

Mesozooplankton distribution in Svalbard waters

Calanus spp. and its relationship to
hydrographic variability

Malin Daase



The University Centre in Svalbard
and
Department of Biology
University of Bergen, Norway



Thesis submitted for the degree of philosophiae doctor

Longyearbyen, October 2007

Doctoral thesis for the degree of philosophiae doctor (PhD)
Defence at The University Centre in Svalbard, Longyearbyen, Norway
6 February 2008

Leader of the committee: Thorolf Magnesen
Department of Biology
University of Bergen

Opponents: Sigrún Jónásdóttir
Department of Marine Ecology and Aquaculture
Danish Institute for Fisheries Research

Frederika Norrbin
Norwegian College of Fishery Science
University of Tromsø

ISBN-Nr.

The people along the sand
All turn and look one way
They turn their back on the land.
They look at the sea all day.

[...]

The land may vary more;
But wherever the truth may be
The water comes ashore,
And the people look at the sea.

They cannot look out far.
They cannot look in deep.
But when was that ever a bar
To any watch they keep?

Robert Frost

“Yet with the Pole actually in sight I was too weary to take the last few steps. The accumulated weariness of all those days and nights of forced marches and insufficient sleep, constant peril and anxiety, seemed to roll across me all at once. I was actually too exhausted to realize at the moment that my life's purpose had been achieved.”

Robert E. Peary, The North Pole

Preface

Well, it looks like I might have conquered the pole after all, although at the moment I still feel too exhausted to realize that my PhD times are actually over. But with “those days and nights of forced marches and insufficient sleep, constant peril and anxiety” finally coming to an end it is time for some Thank You's.

First I like to thank my supervisor at UNIS, Ketil Eiane on whose initial ideas this thesis is build. I am grateful for his support, many constructive discussions and most of all for giving me plenty of opportunities to leave my office and be out in the field during scooter season. Thanks also to Dag L. Aksnes, my official supervisor at Bergen University for his input to this thesis. All my samples were taken on cruises that were part of UNIS courses and I am grateful to the “tokt”-leaders Jørgen Berge and Bjørn Gulliksen for always making ship time available for some plankton sampling. I am also indebt to Stig Falk-Petersen who provided additional data, and to Slavek Kwasniewski who taught me how to distinguish all these tiny creatures. I very much appreciated those many hours of constructive discussions with Espen Bagøien via telephone. Thanks also to N.C. Stenseth and Jon-Olav Vik for their interest and collaboration.

UNIS has become a special place for me and I very much enjoyed studying and working here. I like to thank my friends and colleagues at UNIS for contributing to the enjoyable atmosphere encountered in every department. In particular I want to acknowledge former director Lasse Lønnum who funded an extra half year after my initial three year contract came to an end. All those trips to Billefjorden would not have been possible without Daniel Vogedes, most reliable navigator in any white-out and worlds best field assistant (when awake). Berit Jakobsen is still the best librarian on both sides of the Arctic Circle and also a great hostess of many cosy dinner parties. Thanks also to Ragnheid Skogseth and Frank Nilsen, my oceanography advisors and Matlab-support-team. And without the help of Janne Søreide during the last month my synthesis would probably still not be finished.

Life as a PhD student at UNIS wouldn't have been the same without some of my fellow sufferers. Christiaane Hübner and I spend three years in an office together and although our working atmosphere may not have been the most efficient one, at least we had fun! Fortunately the fun did not stop after we got separated into shiny new offices and occasionally we were even discussing our goose and *Calanus* problems (and p-values... again and again...). I am grateful for all the times she led me hide in her office, for showing the only sensible reaction to my panic attacks (ignoring them) and of course for all the scooter trips and film evenings. A big hug to Marta Slubowska, a great companion

in countless lunch breaks (well, afternoon coffee for her, breakfast time for me) and a good friend throughout the years. Thanks also to Carolin Arndt, together we survived our first scooter season and many experimental dinners. I also like to mention Gosia Slubowska who was always up for non-PhD related activities such as an evening in the cinema or a walk with Yang.

Svalbard has been my home for the last nine years and its incredible nature and in particular the different light displays throughout the seasons still amaze me every day. However, being isolated at the rim of the Arctic Ocean I appreciate the people who kept me in touch with the real world down south. Thanks to Anke and Lena for visiting me more often than anyone else and for their constant encouragement. Sünnje was a great conference-travel-companion and helpful in statistical questions. I am grateful to her and Lena for providing a place to stay anytime I was in Tromsø. The same goes to Irene who always provided shelter and 'airport-shuttle-service' in Oslo. Finally, I like to thank my family for their support, in particular my parents who sponsored the first 27 years of my life and who always let me do what I wanted to do.

Summary

This thesis investigates mesozooplankton abundance, composition and distribution in Svalbard waters in relation to hydrography. Sampling was carried out in the archipelago of Svalbard mainly during summer and autumn between 2000 and 2004. From cluster analysis four species assemblages were distinguished and these reflected differences in hydrography and bottom depth. In particular the distribution of the Atlantic *Calanus finmarchicus* relative to that of the Arctic *Calanus glacialis* was associated with different hydrographic regimes. Differences in the species assemblages primarily resulted from variations in species densities rather than from taxonomical variation. For species of Atlantic and Arctic origin significant relationships with temperature and salinity were found. Regression models were used to quantify the influence of water mass characteristics on the abundance of the three different *Calanus* species that co-occur in the study area. About 50% of the variability in abundance of each *Calanus* species could be accounted for by variability in temperature and salinity. *C. finmarchicus* abundance was positively related to warmer and more saline waters, as expected from its distributional southern core area. Conversely, the Arctic species *C. hyperboreus* was more abundant in colder and fresher waters. The numbers of *C. glacialis* decreased with increasing temperature and salinity in shallow areas, while the opposite trend was found in deep locations. Salinity and temperature between 50 - 150 m depth were in most cases better predictors for *Calanus* spp. abundance than near-surface conditions.

Variability in the vertical distribution of the three *Calanus* species and *Metridia longa* reflected life history and behavioural adaptations on diel and seasonal scale. Diel vertical migration was observed for copepodite stages of *M. longa* but generally not for *Calanus* spp. The copepodite stage composition indicated a south to north delay in the succession of *Calanus* development and that the descent to overwintering depth had started at time of sampling. The vertical distribution patterns of *C. finmarchicus* and *M. longa* were found to be consistent with the hypothesis that the developmental stages distributed according to preferences for light intensity.

This thesis includes one of few year-round studies on *Calanus* population dynamics from the high Arctic. The three *Calanus* species co-existed in the studied fjord. The estimated length of the life cycle of *C. glacialis* (1-2 years) and *C. finmarchicus* (1 year) were in

agreement with previous studies in Svalbard and the Arctic in general. For *C. hyperboreus* a one year life cycle was observed which is among the shortest life cycle duration reported for this species. Differences in winter mortality rates for the three *Calanus* populations indicate that these affect the species composition in the study area.

The observed statistical relationships between *Calanus* abundance and hydrography indicate that changes in ocean climate as a consequence of global warming may alter the relative composition of the three *Calanus* species in Svalbard waters. However, lack of such relationship between *Calanus* biomass and hydrography suggests that a changing climate may induce a shift in size structure rather than in biomass which may have repercussions on the pelagic food web.

Contents

List of papers	2
Introduction	3
The physical environment in the study area	9
Results and discussion	12
Mesozooplankton composition, distribution and the relationship to hydrographic variability	12
Potential significance of advection on the <i>C. finmarchicus</i> distribution	22
Vertical distribution and migration	28
Life cycles and population dynamics of co-existing <i>Calanus</i> species	33
Possible effects of global warming on the <i>Calanus</i> community and the pelagic food web	35
References	43

Boxes

1. Redundancy analysis (page 18)
2. Modelling the role of advection and local production in zooplankton population dynamics (page 23-24)

List of papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numbers.

Paper I

Daase M, Eiane K (2007) Mesozooplankton distribution in northern Svalbard waters in relation to hydrography. *Polar Biology* 30 (8):969-981

Paper II

Daase M, Vik JO, Bagøien E, Stenseth NC, Eiane K (2007) The influence of advection on *Calanus* near Svalbard: statistical relations between salinity, temperature and copepod abundance. *Journal of Plankton Research* 29(10):903-911

Paper III

Daase M, Eiane K, Aksnes DL, Vogedes D (in Press) Vertical distribution of *Calanus* spp. and *Metridia longa* at four Arctic locations. *Marine Biology Research*.

Paper IV

Arnkværn G, Daase M, Eiane K (2005) Dynamics of coexisting *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* populations in a high-Arctic fjord. *Polar Biology* 28:528-538

Introduction

The archipelago of Svalbard is located in a border-area between Atlantic and Arctic climatic and biogeographic zones (Stroemberg 1989). Ecological research in this area has mainly focused on the fjords along the western coast such as the Isfjorden area (Digby 1961, Lie 1965), and more recently Hornsundfjorden (Koszteyn and Kwasniewski 1989, Koszteyn et al. 1991, Weslawski et al. 1991) and in particular Kongsfjorden (Hop et al. 2002, Kwasniewski et al. 2003, Basedow et al. 2004, Hop et al. 2006, Willis et al. 2006). Northern and eastern Svalbard waters on the other hand have only occasionally been sampled (Mumm et al. 1998, Walkusz et al. 2003).

The main pathway of Atlantic water into the Arctic Ocean (the West Spitsbergen Current WSC, see also 'The physical environment in the study area') runs along the western coast of Svalbard. A boreal pelagic community characterizes these waters. This community is transported northwards within the WSC and is commonly found as expatriates in the Arctic Ocean (Sars 1900, Hirche and Mumm 1992, Mumm et al. 1998, Hop et al. 2006). There is high inter-annual variability in the strength of the WSC and consequently in the inflow of Atlantic water to the Arctic (Saloranta and Haugan 2001). Observations from fjord plankton populations suggest that variability in abundance and biomass are strongly related to the variability in the influx of Atlantic water mass (Hop et al. 2002, Kwasniewski et al. 2003). Sufficiently strong this inflow alters the species composition towards boreal species, whereas Arctic species dominate if the Atlantic influx is diminished (Hop et al. 2002, Kwasniewski et al. 2003, Willis et al. 2006). In addition, Svalbard waters are often modified by local oceanographic processes (e.g. freshwater runoff, wind driven circulation, and cooling). Thus the plankton communities in Svalbard waters reflect variations in ocean climate in particular due to two main factors: advective input and loss of organisms, and biological responses to regional as well as local variations in water characteristics. Depending on the frequency and strength of the advective input to Svalbard waters relative to local processes the advective signal should be observable on the level of plankton community as a quantifiable relationship between boreal and Arctic forms and hydrographic variability. Exploration of this relationship

between hydrographic variability and variation in the abundance of dominating copepod species was part of the motivation for this study.

Plankton by definition drifts passively with water currents (Hensen 1887) thus their spatial and temporal distribution is linked to hydrodynamic processes such as water mass distribution and circulation patterns. Plankton is the key element of the pelagic foodweb with zooplankton as the main trophic link between primary producers and higher trophic levels. Thus plankton plays an important role in integrating hydroclimatic signals into the pelagic ecosystem since any effect of hydrographic variability on plankton populations will be transferred to the next trophic level (Planque and Taylor 1998, Beaugrand 2005, Hays et al. 2005). The relatively short life cycles of many plankton populations make them well suited for tracing seasonal to inter-annual changes in environmental conditions (Mackas et al. 2004, Hays et al. 2005). In the North Atlantic inter-annual variations in zooplankton abundance has for example been related to hydrodynamic variables such as the Gulf stream index (Reid et al. 1998, Planque and Taylor 1998), sea surface temperature (Conversi et al. 2001, Lindley and Reid 2002), wind direction and intensity (Dickson et al. 1988), circulation patterns (Stephens et al. 1998, Reid et al. 2003), and in particular to the North Atlantic Oscillation (NAO) index (Planque and Taylor 1998, Reid et al. 1998, Greene et al. 2003, Nash and Geffen 2004).

In general one can distinguish between direct and indirect effects of climatic variability on zooplankton populations (Ottersen et al. 2001). Direct effects include changes in development, growth and survival due to changes in temperature (Campbell et al. 2001, Vidal 1980a, Huntley and Lopez 1992, Hirst and Lampitt 1998) as well as changes in the distribution and abundance of organisms through changes in circulation patterns and water mass distribution (Iles and Sinclair 1982, Stephens et al. 1998, Beare et al. 2002, Dalpadado et al. 2003). Indirectly ocean climate variability can influence zooplankton populations through its effect on ecosystem functions such as the timing and magnitude of the spring bloom (Richardson and Schoeman 2004) or through hydrodynamic induced changes in the predator community (Reid et al. 2000, Wespestad et al. 2000, Dalpadado et al. 2001). The interactions between hydrographic variability and direct and indirect

ecosystems responses have been well documented in the Barents Sea (Skjoldal and Rey 1989, Ottersen and Stenseth 2001). Here variability in zooplankton abundance and distribution is suggested to be directly affected by inter-annual variability in the inflow of Atlantic water (Helle 2000, Edvardsen et al. 2003, Dalpadado et al. 2003), but also the timing of the inflow has an effect on the amount of advected zooplankton (Skjoldal et al. 1992). In addition, variability in ice cover and stratification processes affect the timing of the spring bloom and thus the synchronization between primary and secondary producers (Skjoldal et al. 1987). Variability in zooplankton abundance due to variability in ocean climate may have repercussions on the recruitment and population size of fish stocks (Skjoldal et al. 1992, Astthorsson and Gislason 1998, Helle and Pennington 1999, Sundby 2000).

Strong relationships between hydrography and variability in abundance and distribution have in particular been observed for copepods of the genus *Calanus* (Grainger 1963, Jaschnov 1961, van Aken et al. 1991, Edvardsen et al. 2003). *Calanus* spp. dominates the mesozooplankton community in Arctic and Atlantic waters in terms of biomass (Sars 1900, Hirche 1991, Mumm et al. 1998). Therefore I selected these calanoid copepods as target species for this thesis (**papers II, III and IV**). Three *Calanus* species co-occur in the study area: *Calanus finmarchicus* (Gunnerus, 1765), *Calanus glacialis* Jaschnov, 1955 and *Calanus hyperboreus* Krøyer, 1838. *C. finmarchicus* is defined as an Atlantic species (Jaschnov 1966, Jaschnov 1972, Conover 1988). Its occurrence in the Arctic Ocean is typically associated with the inflow of Atlantic water masses (Grainger 1961, Grainger 1963, Jaschnov 1972, Mumm et al. 1998) and it may dominate the calanoid community in areas of strong Atlantic influence (Thibault et al. 1999, Auel and Hagen 2002). However, it is regarded as an expatriated species in the Polar Basin and probably does not reproduce there (Gran 1902, Tande et al. 1985, Diel 1991, Conover and Huntley 1991).

C. glacialis and *C. hyperboreus* are of Arctic origin (Jaschnov 1972, Conover 1988, Hirche 1991) and dominate the mesozooplankton community in the Arctic Ocean in terms of biomass (Sars 1900, Lee 1974, Dawson 1978, Hirche and Mumm 1992, Thibault et al. 1999). *C. glacialis* has its main distribution in the relatively shallow Arctic shelf

seas (Kosobokova et al. 1998, Lischka et al. 2001, Head et al. 2003) whereas *C. hyperboreus* is a more oceanic species penetrating further south into deep Atlantic waters, but most likely with the Greenland Sea as a centre of distribution (Hirche 1991, Richter 1994).

The three species overlap in their distribution where Atlantic and Arctic water masses meet, such as the Barents Sea (Falk-Petersen et al. 1999), the Labrador Sea (Head et al. 2003), the North East Polynya (Ashjian et al. 1995), the Nansen Basin (Mumm 1993) and in fjords of Greenland and Svalbard (Digby 1954, Madsen et al. 2001, Kwasniewski et al. 2003, **paper III**). Where the three species co-occur they can account for up to 75 % of the mesozooplankton standing stock (Auel and Hagen 2002). *Calanus* spp. is a key prey for many fish stocks in the North Atlantic (and adjacent shelf seas) such as cod (*Gadus morhua*) (Helle and Pennington 1999, Sundby 2000), capelin (*Mallotus villosus*) (Gjørøseter et al. 2002) and herring (*Clupea harengus*) (Corten 2001). Also in the Arctic pelagic food web *Calanus* spp. is identified as a key species being the dominant prey species for the main predators here (polar cod (*Boreogadus saida*), *Themisto libellula*, *Mertensia ovum*; Scott et al. 1999, Falk-Petersen et al. 2002, Auel et al. 2002, Hop et al. 2006) and *Calanus* spp. lipid markers can be traced throughout the food web to higher trophic levels (Dahl et al. 2000, Falk-Petersen et al. 2004).

All three species are primarily herbivorous and like many zooplankton species at high latitudes they accumulate energetic reserves in form of lipids during periods of high food abundance (Lee 1975, Scott et al. 2002). These energy reserves sustain the animals during periods of limited food supply (Lee 1974, Sargent and Falk-Petersen 1988), and may fuel reproduction and development in early spring, thereby allowing reproduction to take place before the phytoplankton spring bloom starts (e.g. Smith and Schnack-Schiel 1990, Conover and Huntley 1991, Hirche 1996a, Niehoff et al. 2002, Lee et al. 2006). As another key adaptation to life at high latitudes *Calanus* spp. conducts seasonal ontogenetic vertical migration (Hirche 1996b, Hirche 1997, Kosobokova 1999). After synthesizing large lipid reserves during the productive season (Conover and Huntley 1991, Scott et al. 2000), the animals descend to deeper water where the winter is spent in a non-feeding state with reduced metabolism (Conover and Huntley 1991, Hirche 1996b). Life history strategies of *Calanus* differ between species and populations in a way that

seem to reflect adaptation to different environmental conditions (Conover 1988, **paper IV**).

Observations indicate that the Arctic Ocean is in transition to a warmer state with reduced ice cover (ACIA 2004, Polyakov et al. 2005, Anisimov et al. 2007). This trend is in part attributed to global warming caused by anthropogenic intensification of the global greenhouse effect (Johannessen et al. 2004). It is generally agreed that the effects of climate change may be more pronounced in the Arctic since decreasing ice and snow cover will reduce the albedo and thereby enhance the warming (positive ice-albedo feedback; ACIA 2004, Serreze and Francis 2006). However, there is also high natural annual, decadal and multi-decadal variability (Saloranta and Haugan 2001, Polyakov et al. 2002) in the in- and outflow to and from the Arctic Ocean that is related to large scale atmospheric weather patterns such as the North Atlantic Oscillation (NAO) (Dickson et al. 2000) and the Arctic Oscillation (AO) (Rigor et al. 2002, Zhang et al. 2003).

Over the last decades the inflow of Atlantic water into the Arctic has intensified, and temperature and salinity is increasing over large areas of the Arctic Ocean (Morison et al. 1998, Morison et al. 2000, Schauer et al. 2004). Since variations in the inflow of Atlantic water to the Arctic correlates with fluctuations in the NAO, the warming trend in the Arctic Ocean is interpreted as an advective feature that arises largely outside the Arctic Ocean (Swift et al. 1997, Grotefendt et al. 1998, Dickson et al. 2000). Such variations are likely to have an effect on the pelagic ecosystem since its members are strongly affected by changes in water mass distribution and advection (McGowan 1990, Ottersen and Stenseth 2001, Hays et al. 2005).

Our ability to predict the ecological responses of increased climatic variability in the Arctic is limited. To assess the ecological response a profound knowledge of the current situation is needed, including knowledge about species composition, life history adaptations and distribution patterns. If the observed trend from the temperate regions (Beaugrand et al. 2002b) proceed into the Arctic Ocean we might expect a shift towards more boreal species also here. How the resident food web is able to cope with such changes is uncertain but the implications for the marine ecosystem may be severe. For example, it has been suggested that changes in ocean climate have led to changes in the

structure of the pelagic ecosystem from arctic to sub-arctic conditions in the northern Bering Sea, e.g. to a shift from an ecosystem that favoured benthic communities to an ecosystem that is dominated by pelagic fish (Grebmeier et al. 2006b). This shift has been attributed to increased bottom water temperatures and a subsequent northward shift in the distribution of demersal fish and epifaunal invertebrates. In addition, it has been hypothesised that increased water temperature and reduced sea ice cover may increase the energy flow to the pelagic system in Arctic shelf seas as opposed to a strong carbon flux from ice-algae directly to the benthos in a cold climate with high sea ice cover (Carroll & Carroll 2003, Piepenburg 2005). Thus climate warming may enhance pelagic production thereby reducing carbon flux to the benthos with detrimental effects for benthic communities (Grebmeier et al. 2006a, Grebmeier et al. 2006b).

Increased knowledge on how the boreal and Arctic components of the pelagic community respond to environmental variability is needed to assess effects of global warming in the Arctic.

Therefore, the overall objective of this study was to gain new insight into what governs mesozooplankton abundance, composition and distribution in Svalbard waters. Specific aims were to

- describe the mesozooplankton species composition and abundance in northern Svalbard waters (**paper I**)
- investigate and quantify how variability in the mesozooplankton distribution relates to hydrography in this area (**paper I, II**)
- examine the vertical distribution of developmental stages of dominant copepod species at different locations in Svalbard waters (**paper III**)
- evaluate if congeneric *Calanus* species of Atlantic and Arctic origin do co-exist in an Arctic environment and if so how their population dynamics and life cycle strategies differ (**paper IV**)
- evaluate the possible effects of climatic changes on the *Calanus* community in Svalbard waters

The physical environment in the study area

The data used in this work were collected in waters around the archipelago of Svalbard (Figure 1) and included locations in coastal waters and fjords as well as stations beyond the continental shelf and in ice covered Arctic waters.

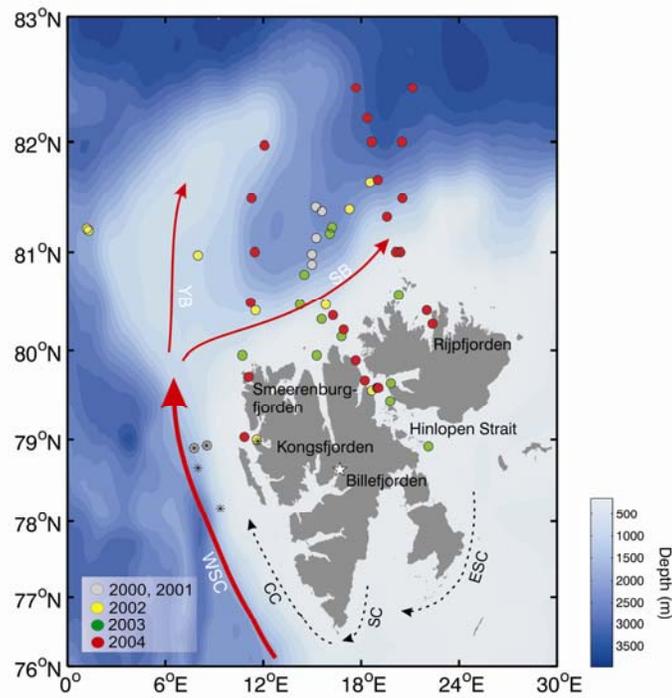


Figure 1. Map of Svalbard together with main current systems in the region and locations of in total 53 sample sites sampled in 2000 and 2001 (grey dots, paper II), in 2002 (yellow dots, paper I, II, III), in 2003 (green dots, paper I, II) and 2004 (red dots, paper I, II). White star marks the sample site in Billefjorden (paper IV). Asterisks mark additional locations that were sampled during the study period and from which data were included in some figures presented in the synthesis. Red arrows indicate warm (Atlantic) currents; black, dashed arrows indicate cold (Arctic) currents. Abbreviations are WSC: West Spitsbergen Current; ESC: East Spitsbergen Current; SC: Sørkapp Current; CC: Coastal Current; YB: Yermak Branch; SB: Svalbard Branch.

The North Atlantic Current (NAC) mainly drives the ocean circulation in the Nordic Seas (Figure 2). In it warm Atlantic waters are transported over the Faeroe - Shetland Ridge into the Norwegian Sea (Rudels et al. 1999). This water mass continues northwards along the Norwegian coast as the Norwegian Atlantic Current (NwAC). Off northern Norway one branch enters the Barents Sea, will eventually cross the Barents Sea and enter the Arctic Ocean via the Kara Sea (Rudels et al. 1994). The other branch of the NwAC continues northwards as the West Spitsbergen Current (WSC) (Aagaard et al. 1987,

Rudels et al. 1999). At the northwestern corner of Svalbard the WSC splits into the ‘Yermak Branch’, which is largely recirculated to the Greenland Sea, and the ‘Svalbard Branch’ (Figure 1), which defines the largest input of Atlantic Water into the Arctic Ocean (Manley 1995). It turns eastwards and enters the Arctic Ocean where it follows the continental slope (Rudels et al. 1999). Together with the inflow over the Barents Sea shelf the inflow of Atlantic water within the WSC constitutes the main inflow of heat to the Arctic Ocean (Aagaard and Greisman 1975, Aagaard and Carmack 1989, Saloranta and Haugan 2001).

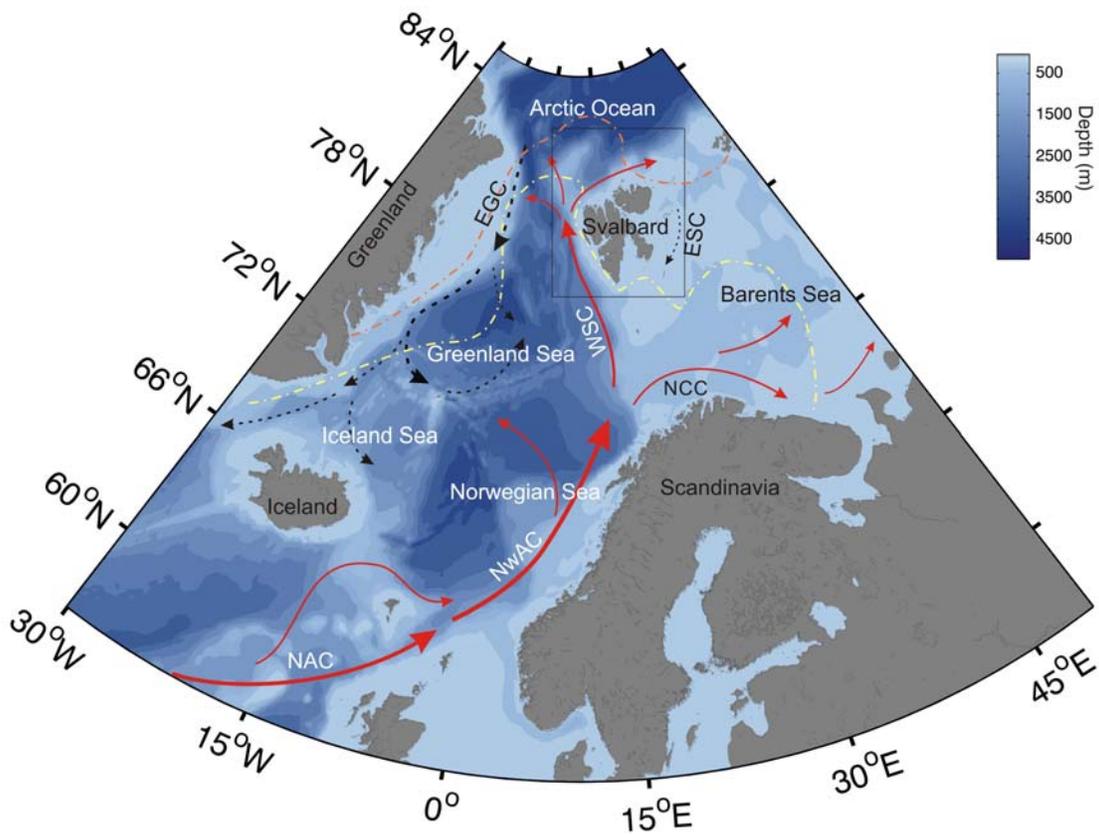


Figure 2. Map over the Nordic Seas together with the main current systems in the region (modified after Blindheim and Østerhus 2005), average winter (yellow dashed-dotted line) and summer (orange dashed-dotted line) sea ice margins (Johannessen et al. 2004). Red arrows indicate warm (Atlantic) water currents; black, dashed arrows indicate cold (Arctic) water currents. Abbreviations are: NAC: North Atlantic Current; NwAC: Norwegian Atlantic Current; NCC: North Cape Current; WSC: West Spitsbergen Current; ESC: East Spitsbergen Current; ECG: East Greenland Current. Square indicates section that is presented in Figure 1.

Variable meteorological conditions affect the strength of the North Atlantic currents and its continuations, and the inter-annual variability in the Atlantic inflow to the Arctic is substantial (Saloranta and Haugan 2001, Ingvaldsen et al. 2002, Furevik and Nilsen 2005). The main outflow from the Arctic Ocean occurs on the western side of the Fram Strait where Arctic water combines with recirculated water from the WSC and flows southwards as the East Greenland Current (EGC) (Figure 2) (Aagaard and Carmack 1989, Schlichtholz and Houssais 1999a, Rudels et al. 1999, Blindheim and Østerhus 2005). The EGC is also the main export path of sea ice from the Arctic Ocean (Saloranta and Haugan 2001).

Shelf- slope interaction

Due to the presence of the warm Atlantic waters within the WSC the marine climate along the western and northern coast of Svalbard is relatively warm as indicated by mostly ice-free conditions. Waters east of Svalbard on the other hand are of more Arctic characteristic due to the East Spitsbergen Current (ESC) that exits the Arctic Ocean between Nordaustlandet and Frans Josef Land and transports cold Arctic water into the northern Barents Sea (Figure 2, Pfirman et al. 1994). The ESC combines with cold waters from Storfjorden to form the Sørkapp Current (SC) that surrounds the southern tip of the Svalbard archipelago and continues northwards as the Coastal Current (CC) with relatively cold and fresh waters (Figure 1, Loeng 1991). The CC runs parallel to the WSC, which results in an Arctic front west of Svalbard that is steered by the bathymetry and normally isolates the Atlantic water in the WSC from cooler coastal waters (Saloranta and Svendsen 2001). Prevailing currents and wind systems (Svendsen et al. 2002, Cottier et al. 2007) as well as instabilities in the front between the WSC and CC (Saloranta and Svendsen 2001, Svendsen et al. 2002) and topographical steering (Saloranta and Svendsen 2001) drive the exchange of water masses between the slope and the shelf. Episodic intrusions of Atlantic water onto the shelf are common while remnants of shelf water within the WSC are rarely observed (Saloranta and Svendsen 2001, Cottier et al. 2005). Fjords along the western coast of Svalbard are thus partially affected by the cold waters of the CC and by the warm and more saline WSC (Koszteyn and Kwasniewski 1989, Saloranta and Svendsen 2001, Cottier et al. 2005).

Results and discussion

Mesozooplankton composition, distribution and the relationship to hydrographic variability

The mesozooplankton community in Svalbard waters was numerical dominated by cosmopolitan species (Figure 3, Table 1, **paper I**). This dominance was in particular due to the high abundance of the copepod *Oithona similis*, but also copepods of the genus *Pseudocalanus* and *Microcalanus* occurred at most location in high numbers (**paper I**). This is in agreement with previous observations in Svalbard waters and in the Eurasian Arctic (Mumm et al. 1998, Walkusz et al. 2003). Atlantic species dominated within the core area of the inflowing Atlantic water (**paper I**). The dominance of Atlantic species compared to Arctic species diminished towards the north and in southern Hinlopen, where cooler and fresher Arctic waters prevailed. Arctic species were also more common in the inner fjords along the west and north coast (Billefjorden, Rijpfjorden, Smeerenburgfjorden, Figure 3, **paper I**).

Table 1: List of species with Arctic, subarctic-boreal or wide spread distribution

Arctic species: cold water species that are endemic to Arctic waters or closely confined to the Arctic and adjacent waters. **Atlantic species:** cold temperate species that are distributed over the North Atlantic and in subarctic areas. **Wide-spread and cosmopolitan species:** species that occur over a wide geographic range in both cold and warm water regions and that have no value as biogeographic indicator species (Grice 1962). Numbers refer to references: 1. Jaschnov (1972), 2. Conover (1988), 3. Grainger (1963), 4. Grice (1962), 5. Raymont (1983), 6. Brodskii (1967), 7. Dunbar (1964), 8. Richter (1994), 9. Ekman (1953), 10. Grainger (1965), 11. Kramp (1947), 12. Dunbar (1962), 13. Conover and Huntley (1991), 14. Gallienne and Robins (2001), 15. Alvariño (1965).

Arctic	Atlantic	Wide spread, cosmopolitan
<i>Calanus glacialis</i> ^{1,2}	<i>Calanus finmarchicus</i> ^{1, 2, 3}	<i>Oithona similis</i> ^{4, 13, 14}
<i>Calanus hyperboreus</i> ^{2,3}	<i>Pareuchaeta norvegica</i> ¹⁰	<i>Microcalanus</i> spp. ^{4,6*}
<i>Metridia longa</i> ^{4,5}	<i>Oithona atlantica</i> ⁵	<i>Pseudocalanus</i> spp. ^{4, 6*}
<i>Chiridius obtusifrons</i> ⁶	<i>Heterorhabdus norvegicus</i> ⁶	<i>Gaidius tenuispinus</i> ^{4, 6}
<i>Themisto libellula</i> ⁷	<i>Cyclopina schneideri</i> ¹⁰	<i>Scaphocalanus magnus</i> ^{4, 6}
<i>Tricona (Oncaea) borealis</i> ^{5, 8}	<i>Thysanoessa longicaudata</i> ⁷	<i>Scolecithricella minor</i> ⁶
<i>Mertensia ovum</i> ⁹	<i>Thysanoessa inermis</i> ⁷	<i>Microsetella norvegica</i> ⁵
	<i>Aglantha digitale</i> ¹¹	<i>Eukrohnia hamata</i> ¹⁵
	<i>Sagitta elegans</i> ¹²	<i>Clione limacine</i> ⁹
		<i>Limacina helicina</i> ⁵

*three species of *Pseudocalanus* (*P. elongatus*, *P. acuspes*, *P. minutus*) and two species of *Microcalanus* (*M. pygmaeus*, *M. pusillus*) are observed in Arctic and Svalbard waters (Grice 1962, Mumm 1991, Koszteyn et al 1991). *M. pygmaeus* and *P. minutus* are found to be more confined to Arctic and subarctic areas (Koszteyn et al 1991). However, since I did not distinguish between species of *Pseudocalanus* and *Microcalanus* these species are included in the wide-spread group following Grice (1962) and Brodskii (1967).

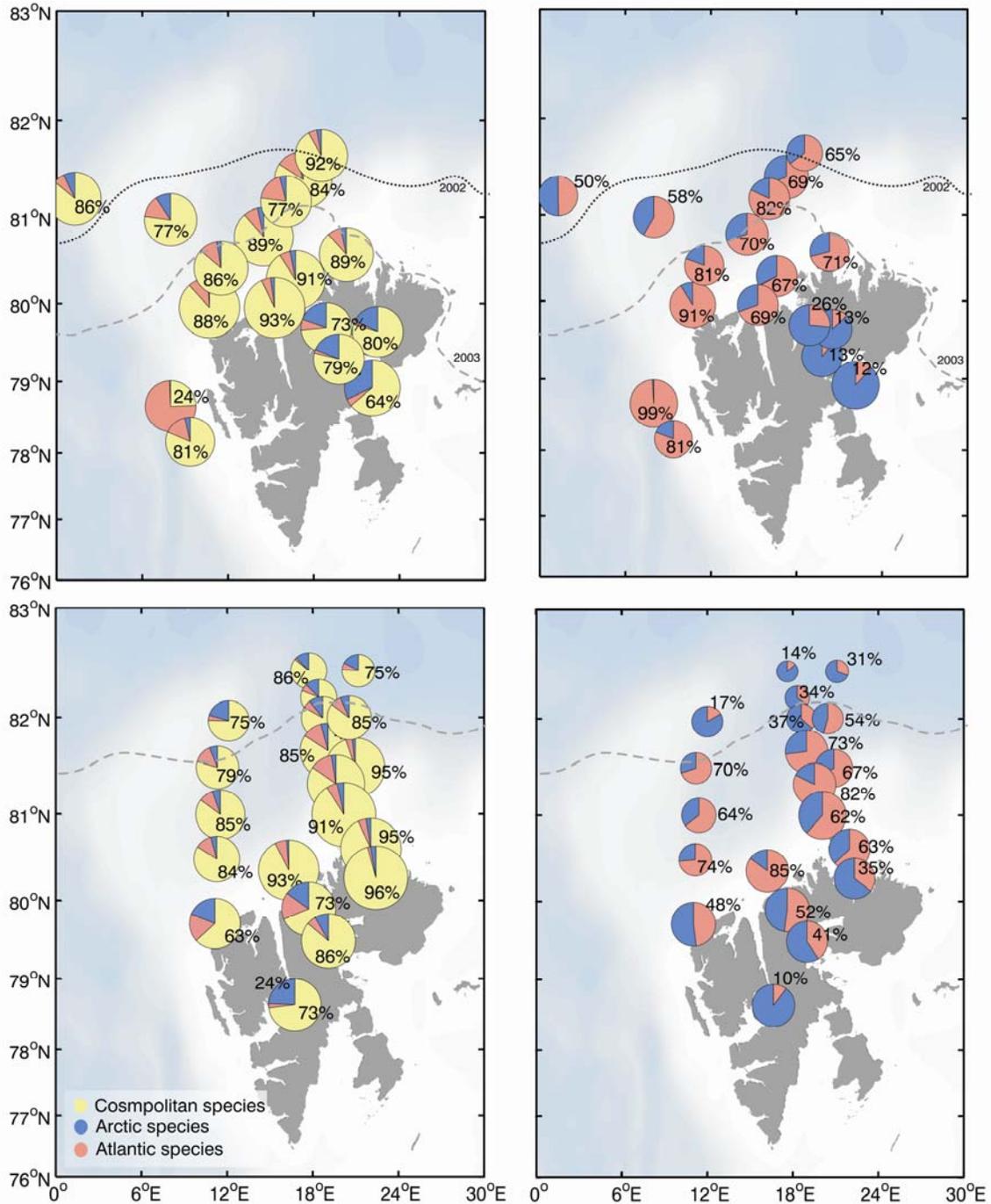


Figure 3: Left panel: relative composition of Atlantic, Arctic and cosmopolitan species around Svalbard sampled in 2002, 2003 (upper panel) and 2004 (lower panel). Numbers refer to percentage represented by cosmopolitan species. Right panel: relative composition of Atlantic and Arctic species, numbers refer to percentage represented by Atlantic species. For definition of cosmopolitan, Atlantic and Arctic species see Table 1. Dashed lines indicate location of ice edge during sampling period (September) in each year. Size of pies reflects log transformed abundance (ind. m⁻³)

Differences in hydrography and bottom depth largely determined the horizontal distribution patterns of the zooplankton (**paper I**). Temperature and salinity co-varied with variation in the zooplankton species composition between assemblages of distinct geographic and hydrographic integrity (**paper I**). Differences in the community structure were primarily caused by variations in species densities rather than differences in the taxonomic composition (**paper I**).

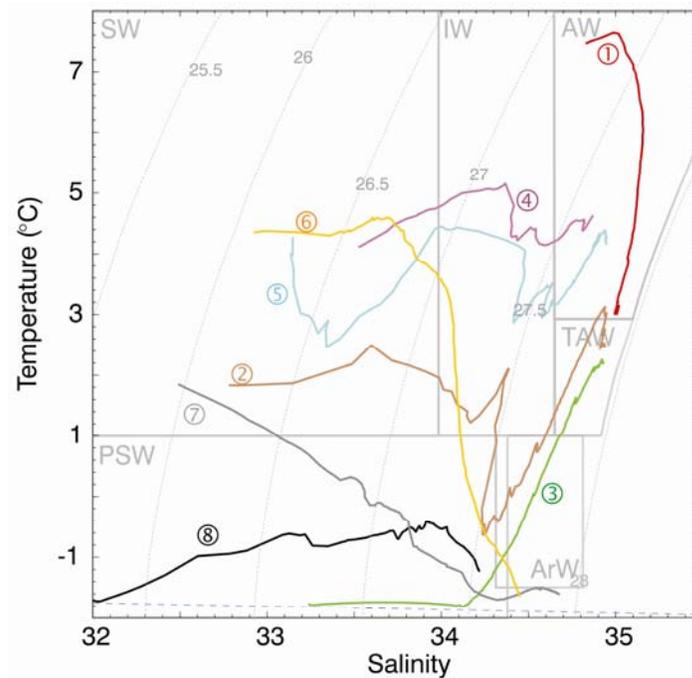


Figure 4: TS diagram of vertical CTD profiles taken at eight selected stations around Svalbard. Each line represents one of the CTD plots in Figure 5, numbers in circles refer to station and CTD plots in Figure 5. The lines are superimposed over water mass domains as defined by Cottier et al. 2005 for Kongsfjorden and the adjacent shelf. Atlantic water (AW): $T > 3^{\circ}\text{C}$, $S > 34.65$, $D > 27.92$; Transformed Atlantic water (TAW) $T: 1$ to 3°C , $S > 34.65$; Arctic Water (ArW) $T: -1.5$ to 1°C , $S: 34.3-34.8$; Surface water (SW) $T > 1^{\circ}\text{C}$, $S < 34.0$, Intermediate water (IW) $T > 1.0^{\circ}\text{C}$, $S: 34-34.65$; the watermass with $T < 0^{\circ}\text{C}$ and $S < 34.7$ is defined as Polar Surface water (PSW) (modified after Rudels et al. 2000) . Isopycnals are in 0.5 intervals, dashed line indicates freezing point.

Water mass characteristics varied substantially around Svalbard (Figure 4). Along the west coast the Atlantic water prevailed. North and east of Svalbard a fresh surface layer was usually observed in the upper 50 m and water masses were modified through mixing processes between Atlantic and Arctic water (Figure 4). Coldest and freshest water masses were observed in southern Hinlopen and in the inner basins of Rijpfjorden and Billefjorden (Figure 4, 5).

This variability in water mass characteristics around Svalbard was well reflected by the *Calanus* species composition, in particular by the abundance of *C. finmarchicus* and *C. glacialis* relative to each other. *C. finmarchicus* was the most common species along the western and northern coast of Svalbard where the influence of Atlantic waters masses was high (Figure 5). Although its abundance and dominance decreased towards the northern oceanic realm it was nevertheless found to dominate within the perennial sea ice zone as far north as 82° 30'N (station 3 in Figure 5, **paper I**). *C. glacialis*, on the other hand, was more common on the north-eastern shelf (Rijpfjorden, Hinlopen) and in the southern Hinlopen Strait where Arctic waters dominated (stations 5, 7 & 8 in Figure 5, **paper I**). It was also found in high abundance in fjords on the west coast (Kongsfjorden, Smeerenburgfjorden, Billefjorden) (station 6 in Figure 5). These are Arctic glacial fjords of which the inner parts are characterized by relatively cold and fresh water masses (Svendsen et al. 2002, Figure 5, **paper IV**), thus providing more 'Arctic-like' conditions than otherwise encountered along the west coast (Figure 4, 5). The observed distribution of *C. glacialis* confirms its status as an Arctic shelf species with a preference for cold waters (Jaschnov 1972, Conover and Huntley 1991, **paper IV**). Thus the horizontal distribution of *C. finmarchicus* and *C. glacialis* and their dominance in different hydrographic regimes agree with observations from the Fram Strait (van Aken et al. 1991, Ashjian et al. 1995), the Canadian archipelago (Grainger 1963) and the Barents Sea (Jaschnov 1972, Tande et al. 1985, Melle and Skjoldal 1998) that describe *C. finmarchicus* and *C. glacialis* as indicator species for Atlantic and Arctic waters, respectively. *C. hyperboreus* was also most abundant in Arctic waters (station 3 in Figure 5,) but it was comparatively rare around Svalbard (Figure 5, **paper I, II**). Similar observations were made by Søreide et al. (submitted) in northern Svalbard waters. However, a large part of the sampling area was outside of this species main distributional area (Conover 1988; Mumm 1993; Hirche 1997). At most of the stations sampled in this study it represented numerically less than 10% of all *Calanus* species. Only at the deeper locations within the marginal ice zone it represented a larger proportion (station 3 in Figure 5).

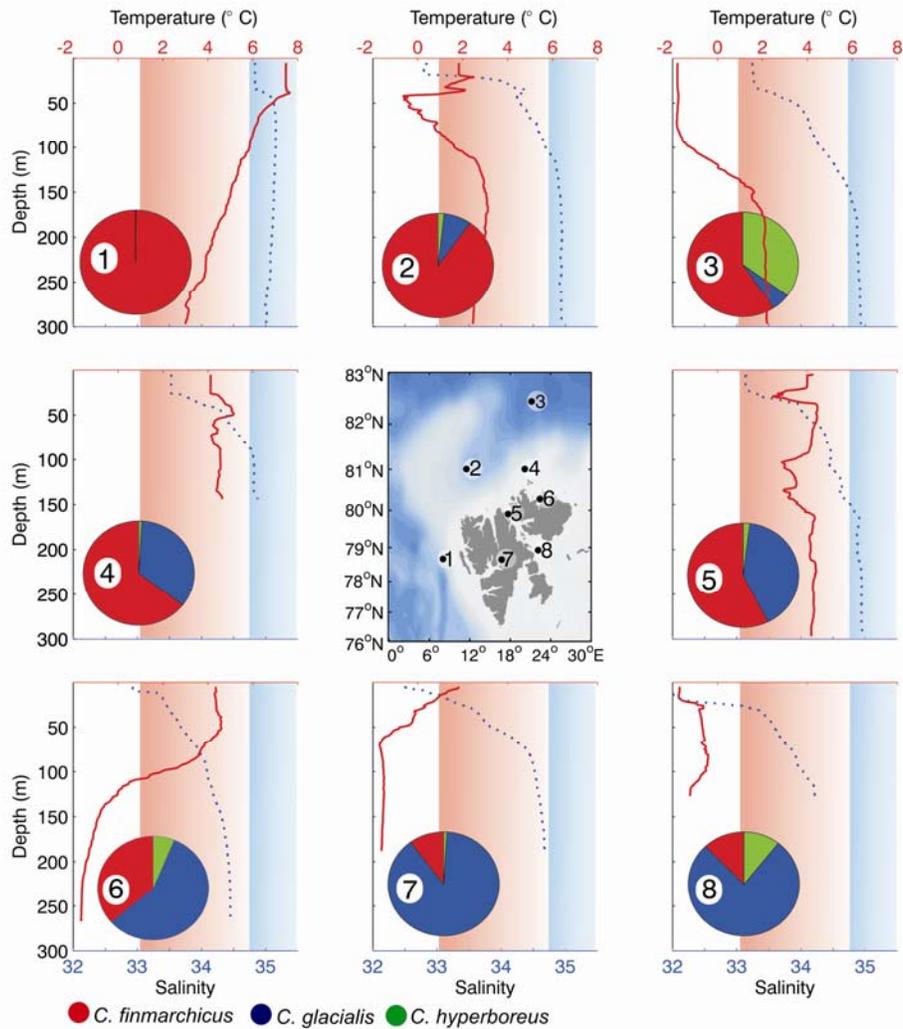


Figure 5: Vertical profiles of temperature (red lines) and salinity (dotted blue lines) at 8 selected stations around Svalbard. Pie charts show relative abundance of the three *Calanus* species at each location. Red shaded area marks temperature >1°C, blue shaded area marks salinity >34.65. Temperature and salinity above these values indicate Transformed Atlantic and Atlantic water masses (see also Figure 4, Cottier et al. 2005)

A number of studies have dealt with the influence of climate variability on Arctic and North Atlantic zooplankton populations and in particular on *Calanus* populations (Pershing et al. 2004, Skjoldal et al. 1992, Helle 2000, Dalpadado et al. 2003). So far there has been made little effort to quantify these relationships using statistical models. This was the motivation for the analyses in **paper II** where regression models were used to analyse the relationship between the variability in *Calanus* abundance and variability in temperature and salinity.

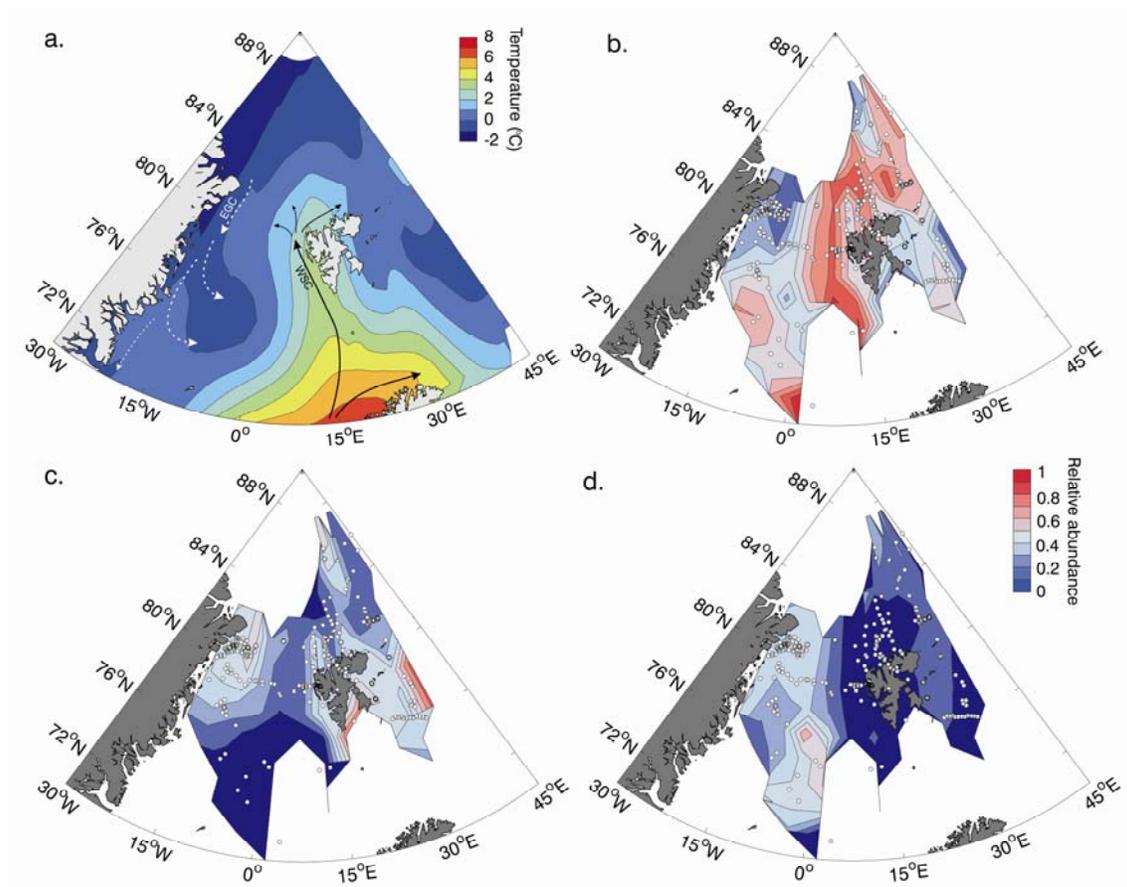


Figure 6. Distribution of water mass and *Calanus* spp. in the North Atlantic.

a) Annual mean of water temperature at 150 m in 2001 (NOAA Atlas NESDIS 45 World Ocean Database 2001). Main current systems are indicated by arrows; black arrows indicate warm (Atlantic) water currents; grey dotted arrows indicate cold (Arctic) water currents. WSC= West Spitsbergen Current; EGC= East Greenland Current; ESC= East Spitsbergen Current (see also Figure 2). Also shown is the relative abundance of b) *C. finmarchicus*, c) *C. glacialis* d) *C. hyperboreus* in the study area. The maps were created from data used in papers I, II, III and from additionally sampled stations (120 records), unpublished data from the northern Barents Sea and Kongsfjorden (89 records, courtesy of Stig Falk-Petersen, Norwegian Polar Institute), and published records of the abundance of all three *Calanus* species from 139 stations from the Greenland Sea, Barents Sea, Northern Norwegian Sea, Svalbard waters and the Polar Ocean (Diel 1991; Hirche 1991; Mumm 1991; Hirche et al. 1994; Ashjian et al. 1995; Ashjian et al. 1997; Mumm et al. 1998; Dale et al. 1999; Thibault et al. 1999; Smith et al. 2003, Basedow et al. 2004). Data from shallow (< 100 m) stations were excluded to reduce any bias that may arise from only sampling the upper layers of the ocean. The relative abundance of the three *Calanus* species was then computed for each geographical position (as indicated by white dots in b, c and d), and distribution maps were created by interpolating between stations over a 5 nm grid using the minimum variance unbiased estimate method (MVUE).

Significant relationships between *Calanus* abundance and salinity and temperature were revealed using linear regression models (**paper II**). This suggests that the abundance of the different *Calanus* species is affected by water mass characteristics. In these regressions, *Calanus* abundance was expressed as a function of temperature and salinity and around 50% of the variability in *Calanus* abundance could be accounted for by the variations in temperature and salinity (**paper II**). Thus I conclude that the biogeography of these species are tightly connected to hydrography (Figure 6, **paper II**).

Another way to analyse the relationship between environmental parameters and biological variance is the use of ordination techniques such as principle component analysis (PCA) or redundancy analysis (RDA) (Legendre and Legendre 1998). RDA, a constrained form of PCA, is related to multiple regression analysis, but while in regression only one response variable can be related to one or several explanatory

Box 1: Redundancy Analysis

Redundancy Analysis (RDA), a multivariate form of regression analysis, was performed on the data used in **paper II** to relate the variability in the abundance of the three *Calanus* species to environmental variables. In contrast to the regression analysis in **paper II** which analyses each species for separately, this method analyses the relationship between the entire *Calanus* population and the environment. The analysis was conducted with CANOCO 5.5 for Windows (ter Braak and Smilauer 2002). The abundance of the three *Calanus* species and a number of potential explanatory environmental variables (average temperature and salinity 0-300 m, average fluorescence 0-100 m, date of sampling, bottom depth, longitude and latitude, and a categorical variable, which could be either “shelf” for stations with bottom depth < 500 m, or “oceanic” for stations with bottom depth >500 m) were analysed simultaneously to determine which of these explanatory variables best explained the variance in the *Calanus* data. *Calanus* abundance data were log transformed prior to analysis for stations. Stations sampled with multiple hauls were pooled. Those environmental variables that best and significantly (Monte Carlo permutation test with 999 random permutations) explained the variability in the three *Calanus* species distribution were chosen (Table 2). Ordination techniques and rules of interpretation of RDA ordination plots are summarized by ter Braak (1995) and ter Braak and Smilauer (2002). The species and explanatory variables are shown as arrows in the RDA ordination plots, and are standardized and centred, and point in the direction of maximum change. The angle between the arrows indicates their correlation, i.e. they are uncorrelated if they are perpendicular to each other and highly correlated if the angle is small (positive correlation) or large (negative correlation) (Figure 7).

variables, a RDA analyses simultaneously several response variables (Legendre and Legendre 1998).

This allows testing a number of environmental parameters simultaneously to find those that best ‘explain’ the observed variance in the species composition. Applying a RDA on the data used in **paper II** (Box 1) showed that over 50% of the variability in the data could be accounted for by the chosen environmental variables (Figure 7, Table 2). The RDA showed a clear separation between samples taken in oceanic locations (bottom depth > 500 m) and samples taken on the comparatively shallow locations above the continental shelf and slope (bottom depth < 500 m; Figure 7). This categorical variable, which could be either “shelf” or “oceanic”, accounted for more of the observed variability in the dataset than any of the other variables (Table 2). This suggests that the classification into shelf and oceanic groups (**paper II**) seems reasonable in a statistical sense. Variability in the *Calanus* abundance was also strongly correlated with temperature and salinity (Table 2, Figure 7), which suggests that the most important variables were chosen for the linear regression models.

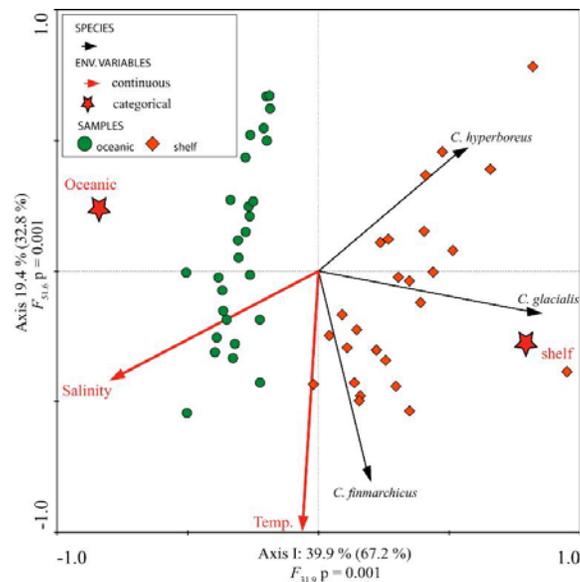


Figure 7. Biplot of redundancy analysis (RDA) (axes I and II) relating the abundance of all three *Calanus* species (black arrows) to environmental variables (red arrows and stars). Temperature and salinity are averaged over 0-300 m (see Box 1 for details). The plot explains 59.3 % of the total variability in the data, and the chosen significant environmental variables (red arrows and stars) account for 100% (in brackets) of this explained variability.

Table 2. Ranking of environmental variables as resulted from the RDA (see Box 2) that significantly influenced abundance of *Calanus* in the study area. The environmental variable that best explained *Calanus* variability is ranked first; additional variables are ranked on the basis of additional fits.

Environmental variable	Explained variance	p	F
Categorical depth variable	32.4%	0.001	23.9
Temperature	21.4%	0.001	22.7
Salinity	5.6%	0.001	6.55

There were no statistical significant relationships between the variability in the abundance of the three *Calanus* species and algal biomass as measured by fluorescence at the time of sampling. Only in one case (*C. glacialis* in shallow waters) could a statistical significant relationship be demonstrated (linear regression, $p < 0.05$, Table 3). However, this relationship was an inverse correlation suggesting that perhaps *C. glacialis* had a negative effect on algal biomass rather than that the abundance of *C. glacialis* was dependent on the available amount of phytoplankton. As *Calanus* spp. are relative long lived with a generation time of more than one year (Conover 1988, **paper IV**) I find it unlikely that a point measurement of food abundance is a good variable to explain variation in abundance. The data were collected in early autumn when fluorescence levels were low at most stations and showed little horizontal variability. Vertical gradients in algal biomass may however have affected the vertical distribution of *Calanus* spp. (Figure 2 in **paper III**).

Table 3. Regression analyses of log-transformed *Calanus* abundance (as ind. m^{-3} for each species, averaged from the surface down to 300 m or bottom depth, whichever was less) against fluorescence (as mV, averaged over upper 100 m). The data are from 41 stations (latitude $> 78^{\circ}54'N$, longitude $< 22^{\circ}22'E$, Julian day 237-269). Repeated samples were pooled within each station before this analysis. The dataset was split in samples taken over “shelf” waters (bottom depth < 500 m) and over “deep” water (bottom depth > 500 m). ns= not significant ($p > 0.05$)

	Shelf			Deep		
	Intercept	Slope	p	Intercept	Slope	p
<i>C. finmarchicus</i>	5.08	0.07	ns	4.03	0.26	ns
<i>C. glacialis</i>	5.40	-1.70	$< 0.05^*$	1.99	-0.06	ns
<i>C. hyperboreus</i>	2.33	-0.65	ns	1.08	0.05	ns

* $R^2 = 0.36$

The strong relationships between plankton abundance and physical variables in the study area corroborate the view that variability in zooplankton abundance and composition may arise mainly from variations in the distribution of water masses. Such variability will primarily reflect the prevailing circulation system, which in the study area is largely driven by variations in the WSC (Aagaard et al. 1987, Saloranta and Haugan 2001, Zhang et al. 2004). This notion is supported by geographical distribution patterns of the three *Calanus* species (Figure 6). Variations in the relative abundance of all three species were largely consistent with the prevailing water mass distribution as indicated by average water temperature at 150 m in the study area (Figure 6 a). *C. finmarchicus* dominated in the main inflow area of warmest water masses i.e. in the northern Norwegian Sea, southern Greenland Sea, along the west coast, and to the northeast of Svalbard, while *C. glacialis* and *C. hyperboreus* were more common where colder water prevailed, i.e. north of 83° N, in the western Fram Strait, and east of 45° E in the northern Barents Sea.

Hydrographic variability is recognized as a major force structuring marine populations (Legendre and Demers 1984, Mann and Lazier 1996, Steele 1998) on meso- to large-scale and regional forces have been shown to be important for the structure of local zooplankton communities (e.g. Aksnes et al. 1997, Eiane et al. 1998). Outside the Arctic seas zooplankton distribution has been linked both to temperature and salinity and to large-scale circulation indices, such as the NAO, for both *Calanus* (Fromentin and Planque 1996; Heath et al. 1999) and many other species (Beaugrand et al. 2002b). Climate related variability in water mass distribution has been shown to influence the dispersal and transport of species (e.g. Arashkevich et al. 2002, Beare et al. 2002, Gislason and Astthorsson 2004) and can thereby alter population dynamics and species composition (Pershing et al. 2005, Planque and Fromentin 1996, Beaugrand and Reid 2003).

In Svalbard waters Willis et al. (2006) demonstrated that changes in the zooplankton community structure in Kongsfjorden were associated with the advection of water masses from the adjacent shelf. Further south the Atlantic inflow to the Barents Sea is subject to strong inter-annual variability (Loeng et al. 1997), which results in high variations in the abundance of *C. finmarchicus* (Sakshaug 1997, Helle and Pennington 1999, Dalpadado et

al. 2003). Similarly, Søreide et al. (2003) found that environmental variables, with water mass distribution being most important, can account for 80% of the variability in macrozooplankton distribution in the Barents Sea. Pedersen (1995a) estimated the advected biomass of *C. finmarchicus* to be 6-10 times higher than the endemic production in the Barents Sea while Edvardsen et al. (2003) report advection of *C. finmarchicus* into the Barents Sea to be four times more important than the local production of this species. Tande et al. (2000) however did not find clear relationships between inter-annual variability in copepod abundance (including *C. finmarchicus*) in the Barents Sea and water temperature. That study was however largely based on zooplankton sampled in the upper 50 m. I found that the variation in salinity and temperature at intermediate depth (50- 150 m) accounted for more of the variation in the abundance of the three *Calanus* species than the temperature and salinity in the upper 50 m (Figure 3 in **paper II**) and that consistent geographical patterns in community structure north of Svalbard were only observed below 50 m (**paper I**). As the hydrographic properties of deep water are more conservative than the atmospherically influenced surface water, the deep water properties more clearly reflect the geographical origin of the water mass.

Potential significance of advection on the *C. finmarchicus* distribution

In the North Atlantic the strongest relationship between ocean climate variability and zooplankton has been established for shelf populations of *C. finmarchicus* (Colebrook 1978, Miller et al. 1998, Heath et al. 1999) and advection of *C. finmarchicus* from the North Atlantic basins to the shelf seas (in particular that of overwintering populations) is identified as an important process for sustaining shelf populations (Heath et al. 1999; Harms et al. 2000; Speirs et al. 2006). Thus shelf populations that rely on advective input from oceanic stocks may be more susceptible to changes in circulation patterns. In waters around Svalbard the association between zooplankton abundance and hydrography was not limited to shelf populations, indeed co-variation between *C. finmarchicus* abundance and temperature and salinity was even stronger in the open ocean (**paper II**). This may not be surprising since the *C. finmarchicus* population in the oceanic areas north of Svalbard are most likely expatriates from North Atlantic populations (Smith and Schnack-Schiel 1990, Mumm 1993) with presumed limited ability for reproduction

(Tande et al. 1985, Diel 1991, Conover and Huntley 1991). Thus their distribution is largely reflecting transport within the major current systems. The impact of Atlantic inflow on shelf and fjord populations is more variable (Cottier et al. 2005, Nilsen et al. 2006) and despite occasional intrusion of Atlantic water from the shelf slope that can refuel the Atlantic part of the community (Svendsen et al. 2002, Basedow et al. 2004, Berge et al. 2005) fjord populations are found to be partly self-sustained (**paper IV**). Local processes may therefore largely balance the importance of transport on the shelf (Scott et al. 2000).

Box 2: Modelling the role of advection and local production in zooplankton population dynamics

Aksnes and Blindheim (1996) proposed a simple model to assess the advective influence on local populations in a habitat volume V (m^3):

$$\frac{dN}{dt} = (b - d)N - eN + iN_b \quad (\text{eq.1})$$

Here N is the abundance of the local population ($\text{ind } m^{-3}$), N_b the abundance of the neighboring population ($\text{ind } m^{-3}$), b the birth rate of the local population (y^{-1}), d the death rate of the local population (y^{-1}), e the emigration rate of the local population (y^{-1}), i the immigration rate of the neighboring population (y^{-1})

If emigration and immigration are dominated by physical transport rather than by swimming which is a likely assumption for plankton (Hensen 1898), then

$$e = i = Av/V \quad (\text{eq.2})$$

where A is the boundary area (m^2), v the current speed (ms^{-1}) across the boundary area and V the habitat Volume (m^3).

Substituting eq.2 into eq.1 yields:

$$\frac{dN}{dt} = (b - d)N + \frac{Av}{V}(N_b - N) \quad (\text{eq.3})$$

This relates the dynamics of a local population to the biological rates ($b-d$), water movement (v) and the spatial scale (A, V) of the habitat in question.

If the physical-spatial term Av/V ('advective renewal rate') is greater than the biological rates b and d then the population dynamics are dominated primarily by the physical environment rather than by the two local biological processes (e.g. $b/(Av/V) < 1$).

Box 2 continued

Advective renewal rate

The advective renewal rate was estimated for a box of a spatial scale of 70 km width, 240 km length and 500 m depth (Figure B1). This area is based on the extension of Atlantic water north of Svalbard that is transported in this region within the Svalbard branch of the WSC (Figure 3 in Manley 1995). This area roughly corresponds to the off shelf area sampled in **paper II** (Figure 1).

The advective renewal rate was computed based on an average current speed in this region of 0.25 ms^{-1} (Schauer et al. 2004), a lower current speed estimate of 0.1 ms^{-1} (Quadfasel et al. 1987, Schlichtholz and Houssais 1999b) and a maximum estimate of 0.55 ms^{-1} (Osinski et al. 2003).

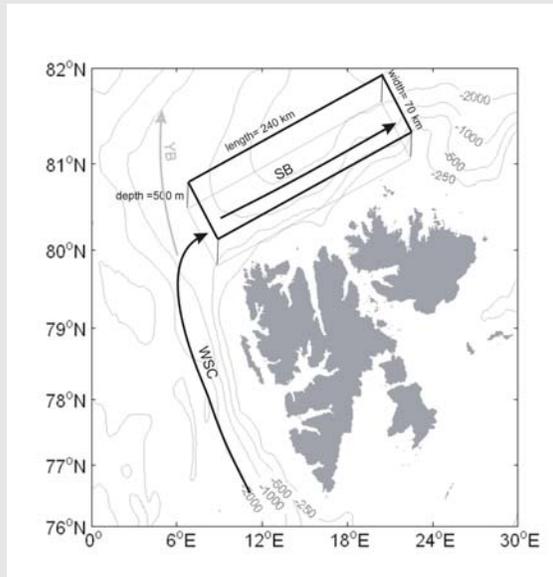


Figure B1: A schematic illustration of the habitat volume the advective renewal rate was calculated for (eq. 2) in relation to the geographical position of Svalbard and the extension of the WSC and its branches (SB= Svalbard branch, YB= Yermark Branch).

Local production

Birth rate b was estimated from life time fecundities (number of eggs produced per female, B) under the assumption that *C. finmarchicus* has a generation time of one year ($T = 1$ year) at high latitudes. Life time fecundity estimates for *C. finmarchicus* vary from 200-300 eggs per female (Marshall and Orr 1955) to 500-900 (Diel and Tande 1992, Plourde and Runge 1993, Hirche 1990) and up a maximum estimates of 3100 (Hirche 1990). This corresponds to Aksnes and Blindheim (1996) who estimated that the average life time fecundity of *C. finmarchicus* is in the order of 100-1000 eggs.

A sex ratio of 1:1 was assumed and the mortality was set to zero ($d=0$) which gives the maximal rate of increase of the population (r_{\max}):

$$b-d = b-0 = b = r_{\max} = \ln(B/2)/T \text{ (year}^{-1}\text{)} \quad (\text{eq.4})$$

The factor 2 appears as a consequence of the chosen sex ratio.

An assessment of the importance of advection in comparison to local production of *C. finmarchicus* in the study area is described in Box 2. In addition to the current velocities the advective influence on a population depends on the spatial scale of the distribution of the population (Aksnes and Blindheim 1996) and the scale used here reflects the study area of **paper I** and **II** and also the approximate distribution of Atlantic water north of Svalbard (Manley 1995).

The ratio between the estimated local production and the advective influence obtained in this manner indicates that population dynamics of *C. finmarchicus* in the study area should be dominated by transport rather than by local biological dynamics (Figure 8). Current speeds in the WSC are highest during winter and early autumn and vary between ca 0.1- 0.5 ms⁻¹ (Quadfasel et al. 1987, Schlichtholz and Houssais 1999b, Osinski et al. 2003, Schauer et al. 2004, Hop et al. 2006). The model predicts that only at current speeds <0.05 ms⁻¹ (Figure 8) population dynamics may be dominated by local production but even then only at high assumed reproductive rates. Velocity within the WSC decreases from east to west and can be <0.05 ms⁻¹ towards the boundary of the southwards flow in the Fram Strait (Fahrbach et al. 2001, Schauer et al. 2004, Hop et al. 2006). Current speeds are also weaker during summer (May-July) and can be <0.1 ms⁻¹ (Hop et al. 2006). Thus during summer when production reaches its peak, local production may be relatively more important.

Zooplankton species are able to adjust their vertical position within the water column and do so on diel to seasonal time scales (Cushing 1951, Longhurst 1976, **paper III, IV**). This may lead to temporal variability in the importance of advection on a population. By conducting seasonal vertical migration during autumn *Calanus* populations move from the surface waters into deeper layers, which often have a different temperature regime, circulation patterns and currents speeds (Ekman 1905, Backhaus et al. 1994, Kaartvedt 1996, Schauer et al. 2004). It has been suggested that seasonal vertical migration is essential for the maintenance of a basin-wide, self-sustaining population of *C. finmarchicus* in the eastern North Atlantic (Backhaus et al. 1994, Bryant et al. 1998). In the Barents Sea differences in the strength but also in the timing of the inflow of Atlantic water was found to affect the abundance of *C. finmarchicus* (Skjoldal and Rey 1989).

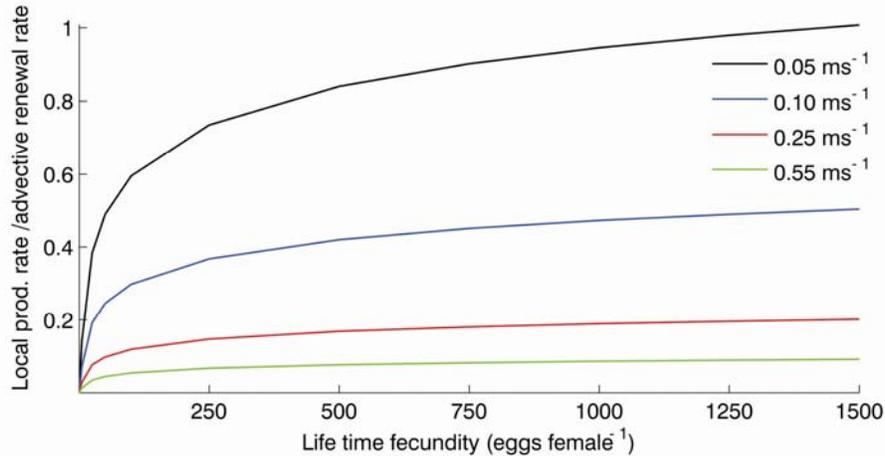


Figure 8. The relative importance of local production and advective renewal rate ($b/(Av/V)$ where b was calculated from Eq. 4 in Box 2 and Av/V is the advective renewal rate defined in Eq. 3 of Box 2) against life time fecundity of *C. finmarchicus*. Advective renewal rate has been calculated based on currents speeds of 0.05, 0.1, 0.25 and 0.55 ms^{-1} for a volume habitat of 8400 km^3 (see Box 2 for details).

This is because the *C. finmarchicus* population in the Atlantic domain will mainly be located at overwintering depth below 600 m during autumn and winter (Østvedt 1955, Hirche 1991, Kaartvedt 1996, Halvorsen et al. 2003). Thus abundance is low in the upper water layers which are brought into the Barents Sea. Atlantic water entering the Barents Sea in spring and summer on the other hand contains higher abundance of *C. finmarchicus* which are accumulated at the surface during the productive season (Skjoldal and Rey 1989, Conover 1988). It is likely that a similar mechanism regulates the advection of *C. finmarchicus* into Svalbard waters. Current velocities within the WSC are strongest in the upper 500 m (Osinski et al. 2003, Schauer et al. 2004) which is above the main overwintering depth of *C. finmarchicus* in most for the North Atlantic basins (Østvedt 1955, Hirche 1991, Kaartvedt 1996). Thus advection of *C. finmarchicus* within the WSC may be strongest during spring and summer when the population is located close to the surface. This implies that the copepods are advected northwards during their early life stages and have to cope with changing environmental condition during their development as they drift northwards. Torgersen and Huse (2005) suggested that planktonic species that live in an advective and variable system may be pre-adapted to cope with temporal fluctuations in the physical and biological environment and thus may be relatively robust to climatic changes.

Hirche (1991) found that part of the *C. finmarchicus* population in the north Atlantic remained in surface water during winter. Similar observations have been made in the Norwegian Sea (Bathmann et al. 1990) and in the Barents Sea (Pedersen et al. 1995b). Since current velocities in the WSC and physical processes that drive advection (such as storm activity over the North Atlantic) tend to be strongest during the winter season (Dickson et al. 2000) it can not be ruled out that advection of older stages of *C. finmarchicus* during winter may also be important. Pedersen (1995a) calculated that around 8×10^3 tons of carbon (C) of *C. finmarchicus* may be advected into the Barents Sea during January and concluded that, although it is far less compared to what may be advected during summer ($660\text{-}1320 \times 10^3$ tons C during May and June), it may nevertheless be an important component seeding the reproductive stock.

Plankton communities are not solely shaped by the transport of water masses, but also by local, ecological dynamics. Presumably, the most important factors determining local population dynamics through their effect on growth, reproduction or mortality are food availability, temperature and predation (Vidal 1980a, Hirche et al. 1997, Campbell et al. 2001, Hirst and Kiorboe 2002, Bagoien et al. 2001). Within the bounds defined by the ecological niche of organisms an increase in temperature typically enhances productivity by increasing growth rate and development rate (Huntley and Lopez 1992, Hirst and Kiorboe 2002, Campbell et al. 2001, Leandro et al. 2006) and thereby decreasing the population loss from eggs to diapause stages. Thus the increasing trend in *C. finmarchicus* abundance (and in *C. glacialis* in open water) with temperature may alternatively be explained as temperature enhanced productivity. However, increased productivity in warmer water can not explain the observed reduction in *C. glacialis* (on the shelf) and *C. hyperboreus* abundance with temperature. I find it therefore unlikely that temperature enhanced productivity alone should account for the observed relationships between *Calanus* abundance and the hydrographic parameters.

C. glacialis and *C. hyperboreus* are subjected to a different advective regime than *C. finmarchicus*. *C. glacialis* may be advected from the Arctic shelf seas, e.g. the northern Barents Sea, and within the East Spitsbergen Current and Coastal Current to the western

coast of Svalbard (Pedersen et al. 1995c, Karnovsky et al. 2003, Willis et al. 2006). *C. hyperboreus* populations may be advected from the Arctic Ocean into Svalbard waters within Arctic waters flowing in between Svalbard and Frans-Josef Land and continuing in the East Spitsbergen Current (Loeng 1989). Both species are also more successful in reproducing in colder water and under seasonal food limitations than *C. finmarchicus* (Tande et al. 1985, but see discussion below). Thus for the *C. glacialis* and *C. hyperboreus* populations in the study area local production may play an important role in sustaining the populations in Svalbard waters. Future studies should aim at clarifying the role of local production for these species.

Conclusion: *The mesozooplankton community in Svalbard waters was dominated by wide spread species. Variation in the community structure was related to variation in hydrography and bottom depth and was primarily caused by variation in species abundance rather than by taxonomical variation. For species of Atlantic and Arctic origin significant relationships with temperature and salinity were found and these relationships tended to be stronger for water mass characteristics deeper in the water column than for characteristics of the surface water. For the study area advection appeared to be more important than local production for sustaining the C. finmarchicus population.*

Vertical distribution and migration

While planktonic organisms have limited abilities to control their position in the horizontal scale they can affect their vertical distribution to a large extent by their own mobility (Longhurst 1976). Vertical gradients in light presumably play an important role for the vertical distribution of zooplankton. The attenuation of light in water restricts the depth range for primary production and thus the distribution of food within the water column (Sverdrup 1953). At the same time the light level restricts the efficiency of visual predators with increasing depth. Therefore the distribution of light in the water column may affect growth and mortality of zooplankton population. Thus to optimise their fitness zooplankton have to choose the optimal vertical position in the water column by balancing feeding conditions against predation risk. Several recent studies suggest that

optical properties are important in shaping abundances and vertical distributions in plankton and fish populations (Aksnes et al. 2004, Sørnes and Aksnes 2006, Sørnes et al. 2007, Aksnes 2007). I observed a positive linear relationship between the vertical range of the depth distribution and the mean depth for the copepodite stages of *C. finmarchicus* and *M. longa* (**paper III**). Although not a proof, this is consistent with the hypothesis that individuals of a species or developmental stages have a preference for ambient light of the water column.

Diel and seasonal migration are considered to be adaptive strategies to cope with vertical gradients in food availability (Unstad and Tande 1991, Hirche 1996b) and predation risk (Lampert 1989, Dale et al. 1999, Bagoien et al. 2001, Fiksen 2000) and changes in light condition are regarded as the most important proximate cue to trigger diel and seasonal vertical migrations (Haney 1988, Miller et al. 1991, Ringelberg and Van Gool 2003).

At high latitudes there is, in contrast to lower latitudes, high seasonal but low diel variability in the light regime. Thus there are large gradients in food abundance on a seasonal scale but the diel variability in predation risk within the water column is relatively small. Consequently, seasonal vertical migrations should be more important than diel vertical migration (DVM) for zooplankton in the Arctic (Kosobokova 1978, Longhurst et al. 1984, Falkenhaus et al. 1997, **paper III**). There are a number of studies on DVM behaviour of copepods at high latitudes but the data remain inconclusive on whether copepods perform DVM here or not. The absence of night (or day) leaves the zooplankton without a temporal refuge for feeding thus eliminating the advantage of DVM and this should depress DVM behaviour in zooplankton populations. This is supported by some observations such as those by Hays (1995b) who reports DVM in *C. hyperboreus* in temperate areas but not in Arctic waters. Digby (1960) concluded that diel changes in light intensity in Svalbard waters were too small to induce extensive migration in zooplankton. For *Calanus* DVM has not been observed in high Arctic locations such as the Nansen Basin (Gröndahl and Hernroth 1986, Mumm 1993) and Svalbard (Blachowiak-Samolyk et al. 2006, **paper III**), neither further south in the Barents Sea (Bogorov 1946) or in northern Norwegian coastal waters Falkenhaus et al. 1997). Dale and Kaartvedt (2000) however found the decrease in surface illumination high enough to reduce night time predation risk at the surface even during midnight sun in the

Norwegian and Greenland Sea. For distinct copepodite stages of *C. finmarchicus* DVM was observed in the Norwegian Sea and northern Norwegian coastal waters (Tande 1988, Dale and Kaartvedt 2000).

C. finmarchicus, *C. glacialis* and *C. hyperboreus* are also observed to conduct DVM in the Canadian archipelago (Sameoto 1984, Runge and Ingram 1991, Fortier et al. 2001).

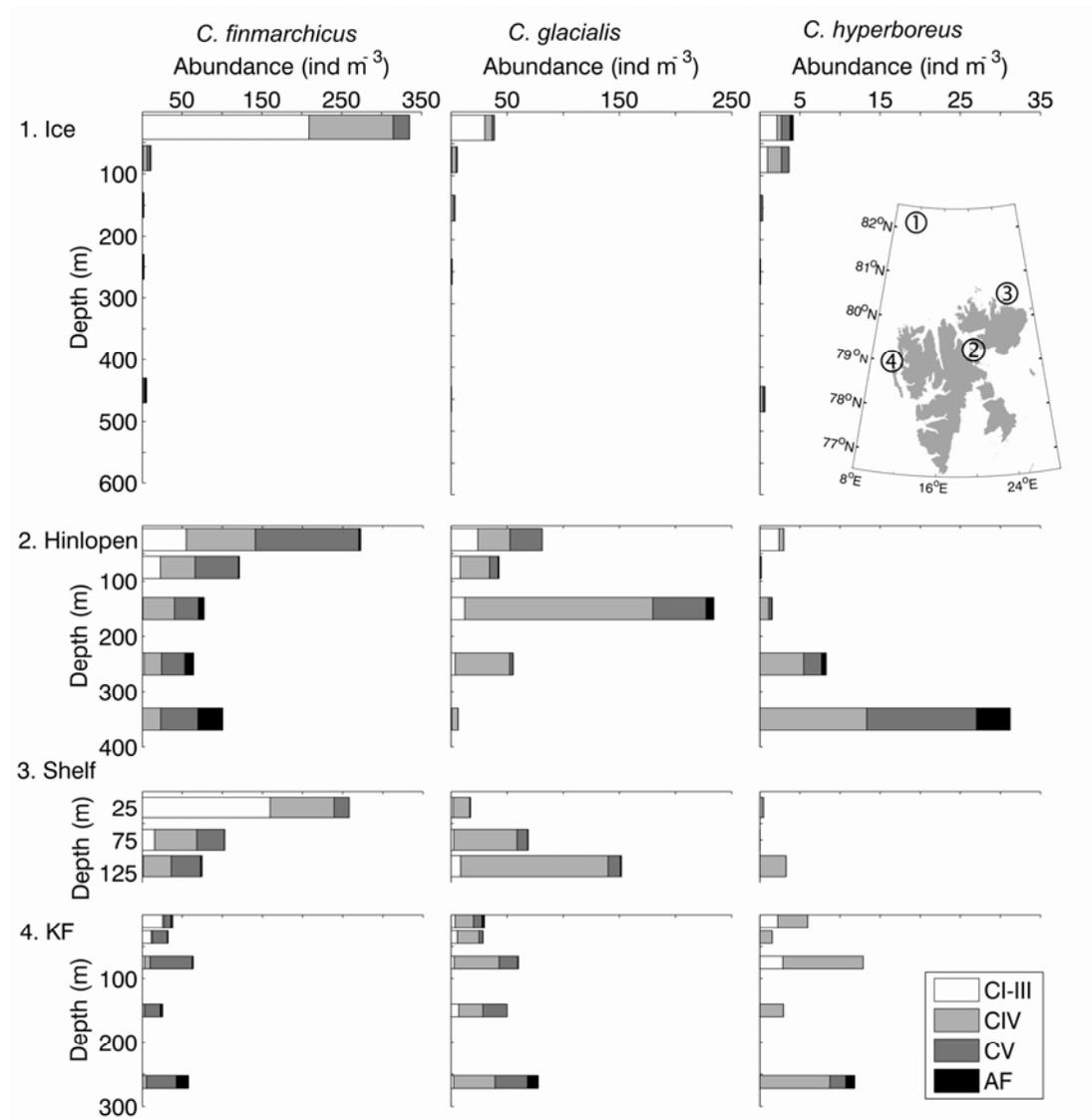


Figure 9: Vertical distribution of copepodite stages of the three *Calanus* species (ind. m⁻³) as observed in 1) oceanic waters north of Svalbard at the marginal ice edge ('Ice'), 2) in Hinlopen, 3) on the shelf north-east of Svalbard and 4) in Kongsfjorden ('KF') in September 2004. Location of each station is indicated by numbers in the inserted map.

Other studies indicate that there is temporal variability in the DVM behaviour of zooplankton in the Arctic, since some species were found to display DVM during autumn but were non-migratory during summer (Kosobokova 1978, Fischer and Visbeck 1993, Cottier et al. 2006). This is in contrast to my findings, which did not reveal DVM behaviour in *Calanus* during autumn (**paper III**). At the end of the productive season (late summer/ early autumn) older and larger copepodites of *Calanus* spp. were generally located deeper in the water column indicating that seasonal migration (the descent to overwintering depth) had started (Figure 3 in **paper III**). Fiksen and Carlotti (1998) suggested that DVM in herbivorous species such as *C. finmarchicus* in a highly seasonal environment will be constrained by the need to gain enough energy for the winter. Their model predicts that copepods risk staying close to the surface to feed in the period just before the descent to overwintering depth. This may explain the lack of DVM observed in Svalbard waters at the end of the productive season (**paper III**).

DVM was however observed for older developmental stages of *Metridia longa* while young stages of *M. longa* remained in deep waters both day and night (**paper III**). *M. longa* is an omnivorous species (Haq 1967) that does not go into diapause (Grønvik and Hopkins 1984, Båmstedt et al. 1985) and it is regularly reported to conduct DVM (Bogorov 1946, Grøndahl and Hernroth 1986, Hays 1995a, Falkenhaus et al. 1997). More opportunistic species which switch to other food resources when primary production is low and feed throughout the winter may be less constrained by the short productive season. These species may not need to spend as much time in the food rich surface layers but can allocate more resources to predator avoidance behaviour such as DVM (e.g. Diel 1991, Hagen 1999, Stevens et al. 2004). A mortality index indicated that non-migrating *Calanus* spp. suffered higher mortality than migrating *M. longa* (**paper III**). Since these observations were made during autumn, diel changes in light intensity may have been large enough to reduce predation risk at night at the surface. Thus during this period migrating animals may have a selective advantage over non-migratory animals that remain in surface waters to feed.

The onset of seasonal migration as indicated by the depth distribution of *Calanus* copepodite stages (Figure 3 in **paper III**) points to some constraints for the analysis in

paper I and **II**, since it implies that a part of the *Calanus* population may have been located below sampling depth at the deeper stations. This raises the question how representative the results are for other areas or season. Observations show that while the population was distributed throughout the water column in the shallow locations, at deep locations highest abundance was observed in the surface layer (Figure 9, Figure 2 in **paper III**). This also implies that even in the deeper locations most of the population was sampled in spite of not sampling the whole water column. The deeper locations were all located further north than the shallow locations. The larger proportion of younger stages at these locations (**paper III**) may therefore indicate a delayed development with latitude. This delay in development may reflect slower development in the colder northern waters (Corkett et al. 1986, Campbell et al. 2001) and also the succession in the onset of the spring bloom with the retreating ice edge. The difference in the timing of ice break up and onset of the phytoplankton bloom from south-western to north-eastern Svalbard waters can be up to four months (Hegseth 1998, Reigstad et al. 2002). Thus part of the variation in population development and abundance may be explained by differences in food availability and life history strategies.

***Conclusion:** Variability in abundance of the three *Calanus* species and *M. longa* on the vertical scale reflected life history and behavioural adaptations on diel and seasonal scale. The older copepodite stages of *Calanus* were located deeper in the water column indicating that the descent to overwintering depth had started. Peak abundance in the upper water column in the more northern stations however indicated a south to north delay in the succession of *Calanus* development. Positive correlations between the mean depth and the spread of *C. finmarchicus* and *M. longa* throughout the water column were consistent with the hypothesis that optical properties may have affected the vertical distribution. DVM was observed for older copepodite stages of *M. longa* but not for *Calanus* spp. This DVM behaviour in *M. longa* may account for the lower mortality rate indicated for this species compared to the non-migratory *Calanus* species.*

Life cycles and population dynamics of co-existing *Calanus* species

C. finmarchicus, *C. glacialis* and *C. hyperboreus* have evolved different life history strategies to cope with the environmental conditions in their main area of distribution, (Tande et al. 1985, Hirche 1997). Conover (1988) suggested that differences in the seasonal timing of reproduction (reviewed in **paper IV**) may be important to understand co-occurrence in *Calanus* spp. All three species show plasticity in the timing of reproduction. It is suggested that *C. finmarchicus* requires external energy supply to start reproduction (Diel and Tande 1992, Hirche et al. 1997) thus the timing of spawning for this species seems to depend on the onset of the spring bloom. *C. finmarchicus* can complete up to three generations per year in the southern parts of its distribution area (Conover 1988, Hirche 1996a) where temperatures are higher and the productive season starts earlier and lasts longer than further north where the generation time is found to be prolonged to a one-year life cycle (Grainger 1961, Tande et al. 1985, Melle and Skjoldal 1998, **paper IV**). *C. glacialis* and *C. hyperboreus* seem to be able to spawn independently of food abundance (Smith 1990, Diel 1991, Hirche and Niehoff 1996) but show also geographical variations in the length of their life cycles (Conover 1988). This might be due to difference in food availability at different locations during the growing season (Tande et al. 1985, Conover 1988, Hirche 1997, Melle and Skjoldal 1998) but also due to temperature dependent differences in development time (Corkett et al. 1986, Campbell et al. 2001).

Co-existing populations of *Calanus* spp. are observed on the shelf (Walkusz et al. 2003, Figure 5, **paper I**) and in fjords of Svalbard (e.g. Hornsundfjorden; Koszteyn and Kwasniewski 1989, Weslawski et al. 1991), Billefjorden (**paper IV**), Kongsfjorden (Kwasniewski et al. 2003, **paper III**). The distribution on the shelf is affected by advective transport but some fjord populations are assumed to be self-sustained (Kwasniewski et al. 2003). The generation time of *C. finmarchicus* and *C. glacialis* in Billefjorden corresponded to observations from other high latitude locations while for *C. hyperboreus* observations indicate a relatively short life cycle (**paper IV**). Environmental conditions in Billefjorden (low temperatures, seasonal ice cover, late spring bloom) resembled the Arctic shelf seas which presumably is a benefit for *C. glacialis*. The much

lower mortality rates observed for this species here compared to the other two species (**paper IV**) is consistent with this assertion.

It has been suggested that *C. finmarchicus* is not able to reproduce under high Arctic conditions (Tande et al. 1985). However, observations in **paper IV** indicated that *C. finmarchicus* did reproduce and maintained a population in Billefjorden. *C. finmarchicus* is capable of reproducing in waters below -1°C (Hirche et al. 1997), and Diel (1991) and Hirche et al. (1997) suggested that it may reproduce under Arctic conditions as long as food is not limiting development and egg production. Søreide et al. (submitted) however suggest that the main constraint for *C. finmarchicus* in Arctic waters are low temperatures and not food since it was found to utilize both ice algae and phytoplankton successfully. Unlike the Polar Basin, Billefjorden is ice-free every summer (July to September) making the onset of annual primary production regular. This regularity might be important for *C. finmarchicus* to maintain a population at this location. It is also likely that such predictability is the reason that *C. hyperboreus* obtained a shorter life cycle in Billefjorden than commonly observed in the high Arctic (**paper IV**) since a multiyear life cycle is regarded as an adaptation to cope with high variations in food supply not only on a seasonal scale but which may vary substantially between years due to variations in ice cover (Conover 1988).

***Conclusion:** The three Calanus species co-existed in Billefjorden. The estimate length of the life cycle of *C. glacialis* and *C. finmarchicus* was in agreement with previous studies in Svalbard and the Arctic. Observation of the stage development of *C. hyperboreus* suggest that it has a one year life cycle which is among the shortest life cycle durations reported for this species. Ice free conditions during summer may provide more stable conditions to complete the life cycle in one year in contrast to areas with more permanent ice cover.*

Possible effects of global warming on the *Calanus* community and the pelagic food web

An increase in air and water temperature in the Arctic has been observed over the past decades and temperatures are predicted to increase further over the next hundred years (Furevik et al. 2002, ACIA 2004). This warming has led to a decline in the sea ice extent throughout the last half of the twentieth century (Stroeve et al. 2007) and models predict further reductions that will eventually result in a sea-ice free summer in the Arctic Ocean (Johannessen et al. 2004, ACIA 2004, Polyakov et al. 2005, Zhang and Walsh 2006). This is likely to have an effect on the Arctic pelagic ecosystems since pelagic primary production is strongly related to the seasonality in ice cover and light. Thus the reduction in sea ice extent may open up new areas for phytoplankton production, in particular along the southern margin of the Arctic Ocean. In addition, increased air and water temperature may affect the timing of ice break up in spring and freeze up in autumn as well as stratification processes. A prolonged productive season may be a probable consequence since an earlier ice retreat may promote the onset of the spring bloom (Rysgaard et al. 1999, Carmack et al. 2006, Wu et al. 2007) while a delayed freeze-up may prolong the productive season in autumn as long as light is available. Carmack et al. (2006) pointed out that reduced ice cover will also subject larger areas of open water for longer time to wind convection and thereby affect vertical stratification and distribution of nutrients, which are important factors determining the onset of the spring bloom onset and the productivity. In the Bering Sea the pelagic spring bloom was found to be delayed in warm years of early ice retreat (before mid March) due to insufficient sun light and late thermal stratification. In colder years of late ice retreat however, the pelagic spring bloom occurred early since it was triggered by an ice associated bloom and supported by a stable stratification due to ice melt (Hunt et al. 2002).

If an earlier ice break up is followed by an early spring bloom this would most likely be advantageous for *C. finmarchicus*, since this species presumably needs the energy input of the bloom for reproductive success (Hirche et al. 1997). Recruitment is therefore likely to increase provided that the pre-bloom spawning observed now (**paper IV**) will occur under more favourable conditions. However, the reproductive success of the *Calanus*

population would also depend on their capability to synchronize diapause termination with an earlier productive season. Otherwise a mismatch between an early phytoplankton peak and occurrence of the herbivorous offspring might occur, resulting in low copepod production as suggested for ice-free conditions in Disko Bay (Hansen et al. 2003).

Changes in water temperature and ice cover may also shift the distribution and the generation time of species. Temperature in particular has a direct impact on development rate and generation time (Campbell et al. 2001), growth rates (Vidal 1980a, Vidal 1980b, Huntley and Lopez 1992a), body size (Hirst and Lampitt 1998) and reproduction (Hirche et al. 1997, Mauchline 1998). Increased water temperature and primary production may provide more favourable conditions for *C. finmarchicus* in more northern waters enabling it to reproduce successfully in areas where it was excluded before. In addition, it may also be able to adopt a shorter life cycle in Svalbard waters comparable to what is currently observed further south in the Norwegian Sea and along the Norwegian coast (Conover 1988, Hirche 1996a). This is supported by studies from the eastern Barents Sea that concluded that *C. finmarchicus* has a one-year life cycle in cold years but may produce two generations in warm years (Zelikman 1982 cited in Matishov et al. 2000).

Extrapolations of the results from **paper I** indicate that an increase in temperature in the study area may lead to an increase in the total zooplankton abundance. *C. finmarchicus* in particular showed a strong positive correlation with temperature (**paper II**) especially in the open ocean. The regression model in **paper II** predicts that *C. finmarchicus* abundance will increase with 120% at a temperature increase of one degree. The actual mechanisms behind such an increase are most likely multifaceted, involving a direct effect of warming that leads to increased local production as discussed above. On the other hand, warming resulting from a larger amount of warm water being advected into an area is likely to bring a higher number of individuals into this area.

In Svalbard waters in particular the inflow of Atlantic water within the WSC is predicted to increase (Walczowski and Piechura 2006). This may increase the amount of advected plankton from the Atlantic and the Arctic shelf seas to the Arctic Ocean. Olli et al. (2007) suggest that the copepod biomass in the central Arctic Ocean is largely due to lateral advection of allochthonous copepod populations (such as *C. glacialis* and *C.*

hyperboreus) from the more productive shelf areas rather than due to local, autochthonous production. Thus increased advection into the Arctic may also affect the pelagic production in the polar basin. In addition, an increased pelagic production and a prolonged productive season in the central Arctic Ocean season due to reduced ice cover may also benefit the autochthonous pelagic production.

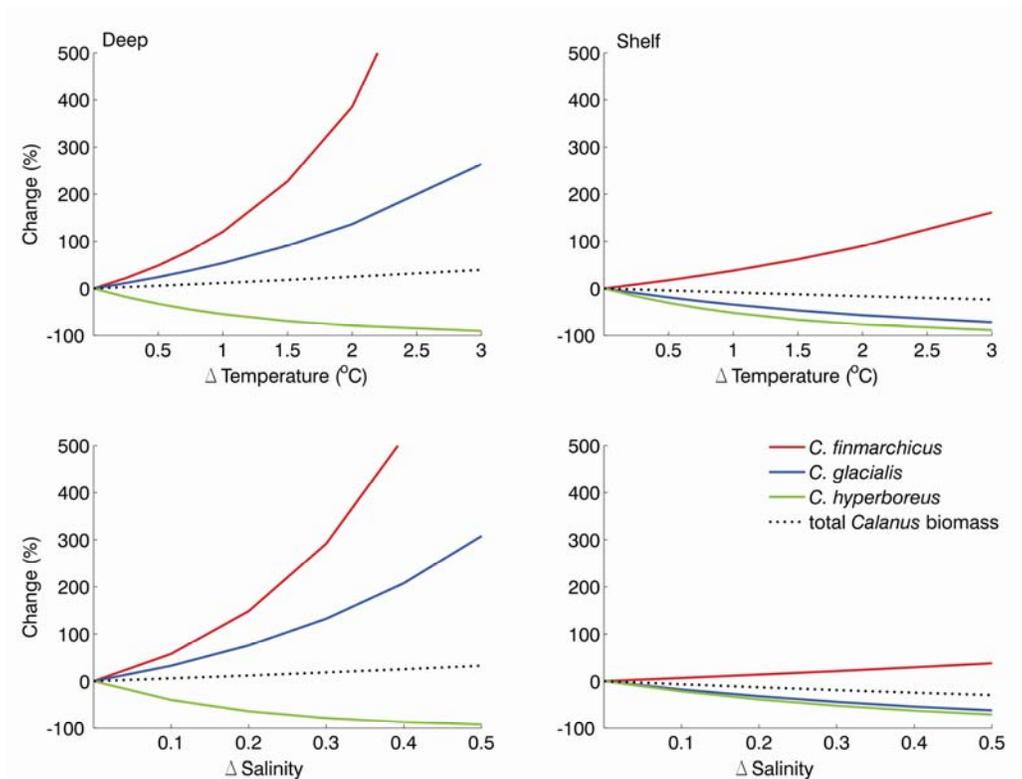


Figure 10: Predicted changes in the abundance of the three *Calanus* species (coloured lines) and in total *Calanus* biomass (black dotted line) with changes in temperature (upper panel) and salinity (lower panel) in oceanic waters (left panel) and on the shelf (right panel). Calculations are based on regression models (paper II).

Models predict a warming of the Nordic Seas of 1-2 degrees until 2080 (Furevik et al. 2002). By using the empirical relationships between *Calanus* abundance and temperature and salinity (paper II) as predictive tools I investigated the effect such a warming may have on the *Calanus* population. Figure 10 illustrates the changes in abundance of each species and in total *Calanus* biomass with increasing temperature and salinity in oceanic and shelf waters. While an increase in temperature or salinity leads to a large increase in the *C. finmarchicus* abundance, the total *Calanus* biomass increases only slightly and

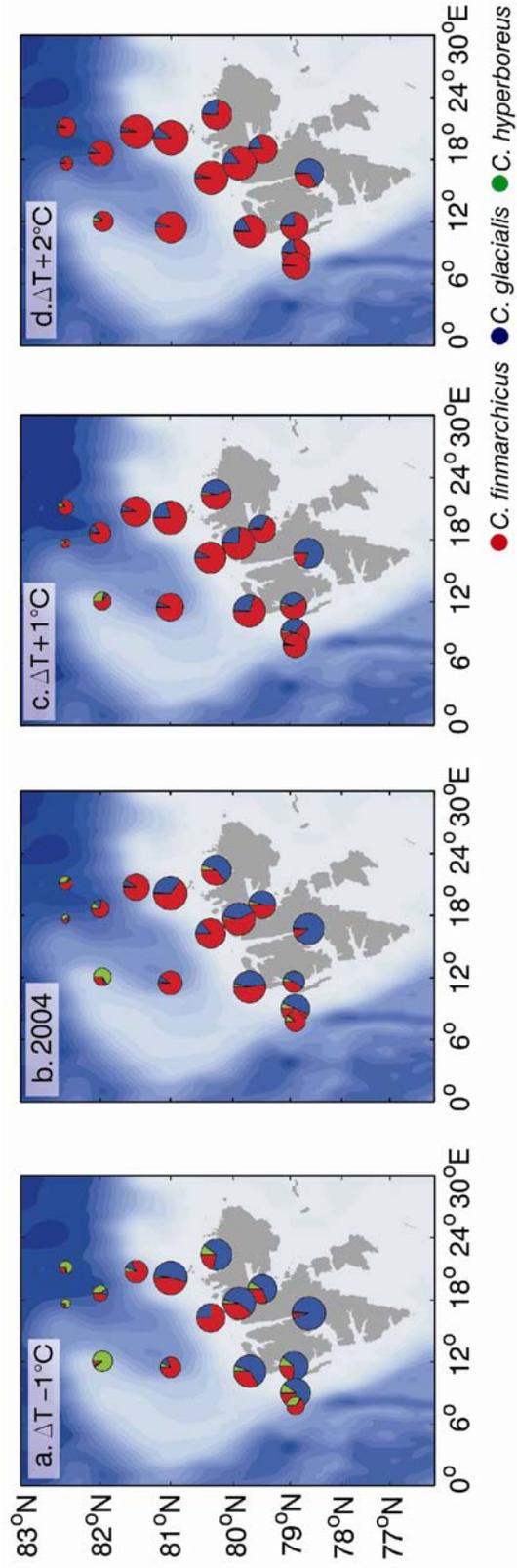


Figure 11: *Calanus* composition and abundance at selected station around Svalbard at different temperature scenarios. Based on observations of *Calanus* composition and abundance made in September 2004 (b.) the abundance of all three species was predicted for (a.) a temperature decrease of 1°C, (c.) a temperature increase of 1°C and (d.) 2°C. Predictions made based on models in paper II. Size of pies reflects log transformed abundance.

even decreases in shelf waters. In oceanic waters *C. glacialis* is also predicted to increase, but its abundance there is low (**paper II**). *C. hyperboreus* would also decrease in abundance and since this is the largest of the three species this should result in a decrease of the total *Calanus* biomass. However, in oceanic waters this biomass decrease is counteracted by a large increase in *C. finmarchicus* abundance. On the shelf both *C. glacialis* and *C. hyperboreus* decrease with increasing temperature and salinity. This decrease of the lipid rich Arctic species is large enough to cause a decrease in total biomass that is not balanced by the increase in *C. finmarchicus*.

The model also indicates that the changes will differ between oceanic and shelf waters. Assuming that advection is stronger in the open water (**paper II**) the large increase in *C. finmarchicus* here is likely to reflect increased inflow of Atlantic water. Taking observed abundance in 2004 as a starting point, a temperature increase of 1 or 2 degrees would shift the *Calanus* community composition in Svalbard waters to a stronger dominance of *C. finmarchicus* (Figure 11). A decrease in water temperature of 1 degree on the other hand would lead to a dominance of *C. glacialis* on the shelf and increases the importance of *C. hyperboreus* in the open water (Figure 11). The differences between the colder and warmer climate scenario is mainly reflected in the relative composition of the *Calanus* species. In 2004 *C. finmarchicus* represented on average 53% of all *Calanus* species at the selected stations. In the colder scenario (-1°C) it only represents 33% whereas in the warmer scenarios it dominates the *Calanus* community with 73% (+1°C) and up to 86% (+2°C). Since total biomass changes are minor, the implication for the ecosystem may mainly be associated with a shift in size structure. A shift in the size of the dominant zooplankton species in the system can have direct effects on the amount of biological energy available for the next trophic level since the lipid content of *C. glacialis* and *C. hyperboreus* is 10, respectively 25 times higher than in *C. finmarchicus* (mean lipid content for stage CV in *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* is 0.04, 0.38, and 1.03 mg ind⁻¹, respectively; Scott et al. 2000, Scott et al. 2002).

As planktivorous species tend to be size selective (Yen 1983, Greene and Landry 1985, Munk 1997, Puvanendran et al. 2004) it is likely that this change in mean size and energy content will have consequences for the pelagic food web. Beaugrand et al. (2003) related the survival of larval cod to changes in the mean size of calanoid copepods in the North

Sea. Here the smaller *C. helgolandicus* progressively substituted *C. finmarchicus*, probably as a consequence of a major shift in the zooplankton community structure detected in the North East Atlantic which has been attributed to increased temperatures (Beaugrand et al. 2002a, Beaugrand 2003, Beaugrand 2004).

This diminution of the mean size of available prey for juvenile cod is regarded as one of the main factors contributing to poor cod recruitment since the mid 80s (Beaugrand et al. 2003). In Arctic-Atlantic waters little auk (*Alle alle*) and polar cod (*Boreogadus saida*) are among the main predators of *Calanus* spp. (Bradstreet et al. 1986, Weslawski et al. 1999). As little auks are size-selective planktivores with a strong preference for larger prey items, a shift towards the small boreal species is proposed to lead to a reduction in available feeding grounds and reduced population size of little auks (Weslawski et al. 1999, Karnovsky et al. 2003). Polar cod is a visual predator (Bradstreet et al. 1986) and a decrease in prey size may affect its efficiency to catch prey. This may however be counterbalanced by feeding in a higher density of smaller prey. Polar cod is a generalist that tends to switch its food preferences to what is locally available and even adult fishes are often found to feed on smaller prey items (Bradstreet et al. 1986, Lønne and Gulliksen 1989).

Consequently, Falk-Petersen et al. (2006) proposed that a shift in the zooplankton community structure towards the smaller *C. finmarchicus* may lead to a change in the pelagic ecosystem structure where piscivorous predators are favoured rather than planktivorous seabirds that profit from a zooplankton community dominated by larger species such as *C. glacialis* and *C. hyperboreus*. Observations made in the north-western Pacific seem to support this notion. Here changes in the size spectra of the zooplankton community have been attributed to variations in ocean climate (Kitaysky and Golubova 2000). High production of mesozooplankton in warm years is assumed to profit fish recruitment which probably increased the reproductive success of piscivorous seabirds. During cold years high abundance of macrozooplankton provided better feeding conditions for planktivore seabirds which were more abundant during these periods (Kitaysky and Golubova 2000).

Conclusion: Projections made from the results of this thesis suggest that predicted climate change may affect the Calanus community in Svalbard waters by altering the abundance of the three Calanus species differently and thereby changing the relative species composition. The abundance of *C. finmarchicus* is expected to increase, whereas *C. hyperboreus* and *C. glacialis* are likely to decrease. Thus the Calanus community will shift towards a dominance of the small Atlantic species. Total Calanus biomass however is less affected. Thus the effect of ocean climate changes on the Calanus species composition may first and foremost be associated with a shift in size structure. This may have implication for the structure of the pelagic food web since the members of the next trophic level have different preferences for prey of different size.

References

- Aagaard K, Greisman P (1975) Toward new mass and heat budgets for Arctic Ocean. *J Geophys Res C* 80:3821-3827
- Aagaard K, Foldvik A, Hillman SR (1987) The West Spitsbergen Current - disposition and water mass transformation. *J Geophys Res C* 92:3778-3784
- Aagaard K, Carmack EC (1989) The role of sea ice and other fresh-water in the Arctic Circulation. *J Geophys Res C* 94:14485-14498
- ACIA (2004) Impacts of warming in the Arctic: Arctic Climate Impact Assessment. Cambridge University Press, www.acia.uaf.edu
- Aksnes DL, Blindheim J (1996) Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. *Ophelia* 44:7-28
- Aksnes DL, Miller CB, Ohman MD, Wood SN (1997) Estimation techniques used in studies of copepod population dynamics - A review of underlying assumptions. *Sarsia* 82:279-296
- Aksnes DL, Nejtgaard J, Soedberg E, Sørnes T (2004) Optical control of fish and zooplankton populations. *Limnol Oceanogr* 49:233-238
- Aksnes DL (2007) Evidence for visual constraints in large marine fish stocks. *Limnol Oceanogr* 52:198-203
- Alvariño A (1965) Chaetognaths. In: Barnes H (ed) *Oceanography and Marine Biology- An Annual Review*, Vol. 3. Aberdeen University Press, pp 115-194
- Anisimov OA, Vaughan DG, Callaghan TV, Furgal C, Marchant H, Prowse TD, Vilhjalmsón H, Walsh JE (2007) *Climate Change 2007: Impacts, Adaptations and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*, Cambridge University Press
- Arashkevich E, Wassmann P, Pasternak A, Riser CW (2002) Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. *J Mar Syst* 38:125-145
- Ashjian C, Smith S, Bignami F, Hopkins T, Lane P (1997) Distribution of zooplankton in the Northeast Water Polynya during summer 1992. *J Mar Syst* 10:279-298
- Ashjian CJ, Lane PVZ, Smith SL (1995) The Northeast Water Polynya during summer 1992 - Distribution and aspects of secondary production of copepods. *J Geophys Res C* 100:4371-4388
- Astthorsson OS, Gislason A (1998) Environmental conditions, zooplankton, and capelin in the waters north of Iceland. *ICES J Mar Sci* 55:808-810
- Auel H, Hagen W (2002) Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. *Mar Biol* 140:1013-1021
- Auel H, Harjes M, da Rocha R, Stubing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. *Polar Biol* 25:374-383

- Backhaus JO, Harms IH, Krause M, Heath MR (1994) A hypothesis concerning the space-time succession of *Calanus finmarchicus* in the northern North-Sea. ICES J Mar Sci 51:169-180
- Bagoien E, Kaartvedt S, Aksnes DL, Eiane K (2001) Vertical distribution and mortality of overwintering *Calanus*. Limnol Oceanogr 46:1494-1510
- Basedow SL, Eiane K, Tverberg V, Spindler M (2004) Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard). Est Coast Shelf Sci 60:113-124
- Bathmann UV, Noji TT, Vonbodungen B (1990) Copepod grazing potential in late winter in the Norwegian Sea - a factor in the control of spring phytoplankton growth. Mar Ecol Prog Ser 60:225-233
- Beare DJ, Batten S, Edwards M, Reid DG (2002) Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. J Sea Res 48:29-49
- Beaugrand G, Ibanez F, Lindley JA, Reid PC (2002a) Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. Mar Ecol Prog Ser 232:179-195
- Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M (2002b) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692-1694
- Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fish Oceanogr 12:270-283
- Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661-664
- Beaugrand G, Reid PC (2003) Long-term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology 9:801-817
- Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog Oceanogr 60:245-262
- Beaugrand G (2005) Monitoring pelagic ecosystems using plankton indicators. ICES J Mar Sci 62:333-338
- Berge J, Johnsen G, Nilsen F, Gulliksen B, Slagstad D (2005) Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Mar Ecol Prog Ser 303:167-175
- Blachowiak-Samolyk K, Kwasniewski S, Richardson K, Dmoch K, Hansen E, Hop H, Falk-Petersen S, Mouritsen LT (2006) Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. Mar Ecol Prog Ser 308:101-116
- Blindheim J, Østerhus S (2005) The Nordic Seas, main Oceanographic Features. In: Drange H, Dokken T, Furevik T, Gerdes R, Berger W (eds). Geophysical Monograph 158: The Nordic Seas: An integrated perspective. Oceanography, Climatology, Biochemistry, and Modeling., The American Geophysical Union, pp 11-38
- Bogorov BG (1946) Peculiarities of diurnal vertical migrations of zooplankton in Polar Seas. J Mar Res 6:25-32
- Bradstreet MSW, Finley KJ, Sekerak AD, Griffiths WB, Evans CR, Fabijan MF, Stallard HE (1986) Aspects of the biology of Arctic cod (*Boreogadus saida*) in Arctic marine food chains. Can Tech Rep Fish Aqua Sci 4, 193 pp

- Brodskii KA (1967) Calanoida of the Far Eastern Seas and the Polar Basin of the USSR. In: Strelkov AA (ed) Keys to the Fauna of the USSR, The Zoological Institute of the Academy of Sciences of the USSR No.35, Israel Program for Scientific Translations
- Bryant AD, Hainbucher D, Heath M (1998) Basin-scale advection and population persistence of *Calanus finmarchicus*. Fish Oceanogr 7:235-244
- Båmstedt U, Tande K, Nicolajsen H (1985) Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: physiological adaptations in *Metridia longa* (copepoda) to the overwintering periods. In: Gray JS, Christiansen ME (eds). Marine Biology of polar regions and effects of stress on marine organisms, John Wiley & Sons Ltd, pp 313-327
- Campbell RG, Wagner MM, Teegarden GJ, Boudreau CA, Durbin EG (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Mar Ecol Prog Ser 221:161-183
- Carmack E, Barber D, Christensen J, Macdonald R, Rudels B, Sakshaug E (2006) Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. Prog Oceanogr 71:145-181
- Carroll ML, Carroll J (2003) The Arctic seas. In: Black K, Shimmiel G (eds) Biogeochemistry of Marine Systems. Blackwell Publ Ltd, Oxford, pp 127-156
- Colebrook JM (1978) Continuous plankton records: zooplankton and environment, North-East Atlantic and North Sea, 1948-1975. Oceanol Acta 1:9-23
- Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167:127-142
- Conover RJ, Huntley M (1991) Copepods in ice-covered seas- Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. J Mar Res 2:1-41
- Conversi A, Piontkovski S, Hameed S (2001) Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US shelf) with reference to the North Atlantic Oscillation. Deep Sea Res Part II 48:519-530
- Corkett CJ, McLaren IA, Sevigny JM (1986) The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Krøyer with comment on the equiproportional rule. In: Schriever G, Schminke HK, Shih CT (eds) Syllogeus 58, Proceedings of the second international Conference on Copepoda 13.-17. August, Ottawa, Canada, pp 539-546
- Corten A (2001) Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. Fish Res 50:189-204
- Cottier F, Tverberg V, Inall M, Svendsen H, Nilsen F, Griffiths C (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. J Geophys Res C 110: C12005, doi:10.1029/2004JC002757
- Cottier FR, Tarling GA, Wold A, Falk-Petersen S (2006) Unsynchronized and synchronized vertical migration of zooplankton in a high arctic fjord. Limnol Oceanogr 51:2586-2599
- Cottier FR, Nilsen F, Inall ME, Gerland S, Tverberg V, Svendsen H (2007) Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. Geophys Res Lett 34: L10607, doi:10.1029/2007GL029948

- Cushing DH (1951) The vertical migration of planktonic crustacea. *Biological Reviews of the Cambridge Philosophical Society* 26:158-192
- Dahl TM, Lydersen C, Kovacs KM, Falk-Petersen S, Sargent J, Gjertz I, Gulliksen B (2000) Fatty acid composition of the blubber in white whales (*Delphinapterus leucas*). *Polar Biol* 23:401-409
- Dale T, Bagoien E, Melle W, Kaartvedt S (1999) Can predator avoidance explain varying overwintering depth of *Calanus* in different oceanic water masses? *Mar Ecol Prog Ser* 179:113-121
- Dale T, Kaartvedt S (2000) Diel patterns in stage-specific vertical migration of *Calanus finmarchicus* in habitats with midnight sun. *ICES J Mar Sci* 57:1800-1818
- Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of *Themisto* (Amphipoda) spp in the Barents Sea and predator-prey interactions. *ICES J Mar Sci* 58:876-895
- Dalpadado P, Ingvaldsen R, Hassel A (2003) Zooplankton biomass variation in relation to climatic conditions in the Barents Sea. *Polar Biol* 26:233-241
- Dawson JK (1978) Vertical distribution of *Calanus hyperboreus* in Central Arctic Ocean. *Limnol Oceanogr* 23:950-957
- Dickson RR, Kelly PM, Colebrook JM, Wooster WS, Cushing DH (1988) North winds and production in the eastern North-Atlantic. *J Plankton Res* 10:151-169
- Dickson RR, Osborn TJ, Hurrell JW, Meincke J, Blindheim J, Adlandsvik B, Vinje T, Alekseev G, Maslowski W (2000) The Arctic Ocean response to the North Atlantic oscillation. *J Clim* 13:2671-2696
- Diel S (1991) On the life history of dominant copepod species (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia longa*) in the Fram Strait. *Ber Polarforsch* 88:1-113
- Diel S, Tande K (1992) Does the spawning of *Calanus finmarchicus* in high-latitudes follow a reproducible pattern. *Mar Biol* 113:21-31
- Digby PSB (1954) The biology of the marine planktonic copepods of Scoresby-Sound, East Greenland. *J Anim Ecol* 23:298-338
- Digby PSB (1960) Midnight-sun illumination above and below the sea-surface in the Spitsbergen, N.W. and its significance to plankton. *J Anim Ecol* 29:273-297
- Digby PSB (1961) The vertical distribution and movement of marine plankton under midnight-sun conditions in Spitsbergen. *J Anim Ecol* 30:9-25
- Dunbar MJ (1962) The Life Cycle of *Sagitta elegans* in Arctic and subarctic seas, and the modifying effects of hydrographic differences in the environment. *J Mar Res* 20:76-91
- Dunbar MJ (1964) Serial Atlas of the Marine Environment, Folio 6: Euphausiids and pelagic amphipods: distribution in North Atlantic and Arctic waters. American Geographical Society, 8 Plates
- Edvardsen A, Tande KS, Slagstad D (2003) The importance of advection on production of *Calanus finmarchicus* in the Atlantic part of the Barents Sea. *Sarsia* 88:261-273
- Eiane K, Aksnes DL, Ohman MD (1998) Advection and zooplankton fitness. *Sarsia* 83:87-93
- Ekman VW (1905) On the influence of the earth's rotation on ocean-currents. *Arkiv för Matematik, Astronomi och Fysik* 2:1-52

- Ekman S (1953) Zoogeography of the Sea. Sigwick & Jackson, London, 417p.
- Fahrbach E, Meincke J, Osterhus S, Rohardt G, Schauer U, Tverberg V, Verduin J (2001) Direct measurements of volume transports through Fram Strait. *Polar Res* 20:217-224
- Falkenhaug T, Tande KS, Semenova T (1997) Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. *Mar Ecol Prog Ser* 149:1105-1119
- Falk-Petersen S, Pedersen G, Kwasniewski S, Hegseth EN, Hop H (1999) Spatial distribution and life-cycle timing of zooplankton in the marginal ice zone of the Barents Sea during the summer melt season in 1995. *J Plankton Res* 21:1249-1264
- Falk-Petersen S, Dahl TM, Scott CL, Sargent JR, Gulliksen B, Kwasniewski S, Hop H, Millar RM (2002) Lipid biomarkers and trophic linkages between ctenophores and copepods in Svalbard waters. *Mar Ecol Prog Ser* 227:187-194
- Falk-Petersen S, Haug T, Nilssen KT, Wold A, Dahl TM (2004) Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. *Polar Res* 23:43-50
- Falk-Petersen S, Timofeev S, Pavlov V, Sargent JR (2006) Climate variability and the effect on arctic food chains. The role of *Calanus*. In: Orbaek JB, Tombre T, Kallenborn R, Hegseth E, Falk-Petersen S, Hoel A H (eds). Arctic-alpine ecosystems and people in a changing environment, Springer Verlag, pp 147-166
- Fiksen Ø, Carlotti F (1998) A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. *Sarsia* 83:129-147
- Fiksen Ø (2000) The adaptive timing of diapause - a search for evolutionarily robust strategies in *Calanus finmarchicus*. *ICES J Mar Sci* 57:1825-1833
- Fischer J, Visbeck M (1993) Seasonal-Variation of the Daily Zooplankton Migration in the Greenland Sea. *Deep Sea Res Part I* 40:1547-1557
- Fortier M, Fortier L, Hattori H, Saito H, Legendre L (2001) Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. *J Plankton Res* 23:1263-1278
- Fromentin JM, Planque B (1996) *Calanus* and environment in the eastern North Atlantic 2. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar Ecol Prog Ser* 134:111-118
- Furevik T, Drange H, Sorteberg A (2002) Anticipated changes in the Nordic Seas marine climate: Scenarios for 2020, 2050 and 2080. *Fisken og Havet* 4/2002:1-13
- Furevik T, Nilsen JEØ (2005) Large-scale atmospheric circulation variability and its impact on the Nordic Seas ocean climate - a review. In: Drange H, Dokken T, Furevik T, Gerdes R, Berger W (eds). Geophysical Monograph 158: The Nordic Seas: An integrated perspective. Oceanography, Climatology, Biochemistry, and Modeling., The American Geophysical Union, pp 105-136
- Gallienne CP, Robins DB (2001) Is *Oithona* the most important copepod in the world's oceans? *J Plankton Res* 23:1421-1432
- Gislason A, Astthorsson OS (2004) Distribution patterns of zooplankton communities around Iceland in spring. *Sarsia* 89:467-477

- Gjørseter H, Dalpadado P, Hassel A (2002) Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance. *ICES J Mar Sci* 59:959-967
- Grainger EH (1961) The copepods *Calanus glacialis* Jaschnov and *Calanus finmarchicus* (Gunnerus) in Canadian Arctic-Subarctic Waters. *J Fish Res Board Can* 18:663-678
- Grainger EH (1963) Copepods of the genus *Calanus* as indicators of Eastern Canadian Waters. In: Dunbar MJ (ed). *Marine Distributions*, The Royal Society of Canada, Special Publications No.5, University of Toronto Press, pp 68-94
- Grainger EH (1965) Zooplankton from Arctic Ocean and adjacent Canadian waters. *J Fish Res Board Can* 22:543-564
- Gran HH (1902) Das Plankton des Norwegischen Nordmeeres von biologischen und hydrographischen Gesichtspunkten behandelt. *Rep Norweg Fish Invest* 2:222
- Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006a) Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Prog Oceanogr* 71:331-361
- Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006b) A major ecosystem shift in the northern Bering Sea. *Science* 311:1461-1464
- Greene CH, Landry MR (1985) Patterns of prey selection in the cruising calanoid predator *Euchaeta elongata*. *Ecology* 66:1408-1416
- Greene CH, Pershing AJ, Conversi A, Planque B, Hannah C, Sameoto D, Head E, Smith PC, Reid PC, Jossi J, Mountain D, Benfield MC, Wiebe PH, Durbin E (2003) Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. *Prog Oceanogr* 58:301-312
- Grice GD (1962) Copepods collected by the nuclear submarine Seadragon on a cruise to and from the North Pole, with remarks on their geographic distribution. *J Mar Res* 20:97-109
- Grotefendt K, Logemann K, Quadfasel D, Ronski S (1998) Is the Arctic Ocean warming? *J Geophys Res C* 103:27679-27687
- Grøndahl F, Hernroth L (1986) Vertical distribution of copepods in the eurasian part of the Nansen Basin, Arctic Ocean. In: Schriever G, Schminke HK, Shih CT (eds) *Syllogeus* 58, Proceedings of the second international Conference on Copepoda 13.-17. August, Ottawa, Canada, pp 311-320
- Grønvik S, Hopkins CCE (1984) Ecological investigations of the zooplankton community of Balsfjorden, Northern Norway: Generation cycle, seasonal vertical distribution and seasonal variations in body weight and carbon and nitrogen content of the copepod *Metridia longa* (Lubbock). *J Exp Mar Biol Ecol* 80:93-107
- Hagen W (1999) Reproductive strategies and energetic adaptations of polar zooplankton. *Invertebrate Reproduction & Development* 36:25-34
- Halvorsen E, Tande KS, Edvardsen A, Slagstad D, Pedersen OP (2003) Habitat selection of overwintering *Calanus finmarchicus* in the NE Norwegian Sea and shelf waters off Northern Norway in 2000-02. *Fish Oceanogr* 12:339-351
- Haney JF (1988) Diel patterns of zooplankton behavior. *Bull Mar Sci* 43:583-603

- Hansen AS, Nielsen TG, Levinsen H, Madsen SD, Thingstad TF, Hansen BW (2003) Impact of changing ice cover on pelagic productivity and food web structure in Disko Bay, West Greenland: a dynamic model approach. *Deep Sea Res Part I* 50:171-187
- Haq SM (1967) Nutritional physiology of *Metridia lucens* and *M. longa* from Gulf of Maine. *Limnol Oceanogr* 12:40-51
- Harms JH, Heath MR, Bryant AD, Backhaus JO, Hainbucher DA (2000) Modelling the Northeast Atlantic circulation: implications for the spring invasion of shelf regions by *Calanus finmarchicus*. *ICES J Mar Sci* 57:1694-1707
- Hays GC (1995a) Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*. *Limnol Oceanogr* 40:1461-1465
- Hays GC (1995b) Diel vertical migration behavior of *Calanus hyperboreus* at temperate latitudes. *Mar Ecol Prog Ser* 127:301-304
- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends Ecol Evol* 20:337-344
- Head EJH, Harris LR, Yashayaev I (2003) Distributions of *Calanus* spp. and other mesozooplankton in the Labrador Sea in relation to hydrography in spring and summer (1995-2000). *Prog Oceanogr* 59:1-30
- Heath MR, Backhaus JO, Richardson K, McKenzie E, Slagstad D, Beare DJ, Dunn J, Fraser JG, Gallego A, Hainbucher DA, Hay SJ, Jonasdottir SH, Madden H, Mardaljevic J, Schacht A (1999) Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fish Oceanogr* 8 (Suppl.1):163-176
- Hegseth EN (1998) Primary production of the northern Barents Sea. *Polar Res* 17:113-123
- Helle K, Pennington M (1999) The relation of the spatial distribution of early juvenile cod (*Gadus morhua* L.) in the Barents Sea to zooplankton density and water flux during the period 1978-1984. *ICES J Mar Sci* 56:15-27
- Helle K (2000) Distribution of the copepodite stages of *Calanus finmarchicus* from Lofoten to the Barents Sea in July 1989. *ICES J Mar Sci* 57:1636-1644
- Hensen V (1887) Über die Bestimmung des Planktons oder des im Meere treibende Materials an Pflanzen und Thieren. *Berichte der Kommission zur Wissenschaftlichen Untersuchung der Deutschen Meere* 5
- Hirche HJ (1990) Egg-production of *Calanus finmarchicus* at low temperature. *Mar Biol* 106:53-58
- Hirche HJ (1991) Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. *Polar Biol* 11:351-362
- Hirche HJ, Mumm N (1992) Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. *Deep Sea Res Part A* 39:S485-S505
- Hirche HJ, Hagen W, Mumm N, Richter C (1994) The northeast water polynya, Greenland Sea. III. Mesozooplankton and macrozooplankton distribution and production of dominant herbivorous copepods during spring. *Polar Biol* 14:491-503
- Hirche HJ (1996a) The reproductive biology of the marine copepod, *Calanus finmarchicus* - A review. *Ophelia* 44:111-128

- Hirche HJ (1996b) Diapause in the marine copepod, *Calanus finmarchicus* - A review. *Ophelia* 44:129-143
- Hirche HJ, Niehoff B (1996) Reproduction of the Arctic copepod *Calanus hyperboreus* in the Greenland Sea- field and laboratory observations. *Polar Biol* 16:209-219
- Hirche HJ (1997) Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Mar Biol* 128:607-618
- Hirche HJ, Meyer U, Niehoff B (1997) Egg production of *Calanus finmarchicus*: Effect of temperature, food and season. *Mar Biol* 127:609-620
- Hirst AG, Lampitt RS (1998) Towards a global model of in situ weight-specific growth in marine planktonic copepods. *Mar Biol* 132:247-257
- Hirst AG, Kiorboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. *Mar Ecol Prog Ser* 230:195-209
- Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowaleczuk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey RJG, Lonne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wangberg SA, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. *Polar Res* 21:167-208
- Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. *Prog Oceanogr* 71:182-231
- Hunt GL, Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep Sea Res Part II* 49:5821-5853
- Huntley M, Lopez MDG (1992) Temperature dependent production of marine copepods- A global synthesis. *Am Nat* 140:201-242
- Iles TD, Sinclair M (1982) Atlantic Herring - stock discreteness and abundance. *Science* 215:627-633
- Ingvaldsen R, Loeng H, Asplin L (2002) Variability in the Atlantic inflow to the Barents Sea based on a one-year time series from moored current meters. *Contl Shelf Res* 22:505-519
- Jaschnov WA (1961) Water masses and plankton. 1. Species of *Calanus finmarchicus* s.l. as indicators of definite water masses. *Zoologeskij zurnal* 40:1314-1334
- Jaschnov WA (1966) Water mass and Plankton: 4. *Calanus finmarchicus* and *Dimophysys arctica* as indicators of Atlantic waters in the Polar Basin. *Oceanol Acad Sci USSR* 6:404-412
- Jaschnov WA (1970a) Distribution of *Calanus* species in the seas of the northern hemisphere. *Int Rev Gesamten Hydrobiol* 55:197-212
- Jaschnov WA (1972) On the systematic status of *Calanus glacialis*, *Calanus finmarchicus* and *Calanus hyperboreus*. *Crustaceana* 22:279-284
- Johannessen OM, Bengtson L, Miles MW, Kuzmina SI, Semenov VA, Alekseev GV, Nagurnyi AP, Zakharov VF, Bobylev LP, Petterson LH, Hasselmann K, Cattle HP (2004) Arctic climate change: observed and modelled temperature and sea-ice variability. *Tellus* 56A:328-341

- Kaartvedt S (1996) Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. *Ophelia* 44:145-156
- Karnovsky NJ, Kwasniewski S, Weslawski JM, Walkusz W, Beszczynska-Moller A (2003) Foraging behavior of little auks in a heterogeneous environment. *Mar Ecol Prog Ser* 253:289-303
- Kitaysky AS, Golubova EG (2000) Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. *J Anim Ecol* 69:248-262
- Kosobokova K (1978) Diurnal vertical distribution of *Calanus hyperboreus* Kroyer and *Calanus glacialis* Jaschnov in Central Polar Basin. *Oceanology* 18:722-728
- Kosobokova KN, Hanssen H, Hirche HJ, Knickmeier K (1998) Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993. *Polar Biol* 19:63-76
- Kosobokova KN (1999) The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. *Polar Biol* 22:254-263
- Koszteyn J, Kwasniewski S (1989) Comparison of fjord and shelf mesozooplankton communities of southern Spitsbergen region. *Rapp. P.-v. Reun. Cons. int. Explor. Mer* 188:164-169
- Koszteyn J, Kwasniewski S, Rozycki O, Weslawski JM (1991) Atlas of the marine fauna of southern Spitsbergen, Vol. 2 Invertebrates Part 1. In: Klekowski R, Weslawski JM (eds) Polish Academy of Sciences, Institute of Ecology, Institute of Oceanology, 550 pp
- Kramp PL (1947) Medusae- Part III Trachylina and Scyphozoa. *Dan Ingolf-Exped* 5, 14:1-66
- Kwasniewski S, Hop H, Falk-Petersen S, Pedersen G (2003) Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *J Plankton Res* 25:1-20
- Lampert W (1989) The adaptive significance of diel vertical migration of zooplankton. *Funct Ecol* 3:21-27
- Leandro SM, Queiroga H, Rodriguez-Grana L, Tiselius P (2006) Temperature-dependent development and somatic growth in two allopatric populations of *Acartia clausi* (Copepoda: Calanoida). *Mar Ecol Prog Ser* 322:189-197
- Lee RF (1974) Lipid-composition of copepod *Calanus hyperboreus* from Arctic Ocean - Changes with depth and season. *Mar Biol* 26:313-318
- Lee RF (1975) Lipids of Arctic zooplankton. *Comp Biochem Physiol* 51:263-266
- Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. *Mar Ecol Prog Ser* 307:273-306
- Legendre L, Demers S (1984) Towards dynamic biological oceanography and limnology. *Can J Fish Aquat Sci* 41:2-19
- Legendre P, Legendre L (1998) Numerical Ecology. Elsevier Science B.V., 853pp
- Lie U (1965) Quantities of zooplankton and propagation of *Calanus finmarchicus* at permanent stations on the Norwegian Coast and at Spitsbergen, 1959-1962. *Fiskeridir Skr Ser Havunders* 13:1-19
- Lindley JA, Reid PC (2002) Variations in the abundance of *Centropages typicus* and *Calanus helgolandicus* in the North Sea: deviations from close relationships with temperature. *Mar Biol* 141:153-165

- Lischka S, Knickmeier K, Hagen W (2001) Mesozooplankton assemblages in the shallow Arctic Laptev Sea in summer 1993 and autumn 1995. *Polar Biol* 24:186-199
- Loeng H (1989) Ecological Features of the Barents Sea. In: Rey L, Alexander V (eds) Proceedings 6th Conference of the Comité Arctique International 13-15 May 1985, pp 327-365
- Loeng H (1991) Features of the physical oceanographic conditions of the Barents Sea. *Polar Res* 10:5-18
- Loeng H, Ozhigin V, Adlandsvik B (1997) Water fluxes through the Barents Sea. *ICES J Mar Sci* 54:310-317
- Longhurst A (1976) Vertical migration. In: Cushing D H Walsh J J (ed). *The Ecology of the Seas*, Blackwell Scientific Publications, pp116-137
- Longhurst A, Sameoto D, Herman A (1984) Vertical distribution of Arctic zooplankton in summer - Eastern Canadian Archipelago. *J Plankton Res* 6:137-168
- Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773) in ice covered waters. *Polar Biol* 9:187-191
- Mackas DL, Peterson WT, Zamon JE (2004) Comparisons of interannual biomass anomalies of zooplankton communities along the continental margins of British Columbia and Oregon. *Deep Sea Res Part II* 51:875-896
- Madsen SD, Nielsen TG, Hansen BW (2001) Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. *Mar Biol* 139:75-93
- Manley TO (1995) Branching of Atlantic water within the Greenland-Spitsbergen passage - an estimate of recirculation. *J Geophys Res C* 100:20627-20634
- Mann KH, Lazier JRN (1996) Dynamics of marine ecosystems. Biological-physical interactions in the oceans. Blackwell Science Inc, 394 pp
- Marshall SM, Orr AP (1955) *The Biology of a marine copepod (Calanus finmarchicus Gunnerus)*. Oliver & Boyd (eds), Springer-Verlag, 195 pp
- Matishov G, Makarevich P, Timofeev S, Kuznetsov L, Druzhkov N, Lariono V, Golubev V, Zuyev A, Adrov N, Denisov V, Iliyan G, Kuznetsov A, Denisenko SG, Savinov V, Shavikyn A, Smolyar I, Levitus S, O'Brien T, Baranova O (2000) Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas. International Ocean Atlas Series. Volume 2. www.nodc.noaa/OC5/
- Mauchline J (1998) *The biology of marine copepods*. *Avances in Marine Biology*, Academic Press, 710 pp
- McGowan JA (1990) Climate and change in oceanic ecosystems - the value of time-series data. *Trends Ecol Evol* 5:293-295
- Melle W, Skjoldal HR (1998) Reproduction and development of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the Barents Sea. *Mar Ecol Prog Ser* 169:211-228
- Miller CB, Cowles TJ, Wiebe PH, Copley NJ, Grigg H (1991) Phenology in *Calanus finmarchicus*-Hypotheses about control mechanisms. *Mar Ecol Prog Ser* 72:79-91
- Miller CB, Lynch DR, Carlotti F, Gentleman W, Lewis CVW (1998) Coupling of an individual-based population dynamic model of *Calanus finmarchicus* to a circulation model for the Georges Bank region. *Fish Oceanogr* 7:219-234

- Morison J, Steele M, Andersen R (1998) Hydrography of the upper Arctic Ocean measured from the nuclear submarine USS Pargo. *Deep Sea Res Part I* 45:15-38
- Morison J, Aagaard K, Steele M (2000) Recent environmental changes in the Arctic: A review. *Arctic* 53:359-371
- Mumm N (1991) On the summerly distribution of mesozooplankton in the Nansen Basin, Arctic Ocean. *Ber Polarforsch* 92:1-146
- Mumm N (1993) Composition and distribution of mesozooplankton in the Nansen Basin, Arctic Ocean, during summer. *Polar Biol* 13:451-461
- Mumm N, Auel H, Hanssen H, Hagen W, Richter C, Hirche HJ (1998) Breaking the ice: large-scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises. *Polar Biol* 20:189-197
- Munk P (1997) Prey size spectra and prey availability of larval and small juvenile cod. *J Fish Biol* 51:340-351
- Nash RDM, Geffen AJ (2004) Seasonal and interannual variation in abundance of *Calanus finmarchicus* (Gunnerus) and *Calanus helgolandicus* (Claus) in inshore waters (west coast of the Isle of Man) in the central Irish Sea. *J Plankton Res* 26:265-273
- Niehoff B, Madsen SD, Hansen BW, Nielsen TG (2002) Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. *Mar Biol* 140:567-576
- Nilsen F, Gjevik B, Schauer U (2006) Cooling of the West Spitsbergen Current: Isopycnal diffusion by topographic vorticity waves. *J Geophys Res C* 111: C08012, doi:10.1029/2005JC002991
- Olli K, Wassmann P, Reigstad M, Ratkova TN, Arashkevich E, Pasternak A, Matrai PA, Knulst J, Tranvik L, Klais R, Jacobsen A (2007) The fate of production in the central Arctic Ocean - Top-down regulation by zooplankton expatriates? *Prog Oceanogr* 72:84-113
- Osinski R, Wieczorek P, Beszczynska-Moller A, Goszczko I (2003) ADCP-referenced geostrophic velocity and transport in the West Spitsbergen Current. *Oceanologia* 45:425-435
- Østvedt OJ (1955) Zooplankton investigation from weather-ship M in the Norwegian Sea 1948-1949. *Hvalrådets Skrifter* 40:1-93
- Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. *Oecologia* 128:1-14
- Ottersen G, Stenseth NC (2001) Atlantic climate governs oceanographic and ecological variability in the Barents Sea. *Limnol Oceanogr* 46:1774-1780
- Pedersen G (1995a) Factors influencing the size and distribution of the copepod community in the Barents Sea with special emphasis on *Calanus finmarchicus* (Gunnerus). Dr scient thesis, Norwegian College of Fishery Science, University of Tromsø, Tromsø
- Pedersen G, Tande K, Ottesen GO (1995b) Why does a component of *Calanus finmarchicus* stay in the surface waters during the overwintering period in high latitudes. *ICES J Mar Sci* 52:523-531
- Pedersen G, Tande KS, Nilssen EM (1995c) Temporal and regional variation in the copepod community in the central Barents Sea during spring and early summer 1988 and 1989. *J Plankton Res* 17:263-282

- Pershing AJ, Greene CH, Planque B, Fromentin JM (2004) The influence of climate variability on North Atlantic zooplankton populations. In: Stenseth NC, Ottersen G, Hurrell J, Belgrano A (eds). Marine Ecosystems and Climate variation - The North Atlantic. A comparative perspective. Oxford University Press, pp 59-69
- Pershing AJ, Greene CH, Jossi JW, O'Brien L, Brodziak JKT, Bailey BA (2005) Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. ICES J Mar Sci 62:1511-1523
- Pfirman SL, Bauch D, Gammelsrød T (1994) The Northern Barents Sea: Water mass distribution and modification. Geophys Monogr 85:77-94
- Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. Polar Biol 28:733-755
- Planque B, Fromentin JM (1996) *Calanus* and environment in the eastern North Atlantic: 1. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. Mar Ecol Prog Ser 134:101-109
- Planque B, Taylor AH (1998) Long-term changes in zooplankton and the climate of the North Atlantic. ICES J Mar Sci 55:644-654
- Plourde S, Runge JA (1993) Reproduction of the planktonic copepod *Calanus finmarchicus* in the lower St. Lawrence estuary - Relation to the cycle of phytoplankton production and evidence for a *Calanus* pump. Mar Ecol Prog Ser 102:217-227
- Polyakov IV, Alekseev GV, Bekryaev RV, Bhatt U, Colony RL, Johnson MA, Karklin VP, Makshtas AP, Walsh D, Yulin AV (2002) Observationally based assessment of polar amplification of global warming. Geophys Res Lett 29: NO. 18, 1878, doi:10.1029/2001GL0
- Polyakov IV, Beszczynska A, Carmack EC, Dmitrenko IA, Fahrbach E, Frolov IE, Gerdes R, Hansen E, Holfort J, Ivanov VV, Johnson MA, Karcher M, Kauker F, Morison J, Orvik KA, Schauer U, Simmons HL, Skagseth O, Sokolov VT, Steele M, Timokhov LA, Walsh D, Walsh JE (2005) One more step toward a warmer Arctic. Geophys Res Lett 32: L17605, doi:10.1029/2005GL023740
- Puvanendran V, Salies K, Laurel B, Brown JA (2004) Size-dependent foraging of larval Atlantic cod (*Gadus morhua*). Can J Zoo 82:1380-1389
- Quadfasel D, Gascard JC, Koltermann KP (1987) Large-scale oceanography in Fram Strait during the 1984 Marginal Ice-Zone Experiment. J Geophys Res C 92:6719-6728
- Raymont JEG (1983) Plankton and Productivity in the Oceans, 2. Zooplankton. Pergamon Press, 824 pp
- Reid PC, Planque B, Edwards M (1998) Is observed variability in the long-term results of the Continuous Plankton Recorder survey a response to climate change? Fish Oceanogr 7:282-288
- Reid PC, Battle EJV, Batten SD, Brander KM (2000) Impacts of fisheries on plankton community structure. ICES J Mar Sci 57:495-502
- Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish Oceanogr 12:260-269
- Reigstad M, Wassmann P, Riser CW, Oygarden S, Rey F (2002) Variations in hydrography, nutrients and chlorophyll a in the marginal ice-zone and the central Barents Sea. J Mar Syst 38:9-29

- Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305:1609-1612
- Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. *Ber Polarforsch* 154:1-87
- Rigor IG, Wallace JM, Colony RL (2002) Response of sea ice to the Arctic oscillation. *J Clim* 15:2648-2663
- Ringelberg J, Van Gool E (2003) On the combined analysis of proximate and ultimate aspects in diel vertical migration (DVM) research. *Hydrobiologia* 491:85-90
- Rudels B, Friedrich HJ, Quadfasel D (1999) The Arctic circumpolar boundary current. *Deep Sea Res Part II* 46:1023-1062
- Rudels B, Meyer R, Fahrbach E, Ivanov VV, Osterhus S, Quadfasel D, Schauer U, Tverberg V, Woodgate RA (2000) Water mass distribution in Fram Strait and over the Yermak Plateau in summer 1997. *Ann Geoph Atmos Hydrosph Space Sci* 18:687-705
- Runge JA, Ingram RG (1991) Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. *Mar Biol* 108:217-225
- Rysgaard S, Nielsen TG, Hansen BW (1999) Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. *Mar Ecol Prog Ser* 179:13-25
- Sakshaug E (1997) Biomass and productivity distributions and their variability in the Barents Sea. *ICES J Mar Sci* 54:341-350
- Saloranta TM, Haugan PM (2001) Interannual variability in the hydrography of Atlantic water northwest of Svalbard. *J Geophys Res C* 106:13931-13943
- Saloranta TM, Svendsen H (2001) Across the Arctic front west of Spitsbergen: high-resolution CTD sections from 1998-2000. *Polar Res* 20:177-184
- Sameoto DD (1984) Vertical distribution of zooplankton biomass and species in Northeastern Baffin-Bay related to temperature and salinity. *Polar Biol* 2:213-224
- Sargent JR, Falk-Petersen S (1988) The lipid biochemistry of calanoid copepods. *Hydrobiologia* 167:101-114
- Sars GO (1900) Crustacea In: Nansen F (ed) *Norwegian North Pole Expedition 1893-1896. Scientific Results*, pp 1-137
- Schauer U, Fahrbach E, Osterhus S, Rohardt G (2004) Arctic warming through the Fram Strait: Oceanic heat transport from 3 years of measurements. *J Geophys Res C* 109:C06026, doi:06010.01029/02003JC001823
- Schlichtholz P, Houssais MN (1999a) An inverse modeling study in Fram Strait. Part II: water mass distribution and transports. *Deep Sea Res Part II* 46:1137-1168
- Schlichtholz P, Houssais MN (1999b) An inverse modeling study in Fram Strait. Part I: dynamics and circulation. *Deep Sea Res Part II* 46:1083-1135

- Scott CL, Falk-Petersen S, Sargent JR, Hop H, Lønne OJ, Poltermann M (1999) Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea. *Polar Biol* 21:65-70
- Scott CL, Kwasniewski S, Falk-Petersen S, Sargent JR (2000) Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. *Polar Biol* 23:510-516
- Scott CL, Kwasniewski S, Falk-Petersen S, Sargent JR (2002) Species differences, origins and functions of fatty alcohols and fatty acids in the wax esters and phospholipids of *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* from Arctic waters. *Mar Ecol Prog Ser* 235:127-134
- Serreze MC, Francis JA (2006) The arctic amplification debate. *Clim Chang* 76:241-264
- Skjoldal HR, Hassel A, Rey F, Loeng H (1987) Spring phytoplankton development and zooplankton reproduction in the central Barents Sea in the period 1979-1984. In: Loeng H (ed) The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea. Proceedings of the third Soviet-Norwegian Symposium, Murmansk 26-28 May 1986., pp 59-90
- Skjoldal HR, Rey F (1989) Pelagic production and variability of the Barents Sea ecosystem. In: Sherman K, Alexander LM (eds). Biomass yields and geography of large marine ecosystems. AAAS Selected Symposium 111, Westview Press Inc., pp241-286
- Skjoldal HR, Gjørseter H, Loeng H (1992) The Barents Sea ecosystem in the 1980s: ocean climate, plankton and caplin growth. *ICES mar. Sci. Symp.* 195:278-290
- Smith SL (1990) Egg-production and feeding by copepods prior to the spring bloom of phytoplankton in Fram Strait, Greenland Sea. *Mar Biol* 106:59-69
- Smith SL, Schnack-Schiel SB (1990) Polar Zooplankton. In: Smith Jr WO (ed). *Polar Oceanography Part B Chemistry, Biology and Geology*, Academic Press Inc., pp 529-598
- Smith WO, Lane PVZ, Smith SL, Ashjian C (2003) Distribution of zooplankton in the Northeast Water Polynya Project, summer 1992 and 1993. Boulder, CO: National Snow and Ice Data Center. Digital media.
- Speirs DC, Gurney WSC, Heath MR, Horbelt W, Wood SN, de Cuevas BA (2006) Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*. *Mar Ecol Prog Ser* 313:173-192
- Steele JH (1998) From carbon flux to regime shift. *Fish Oceanogr* 7:176-181
- Stephens JA, Jordan MB, Taylor AH, Proctor R (1998) The effects of fluctuations in North Sea flows on zooplankton abundance. *J Plankton Res* 20:943-956
- Stevens CJ, Deibel D, Parrish CC (2004) Species-specific differences in lipid composition and omnivory indices in Arctic copepods collected in deep water during autumn (North Water Polynya). *Mar Biol* 144:905-915
- Stroemberg J-O (1989) Northern Svalbard Waters. In: Rey L, Alexander V (eds) Proceedings 6th Conference of the Comité Arctique International 13-15 May 1985., pp 402-426
- Stroeve J, Holland MM, Meier W, Scambos T, Serreze M (2007) Arctic sea ice decline: Faster than forecast. *Geophys Res Lett* 34:

- Sundby S (2000) Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* 85:277-298
- Svendsen H, Beszczynska-Moller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Orbaek JB, Bischof K, Papucci C, Zajackowski M, Azzolini R, Bruland O, Wiencke C, Winther JG, Dallmann W (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res* 21:133-166
- Sverdrup HU (1953) On conditions for the vernal blooming of phytoplankton. *Journal Cons -Perm Int Explor Mer* 18:287-295
- Swift JH, Jones EP, Aagaard K, Carmack EC, Hingston M, MacDonald RW, McLaughlin FA, Perkin RG (1997) Waters of the Makarov and Canada basins. *Deep Sea Res Part II* 44:1503-1529
- Sørøide JE, Hop H, Falk-Petersen S, Gulliksen B, Hansen E (2003) Macrozooplankton communities and environmental variables in the Barents Sea marginal ice zone in late winter and spring. *Mar Ecol Prog Ser* 263:43-64
- Sørøide JE, Falk-Petersen S, Nøst Hegseth E, Hop H, Carroll ML, Hobson KA, Blachowiak-Samolyk K (submitted) *Calanus* feeding strategies and population dynamics in Svalbard waters (77-81°N).
- Sørnes TA, Aksnes DL (2006) Concurrent temporal patterns in light absorbance and fish abundance. *Mar Ecol Prog Ser* 325:181-186
- Sørnes TA, Aksnes DL, Båmstedt U, Youngbluth MJ (2007) Causes for mass occurrences of the jellyfish, *Periphylla periphylla*; an hypothesis that involves optically conditioned retention. *J Plankton Res* 29:157-167
- Tande K, Hassel A, Slagstad D (1985) Marine biology of polar regions and effects of stress on marine organisms, Wiley
- Tande K (1988) An evaluation of factors affecting vertical distribution among recruits of *Calanus finmarchicus* in three adjacent high latitude localities. *Hydrobiologia* 167:115-126
- Tande KS, Drobysheva S, Nesterova V, Nilssen EM, Edvardsen A, Tereschenko V (2000) Patterns in the variations of copepod spring and summer abundance in the northeastern Norwegian Sea and the Barents Sea in cold and warm years during the 1980s and 1990s. *ICES J Mar Sci* 57:1581-1591
- ter Braak CJF (1995) Ordination. In: Jongman RGH, ter Braak CJF, van Tongeren OFR (eds). *Data Analysis in Community and Landscape Ecology*, Cambridge University Press, pp 91-173
- ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows, User's guide: Software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, NY, USA, 500pp
- Thibault D, Head EJH, Wheeler PA (1999) Mesozooplankton in the Arctic Ocean in summer. *Deep Sea Res Part I* 46:1391-1415
- Torgersen T, Huse G (2005) Variability in retention of *Calanus finmarchicus* in the Nordic Seas. *ICES J Mar Sci* 62:1301-1309
- Unstad KH, Tande K (1991) Depth distribution of *Calanus finmarchicus* and *C. glacialis* in relation to environmental conditions in the Barents Sea. *Polar Res* 10:409-420

- van Aken HM, Quadfasel D, Warpakowski A (1991) The Arctic Front in the Greenland Sea during February 1989-Hydrographic and biological observations. *J Geophys Res C* 96:4739-4750
- Vidal J (1980a) Physio-ecology of zooplankton 1. Effects of phytoplankton concentration, temperature and body size on the growth-rate of *Calanus pacificus* and *Pseudocalanus* sp. *Mar Biol* 56:111-134
- Vidal J (1980b) Physio-ecology of zooplankton .2. Effects of phytoplankton concentration, temperature, and body size on the development and moulting rates of *Calanus pacificus* and *Pseudocalanus* sp. *Mar Biol* 56:135-146
- Walczowski W, Piechura J (2006) New evidence of warming propagating toward the Arctic Ocean. *Geophys Res Lett* 33: L12601, doi:10.1029/2006GL025872
- Walkusz W, Storemark K, Skau T, Gannefors C, Lundberg M (2003) Zooplankton community structure; a comparison of fjords, open water and ice stations in the Svalbard area. *Pol Polar Res* 24:149-165
- Weslawski JM, Kwasniewski S, Wiktor J (1991) Winter in a Svalbard fjord ecosystem. *Arctic* 44:115-123
- Weslawski JM, Stempniewicz L, Mehlum F, Kwasniewski S (1999) Summer feeding strategy of the little auk (*Alle alle*) from Bjørnøya, Barents Sea. *Polar Biol* 21:129-134
- Wespestad VG, Fritz LW, Ingraham WJ, Megrey BA (2000) On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye pollock (*Theragra chalcogramma*). *ICES J Mar Sci* 57:272-278
- Willis K, Cottier F, Kwasniewski S, Wold A, Falk-Petersen S (2006) The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). *J Mar Syst* 61:39-54
- Wu YS, Peterson IK, Tang CCL, Platt T, Sathyendranath S, Fuentes-Yaco C (2007) The impact of sea ice on the initiation of the spring bloom on the Newfoundland and Labrador Shelves. *J Plankton Res* 29:509-514
- Yen J (1983) Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. *Mar Biol* 75:69-77
- Zhang JL, Steele M, Rothrock DA, Lindsay RW (2004) Increasing exchanges at Greenland-Scotland Ridge and their links with the North Atlantic Oscillation and Arctic Sea Ice. *Geophys Res Lett* 31: L09307, doi:10.1029/2003GL019304
- Zhang XD, Ikeda M, Walsh JE (2003) Arctic sea ice and freshwater changes driven by the atmospheric leading mode in a coupled sea ice-ocean model. *J Clim* 16:2159-2177
- Zhang XD, Walsh JE (2006) Towards a seasonally ice-covered Arctic Ocean: Scenarios from the IPCC AR4 model simulations. *J Clim* 19:1730-1747