbon $cell^{-1}$ for *T. weissflogii* was obtained from Dutz *et al.* (Dutz *et al.*, 2008) measured on the same stock culture, whereas carbon content of 1220 pg carbon $cell^{-1}$ for *S. sulcatum* was obtained from Broglio *et al.* (Broglio *et al.*, 2003).

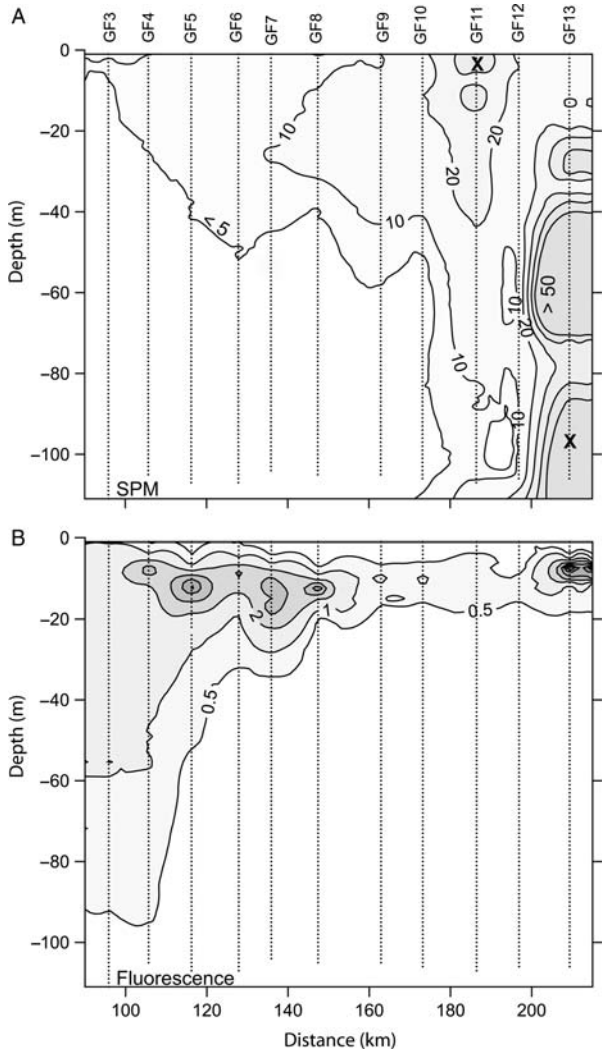


Fig. 2. (**A**) Vertical distribution of SPM along the Godthåbsfjord (marking represent samples for sediment stock solutions in the water column), and (**B**) fluorescence, dotted lines represent CTD casts.

Copepods

Copepods for the experiment were collected mid-May 2009 in the central part of the Godthåbsfjord Stn GF7 (Fig. 1B) by vertically towing a 200-μm WP-2 net equipped with a non-filtering cod end from 0 to 100 m. The samples were brought into the laboratory where living, healthy looking females (*Calanus finmarchicus*, *Pseudocalanus* sp. and *Metridia longa*) were picked and incubated in GF/C filtered sea water for 12 h at 5°C before being introduced to the experimental food and sediment concentrations.

Experimental setup

Food suspensions of 300 μg C L^{-1} *Thalassiosira weissflogii* were prepared with a series of the desired sediment concentrations of 0, 2.5, 5, 10, 20, 50 and 100 mg sediment L^{-1}, and 40 μg C L^{-1} of *Strombidium sulcatum* with sediment concentrations of 0, 20, 50 and 100 mg sediment L^{-1}. The food/sediment suspension was made in GF/F filtered seawater and was gently mixed before triplicate samples were taken for measurement of the initial Chlorophyll *a* (Chl *a*) concentrations. Each suspension was distributed between 18 530 mL polycarbonate bottles. Of these, three bottles without animals were run as controls, while a set of five bottles each received either two *Calanus finmarchicus* females, five *Pseudocalanus* sp. females or two *Metridia longa* females. The bottles were sealed without air bubbles and placed on a plankton wheel at 2 rpm at 5°C in the dark. Every 24 h, samples for Chl *a* (experiments with *T. weissflogii*) or cell counts (experiments with *S. sulcatum*) were taken, the remaining test suspension was gently sieved through a 450 μm mesh to retain copepods and hereafter sieved through a 20 μm mesh to collect eggs and FPs. Living copepods were transferred to bottles with new food and silt suspensions. Dead copepods were replaced by new individuals that had been treated and acclimated in the same way as the experimental copepods. The experiment was run for a total of 4 days.

Analytical procedures

In the experiments with *Thalassiosira weissflogii* as food, three samples of 50 mL were filtered onto 25 mm GF/C filters (pressure <0.2 bar) for Chl *a* analysis after each experimental day. Filters were extracted in 5 mL 96% ethanol for 18 h in the dark at 20°C before fluorescence was measured with a fluorometer (TD-700, Turner Designs, California, USA) calibrated against a pure Chl *a* standard (Turner Designs). In experiments with *Strombidium sulcatum*, four samples of 3 mL each were drawn from each of the suspensions and transferred to a micro titer plate with 3.5 mL chambers containing three drops of Lugol's solution. Samples were allowed to settle for 12 h before they were counted under an inverted microscope. Clearance rate (F) and ingestion rate (I) were calculated based on initial and final Chl *a* measurements (experiments with *T. weissflogii*) or cell counts (experiments with *S. sulcatum*) using the equation of Frost (Frost, 1972). Eggs and FPs were counted under a stereo microscope. Length and width of FPs and the prosome length of the copepods were measured using a calibrated ocular micrometer. The volume of FP was calculated assuming a cylindrical shape. The carbon content of the copepods was calculated using published length–weight regressions (given in Thor *et al.*, 2005). The carbon-SIR was calculated as the daily carbon ingestion divided by copepod carbon

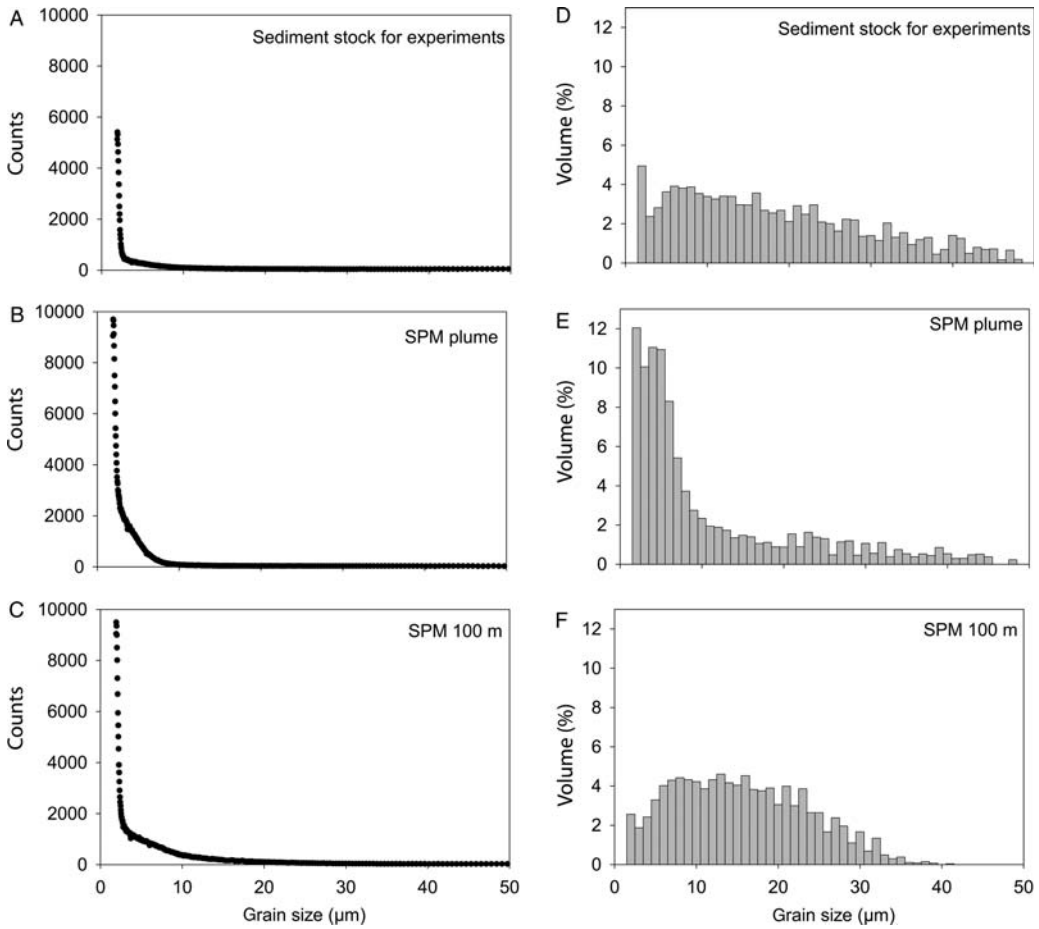


Fig. 3. (**A–C**) Concentration (counts) and (**D–F**) distribution of total volume (%) as function of grain size (µm) (2–50 µm) in the stock solutions; sediment stock used in the experiments (from melted ice), SPM plume (sampled in the fjord Stn GF11, 1 m) and SPM 100 m (sampled in the fjord Stn GF13, 100 m).

content (SIR, µg C day^{-1} µg C^{-1} gives the rate day^{-1}). The influence of increasing sediment concentrations on SIR was fitted to functions in Solver Excel, and statistical analysis and nonparametric Wilcoxon test were performed using JMP® 8.0.1.

RESULTS

SPM, field

Concentrations of SPM ranged from 4.2 to 48.3 mg L^{-1} in the water samples from 2009. The SPM had a positive correlation with the *in situ* turbidity measurements (FTU) ($R^2 = 0.94$, $F = 323.11$, $P < 0.0001$) and therefore concentrations of SPM (mg L^{-1}) were estimated from the FTU measurements following a linear relationship (Domack *et al.*, 1994):

$$\mathrm{SPM} = 2.66\,\mathrm{FTU} + 5.45 \quad (1)$$

The FTU measurements on the transect sampled in 2008 were accordingly converted to concentrations of SPM (mg L^{-1}) (Fig. 2A). The field study showed that the concentrations of SPM can be very high in subsurface plumes close to the outlet glaciers (>50 mg L^{-1}) and in the surface water near the outlet of Lake Tasersuaq at Stn GF11 (>40 mg L^{-1}). The concentrations of SPM decreased towards the fjord mouth to less than 5 mg L^{-1} (Fig. 2A). In contrast, the fluorescence increased towards the fjord mouth (Fig. 2B). We therefore assume that the high concentration of SPM close to the glacial outlet and its decrease towards the fjord mouth largely reflect the inorganic mineral load of seawater and not the phytoplankton concentration, which is by definition part of the SPM.

Stock solutions

Particle size distributions (2–50 µm) in terms of concentration and total volume (%) of the three SPM 'stock

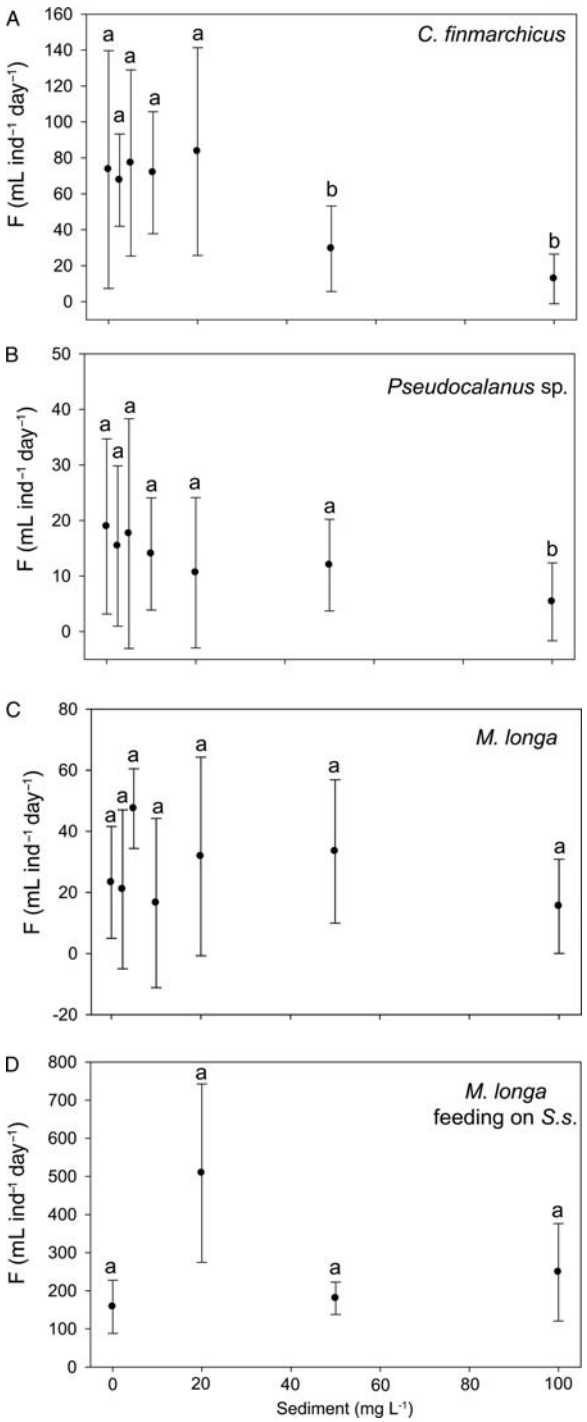


Fig. 4. Clearance rate F (mL ind^{-1} day^{-1}) ± standard deviation, for (**A**) *Calanus finmarchicus*, (**B**) *Pseudocalanus* sp. and (**C** and **D**) *Metridia longa* at variable sediment concentrations when feeding on *Thalassiosira weissflogii* or *Strombidium sulcatum*. Different letters denote treatments that are significantly different from each other ($P < 0.05$).

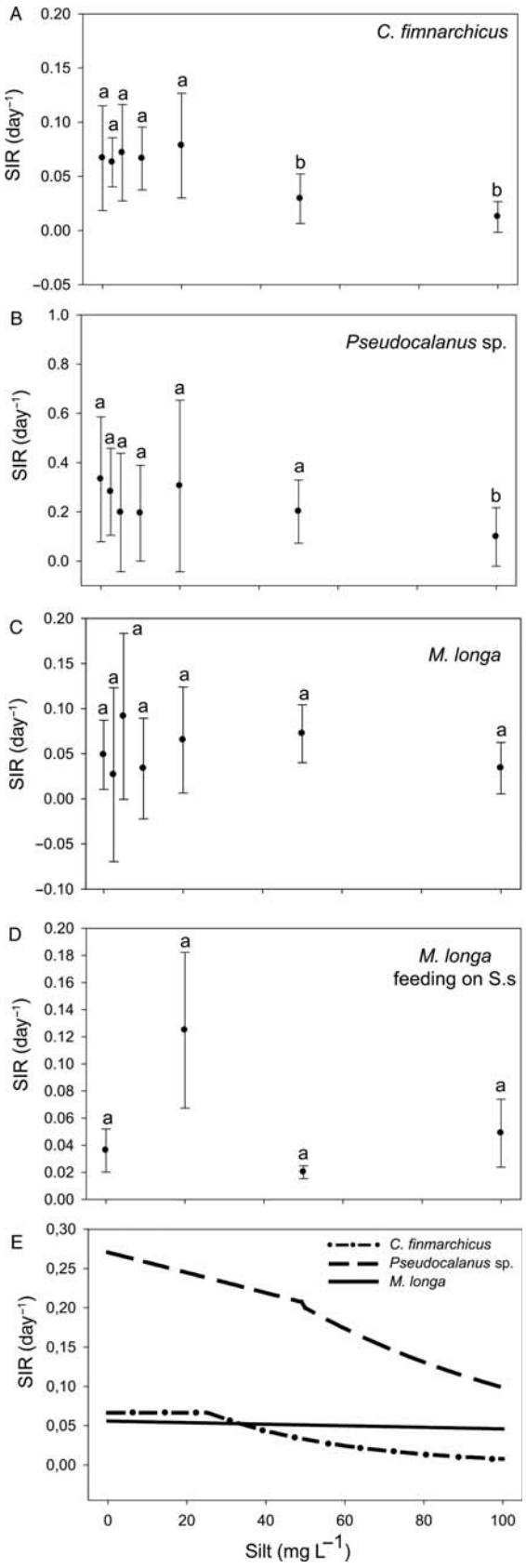
solutions'; sediment stock (melted ice), SPM surface plume and SPM 100 m (Fig. 2A) are shown in Fig. 3. For all three samples, clay (2–3 μm) was the most abundant particle size (Fig. 3A–C). In terms of volume, 90% of the sediment stock solution was made of silt grains (>5 μm), while 93% of the total volume was made of silt grains in the stock solution SPM 100 m. Fine clay material made up larger part of the SPM surface plume stock solution, hereof 33% of total volume were clay particles and 67% of the total volume were silt grains.

Clearance rate

There were no significant differences in clearance rates (F, mL ind^{-1} day^{-1}) at the tested sediment concentrations over the four experimental days ($P > 0.05$, $n \geq 18$, Wilcoxon test). Clearance rate, F, is therefore pooled over the whole experimental period for each copepod species at each sediment concentration. Clearance rate of *Thalassiosira weissflogii* by *Calanus finmarchicus* and *Pseudocalanus* sp. decreased with increasing sediment concentrations, whereas no significant effect of sediment on F was observed for *Metridia longa* (Fig. 4). The strongest reduction in F for *C. finmarchicus* was found between 20 and 100 mg sediment L^{-1} ($P < 0.01$, $n = 38$, Wilcoxon test), whereas no difference in F was observed at either of the incubations at 0–20 mg sediment L^{-1} or at 50 and 100 mg sediment L^{-1} (Fig. 4A). Clearance rate varied between 67.6 ± 25.7 and 83.5 ± 57.8 mL ind^{-1} day^{-1} for *C. finmarchicus* exposed to 0–20 mg sediment L^{-1}, whereas F decreased to <12.0 ± 13.7 mL ind^{-1} day^{-1} for the incubation with 50 and 100 mg sediment L^{-1}. A significant reduction in F for *Pseudocalanus* sp. was found at the highest sediment concentration of 100 mg sediment L^{-1} ($P < 0.02$, $n = 143$, Wilcoxon test). F decreased from 11.9 ± 15.8–18.9 ± 15.8 mL ind^{-1} day^{-1} at 0–50 mg sediment L^{-1} to 5.3 ± 7.0 mL ind^{-1} day^{-1} at 100 mg sediment L^{-1}; however, there was no difference in F when exposed to 0–50 mg sediment L^{-1} (Fig. 4B). Clearance rate for *M. longa* varied between 15.5 ± 15.4 mL ind^{-1} day^{-1} at 100 mg sediment L^{-1} and 47.4 ± 13.1 mL ind^{-1} day^{-1} at 5 mg sediment L^{-1} without any significant difference between the experiments (Fig. 4C). F was significantly higher when *M. longa* was feeding on *Strombidium sulcatum* compared to the rates when feeding on *T. weissflogii* ($P < 0.01$, $n = 34$, Wilcoxon test; Fig. 4D). Clearance rate was highly variable when feeding on *S. sulcatum* and varied between 158.0 ± 69.8 and 508.6 ± 234.0 mL ind^{-1} day^{-1}, but the difference in F on the ciliates was not significant between the four silt concentrations.

Specific ingestion rate

Carbon-SIR (Fig. 5) was calculated directly as a function of the clearance rate F and, as the same individual copepods were used during the four experimental days,



the copepod carbon content did not vary over time. Therefore, the statistics of SIR followed the statistics for F. SIR of *Calanus finmarchicus* varied from 0.06 ± 0.02 to 0.08 ± 0.05 day^{-1}, whereas it decreased to 0.03 ± 0.02 and 0.01 ± 0.01 day^{-1} at sediment concentrations of 50 and 100 mg sediment L^{-1}, respectively (Fig. 5A). SIR of *Pseudocalanus sp.* was clearly the highest of the three copepod species, with up to 0.33 ± 0.25 day^{-1} (Fig. 5B). *Metridia longa* showed no general response in SIR with rising sediment concentration (Fig. 5C), SIR varied from 0.03 ± 0.06 to 0.09 ± 0.09 day^{-1}. SIR of *M. longa* was in the same range when feeding on *S. sulcatum* 0.05 ± 0.05 day^{-1} (all data) compared to when *T. weissflogii* was offered as food (Fig. 5C and D), still with no significant differences when exposed to the various sediment concentrations.

SIR for the three copepod species feeding on *T. weissflogii* at increasing sediment concentrations is illustrated in Fig. 5. The best fit to the data showed an exponential decrease in SIR for *C. finmarchicus* and *Pseudocalanus* sp., while the slope was not significant for *M. longa*. Therefore, an average of SIR at all sediment concentrations is shown. When the SIRs of all three species are shown in same figure (Fig. 5E), this clearly demonstrates that *Pseudocalanus* sp. has the highest SIR of the three species at all sediment concentrations. *Metridia longa* showed the lowest SIR at sediment concentrations <20 mg sediment L^{-1}, whereas *C. finmarchicus* showed lowest SIR at sediment concentrations >20 mg sediment L^{-1} (Fig. 5E).

Fecal pellet production

There were no significant differences in FPP of any of the species (FPP, fecal pellets fem^{-1} day^{-1}) at each of the sediment concentrations tested over the four experimental days ($P > 0.05$, $n = 20$, Wilcoxon test). The FPP is therefore pooled over the whole experimental period for each copepod species at each sediment concentration (Table I). There were no significant differences in FPP of *Calanus finmarchicus* or *Metridia longa* feeding on *T. weissflogii* (all data). In contrast, a significant effect was observed in *Pseudocalanus* sp. FPP ($P < 0.01$, $n = 160$, Wilcoxon test). FPP was low in the control experiment (0 mg sediment L^{-1}), increased at

Fig. 5. SIR ± standard deviation, for (**A**) *Calanus finmarchicus*, (**B**) *Pseudocalanus* spp. and (**C** and **D**) *Metridia longa* at variable sediment concentrations when feeding on *Thalassiosira weissflogii* or *Strombidium sulcatum*. Different letters denote treatments that are significantly different from each other ($P < 0.05$). (**E**) Function fit of SIR for *Calanus finmarchicus*, *Pseudocalanus* spp. and *Metridia longa* at variable sediment concentrations when feeding on *Thalassiosira weissflogii*.

Table I: FPP (fecal pellets fem^{-1} day^{-1}) for the three copepod species Calanus finmarchicus, Pseudocalanus sp. and Metridia longa at the different sediment concentrations (mg L^{-1}) feeding on Thalassiosira weissflogii (T. w) or Strombidium sulcatum (S. s)

	C. finmarchicus		*Pseudocalanus* sp.		*M. longa*		*M. longa*	
Sediment (mg L^{-1})	FPP *T. w*	± SD (*n*)	FPP *T. w*	± SD (*n*)	FPP *T. w*	± SD (*n*)	FPP *S. s*	± SD (*n*)
0	52.4	31.8 (40)	20.5	14.1 (37)	6.7	4.6 (32)	15.2	5.5 (10)
2.5	58.7	16.1 (20)	56.7	16.0 (20)	5.7	3.5 (20)		
5	49.4	18.5 (20)	57.6	13.7 (20)	9.9	5.1 (20)		
10	60.8	16.2 (20)	72.4	25.5 (19)	6.3	4.4 (20)		
20	54.4	25.9 (20)	62.0	26.0 (20)	6.6	4.4 (20)	8.1	4.8 (10)
50	43.6	14.3 (19)	34.4	18.2 (20)	9.1	2.3 (12)	5.7	3.8 (8)
100	46.6	16.5 (20)	41.1	24.6 (20)	8.8	2.0 (12)	7.4	5.2 (10)

Values are means over the four experimental days (± standard deviation (SD), *n* number of replicates).

2.5–20 mg sediment L^{-1}, but decreased when females were exposed to 50 and 100 mg sediment L^{-1} (Table I). In the control experiment (0 mg sediment L^{-1}), a significant difference was observed in the FPP of *M. longa* when fed *S. sulcatum* compared to *Thalassiosira weissflogii* (Table I) ($P < 0.05$, $n = 41$, Wilcoxon test). On the other hand, there was no significant difference in the FPP from the two food items when exposed to sediment concentrations above 20 mg sediment L^{-1} (Table I). FP volume (μm^3) increased with increasing sediment concentration for *C. finmarchicus* and *M. longa*, while there was no general trend for the pellets of *Pseudocalanus* sp. (Fig. 6A–C). There was a significant difference ($P < 0.01$, $n = 138$, Wilcoxon test) of FP volume for *C. finmarchicus* when feeding at 0 and 100 mg sediment L^{-1} and for *M. longa* feeding at 5 and 50 mg sediment L^{-1} ($P < 0.01$, $n = 122$, Wilcoxon test). FP volumes were significantly higher at 2.5 mg sediment L^{-1} than for any of the other sediment concentrations ($P < 0.05$, $n = 138$, Wilcoxon test). There was no relationship between excretion measured as total FP volume (μm^3 fem^{-1} day^{-1}) and ingestion (μg C fem^{-1} day^{-1}) when *T. weissflogii* was fed to the three copepod species (*C. finmarchicus*, $r^2 = 0.01$; *Pseudocalanus* sp., $r^2 = 0.02$; *M. longa*, $r^2 = 0.04$). No difference was observed in FP volume when *M. longa* fed on *T. weissflogii* compared to *Strombidium sulcatum* (Fig. 6C).

Egg production rate

The EPR (egg fem^{-1} day^{-1}) varied over time in all incubations. The three first experimental days were considered as an acclimation period and EPR here is compared only at Day 4 in Table II. There was a significant difference ($P < 0.01$, $n = 35$, Wilcoxon test) in EPR for *Calanus finmarchicus* at the sediment concentrations 0 and 50 mg L^{-1} (22.9 ± 13.7 and 0.2 ± 0.4 eggs fem^{-1} day^{-1}, respectively), however no difference was observed in EPR between 0–20 mg sediment L^{-1} or 50–100 mg sediment L^{-1}. Egg production for *Metridia longa* was low; maximum EPR observed was 1.5 eggs fem^{-1} day^{-1}, with no significant differences between the sediment concentrations. The EPR of *M. longa* did not differ significantly when feeding on *Thalassiosira weissflogii* or *Strombidium sulcatum* (Table II). *Pseudocalanus* sp. females were carrying eggs during the four incubation days. There was no significant difference in numbers of eggs in the eggs sac at the different sediment concentrations at Day 4 (Table II). Survival of the copepod females was >95% at the end of the experiment (Day 4) for all concentrations of suspended sediments and copepod species.

DISCUSSION

The concentrations of SPM in the Godthåbsfjord measured >50 mg L^{-1} and turbidity measurements indicated that *in situ* concentrations could be even higher. Therefore, the level of suspended sediment in the laboratory experiments represents sediment loads that copepods can encounter in a fjord with a glacial outlet.

In situ SPM concentrations along the Godthåbsfjord were highly variable. High concentrations of more than 20 mg L^{-1} were observed in restricted areas near the glacier and the melt-water outflow (Stn GF13 and GF11, Fig. 2A). Concentrations of 20–10 mg L^{-1} were found from the inner parts to the central parts of the fjord (Fig. 2A), whereas the fjord mouth towards the off shore area had concentrations <5 mg L^{-1}. The analysis of the particle size distribution and concentration showed a strong similarity between the sediment stock solutions used in the experiment (melted ice block) and the SPM found in the fjord. In terms of particle

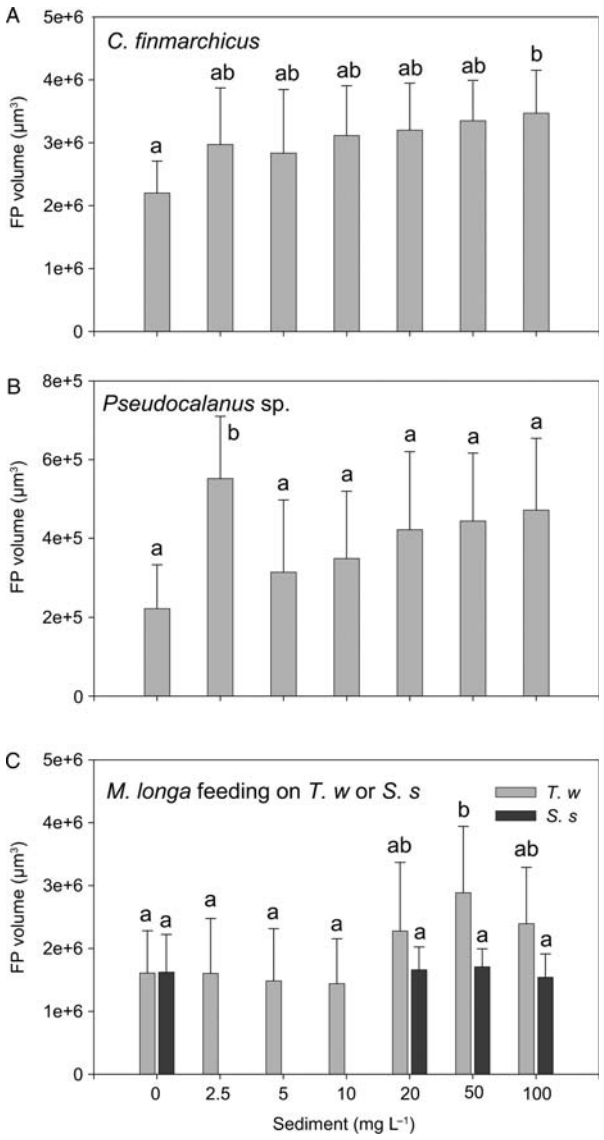


Fig. 6. Average FP volume for (**A**) *Calanus finmarchicus*, (**B**) *Pseudocalanus* sp. and (**C**) *Metridia longa* at variable sediment concentrations when feeding on *Thalassiosira weissflogii* (*T. w*) or *Strombidium sulcatum* (*S. s*). Whiskers indicate ±standard deviation. Different letters denote treatments that are significantly different from each other ($P < 0.05$).

abundance, clay grains (2–3 µm) had the highest concentration in the surface plume (Fig. 2A and E) due to the high sinking rate of large particles. However, in terms of total volume, silt grains dominated in all three stock solutions. In the field, the inorganic particles encountered by copepods might differ from these spectra. For instance, mineral particles are known to flocculate and aggregate (Stumm, 1990; Brown *et al.*, 2002) which results in increasing size of particles and higher sinking rates. In nature, copepods are therefore likely to encounter a variety of aggregate types, including organic material and particulate organic matter. Distinction between non-organic and organic particles was not made in the particle analysis and also could not be distinguished in the *in situ* turbidity (FTU) measurements. The correlation of SPM and FTU is less pronounced at FTU <3, which could be due to high proportion of organic material compared to sediment in the particle spectra. Therefore, direct correlations between suspended sediment and FTU measurements should be made with caution at low concentrations of SPM. However, in this study, the areal distribution of fluorescence and FTU was not similar (Fig. 2), which means that phytoplankton were not the primary source for the turbidity. Our measurements also do not take into account clay particles smaller than 1 µm, although these flocculate and therefore appear as larger size particles. At the highest *in situ* SPM concentrations found in the Godthåbsfjord, we would expect some effect on the feeding efficiency of the copepods. On the other hand, survival of all three copepod species was surprisingly high even at the highest concentrations of suspended sediments in the bottle incubations. This indicates that the copepods can handle very high sediment loads at least for a short period of time (here 4 days).

Effects of increasing suspended sediment concentration on vital rates were observed for *Calanus finmarchicus* and *Pseudocalanus* sp., but not for *Metridia longa*. The three copepod species tested were likely impacted differently by the increasing sediment concentrations. In *C. finmarchicus* and *Pseudocalanus* sp. F, IR and SIR were significantly reduced at the highest sediment concentrations. For *C. finmarchicus*, a reduced ingestion of Chl *a* in conjunction with no effects on FPP and total FP volume suggests ingestion of sediment that replaced food particles in the gut. This was verified by direct observation of sediment particles occurring in FPs of *C. finmarchicus* (Arendt *et al.*, 2010b) indicating the low ability of this species to distinguish between food and non-food particles. Therefore, at high sediment concentrations, the ingestion of clay/silt likely reduced the food uptake and resulted in reduction of egg production by *C. finmarchicus*. At high sediment concentrations, both IR and FPP for *Pseudocalanus* sp. were reduced. However, a reduction in EPR for *Pseudocalanus* sp. was not observed despite the reduction in food uptake, probably due to time-lag differences in egg production between egg carrying *Pseudocalanus* and free spawning species such as *Calanus*. There was no impact on IR and FPP for *M. longa* when exposed to high sediment loads indicating a high ability to distinguish between

Table II: EPR (eggs female^{-1} day^{-1}) for Calanus finmarchicus and Metridia longa and eggs in egg sac of Pseudocalanus sp. feeding on Thalassiosira weissflogii (T. w) or Strombidium sulcatum (S. s) at different silt concentrations (mg L^{-1})

	C. finmarchicus		*Pseudocalanus* sp.		*M. longa*		*M. longa*	
Silt (mg L^{-1})	EPR *T. w*	± SD (*n*)	Egg fem^{-1} *T. w*	± SD (*n*)	EPR *T. w*	± SD (*n*)	EPR *S. s*	± SD (*n*)
0	22.9	13.7 (5)	1.2	2.3 (5)	0.0	0.3 (5)	0.2	0.5 (5)
2.5	20.4	7.7 (5)	1.0	1.4 (5)	0.0	0.0 (5)		
5	16.9	14.1 (5)	0.3	0.5 (5)	0.0	0.1 (5)		
10	19.2	8.5 (5)	3.2	4.9 (5)	0.0	0.2 (5)		
20	15.1	11.0 (5)	0.3	0.2 (5)	0.0	0.1 (5)	0.1	0.2 (10)
50	0.2	0.4 (5)	0.5	0.7 (5)	0.2	0.3 (5)	0.0	0.0 (8)
100	0.3	0.4 (5)	0.1	0.2 (5)	0.0	0.0 (5)	0.0	0.0 (10)

Values are given for experimental Day 4 (± standard deviation (SD), *n* number of replicates).

food and non-food particles for both food types tested (diatom or ciliates).

The significant impact of suspended sediment on vital rates was only observed at very high concentrations (>20 mg L^{-1} for *C. finmarchicus* and >50 mg L^{-1} for *Pseudocalanus* sp.). At lower sediment concentrations, ingestion, FPP and EPR of *C. finmarchicus* corresponded well with published data at food concentration of 300 μg C L^{-1} (Båmstedt *et al.*, 1999), while high SIR (>1 day^{-1}) rates have been reported for *Pseudocalanus* spp. (Paffenhöfer and Harris, 1976). The relatively high tolerance of the copepods to suspended sediments can be due to their ability to ingest particles of high nutritional quality even when particles of low value are more abundant (Paffenhöfer and Van Sant, 1985; Cowles *et al.*, 1988). We conclude that in accordance with results of other studies (Paffenhöfer, 1972; White and Dagg, 1989), *C. finmarchicus* ingests suspended sediments at the high concentrations but the ability of selective feeding seems to be impaired at high sediment concentration. Other studies have shown that the capability to feed selectively may be sensitive and reduced at low food concentrations (Paffenhöfer, 1972; Roman, 1984). This may explain the relatively high tolerance to suspended sediment in the present study where food concentration was high. *In situ* food concentrations are normally lower than in our experimental setup (Rysgaard *et al.*, 2008; Arendt *et al.*, 2010a) and we could expect that it would take more time and energy to search for food particles in mixtures with suspended sediment. Therefore, effects on copepod vital rates are probably more pronounced *in situ* in the Godthåbsfjord where food availability is generally lower than in our experimental setup. Furthermore, high sediment load could negatively affect primary production by reducing the light penetration and consequently indirectly negatively affect secondary production as previously reported from highly turbid estuaries or glacial lakes (Kirk, 1991; Lehman 1992; Gasparini *et al.*, 1999).

Metridia longa showed the same ingestion (F and SIR) at all sediment concentrations regardless of food type offered (diatom or ciliate) as single food type. The SIR did not differ in spite of a tenfold difference in food concentration (300 μg C L^{-1} for *T. weissflogii* versus 40 μg C L^{-1} for *S. sulcatum*). This might be due to a shift in feeding pattern from filter feeding to active hunting as suggested by Haq (Haq, 1967). The low EPR of *M. longa* observed in our study could be due to a low utilization efficiency known for this species as suggested by Hopkins *et al.* (Hopkins *et al.*, 1984) or due to cannibalism of the eggs (Plourde and Joly, 2008). *Metridia longa* is known to feed actively in winter (Hopkins *et al.*, 1984) where it feeds omnivorously on protozooplankton and has also been shown to exhibit coprophagy (Sampei *et al.*, 2009). Therefore, ecosystems that can offer some food during winter could provide a sufficient overwintering habitat for this species, which may explain the dominance of *M. longa* in the Godthåbsfjord over *Calanus*.

Increased melting of the Greenland Ice Sheet and, as a result, increased fresh water runoff is expected to occur in the future as a consequence of global warming (Kattsov and Källén, 2005). This would also increase the expected load of SPM into the fjord. However, concentrations >20 mg L^{-1} would only be expected to occur very close to the glacier melt water outlets. This study shows that high sediment concentrations influence the capability of carbon turnover for *Calanus finmarchicus* and *Pseudocalanus* sp., whereas *Metridia longa* is able to sustain stable carbon ingestion. Significant effects on the copepods were only observed at sediment loads >50 mg sediment L^{-1} which is expected to occur in confined areas. These results could prove to be useful in

understanding the geographical distribution of copepod species in glacial marine environments. The species distribution shown in previous studies (Arendt *et al.*, 2010a) cannot be explained solely by high loads of SPM. The observed pattern is rather a result of combined interaction of hydrographic conditions (Mortensen *et al.*, 2011), differences in species fitness (Kiørboe, 2008), predation (Tang *et al.*, 2011) and long-term influence of sediment plumes on the ecosystem (Dagg *et al.*, 2004). However, it is evident that increased load of suspended sediments to the fjord due to increased runoff from the Greenland Ice Sheet will have an effect on the pelagic zooplankton feeding efficiency and production rates and therefore affect their survival in these waters.

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Succession and fate of the spring diatom bloom in Disko Bay, western Greenland

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Succession and fate of the spring diatom bloom in Disko Bay, western Greenland

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ABSTRACT: Phytoplankton and copepod succession was investigated in Disko Bay, western Greenland from February to July 2008. The spring phytoplankton bloom developed immediately after the breakup of sea ice and reached a peak concentration of 24 mg chl *a* m^{-3} 2 wk later. The bloom was analyzed during 3 phases: the developing, the decaying, and the post-bloom phases. Grazing impact by the copepod community was assessed by 4 methods; gut fluorescence, *in situ* faecal pellet production, and egg and faecal pellet production from bottle incubations. *Calanus* spp. dominated the mesozooplankton community. They were present from the initiation of the bloom but only had a small grazing impact on the phytoplankton. Consequently, there was a close coupling between the spring phytoplankton bloom and sedimentation of particulate organic carbon (POC). Out of 1836 ± 180 mg C m^{-2} d^{-1} leaving the upper 50 m, 60 % was phytoplankton based carbon (PPC). The composition and quality of the sedimenting material changed throughout the bloom succession from PPC dominance in the initial phase with a POC/PON ratio close to 6.6 to a dominance of amorphous detritus with a higher POC/PON ratio (>10) in the post-bloom phase. The succession and fate of the phytoplankton spring bloom was controlled by nitrogen limitation and subsequent sedimentation, while grazing-mediated flux by the *Calanus*-dominated copepod community played a minor role in the termination of the spring bloom of Disko Bay.

KEY WORDS: Spring bloom · *Calanus* spp. · Grazing · Faecal pellets · Sedimentation · Arctic · Greenland

INTRODUCTION

The spring phytoplankton bloom is a key event in high-latitude marine ecosystems, responsible for fueling high secondary production. It is triggered by the break-up of sea ice, combined with a warming and freshening of the surface layer stratifying the water column. The bloom is characterized by a short and pronounced growth peak of diatoms that depletes the surface layer of nitrate (Andersen 1981) and subsequently sediments (Nielsen & Hansen 1995, Poulsen & Reuss 2002).

Sedimentation of phytoplankton from the euphotic zone is the principal mechanism in transport of organic material to benthic communities. Transport occurs directly as intact cells or indirectly as faecal pellets from pelagic grazers, aggregates, and amorphous detritus (Turner 2002, De La Rocha & Passow 2007). During its transit to the sea bed, the organic material is modified by the pelagic heterotrophs in a way that

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influences its quantity and quality as a carbon source for the benthic community (Kiørboe et al. 1996, Kiørboe 1998, Wassmann 1998, Turner 2002, Riser et al. 2008).

Grazing is a key process that reduces the sedimentation of phytoplankton while simultaneously accelerating the sedimentation through production of fast-sinking faecal pellets (Juul-Pedersen et al. 2006). However, a large portion of the faecal pellets may be retained in the water column due to grazing, disintegration, and remineralisation (Noji et al. 1991, Riser et al. 2002, 2007, Turner 2002, Reigstad et al. 2008). Copepods often only graze a minor fraction of the spring phytoplankton bloom, because their longer generation time compared to that of phytoplankton limits them in numerically responding to the bloom (Kiørboe 1998). This results in a high sedimentation of ungrazed phytoplankton. In Arctic areas however, where overwintering stocks of copepods like *Calanus* exist, the copepod grazing impact on the bloom dynamics may be larger, depending on whether ascending *Calanus* match the spring phytoplankton bloom or not (Bathmann et al. 1990, Wassmann 1998, Wassmann et al. 2004, 2006).

The pelagic food web structure and production in Disko Bay, western Greenland, has been intensively investigated since the early 1990s (Nielsen & Hansen 1995). The original focus was mainly on baseline descriptions of composition and trophodynamics of the pelagic food webs (Levinsen et al. 2000a, Madsen et al. 2001, Madsen et al. 2008b). Few studies have considered the sedimentation of organic matter from the surface layer in this region (Juul-Pedersen et al. 2006, Sejr et al. 2007), and investigations resolving the contribution from the spring bloom are lacking. A match between copepod ascent to the surface and the spring phytoplankton bloom would lead to a large grazing impact on the phytoplankton biomass, while a mismatch would result in a larger contribution of ungrazed phytoplankton to the sedimentation.

Over the last decades, the physical forcing of the plankton succession in Disko Bay has changed. Recently an acceleration of the melt water input from the Jakobshavn Isbræ glacier to the bay has been documented (Holland et al. 2008), which, in combination with the general reduction of the sea ice cover (IPPC 2008), potentially impacts stratification, light conditions for the plankton, and consequently the timing and succession of the lower trophic levels of the food chain. Therefore baseline knowledge of carbon flow during the short and pronounced spring diatom bloom needs to be acquired if the ecological impact of future environmental disturbances associated with climate change and increased human activities (e.g. oil exploration) is to be be understood. The aim of the present study was to investigate the succession and fate of the spring diatom bloom in Disko Bay, with emphasis on evaluating the role of sedimentation versus grazing impact by the *Calanus* dominated zooplankton community.

MATERIALS AND METHODS

Study site. The study site was located in the Disko Bay off Qeqertarsuaq, western Greenland (Fig. 1). Due to land-connected sea ice coverage during winter, 2 sampling sites were combined. At the first site in winter (21 February to 23 March 2008), sampling was conducted through a hole in the ice at ca. 65 to 160 m depth approximately 0.5 nautical mile (n mile) south of Qeqertarsuaq (69° 14′ N, 53° 29′ W). In spring and summer (9 April to 18 July), sampling was done at a monitoring station 1 n mile south from Qeqertarsuaq (69° 14′ N, 53° 23′ W) (Fig. 1) at 300 m depth, onboard RV 'Porsild' (Arctic station, University of Copenhagen) and 'Maja S' (Finn Steffens, Qeqertarsuaq).

Sampling. Sampling was carried out between 10:00 and 17:00 h. Vertical profiles of water temperature and salinity were measured down to 150 m during winter and down to 250 m during spring and summer, using a

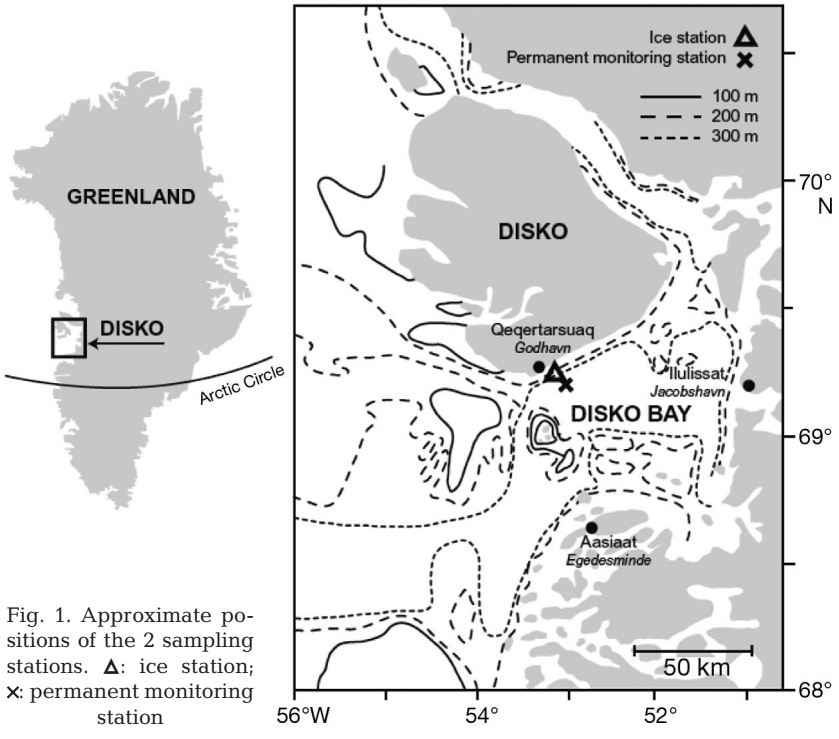

Fig. 1. Approximate positions of the 2 sampling stations. Δ: ice station; ×: permanent monitoring station

Seabird SBE25-01-CTD. Salinity measurements were calibrated against salinity samples taken approximately once a month (n = 4) throughout the study phase, and analyzed on an 8410-Portasal salinometer (Guildline).

Samplings for chemical and biological variables were taken at 6 depths (1, 20, 50, 75, 100, and 150 m) using a 10 l Niskin bottle. Two additional depths (200 and 250 m) were included after ship-based sampling was initiated. Chlorophyll *a* (chl *a*), particulate organic carbon (POC), and particulate organic nitrogen (PON) samples were siphoned directly to 10 l acid cleaned dark carboys and kept in the dark until filtering (max. 1 h after arrival to laboratory). Inorganic nutrient samples (phosphate, nitrate, ammonia, and silicate) were immediately frozen (–30°C) for later analysis on a Skalar autoanalyser (Breda), following the procedures of Grasshoff (1976). Nutrient sample precisions were 0.06, 0.1, 0.3, and 0.2 µM for phosphate, nitrate, ammonia, and silicate, respectively. For analysis of size-fractionated chl *a* and phaeopigments (phaeo), triplicate subsamples (200 to 500 ml) were filtered onto Whatman GF/F filters (0.7 µm) and mesh nets (10 µm and 50 µm). The filters were extracted in 5 ml 96% ethanol overnight (Jespersen & Christoffersen 1987), and pigments were measured on a TD-700 fluorometer (Turner) and calibrated against a chl *a* standard before and after acidification (Yentsch & Menzel 1963).

Samples of POC and PON were collected at 3 depths (1, 20, 50 m) from the ice station, with an additional fourth depth (100 m) from 30 April onwards. Samples (0.7 to 4.5 l) were filtered onto pre-combusted (400°C for 2 h) Whatman GF/F filters, which were stored frozen (–30°C) until analysis on a CHNS Automatic Elemental Analyzer (EA 1110, CE Instruments) after drying at 60°C for 24 h. POC was divided into 3 fractions: chl *a*-based POC (PPC), faecal pellet-based POC (FPC), and amorphous detritus-based POC (amorphous detritus). PPC was estimated from a regression line between chl *a* and water column POC (see Eq. 7 in 'Results'). The amorphous detritus fraction was estimated by subtracting PPC and FPC from POC.

Mesozooplankton. During sampling from the ice, mesozooplankton was collected using a modified WP-2 net (45 µm) equipped with a closing mechanism (Hydrobios). Samples were collected in 3 depth strata (0–50, 50–100, and 100–150 m). During ship-based sampling, mesozooplankton was collected with a multinet (50 µm) equipped with a flow meter (Multinet, Hydrobios type midi), and 2 additional depth strata (150–200 and 200–250 m) were included. In addition to the seasonal study one diurnal investigation with sampling every 6 h was conducted from 29 April at 12:00 h to 30 April 30 at 12:00 h. Samples were immediately preserved in buffered formalin (5% final concentration) for later analyses. Biomass values of the different copepod species were calculated based on measurements of prosome length, and length/weight relationships. Two regressions for *Calanus* spp. were established for biomass calculations: one applicable prior to and during the phytoplankton bloom until 4 May, and another from 9 May onwards (R. Swalethorp et al. unpubl.). Regressions for the remaining copepod species were taken from the literature (Satapoomin 1999, Thor et al. 2005, and references therein).

Gut fluorescence. Gut fluorescence were measured on females of *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* collected using a WP-2 net towed at 0.5 m s^{-1} from 100 m to the surface. A subsample of the cod-end was immediately concentrated on a piece of 100 µm plankton gauze and frozen to –40°C by freeze spraying (75 super, Kontakt Chemie) and then stored frozen (–30°C). Females of *C. hyperboreus* were gently collected from the rest of the cod-end and transferred individually into vials containing 5 ml 96% ethanol and kept dark for later analysis. The full operation took less than 5 min. In the laboratory, samples of *C. glacialis* and *C. finmarchicus* were gently thawed under dim light, diluted with 0.2 µm ice-cold filtered seawater, and triplicate pools of *C. finmarchicus* (n = 5) and *C. glacialis* (n = 3) were extracted in 5 ml 96% ethanol. All samples were analyzed for chl *a* and phaeo as described above. Background values of *C. finmarchicus* (n = 45), *C. glacialis* (n = 25), and *C. hyperboreus* (n = 20) were estimated after incubation for 24 h in 0.2 µm filtered seawater that was renewed after 12 h. Background values were subtracted from all the *Calanus* spp. gut fluorescence measurements.

Ingestion rate (I; µg C individual^{-1} d^{-1}) was calculated using the following equation (modified from Harris et al. 2000)

$$I = K \times G \times 60 \times 24 \quad (1)$$

where K is the instantaneous gut defecation rate constant (min^{-1}) and G is the gut pigment (µg chl *a*). The gut pigment was converted to carbon by application of a conversion factor of 29.9 measured during the present investigation. Instantaneous gut defecation values of 0.032 for *C. finmarchicus* (Maar et al. 2002), 0.017 for *C. glacialis*, and 0.015 for *C. hyperboreus* (Hansen et al. 1990) were used and corrected to *in situ* temperature by applying a Q_{10} value of 2.8 (Hansen et al. 1997). Specific ingestion rate (% d^{-1}) was calculated using *in situ* carbon contents of the 3 *Calanus* spp. (R. Swalethorp et al. unpubl.).

***In situ* faecal pellet production.** Faecal pellet production of the copepod community was measured in short time incubations during ship-based sampling from 23 April to 9 June. Copepods were collected using a WP-2 net (200 µm) from 100 m to the surface. Subsamples of the cod-end were immediately distrib-

uted into 8 fecatrons made of clear PVC (polyvinyl chloride) tubes (inner diameter 8 cm, height 40 cm) filled with 45 µm filtered surface water. One additional subsample was immediately fixed in 2% (v/v) acidic Lugol's solution and served as a start sample. Four fecatrons were equipped with a 200 µm and 4 with a 400 µm false mesh bottom. The procedure from sampling of copepods to incubation start took less than 5 min. Concentrations in the fecatrons were between 20 and 385 copepods l^{-1}, and they were incubated for 1 to 2.5 h in a 100 l container cooled with surface water. Present copepod predators (primarily *Sagitta* spp. and *Pareuchaeta* sp.) were removed before the start of the experiment. At the end of the incubations the samples were preserved with 2% (v/v) acidic Lugol's solution. In the laboratory, faecal pellets and copepods were concentrated on a 20 µm sieve and counted and measured using a stereo light microscope (Olympus SZ40, 40× magnification for faecal pellets and 20× for copepods). The dimensions of maximum 30 faecal pellets and 60 copepods were measured and the rest were counted. Faecal pellet measurements and counting criteria were determined, so that the faecal pellets had to be a minimum of 3× longer than wide. Faecal pellet volume was calculated assuming cylinder shape. FPC was estimated applying a volume to carbon conversion factor of 0.043 pg C μm^{-3} (R. Swalethorp et al. unpubl.). Copepod carbon content was calculated from a combined length/weight regression of *Calanus finmarchicus* and *C. glacialis* in the 2 time series as described above (R. Swalethorp et al. unpubl.).

Specific faecal pellet production rate (SPP, µg C_{pellet} µg C^{-1}_{cop} d^{-1}) was calculated using the following equation:

$$SPP = FPC_{prod}/(C_{cop} \times t) \quad (2)$$

where FPC_{prod} is the carbon content of the faecal pellets produced (µg C_{pellet}) during the experiment. C_{cop} is the biomass of the copepods (µg C_{cop}), and t is the duration of the experiment in days. Specific ingestion rate (% d^{-1}) was calculated assuming an assimilation efficiency of 68.2% (Conover 1966).

Sedimentation. Sedimentation measurements were conducted from 23 April to 9 June using free-floating sediment traps fitted on a buoy (0.5 m^3, 75 kg buoyancy) and moored with a weight (20 kg) to reduce water resistance and upward drift. The sediment traps (KC Denmark) consisted of 2 parallel acrylic cylinders mounted in a gimballed frame equipped with steering fins and pivot joints to ensure a vertical position perpendicular to the current. The traps had an internal diameter of 0.052 m with an aspect ratio (height:diameter) of 6.35. The sediment traps were deployed at 20, 50, and 100 m, with an average deployment time of 5.35 ± 0.1 h (10:00 to 16:00 h). During deployment, the sediment traps did not drift more than 1 n mile away from the sampling position, except on one occasion where tracking of the traps was temporarily interrupted and deployment time was 24 h (23 April). Prior to deployment, the traps were filled with 0.2 µm filtered seawater from depths >100 m with added salt to increase the salinity by 5 psu (Knap et al. 1996). Hereby, advective diffusive exchange between the higher density, particle-free water and the ambient seawater was reduced in the traps during deployment. No preservative was added.

Immediately after recovery, the sedimentation traps were sealed with a clean lid and protected from direct light. In the laboratory, samples were visually inspected for swimmers, which were removed, and kept at 5°C in darkness until analysis (<2 h). The trap contents were carefully mixed before subsampling. To ensure minimal disturbance of the collected material, samples for microscopic examination were taken first. Subsamples for faecal pellets (600 to 900 ml) were preserved with 2% (v/v) acidic Lugol's solution. Analyses for total chl *a*, phaeo (100 ml in triplicates), POC and PON (500 ml), and for faecal pellets were performed as described above for the *in situ* faecal pellet production experiment.

Suspended faecal pellets. Parallel to the trap deployment, water samples were collected using a 30 l Niskin bottle at 3 trap deployment depths (20, 50, and 100 m) for quantification of suspended faecal pellets. The water samples were concentrated on a 20 µm sieve, fixed in 2% (v/v) acidic Lugol's solution, and analysed for faecal pellets and copepod abundance and biomass as described above.

Calculations. The sedimentation rate (mg m^{-2} d^{-1}) of the measured variables was calculated from the following equation (Knap et al. 1996):

$$\text{Sedimentation rate} = (C_{trap} \times V_{trap})/(A_{trap} \times t_{dep}) \quad (3)$$

where C_{trap} (mg m^{-3}) is the concentration of the measured variable in the sediment trap, V_{trap} (m^3) is the volume of the sediment trap, A_{trap} (m^2) is the sediment trap surface area, and t_{dep} (d) is the deployment time. Sinking velocity (m d^{-1}) was estimated for different variables using the following equation (Kiørboe et al. 1994):

$$\text{Sinking velocity} = \text{Sedimentation rate}/C_{in\ situ} \quad (4)$$

where the sedimentation rate is from Eq. (3) and $C_{in\ situ}$ (mg m^{-3}) is the *in situ* concentration of the variables at 50 m depth.

The daily loss rate (% d^{-1}) of chl *a* biomass in the 0–50 m depth stratum due to sinking export was estimated using the following equation (Olli et al. 2002):

$$\text{Daily loss rate} = \text{Sedimentation rate} \times 100/C_{int} \quad (5)$$

where sedimentation rate is from Eq. (3) and C_{int} (mg m^{-2}) is the integrated biomass of chl *a*, estimated vertically from integration of the water column measurements at 0–50 m.

The daily loss (% d^{-1}) of phytoplankton due to copepod grazing was estimated using Eq. (5) by replacing the sedimentation rate with the copepod grazing calculated from faecal pellet production, i.e. the specific faecal pellet production multiplied by the integrated biomass of copepods (mg C m^{-2}) in the 0–50 m depth stratum and assuming an assimilation efficiency of 68.2% (Conover 1966). The present estimate assumes that the copepod prey is dominated by phytoplankton, which is most valid during the bloom. Outside the bloom, protozooplankton can contribute significantly to the diet of *Calanus* spp. (Levinsen et al. 2000b), and the daily ratio will then be overestimated accordingly.

Statistical procedures. Data was tested for normal distribution using the Shapiro-Wilks test and, if necessary, log transformed. Effects of different mesh sizes in the fecatrons were tested with 1-way ANOVA (Statistica 2004, version 7.0; Statsoft). Linear regressions were determined using ANOVA tests (Sigmaplot 2004, version 10.0, Systat Software) to examine potential relationships between carbon and chl *a* of the suspended or settled material as well as the relationship between food size and specific ingestion rate. Comparisons of regression lines were done with a 2-tailed *t*-test and accepted as significantly different if $p < 0.05$. The comparison of faecal pellet sizes and sedimentation fluxes could not be fitted to a normal distribution, and a non-parametric analysis followed by a Kruskal-Wallis test was used. Velocity difference of the organic materials was tested with 1-way ANOVA as were differences between the 4 methods for estimate specific ingestion rates. All data are presented as means ± SE.

RESULTS

Hydrography and nutrient distribution

The ice coverage in Disko Bay was 60% until breakup, between 23 March and 9 April, after which it melted and advected out of the bay. During winter, when sampling took place from the ice station, the water column was stratified with colder (–1.7°C) surface water separated from a warmer (1.7°C) bottom

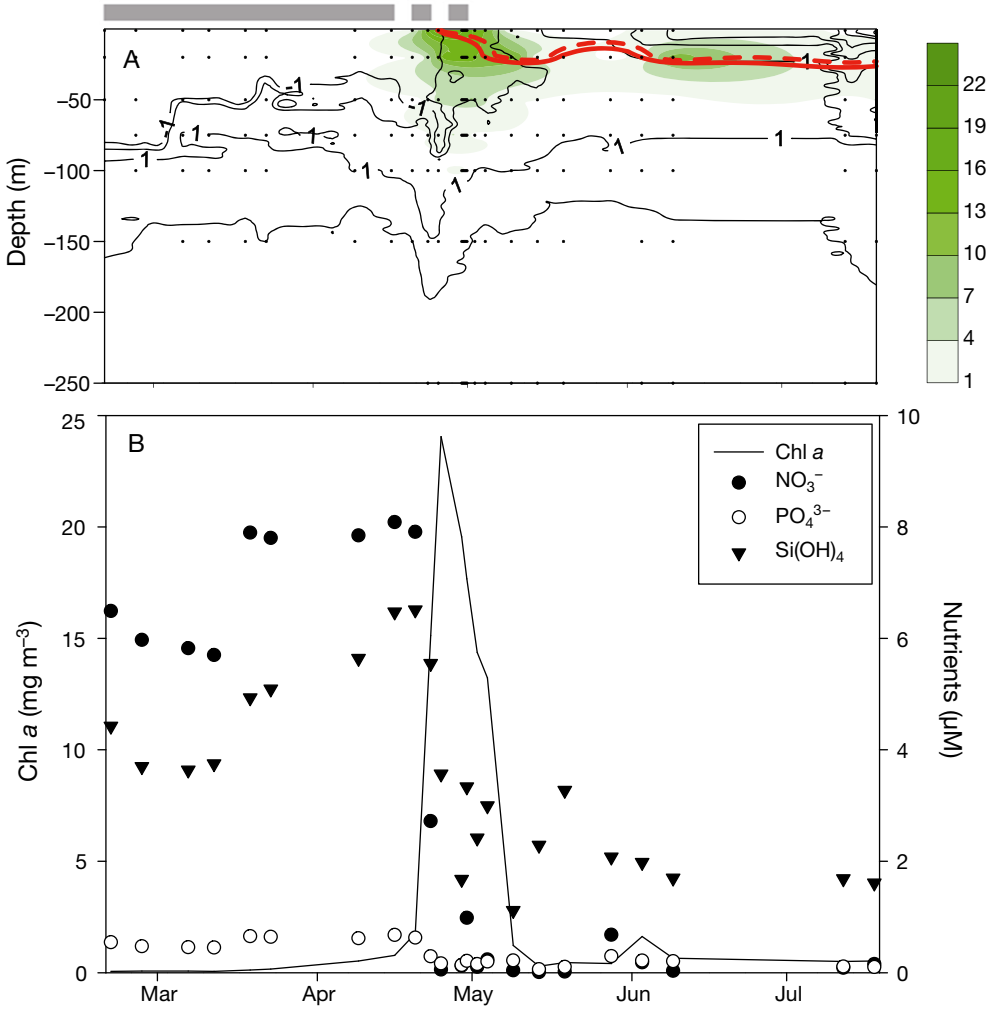

Fig. 2. Water column characteristics over the course of the investigation. (A) Isolines are water temperature (°C) and the green coloration illustrates chlorophyll *a* (chl *a*) concentrations (mg m^{-3}). The concentration of the limiting nutrient nitrate is displayed as red isolines (solid: 1.0 µM, broken: 0.5 µM). Points: sampling depths. Grey bars indicate ice cover. (B) Succession in the surface layer (1 m) of chl *a* and nutrient concentrations

layer by a thermocline at approximately 60 m depth (Fig. 2A). During ship-based sampling from 9 April, the weather was dominated by a high pressure system with high irradiance and no wind. The thermocline remained at approximately 60 m depth as the temperature in the upper layers increased to an average of –0.9°C (Fig. 2A). Towards the end of the investigation, from 9 May, the thermocline approached 20 m, separating the water column into 3 water layers with a warm surface layer, an intermediate layer of cold water (<0.5°C), and a warm bottom layer (Fig. 2A).

Nitrate was uniformly distributed in the water column at the initiation of the investigation. During the bloom phase the average nitrate concentration in the upper 50 m stratum decreased from 5.4 ± 1.5 to 2.1 ± 1.0 µM as a result of the developing bloom (Fig. 2A,B). Nitrate concentrations decreased below detection level above 20 m after 14 May. Phosphorus and silicate distributions mirrored the nitrate development but were not fully depleted. The surface nitrate concentration remained low after the sedimentation of the bloom, and the nutricline followed the stratification for the rest of the study. Comparison of the major nutrients species (Fig. 3) suggests nitrogen limitation of the primary producers, since nitrate became depleted relative to the Redfield ratios with respect to phosphorus (Fig. 3A) and silicate (Fig. 3B) after the ice break-up and initiation of the bloom.

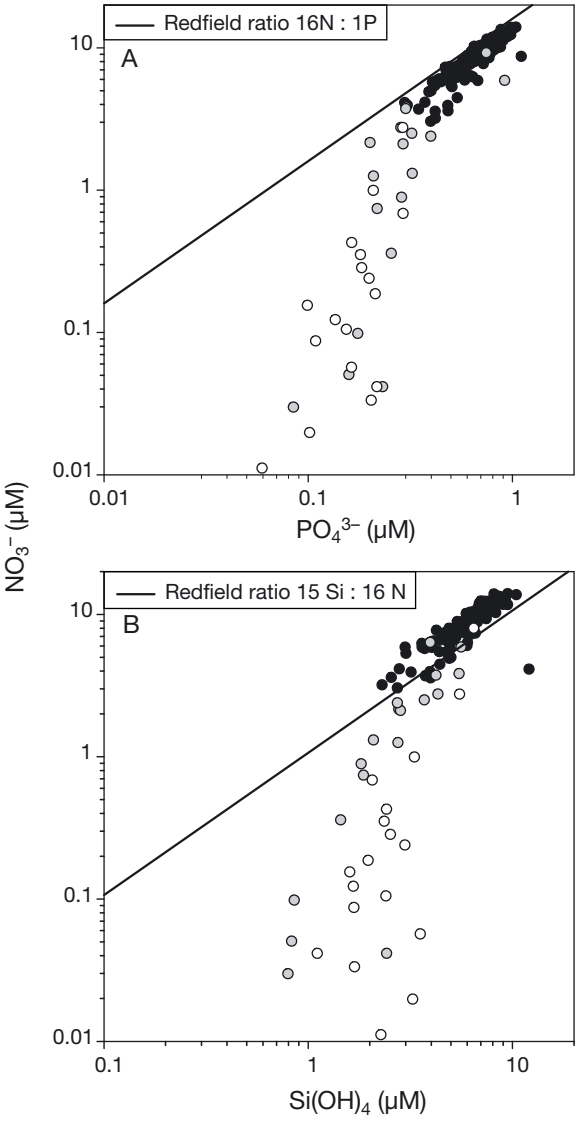

Fig. 3. Relationship between (A) phosphorus and nitrate and (B) silicate and nitrate in the water samples taken from 21 February to 18 July 2008. (●) samples taken throughout the water column before the initiation of the spring bloom and below the photic zone thereafter >50 m; (⊙) samples from 20 m after 20 April and (○) surface samples after 20 April. Lines indicate the Redfield ratios of the nutrients in consideration

Phytoplankton biomass

The initiation of the spring bloom (9 April) began at the break-up of sea ice and establishment of the pycnocline. The bloom developed in the upper 20 m from 23 April and averaged at 11.8 ± 1.7 mg chl *a* m^{-3} (n = 20) during the bloom phase, with a peak of 24.1 mg m^{-3} on 25 April, followed by a rapid sedimentation out of the photic zone (Fig. 4).

In the present study we divided the phytoplankton bloom into 3 phases. The first phase was defined as the bloom developing phase, (23 to 30 April), followed by the decaying bloom phase (2 to 19 May) as the second phase, and the post-bloom phase (28 May to 9 June) as the third phase. The following results are confined to these phases.

Across the 3 depths sampled there was a clear seasonal succession in the size classes of chl *a*. In the beginning of March, chl *a* <10 µm dominated the phytoplankton (Fig. 3). During the spring bloom phase, a succession of the 3 size classes was observed initiated by a peak of chl *a* <10 µm, followed by a 10–50 µm peak, and culminating with a peak of chl *a* >50 µm. The post-bloom period was dominated by the smallest fraction, i.e. <10 µm.

The same overall patterns were observed at all depths, with the bloom peaking first in the surface. Total chl *a* averaged 12.3 ± 3.4, 5.9 ± 2.7, and 1.9 ± 2.2 mg m^{-3} at 0 to 50 m depth during the 3 bloom phases, respectively.

The smallest chl *a* fraction (0.7 to 10 µm) contributed on average 31% to the total chl *a* in the upper 50 m (Fig. 4). At the surface, this fraction had a high average concentration of 5.0 ± 2.2 mg m^{-3} in the bloom developing phase, followed by a subsurface bloom (20 m) with a maximum concentration of 11.9 ± 0.1 mg m^{-3} on June 9.

The medium chl *a* fraction (10 to 50 µm) contributed on average 36% to the total chl *a* in the upper 50 m

Table 1. Taxonomic composition of the dominating phytoplankton community during the 3 phases of the bloom (S. Soylu unpubl.)

Size fraction (µm)	Developing bloom 23–30 April	Decaying bloom 2–19 May	Post bloom 28 May–9 June
<10	*Phaeocystis pouchetti*	*P. pouchetii*	*Chrysochromulina* spp., *Pyramimonas* spp., *P. pouchetii*
>10	*Fragilariopsis cylindrus*, *F. pseudonana*, *Navicula pelagica*, *P. pouchetii*	*F. cylindrus*, *F. pseudonana*, *Heterocapsa triquetra*, *N. pelagica*, *P. pouchetii*	
>50	*F. cylindrus*, *F. pseudonana*, *N. pelagica*	*F. cylindrus*, *F. pseudonana*, *N. pelagica*	

(Fig. 4). The fraction showed a clear unimodal distribution, with high average values both at the surface and subsurface of 7.7 ± 1.3 and 6.8 ± 2.1 mg m^{-3}, respectively, during the bloom developing phase.

The large chl *a* fraction (>50 µm) contributed 33% to the total chl *a* in the upper 50 m (Fig. 4), with average concentrations at the surface up to 6.4 ± 2.5 mg m^{-3} during the bloom developing phase. Subsurface concentrations showed a clear bimodal distribution during the developing and decaying bloom phase, with a maximum of 14.2 ± 0.04 mg m^{-3} on 9 May, and an average of 5.0 ± 2.5 mg m^{-3}.

All chl *a* fractions at 50 m depth had maximum values approximately 3 to 4× lower than the concentrations in the depths above (Fig. 4).

The succession illustrated by the size fractionated chl *a* measurements (Fig. 4) was corroborated by microscopic examinations of the Lugol's fixed samples (Table 1). The winter plankton was dominated by haptophytes (primarily *Phaeocystis pouchetii*). Single cells of *P. pouchetii* also dominated the initial phase (chl *a* <10 µm) of the spring bloom (Fig. 4), followed by a gradual shift to the diatom species of *Fragilariopsis cylindrus* and *Navicula pelagica* after the bloom, first as single cells and later as chain formations during the exponential growth of the bloom. After the bloom peaked and became nutrient-depleted, chains of *F. cylindrus* and *N. pelagica* (>50 µm) sedimented out of the euphotic zone. The summer plankton was dominated by small flagellates <10 µm (Table 1). The same succession patterns were observed in all 3 strata investigated. Further details on the phytoplankton succession and sedimentation are presented in S. Soylu et al. (unpubl.).

Copepod biomass

In all 5 depth strata sampled, a clear seasonal succession was observed in the species composition of the copepods. The bulk part of the biomass was mainly located in the upper 50 m, with an average biomass of 3200 ± 800 mg C m^{-2}, where *Calanus* spp. constituted 96% of the total biomass during all 3 bloom phases. Before the bloom, the biomass consisted primarily of *Oithona* spp., *Pseudocalanus* spp., and *Microcalanus* spp. (Fig. 5). A shift in the biomass composition towards *C. finmarchicus* and *C. glacialis* was observed later in March. During the spring bloom phase, *Calanus* spp. dominated with peaks of high biomasses of *Metridia longa* and *Pseudocalanus* spp. (Fig. 5A). In this phase, the *Calanus* species was mainly represented as adult females (R. Swalethorp et al. unpubl.). During the decaying bloom phase, the biomass consisted mainly of *C. hyperboreus*, which peaked in early May. During the post-bloom phase the biomass of copepods decreased with *C. hyperboreus* as the dominating *Calanus* spp. and *Pseudocalanus* spp. contributing to the main biomass of the smaller copepods. The biomass decreased with depth, although large biomasses were located in the 50–100 m depth stratum, averaging 2200 ± 600 mg C m^{-2}, and dominated by *Calanus* (93% of the total biomass) during all 3 bloom phases (Fig. 5B). However, *M. longa* increased in biomass with depth (Fig. 5C,D). A high biomass of *C. hyperboreus* was observed during the spring bloom phase at the deepest sampling depth (Fig. 5E), followed by a low biomass during the decaying bloom phase, which suggests a vertical ascent of *C. hyperboreus* towards the surface during this phase. An increase in the biomass of *C. hyperboreus* was observed during the post-bloom phase at the 2 deepest depth strata (Fig. 5D,E). Here *C. hyperboreus* contributed with 63 and 89% to the biomass, respectively, suggesting a vertical migration of *C. hyperboreus* towards the overwintering depths at the bottom.

Gut fluorescence

Overall, the specific ingestion rate ranged between 0.01 and 74% d^{-1} for the *Calanus* spp., with an overall average of 10.3 ± 2.2% d^{-1} (n = 38) (Fig. 6, Table 2). The specific ingestion rate for *C. finmarchicus* at the initiation of the bloom reached 74% d^{-1} on 30 April (Fig. 6B). The average specific ingestion rate for *C. finmarchicus* was 17.5 ± 5.7% d^{-1} (n = 13) during all 3 bloom phases and decreased significantly in the post-bloom phase ($p < 0.01$, n = 13).

The specific ingestion rate for *Calanus glacialis* followed the pattern of *C. finmarchicus*, reaching 20%

d^{-1} on 9 May. It decreased significantly in the post-bloom phase ($p < 0.01$, n = 13), and the average specific ingestion rate for *C. glacialis* was 7.0 ± 1.9% d^{-1} (n = 13) during all 3 bloom phases (Fig. 6C). The specific ingestion rate for *C. hyperboreus* reached 15% d^{-1} on 4 May, with an average of 2.1 ± 0.5% d^{-1} (n = 12) during all 3 bloom phases (Fig. 6D) and a significant decrease in the post-bloom phase ($p < 0.01$, n = 12).

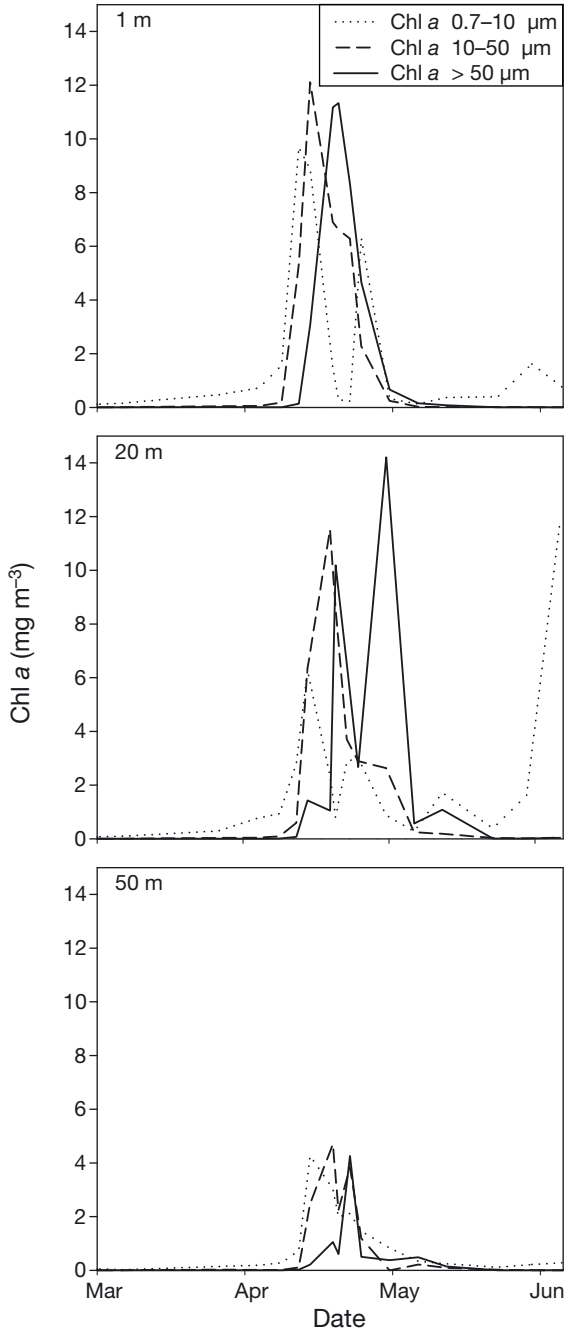

Fig. 4. Size fractionated chl *a* concentrations (0.7–10 µm, 10–50 µm, and >50 µm) at 1, 20, and 50 m depths

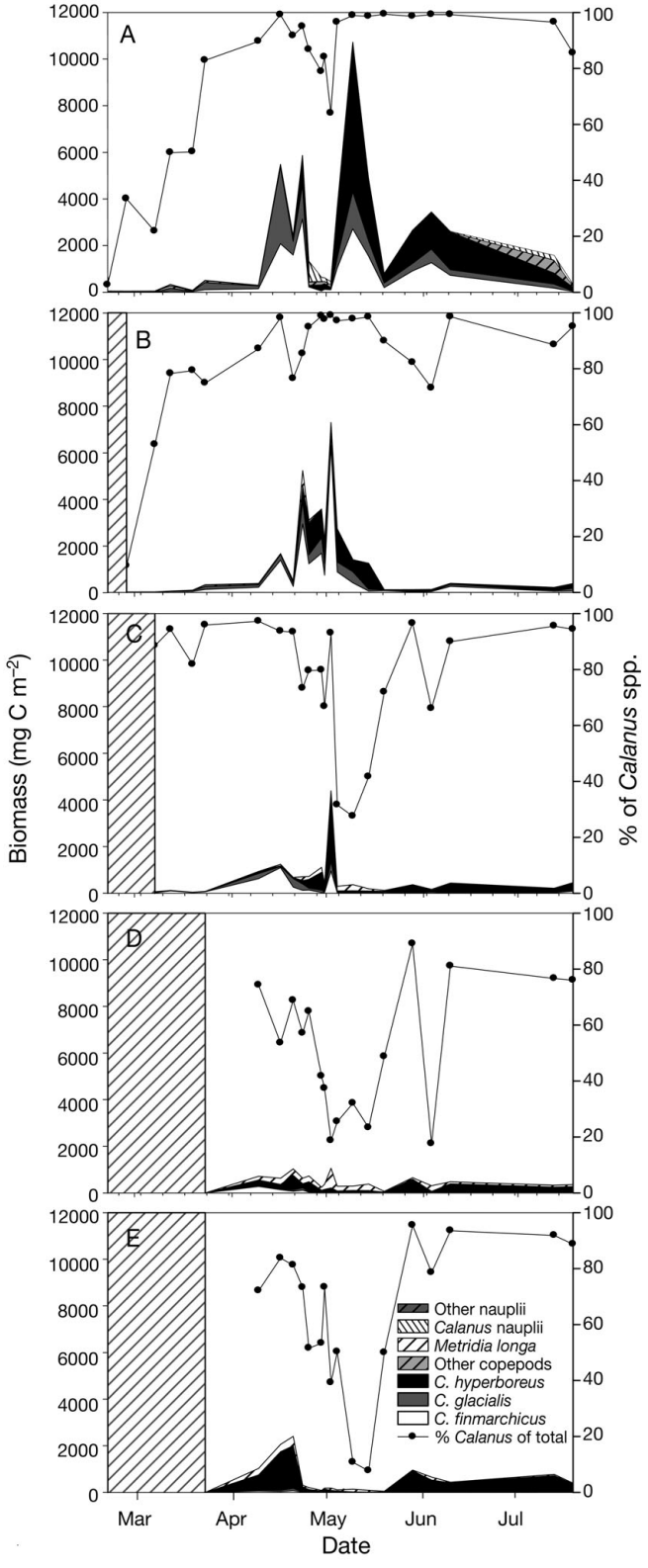

Fig. 5. Integrated biomasses of copepods (mg C m^{-2}) in (A) 0–50 m depth, (B) 50–100 m depth, (C) 100–150 m depth, (D) 150–200 m depth, and (E) 200–250 m depth stratum. Solid line: contribution of *Calanus* spp. (%) to total copepod biomass. Vertical black line: initiation of sampling at depths

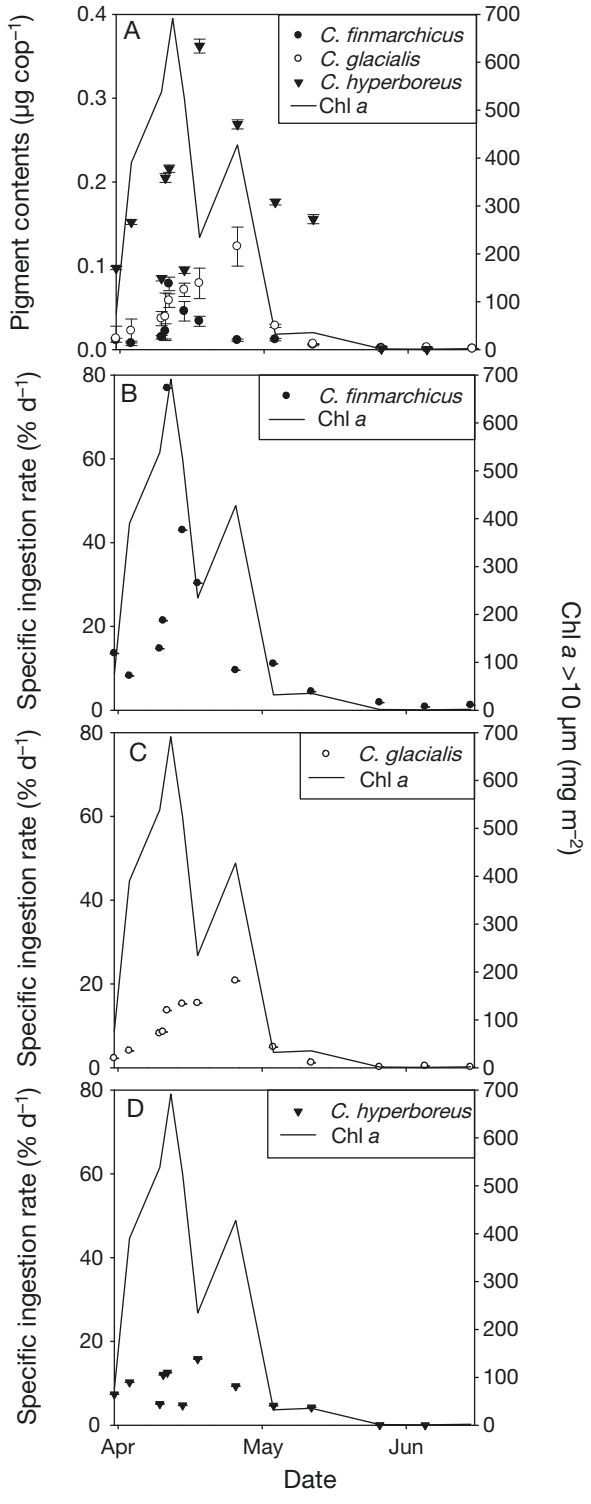

Fig. 6. (A) Gut pigment content (µg) of *Calanus* spp. from gut fluorescence measurements. (B,C,D) Specific ingestion rates (% d^{-1}) calculated from gut fluorescence measurements for (B) *C. finmarchicus*, (C) *C. glacialis*, and (D) *C. hyperboreus*. Data are averages ± SE. Solid line: integrated chl *a* >10 µm (mg m^{-2}) for the 0–50 m depth stratum

A correlation analysis of the specific ingestion rates of *Calanus* spp. and the integrated chl *a* size fractions from 0 to 50 m showed that 74, 72, and 57 % of the variation in specific ingestion rates could be explained by the integrated concentration of the chl *a* >10 µm for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*, respectively, although not significantly for *C. hyperboreus* ($p > 0.05$, n = 12). Furthermore, correlation analyses for chl *a* >50 µm revealed a significant correlation of 89 % of specific ingestion rate by *C. glacialis*, while the correlations of *C. finmarchicus* and *C. hyperboreus* remained unchanged compared to the chl *a* >10 µm. Consequently, the ingestion calculated from the gut pigment of *Calanus* spp. was compared with chl *a* >10 µm representing the potential food for *Calanus* (Fig. 6).

All the *Calanus* spp. responded positively to the developing bloom (Fig. 6). A clear response was observed in the gut pigment content of *C. hyperboreus* at the initiation of the bloom, while the responses were more modest for *C. finmarchicus* and *C. glacialis* (Fig. 6A). Likewise, the gut pigment content of all *Calanus* spp. decreased with the termination of the chl *a* bloom.

All background values measured were low; 0.001 ± 0.02 (n = 45), 0.002 ± 0.02 (n = 25), and 0.01 ± 0.001 µg female^{-1} (n = 20) for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*, respectively.

In situ faecal pellet production experiment

There was no difference between the *in situ* faecal pellet production measured using the 2 types of fecatrons with different mesh sizes ($p > 0.05$, n = 89). Consequently, the results represent an average of the 2 fractions (n = 8). No correlation was found between specific ingestion rate by copepod spp. and chl *a* size fractions from the surface water (1 m) ($p > 0.05$, n = 11). It was assumed that the food size spectra for the copepod spp. were the same as observed for the specific ingestion rate during the gut pigment measurements and observed in the incubations of individual *Calanus* for faecal pellet production measurements from R. Swalethorp et al. (unpubl.). Consequently, production measurements by the *in situ* faecal pellet productions experiment of *Calanus* spp. are presented along with chl *a* >10 µm representing the potential food for the copepods (Fig. 7).

Faecal pellet production rate (FPR) followed the bloom, with a peak after the culmination of the bloom and a decrease to a stable FPR during the post-bloom phase (Fig. 7A). Overall average FPR was 20 ± 2.2 pellets ind.$^{-1}$ d^{-1} (n = 89), with a maximum during the decaying bloom of 27 ± 2.9 pellets animal^{-1} d^{-1} (n = 37). Faecal pellet volumes increased significantly ($p < 0.01$,

Table 2. Integrated phytoplankton and copepod biomass in the upper 50 m and specific ingestion rates and corresponding grazing impact (% of phytoplankton biomass d^{-1}; PB) estimated by 4 methods: (A) *in situ* faecal pellet production experiment, (B) average gut fluorescence in 3 *Calanus* spp., (C) average faecal pellet (FP) production from bottle incubations of 3 *Calanus* spp., and (D) egg production by *C. finmarchicus* and *C. glacialis.* Data are averages ± SE. No. of samples given in parentheses

Phase	Biomass (g C m^{-2})		Specific ingestion rate and grazing impact								(A,B,C,D)	%
	Phyto-plankton	Cope-pod	(A) *In situ* FP pro-duction (% d^{-1})	% of PB	(B) Gut fluores-cence (% d^{-1})	% of PB	(C) FP pro-duction (% d^{-1})	% of PB	(D) Egg pro-duction (% d^{-1})	% of PB	Average produc-tion (% d^{-1})	of PB
Developing bloom												
23–30 April	18.3 ± 2.7 (5)	2.7 ± 1.1 (5)	2.9 ± 0.6 (29)	0.4	14.1 ± 4.4 (15)	2.1	2.2 ± 0.3 (164)	0.3	5.6 ± 0.4 (93)	0.8	6.4	1.0
Decaying bloom												
2–19 May	9.4 ± 3.3 (5)	4.0 ± 1.9 (5)	6.0 ± 1.3 (37)	2.5	12.5 ± 2.8 (15)	5.3	2.1 ± 0.3 (197)	0.9	7.4 ± 0.5 (133)	3.2	7.2	3.4
Post bloom												
28 May–9 June	3.8 ± 2.7 (3)	2.9 ± 0.3 (5)	3.1 ± 0.9 (23)	2.3	0.7 ± 0.3 (9)	0.5	0.5 ± 0.1 (164)	0.4	1.8 ± 0.3 (47)	1.4	1.6	1.6

n = 5563) throughout the 3 phases, with averages of 1.1 ± 0.02 × 10^6 µm^3 (n = 1920), 1.5 ± 0.02 × 10^6 µm^3 (n = 2283), and 1.6 ± 0.04 × 10^6 µm^3 (n = 1360), respectively (Fig. 8A).

Specific ingestion rates showed a delayed response to increased chl *a*. Specific ingestion rates peaked during the decaying bloom phase at 15.6 ± 3.8% d^{-1} (n = 8), then decreased to 4.3 ± 0.6% d^{-1} (n = 8) and remained constant until the last sampling date (Fig. 7C). The overall average was 6.7 ± 0.7% d^{-1} (n = 89) (Fig. 7C, Table 1).

From the 2 independent methods, *in situ* faecal pellet production experiment and gut fluorescence, copepod specific ingestion rates were evaluated and compared. Furthermore, 2 other measures from a concurrent study were included in the comparison (R. Swalethorp et al. unpubl.). Egg and faecal pellet production were measured for adult females of the 3 *Calanus* species individually in bottle incubations. Here, the average of the 3 *Calanus* spp. is presented for faecal pellet production, and the average of *C. finmarchicus* and *C. glacialis* for egg production, since *C. hyperboreus* were not producing any eggs during the time of the study.

Estimated specific ingestion rates from the bottle incubations were calculated from the specific egg and faecal pellet productions assuming a growth and assimilation efficiency of 33 and 68.2%, respectively (Conover 1966, Hansen et al. 1997) and that specific ingestion rates by *Calanus* could be considered representative for the entire copepod community. Grazing impacts on the phytoplankton community assessed using the 4 methods are estimated by multiplying specific ingestion rate by copepod biomass (Table 2). Differences between the estimated ingestion rates of the 4 methods are evaluated in the 'Discussion'.

Sedimentation

POC sedimentation averaged 1.4 ± 0.1 g C m^{-2} d^{-1} (n = 68) from the 0–100 m depth during all 3 phases (Fig. 9). Sedimentation rates at 20 m were approximately 2× higher than at 50 and 100 m. The bulk part of PPC sedimentation was observed in the upper 20 m, with an increasing trend during the developing bloom, ranging from 0.3 to 3.0 g C m^{-2} d^{-1} (Fig. 9). This was reflected by high phytoplankton biomass in the euphotic layer and relatively low grazing rates, suggesting passively sinking PPC from the productive layer. PPC sedimentation rates increased in relation to the subsurface bloom at the end of the post-bloom phase (Fig. 9). PPC contributed with an average of 1.1 ± 0.4 g C m^{-2} d^{-1} (n = 5), equivalent to 60% of POC sedimentation in the upper 50 m during the developing bloom. A relatively lower sedimentation of PPC was observed at 100 m with 0.4 ± 0.2 g C m^{-2} d^{-1}, yet this was equivalent to 57% of POC at 100 m in the developing bloom phase. PPC sedimentation decreased towards the post-bloom phase, with contributions of 18 to 25% of POC in the upper 50 m and 11 to 35% at 100 m in the post-bloom phase. The overall average of PPC was 0.5 ± 0.06 g C m^{-2} d^{-1} (n = 78) at 0 to 100 m depth contributing 36% to the total POC sedimentation.

Seasonal development in sedimentation of amorphous detritus followed the PPC (Fig. 9). Sedimentation of amorphous detritus was of high importance during the post-bloom phase, contributing 71 to 79% to POC sedimentation in the upper 50 m and 10 to 70% at 100 m. On average, the relative importance of sedimenting amorphous detritus exceeded that of PPC both in the decaying and post-bloom phases. The overall average of amorphous detritus was 0.7 ± 0.1 g C m^{-2} d^{-1} (n = 68), contributing 52% to total POC sedimentation.

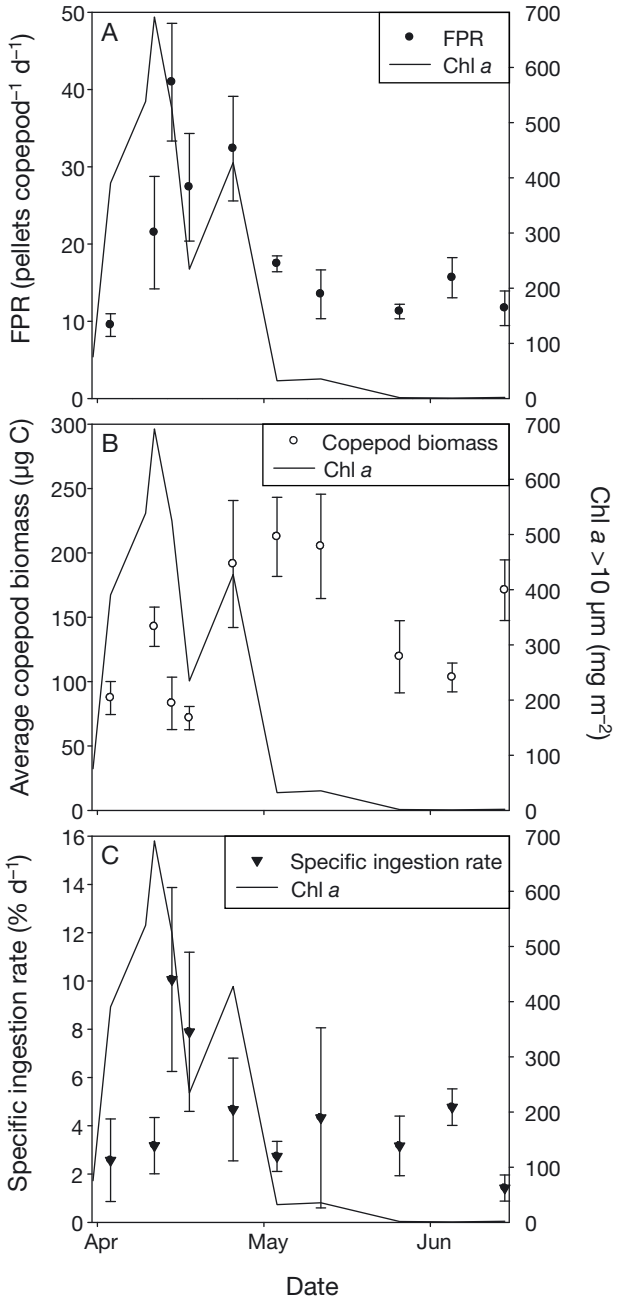

Fig. 7. (A) Faecal pellet production rate (FPR; number of pellets copepod^{-1} d^{-1}) of the *in situ* copepod community. (B) Individual copepod biomass (µg C copepod^{-1}), (C) specific ingestion rates (% d^{-1}). Data are averages ± SE. Solid line: integrated chl *a* >10 µm (mg m^{-2}) for the 0–50 m depth stratum

The highest FPC sedimentation was measured at 100 m depth in the decaying bloom phase, ranging from 0.3 to 0.4 g C m^{-2} (Fig. 9) corresponding to 10 to 43 % of POC. Sedimentation of FPC at 100 m was significantly different between the decaying and post-bloom phases ($p < 0.05$, $n = 26$). These findings correspond well with larger faecal pellets found in the sediment

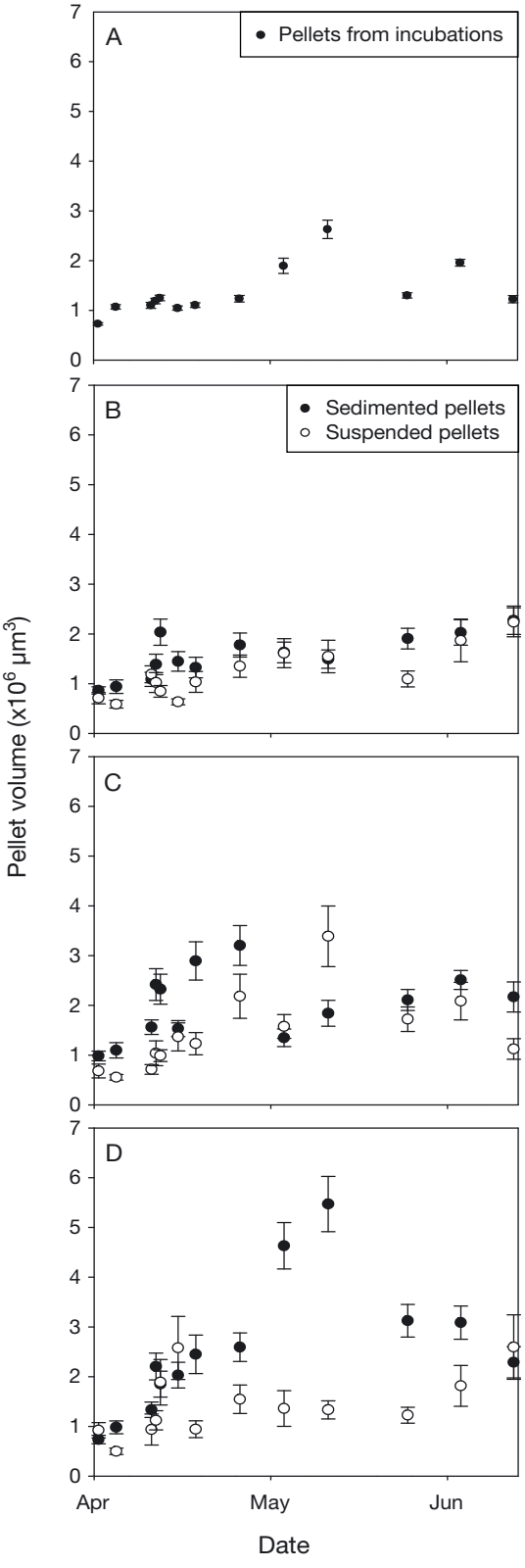

Fig. 8. (A) Volume of faecal pellets from *in situ* faecal pellet production experiments. (B,C,D) Volume of faecal pellets from sediment traps and water column at (B) 20 m, (C) 50 m, and (D) 100 m depths. Data are averages ± SE

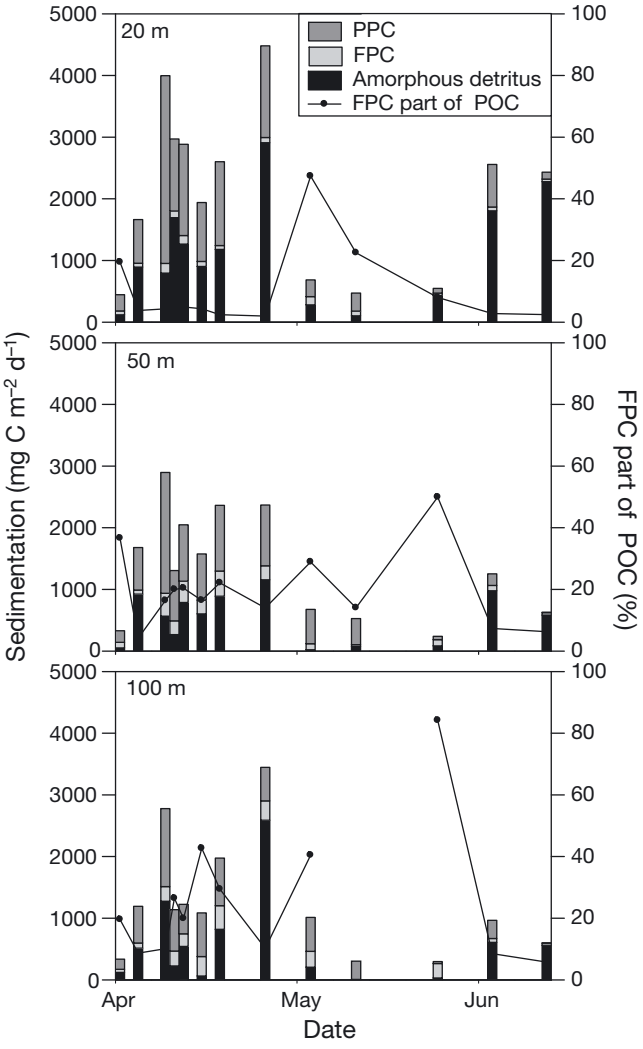

Fig. 9. Seasonal trends in sedimentation of phytoplankton based carbon (PPC), faecal pellet based carbon (FPC), and amorphous detritus fractions of POC (mg C m^{-2} d^{-1}) at 20, 50, and 100 m depths. Solid lines: FPC part of POC sedimentation. The FPC sample is missing on May 19 at 100 m

traps at 100 m during the decaying phase (Fig. 8D). Faecal pellets found in the sediment traps also differed significantly in size from the suspended faecal pellets at 20, 50, and 100 m depths during the developing and post-bloom phases ($p < 0.01$, $n = 1349$) and ($p < 0.01$, $n = 806$), respectively (Fig. 7B,C,D). The overall average of FPC sedimentation was 0.16 ± 0.1 g C m^{-2} d^{-1} ($n = 78$), contributing 12% to total POC sedimentation.

Biochemical composition of the suspended and settled biomass

In general, the bulk of suspended POC and PON was collected in the upper 20 m, where POC peaked at 887 mg C m^{-3} on 29 April. The POC/PON ratio indicates the quality of organic material, as degradation increases the ratio from the Redfield ratio of 6.6. The general trend was that the elementary composition of POC/PON ratios increased with depth and throughout the season (Table 3).

The average suspended POC/PON ratio was ~7 in the upper 50 m during the developing and decaying phases, with an increase in the post-bloom phase. The increase suggests a nitrate limitation, but no significant correlation was observed between the POC/PON ratio and nitrate concentrations ($p > 0.05$, $n = 9$). None of the suspended POC/PON ratios were significantly different between depths during all 3 phases ($p > 0.05$, $n = 40$) (Table 3). The POC/PON ratio of the settled material during the developing bloom phase at 100 m depth was 6.9 (Table 3). The ratio increased during the decaying bloom phase and ended at 16 in the post-bloom phase at 100 m. This suggests that the settling phytoplankton may have been nutrient-limited during the last phase. However, no significant correlation was observed between POC/PON ratio and nitrate concentration ($p > 0.05$, $n = 9$).

The relation between suspended POC and chl *a* was fitted to a linear regression:

$$\text{POC} = 29.9 \pm 1.3 \times \text{chl } a + 113.9 \pm 10.3 \quad (r^2 = 0.87,\ n = 88,\ p < 0.01) \tag{7}$$

The slope of the regression line was used to convert suspended and sedimentated chl *a* measurements into PPC.

The suspended POC/chl *a* ratio increased from ~50, measured during the developing bloom phase, to 300 during the post-bloom phase. The ratio did not change significantly with depth during all 3 phases ($p > 0.05$, $n = 56$).

For the settled material, the linear regression between the POC and chl *a* measurements was:

$$\text{POC} = 40.8 \pm 4.2 \times \text{chl } a + 191.8 \pm 55.2 \quad (r^2 = 0.6,\ n = 68,\ p < 0.01) \tag{8}$$

The POC/chl *a* ratio of 300 measured for the settled material in the post-bloom phase was significantly higher than for the developing and decaying bloom phases ($p < 0.01$, $n = 36$), which suggests that the settling material consisted mainly of degraded material (data not shown).

The chl *a*/phaeo ratio can be taken as a proxy for grazing, since increased degradation of chl *a* to phaeo pigment led to a decrease of the chl *a*/phaeo ratio. The suspended chl *a*/phaeo ratio decreased from 30 in the bloom developing phase to 5 in the post-bloom phase (data not shown). The ratio in the settled material was 2 in the bloom developing phase at 100 m, after which it decreased to <1 during the decaying bloom and the post-bloom phases.

Table 3. Concentrations and ratios of particulate organic material (POC and PON) from water column and sediment traps at 20, 50, and 100 m depths during 3 sampling phases. Sedimented POC and subsequent amorphous detritus at 100 m on 23, 25, and 29 April are missing, as is suspended POC at 100 m on 29 April. Data are averages ± SE. No. of samples given in parentheses

Phase	Depth (m)	Suspended (mg m^{-3})		Sedimented (mg m^{-2})		POC:PON ratio (g:g)			
		POC	PON	POC	PON	Suspended	r^2	Sedimented	r^2
Developing bloom	20	520.7 ± 57.7 (7)	90.2 ± 10.6 (7)	1022.8 ± 103.9 (10)	158.8 ± 14.7 (10)	6.0 ± 0.6 (7)	0.5	6.6 ± 0.5 (10)	0.5
23–30 April	50	236.0 ± 23.2 (7)	40.2 ± 6.1 (7)	644.0 ± 60.9 (10)	103.5 ± 10.2 (10)	6.3 ± 0.6 (7)	0.9	6.4 ± 0.3 (10)	0.6
	100	93.9 ± 13.9 (2)	11.4 ± 2.1 (2)	503.3 ± 27.7 (10)	77.6 ± 6.6 (10)	9.9 ± 0.2 (2)	0.3	6.9 ± 0.7 (10)	0.01
Decaying bloom	20	538.3 ± 90.5 (5)	79.5 ± 15.5 (5)	822.6 ± 192.6 (10)	114.0 ± 25.5 (10)	7.6 ± 1.6 (5)	0.4	7.9 ± 0.7 (10)	0.9
2–19 May	50	201.8 ± 36.8 (5)	34.0 ± 10.2 (5)	499.9 ± 99.0 (10)	70.5 ± 14.0 (10)	6.9 ± 1.1 (5)	0.9	7.4 ± 0.7 (10)	0.7
	100	120.9 ± 13.7 (5)	13.9 ± 1.5 (5)	491 ± 147.6 (7)	45.3 ± 10.3 (7)	8.6 ± 0.4 (5)	0.9	11.6 ± 1.8 (7)	0.4
Post bloom	20	269.6 ± 131.0 (3)	38.0 ± 17.5 (3)	795.8 ± 304.0 (4)	50.9 ± 17.6 (4)	6.9 ± 0.2 (3)	0.9	24.0 ± 4.4 (4)	0.9
28 May–9 June	50	111.7 ± 30.5 (3)	10.4 ± 1.8 (3)	296.1 ± 179.3 (3)	21.2 ± 4.5 (3)	10.8 ± 2.9 (3)	0.2	13.6 ± 4.5 (3)	0.9
	100	89.6 ± 11.5 (3)	8.4 ± 0.6 (3)	298.3 ± 114.8 (4)	18.9 ± 4.7 (4)	10.7 ± 0.9 (3)	0.7	16.0 ± 3.0 (4)	0.7

Loss rates

Sinking velocity of particulate material increased with increasing depth (except amorphous detritus) (Table 4). Sinking velocity of FPC was approximately one order of magnitude higher than PPC and amorphous detritus (Table 4).

Estimated daily loss rates of PPC due to sedimentation were generally high in the first 2 phases (Fig. 10), with an average daily loss rate of 5.1 ± 1.6% d^{-1} (n = 13) equivalent to a loss of 0.6 ± 0.01 g C m^{-2} d^{-1} during all 3 bloom phases. The average daily loss rate of PPC due to copepod grazing was 4.1 ± 1.5% d^{-1} (n = 13). This was equivalent to an average loss of 0.2 ± 0.06 g C m^{-2} d^{-1} during all 3 bloom phases.

Copepod community grazing impact

The specific ingestion rates calculated from the applied methods were variable; however they showed similar trends, with higher rates during the bloom relative to the post-bloom period (Table 2). In general, the lowest estimates originate from bottle incubations (i.e. the egg and faecal pellet production), while the *in situ* measurements (i.e. gut fluorescence and *in situ* faecal pellet production method) resulted in higher rates. Variation in the specific ingestion rate estimates of the different methods varied with bloom phase. The gut fluorescence method values was significantly higher than those originating from the faecal pellet production method, with bottle incubations during the first 2 bloom phases ($p < 0.01$, n = 21) and ($p < 0.01$, n = 25), respectively. Ingestion measured from *in situ* faecal pellet production was significantly higher than that from the faecal pellet production from bottle incuba-

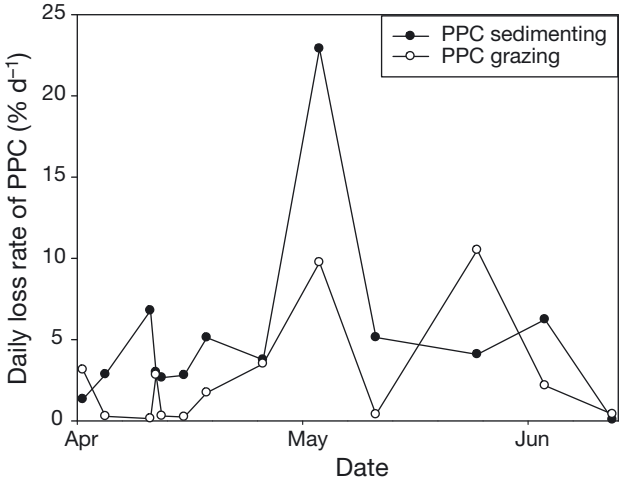

Fig. 10. Daily loss rates (% d^{-1}) of phytoplankton based carbon (PPC), caused by grazing by copepods (Table 1) and sedimentation at the 0 to 50 m depth stratum

Table 4. Sinking velocities of total particulate organic carbon (POC) and its fractions (PPC, FPC, and amorphous detritus) at 20, 50, and 100 m depths during 3 sampling phases. POC and, subsequently, amorphous detritus at 100 m on 23, 25, and 29 April are missing. Data are averages ± SE. No. of samples given in parentheses

Phase	Depth (m)	Velocity (m d^{-1})			Amorphous detritus
		POC	PPC	FPC	
Developing bloom	20	4.1 ± 0.6 (10)	2.7 ± 0.6 (10)	117.4 ± 35.0 (10)	25.5 ± 14.7 (10)
23–30 April	50	6.0 ± 1.0 (10)	5.3 ± 1.6 (10)	174.1 ± 59.7 (10)	19.6 ± 18.3 (10)
	100	10.5 ± 1.0 (4)	18.9 ± 2.7 (10)	108.0 ± 13.7 (10)	6.0 ± 2.1 (4)
Decaying bloom	20	3.3 ± 0.7 (10)	3.2 ± 0.5 (10)	35.5 ± 5.1 (10)	17.6 ± 15.5 (10)
2–19 May	50	6.5 ± 2.0 (10)	4.7 ± 0.7 (10)	48.2 ± 8.8 (10)	29.2 ± 26.3 (10)
	100	9.4 ± 2.8 (10)	10.9 ± 2.9 (10)	188.8 ± 39.1 (10)	9.1 ± 5.4 (10)
Post bloom	20	8.4 ± 2.8 (6)	3.0 ± 1.2 (6)	85.3 ± 20.0 (6)	13.2 ± 5.6 (6)
28 May–9 June	50	5.3 ± 3.1 (6)	3.8 ± 1.7 (6)	140.0 ± 12.0 (6)	2.8 ± 1.2 (6)
	100	6.9 ± 2.1 (6)	10.0 ± 5.6 (6)	321.7 ± 104.5 (6)	6.3 ± 3.9 (6)

tions during the decaying bloom ($p < 0.01$, $n = 25$). During the post bloom, the estimate from the *in situ* faecal pellet production was significantly higher than the other methods (except the egg production [$p < 0.01$, $n = 9$]). The overall averaged grazing rates were significantly lowest in the post-bloom phase ($p < 0.01$, $n = 13$).

Quantification of the daily grazing impact of the copepod community on the phytoplankton based on only daytime measurements of gut fluorescence and *in situ* faecal pellet production requires knowledge about diel feeding periodicity and vertical migration. During the investigation of vertical migration (Fig. 11) we measured gut fluorescence and *in situ* faecal pellet production at 12:00 and 24:00 h (Table 5), and no significant diurnal differences in these rates were detected. However, the biomass of copepods in the upper 50 m doubled from our normal sampling time to around 24:00 h, from 1455 ± 853 to 3147 ± 1168 mg C m^{-2} (Fig. 11) due to vertical migration from deeper layers (data not shown). Consequently, our estimates of grazing impact by the copepod are conservative by not considering the increase in biomass around 24:00 h, and the actual grazing impact could be twice as high as our estimates (Table 2).

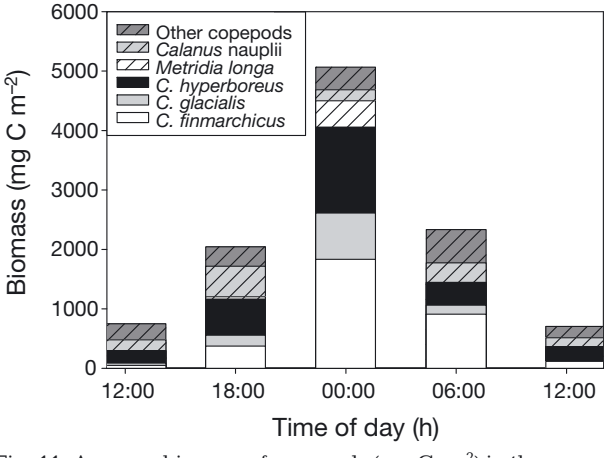

Fig. 11. Average biomass of copepods (mg C m^{-2}) in the upper 50 m during a diurnal study from 29 to 30 April

DISCUSSION

Hydrography and plankton succession

In Disko Bay, the sea ice conditions are highly variable (Hansen et al. 2003). In some years, no stable sea ice establishes (Madsen et al. 2008b), while in other years, the sea ice breaks up as late as June (Nielsen & Hansen 1995). In the present study, the sea ice broke up in early April. The spring phytoplankton bloom developed immediately after the breakup of sea ice. Thus, sea ice conditions are very important for the match between the arrival of overwintering copepods to the surface layers and the high spring phytoplankton production, and therefore also for the subsequent sedimentation.

In 2008 the bloom started on 9 April, and the main bloom event (from 23 April) was triggered by a thermocline at 60 m combined with increasing irradiance. Chl *a* concentration was in the same order of magnitude as previously reported from a shallow cove of Disko Bay (Sejr et al. 2007). It was, however, nearly twice as high as previously recorded spring concentrations from the Disko Bay proper (Levinsen et al. 2000a, Madsen et al. 2001). Generally the 3 chl *a* fractions in this study contributed equally to the phytoplankton biomass. However, distinct underlying successions were observed. Prior to the spring bloom chl *a* <10 µm

Table 5. Comparison of gut pigment contents (GC; ng total pigment fem^{-1}) of *Calanus* spp. and the specific egestion rate (% d^{-1}) of the copepod community from the *in situ* fecal pellet experiment around 12:00 h (29 April) and 24:00 h (30 April). Data are averages ± SE. No. of samples given in parentheses

	12:00 h	24:00 h
Calanus finmarchicus (GC)	40 ± 6 (8)	31 ± 9 (5)
C. glacialis (GC)	60 ± 10 (8)	89 ± 28 (5)
C. hyperboreus (GC)	157 ± 20 (20)	204 ± 24 (10)
Specific egestion rate	1.0 ± 0.3 (13)	0.8 ± 0.2 (8)

dominated; during the spring bloom a succession of the 3 size classes was observed initiated by a peak of chl *a* <10 µm, followed by a 10–50 µm peak and culminating with a peak of chl *a* >50 µm (diatoms) and a post-bloom dominance of chl *a* <10 µm (haptophytes). The same succession was observed throughout the water column. The spring bloom lasted for approximately 1 wk after nitrate depletion. During the second half of May, melt water from glaciers reduced sea surface salinity and the upper 20 m became additionally stratified. At the end of the investigation chl *a* concentration was low in the surface, and the phytoplankton were concentrated at the nutricline/pycnocline.

Generally, the timing of the ascending copepods appears to match the spring bloom (Diel & Tande 1992), which was also confirmed by the present study, where *Calanus* spp. were present in the surface from the initiation of the bloom. Early appearances of *Calanus* in April have been observed in Disko Bay in 1996 and 1997 (Madsen et al. 2001) and in 2005 (Madsen et al. 2008b). However, the main difference between the present study and the 2 latter was the higher biomass of *Calanus* observed already in April and an early maximum biomass peak in early May. It has been suggested that previously sampling of the copepod community with large mesh size nets (e.g. 200 µm) has lead to overestimation of the importance of large species like *Calanus*. We sampled the copepod community with small mesh size nets (50 µm), and still species of *Calanus* comprised up to 99% of the biomass, which is typical for Arctic areas during spring (Hirche 1991, Riser et al. 2007, Madsen et al. 2008a,b). The copepods remained abundant in the upper 100 m throughout the study and did not decrease until early July. *C. hyperboreus* was the only species observed descending to deep waters, whereas *C. finmarchicus* and *C. glacialis* disappeared from the surface but did not aggregate above the bottom as did *C. hyperboreus*. It is possible that they have dispersed out into the bay proper by deeper currents (Holland et al. 2008). This observation is in contrast to the suggestion of a self-sustaining population of *C. finmarchicus* and *C. glacialis* in this area as suggested earlier (Madsen et al. 2001, Niehoff et al. 2002).

Seasonal variability of sedimentation in Disko Bay

During the present study, the sedimentation of organic material increased considerably for all the measured variables. High sedimentation of particulate organic material linked to spring phytoplankton production is common in Disko Bay (Juul-Pedersen et al. 2006, Sejr et al. 2007) and in other Arctic areas (Wassmann 1990, Andreassen et al. 1999, Turner 2002). The POC sedimentation reported in the present study is, to our knowledge, among the highest reported values during an Arctic spring bloom. It resembles estimates from the spring bloom in a shallow cove in Disko Bay in April (ranging from 1200 to 3000 mg C m^{-2} d^{-1} in the upper 5 to 45 m; Sejr et al. 2007), but with a substantial higher PPC fraction of the POC (60% as opposed to 36%), despite the same level of phytoplankton biomass in that study. Sejr et al. (2007) suggested a mismatch between ascending copepods and the spring phytoplankton bloom leads to subsequent low grazing impact by the copepods. In addition, the carbon to chl *a* conversion factor for the sedimented phytoplankton used here was 50% lower, which implies that our PPC contribution to POC could have been 50% higher. Sedimentation of PPC has been reported in similar ranges to ours, during a spring bloom in the central Barents Sea in May-June (Olli et al. 2002, Caron et al. 2004, Reigstad et al. 2008). These studies revealed a close coupling between phytoplankton succession and sedimentation as suggested in the present study. Furthermore, our results of POC sedimentation in the post bloom resembled the values previously found in Disko Bay in June (Juul-Pedersen et al. 2006) and in the central Barents Sea in May (Wassmann et al. 1990, Andreassen & Wassmann 1998). In agreement with the present study, the latter examples report a low contribution of phytoplankton sedimentation relative to carbon in May-June.

Sedimented POC in the present study differed remarkably in composition between two of the bloom phases (developing and post bloom). The above results indicate that much of the vertical reduction (i.e. vertical attenuation) of the settling organic material takes place over a short vertical distance (Fig. 9). The vertical attenuation seems strongest in the upper 50 m, as reported earlier (Riser et al. 2002, Reigstad et al. 2008). The vertical attenuation in the developing bloom of POC was mirrored by amorphous detritus and, to a lesser extent, PPC and FPC. This suggests a selective attenuation of particles where low density particles are being retained above the pycnocline. It is supported by the general lower velocity of PPC in the upper 50 m relative to 100 m depth. This is in contrast to the much higher velocities of the denser faecal pellets observed throughout the water column. If the pycnocline is acting as a barrier to the sedimentation of certain particles, the vertical changes of sedimentation rate would not directly reflect the transformation of the sinking material with depth but rather a differential sedimentation of particles.

In the present study, average FPC contribution to sedimenting POC was low (16%) but within values reported for the Arctic areas in March-May (Wassmann et al. 1999, Riser et al. 2002) and in June

(Andreassen et al. 1996). The relative importance of FPC sedimentation is dependent on copepod abundance, FPR, and faecal pellet size (Besiktepe & Dam 2002, Turner 2002). In the present study, the highest FPC sedimentation was found during the decaying bloom, which is in accordance with the highest FPR (Fig. 7A) and copepod abundance measured.

Nitrogen has previously been shown to be limiting the spring bloom in Disko Bay (Andersen 1981, Nielsen & Hansen 1995, Juul-Pedersen et al. 2006). When nitrate deficiency in phytoplankton growth occurs, an increase in the POC/PON ratio of 6.6 can be expected (Redfield et al. 1963). The high PPC sedimentation during the bloom was probably caused by nitrate limitations, as nitrate decreased in the photic zone (Fig. 2), although average POC/PON ratios found in the suspended and sedimented material were still close to the Redfield ratio. It is likely that phytoplankton aggregation and density dependent coagulation during growth caused the high sedimentation rate (Kiørboe et al. 1994). This is supported by the increased velocity observed at 100 m depth and indicates a depth-related formation of phytoplankton aggregates. During the second half of the decaying bloom, decreased phytoplankton biomass and nitrate depletion led to lower POC sedimentation. PPC attenuation was not observed in the upper 50 m, which suggests that the subsurface bloom was located below the pycnocline and depth of mixing. A majority of the sedimented POC (80%) from the upper 50 m was found at 100 m, thus supporting this notion. Consequently, sedimentation occurs with reduced resuspension and density dependent particle restrictions though the pycnocline. A post-bloom increase of POC sedimentation coincided with a subsurface phytoplankton bloom supported by reintroduced nitrate. The vertical attenuation of POC fractions resembled that observed in the bloom-developing phase. When nitrate was depleted, at the end of the post-bloom phase, both suspended and sedimented POC/PON ratios increased with depth. Phytoplankton growth was probably nitrate-limited, as indicated by POC/PON ratios well above the Redfield ratio in the sedimented material. We cannot, however, exclude a potential influence of increased carbon concentrations from sedimentation of amorphous detritus and faecal pellets, which would increase the POC/PON ratio (Olesen & Lundsgaard 1995, Daly 1996, Daly et al. 1999). Furthermore, potential size dependent sedimentation of phytoplankton (Bienfang 1980, Sarthou et al. 2005) or aggregation (Kiørboe & Hansen 1993, Kiørboe et al. 1994) is not accounted for, which would increase the POC/PON ratio (Olli et al. 2002). The relations between suspended and sedimented carbon and chl *a* were not significantly different ($p > 0.01$, $n = 152$), and the carbon concentration of suspended phytoplankton relative to the sedimented biomass did not change. Sedimented POC/PON ratios found in Greenland Sea in June-August consisting of nutrient deficient diatoms (Daly et al. 1999) resembled the findings of the present study. Accordingly, we did not find any correlation between nitrate concentration and sedimented POC/PON ratios.

The high sedimentations reported here underline the importance of the process as a path of carbon transport in Disko Bay. The results indicate a seasonal variability in magnitude and composition of POC sedimentation, where fresh phytoplankton sedimented in the developing bloom and the quality and quantity of the sedimented material decreased towards the post-bloom phase.

Grazing impact of the copepod community — a comparison of methods

The seasonal variation in composition, biomass, and feeding activity of the copepods strongly influenced the bentho-pelagic coupling by shaping the quality and quantity of organic material sinking to the depths. The timing of mesozooplankton migration to match the spring phytoplankton bloom is essential for an efficient pelagic turnover of phytoplankton and for the magnitude of the secondary production (Diel & Tande 1992, Niehoff et al. 2002). Here we applied 4 methods to quantify the grazing impact on the phytoplankton community. The reliability of the measurements depended on season (i.e. the quantitative and qualitative composition of the prey plankton community). The gut fluorescence method directly quantifies the amount of phytoplankton ingested, while pellet and egg production rates through the application of different conversion factors estimate the carbon ingested (i.e. both autotrophic and heterotrophic prey). In addition, the rates are impacted by diel periodicity in feeding and migration. In the present study, no differences could be detected between midday and midnight rate measurements (Table 5), but significant vertical migration took place increasing the night biomass in the upper 50 m. Consequently, our estimated grazing impact could be higher than reported here (Table 2) based on our normal sampling program.

Ingestion calculated from the egg production rate assumes a direct transfer of the ingested food to egg production. This is not always true for copepods that store large amounts of lipids like *Calanus* (Lee et al. 2006 and references therein). Before the bloom, at low food availability, they may start to produce eggs based on stored lipids (Hirche & Kattner 1993, Hirche & Niehoff 1996). At the termination of the bloom, egg production ceases for *C. glacialis*, as the lipid stores

are refueled (S. Kjellerup et al. unpubl.). During the bloom, however, the assumption of egg production depending on food availability holds true for the 2 smallest *Calanus* spp. (Nielsen & Hansen 1995).

In contrast to egg production, faecal pellet production is more directly related to ingestion (Besiktepe & Dam 2002, Seuthe et al. 2007). Hence, lower faecal pellet production was measured during the developing bloom than later in the bloom where more food was available. The individual faecal pellet production of the 3 *Calanus* species was measured in incubations of 24 to 48 h, and there were indications of chl *a* depletion in the incubation bottles in the post-bloom phase (R. Swalethorp et al. unpubl.) leading to underestimations of the faecal pellet production. Another potential problem is ingestion of faecal pellets during the incubation (coprophagy), as no mesh false bottom was used. However, experiments with *Calanus finmarchicus* have showed that faecal pellets were fragmented (coprorhexy) rather than ingested (Noji et al. 1991). Faecal pellet loss due to coprophagy might be unimportant in the present study, but if coprorhexy disintegrate the faecal pellets completely (Lampitt et al. 1990, Noji et al. 1991) the result would be an underestimated faecal pellet production. The *in situ* faecal pellet production experiment measures the instantaneous faecal pellet production in short time incubations, where coprophagy and food limitation should be of minor importance. Another difference to the bottle experiments was that the *in situ* incubations were made on a mixture of the larger stages (i.e. including copepodites) of the dominating copepods. The smaller copepodites will, on average, have a higher specific pellet production than the adult females (Hansen et al. 1997). Accordingly, the *in situ* pellet production was consequently higher than the faecal pellet production from the long-duration bottle incubation (Table 2).

The gut fluorescence method gave the highest grazing estimate of all the methods during the first 2 bloom phases, mainly as a result of a high specific production by *Calanus finmarchicus*, approximately 60% higher than estimated for *C. glacialis* and *C. hyperboreus*. During the 2 first bloom phases the potential food was completely dominated by diatoms. In such situations, the gut fluorescence method can therefore be expected to produce very reliable estimates of copepod grazing. During the post-bloom phase, the highest estimates came from the *in situ* production. Gut fluorescence may underestimate the grazing rate when phytoplankton biomass is low and/or dominated by small spp., since copepods then ingest non-fluorescent food particles such as protozooplankton to sustain production (Ohman & Runge 1994, Hirche & Kwasniewski 1997, Hansen et al. 1999, Levinsen et al. 2000b). Consequently, successful application of the gut fluorescence method is restricted to phases when herbivory dominates, i.e. during the spring phytoplankton bloom (Kiørboe et al. 1985, Peterson et al. 1990). Thus, a direct correlation between mixed food availability and faecal pellet production seemed to give the most reliable value from the *in situ* production during the post-bloom phase.

The 2 faecal pellet production estimate methods based on direct counting are much more time-consuming than gut fluorescence, but they are a much more reliable tool for estimating the grazing throughout the season. Furthermore, the *in situ* faecal pellet production reduces potential coprophagy and coprorhexy on produced faecal pellets by separating copepods and their pellets. In addition, a short-term incubation period minimized the risk of food depletion during incubation. In contrast, during a long-term experiment, a loss of phytoplankton due to sedimentation and/or grazing during the incubation period can lead to negative effects on the faecal pellet production over time (Besiktepe & Dam 2002, Seuthe et al. 2007), but the long duration is nonetheless necessary when measuring egg production of batch spawning copepods.

In summary, all 4 methods have their strengths and limitations. The choice of method depends on the season, i.e. condition and composition of the phytoplankton community as well as the specific research objective and the time available. Here the overall average was applied to evaluate the copepod community grazing impact on phytoplankton (Fig. 10). Despite a match between the developing bloom and the arrival of *Calanus* to the surface layer, the grazing impact of the copepods was insignificant in the termination of the spring bloom (Table 1, Fig. 10).

The short exponential spring phytoplankton bloom in Disko Bay in 2008 resulted in high phytoplankton sedimentation. The 4 methods used to evaluate the copepod grazing potential concurrently show that grazing impact by copepods played a minor role on the observed phytoplankton succession. Therefore the termination of the phytoplankton spring bloom was primarily caused by sedimentation of nitrogen-limited phytoplankton rather than grazing from the *Calanus*-dominated copepod community.

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Plankton community structure in a West Greenland fjord

Influenced by the Greenland Ice Sheet

Greenlandic fjords are located at the junction between the ocean and the Greenland Ice Sheet and therefore sensitive to future climate change. However, little is known about the fjord-glacier link, and fjords are in general understudied. Furthermore, biological studies and basic ecological understanding remain very incomplete. This PhD thesis describes differences in plankton community structure in the offshore West Greenland system towards a glacial outlet fjord, and the results suggest differences in offshore and fjord systems. The abundance of small copepods is surprisingly high in the fjord and the studies contradict the traditional emphasis on large *Calanus* copepods as the main grazer on an annual basis. Instead the studies demonstrate that small copepods can be a key component in Arctic pelagic food webs. Concentrations of suspended sediments in the fjord are high. However, suspended sediments cannot solely explain the spatial distribution of plankton communities. Instead, the high primary production of the system coupled with ocean-fjord-glacier interaction is suggested as an important driver for the findings.

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