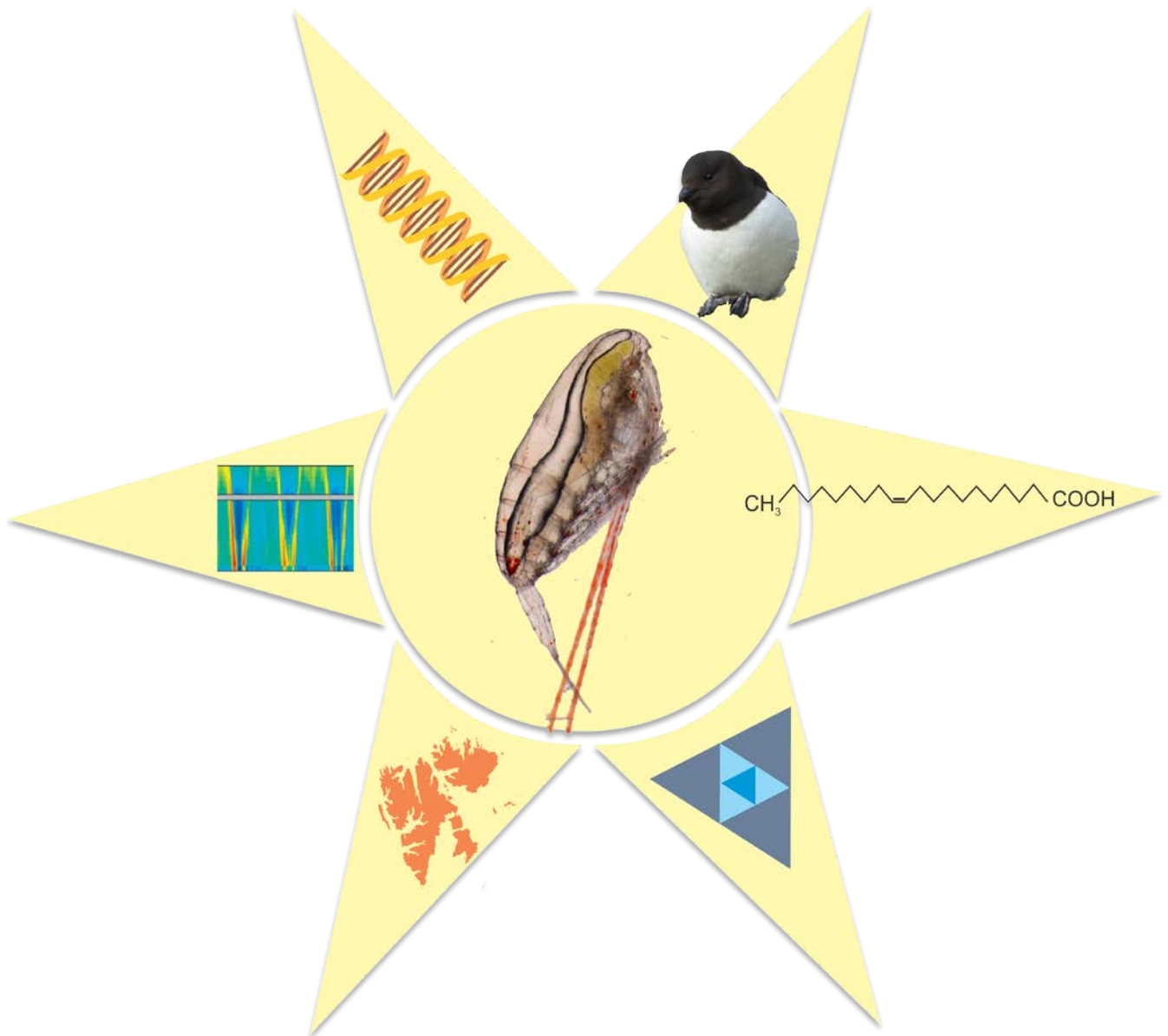# *Calanus* spp. in the Arctic ecosystem

- a story on predation, distribution and methodology

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Daniel Vogedes
A dissertation for the degree of Philosophiae Doctor – November 2014

Acknowledgements

The Sun does not stay up in the sky forever.
There is a season for the moon.
There is a season for the stars.
For now the sun has set … and it is the season of the moon and stars.
The Kiks.ádi Survival March of 1804

Das was das!
Jørgen Berge

Table of contents

List of original papers

1. Gabrielsen, T., Merkel, B., Søreide, J., Johansson-Karlsson, E., Bailey, A., **Vogedes, D**., Nygård, H., Varpe, Ø. and Berge, J. (2012) Potential misidentifications of two climate indicator species of the marine arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*. *Polar Biol.*, 35, 1621-1628. http://dx.doi.org/10.1007/s00300-012-1202-7

2. Steen, H., **Vogedes**, D., Broms, F., Falk-Petersen, S. and Berge, J. (2007) Little auks (*Alle alle*) breeding in a high Arctic fjord system: bimodal foraging strategies as a response to poor food quality? *Polar Res.*, 26, 118-125. http://dx.doi.org/10.1111/j.1751-8369.2007.00022.x

3. **Vogedes, D.**, Eiane, K., Båtnes, A. S. and Berge, J. (2014) Variability in *Calanus* spp. abundance on fine- to mesoscales in an Arctic fjord: implications for little auk feeding. *Mar. Biol. Res.*, 10, 437-448. http://dx.doi.org/10.1080/17451000.2013.815781

4. **Vogedes, D.**, Varpe, Ø., Søreide, J. E., Graeve, M., Berge, J. and Falk-Petersen, S. (2010) Lipid sac area as a proxy for individual lipid content of arctic calanoid copepods. *J. Plankton Res.*, 32, 1471-1477. http://dx.doi.org/10.1093/plankt/fbq068

5. Daase, M., Eiane, K., Aksnes, D. L. and **Vogedes, D.** (2008) Vertical distribution of *Calanus* spp. and *Metridia longa* at four Arctic locations. *Mar. Biol. Res.*, 4, 193-207. http://dx.doi.org/10.1080/17451000801907948

6. Berge, J., Cottier, F., Last, K. S., Varpe, Ø., Leu, E., Søreide, J., Eiane, K., Falk-Petersen, S., Willis, K., Nygard, H., **Vogedes, D.**, Griffiths, C., Johnsen, G., Lorentzen, D. and Brierley, A. S. (2009) Diel vertical migration of Arctic zooplankton during the polar night. *Biology Letters*, 5, 69-72. http://dx.doi.org/10.1098/rsbl.2008.0484

The PDFs of all papers except paper 5 are available for free download under the "doi" link.

Introduction

A sea of *Calanus*

The mesozooplankton biomass in the Arctic and sub-Arctic seas is largely dominated by three copepod species of the genus *Calanus,* the herbivorous *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*. Together they can make up more than 75% of the total mesozooplankton biomass in a given area (Wassmann *et al.*, 2006 ; Błachowiak-Samołyk *et al.*, 2008 ; Søreide *et al.*, 2008). In the scientific literature they are equally "abundant" as in the sea - as of September 2014 Google Scholar had over 9000 hits for a search on *C. finmarchicus* and almost 4000 on the other two *Calanus* spp. This thesis and the papers herein build on some of these publications and suggest directions for further research.

Calanus spp.: crucial for energy accumulation and conversion in the Arctic Ocean

It is not only the mere abundance of these calanoid copepod species that has attracted the attention of researchers. They also play a major role in the Arctic ecosystem by facilitating the transfer of energy from primary producers to higher trophic levels (Lee *et al.*, 2006 ; Falk-Petersen *et al.*, 2007).

Of real importance for the Arctic marine food chain is their ability to convert low-energy carbohydrates and proteins obtained through their diet from the primary producers into high energy storage lipids, comprised mainly of wax esters. These storage lipids can make up 70% of the copepod dry mass (Falk-Petersen *et al.*, 2009). Stored in a conspicuous lipid sac in the centre of the body cavity the lipids can fill up to 60% of the body volume (Sargent and Falk-Petersen, 1988 ; Miller *et al.*, 1998 ; Miller *et al.*, 2000 ; Lee *et al.*, 2006). Their specialised biosynthesis (Sargent and Henderson, 1986) gives *Calanus* spp. the ability to produce wax esters quickly and thus efficiently utilize the short "times of plenty" when the intense phytoplankton blooms occur. The tremendous abundance and the large amount of compact energy make *Calanus* spp. the most significant species for energy accumulation and conversion in the Arctic. The energy rich wax esters are utilized by many commercial and non-commercial fish stocks in the North Atlantic such as capelin (*Mallotus villosus*)(Hop and Gjøsæter, 2013), herring (*Clupea harengus*) (Varpe *et al.*, 2005) and cod (*Gadus morhua*) (Helle and Pennington, 1999). In the high Arctic, *Calanus* spp. are a key prey species for polar cod (*Boreogadus saida*)(Nahrgang *et al.*, 2014), macrozooplankton such as *Themisto libellula*, *Mertensia ovum* (Scott *et al.*, 1999 ; Falk-Petersen *et al.*, 2002 ; Hop *et al.*, 2006 ; Kraft *et al.*, 2013) and some sea birds like the little auk (*Alle alle*) (Weslawski *et al.*, 1994 ; Steen *et al.*, 2007) for which *Calanus* spp. are the single most important prey (e.g. (Karnovsky *et al.*, 2003 ; Wojczulanis *et al.*, 2006).

Season of the sun, season of the moon

The high latitudes are characterized by strong seasonality. Several months of more or less darkness and ice cover, traditionally considered as being of very low productivity, are followed by the sea ice break-up and melting, a stratification of nutrient rich water masses and several months of constant light. These factors trigger prolific but short lived blooms of ice algae and phytoplankton, which in turn fuel the development of the zooplankton community (Leu *et al.*, 2010 ; Søreide *et al.*, 2010 ; Wold, 2012). The onset and duration of the spring bloom is related to the ice break up which starts in the southern areas and proceeds further north during spring and summer. Consequently the duration of the bloom is shorter in the North and the amplitude is higher (Zenkevitch, 1963, Fig. 1). An ice algae bloom usually precedes the pelagic phytoplankton bloom in ice covered waters providing an additional food source for grazers.

This pronounced seasonality in food availability and the high variability along latitudinal gradients can explain the large plasticity in the life history strategies that characterize the three *Calanus* congeners that co-occur in the Arctic and Sub-Arctic seas. All three species have adapted their life cycles to have optimal conditions during their reproduction period. Differences in life history strategies reflect adaptations to the environmental conditions in their main area of distribution and are themselves reflected differences in
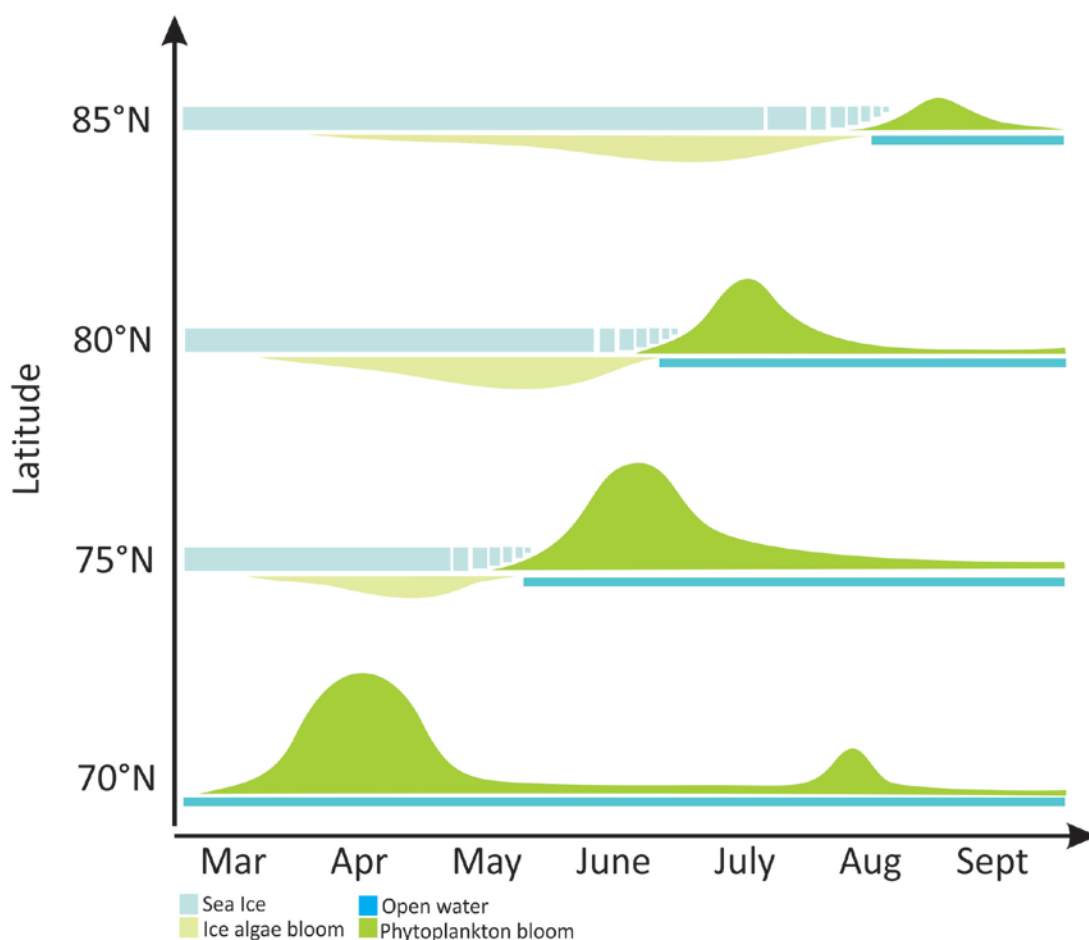
Figure 1. Conceptual model of onset, amplitude and duration of ice algae and phytoplankton blooms on a latitudinal transect.
Figure from Leu *et al.* (2011), modified after Zenkevitch (1963)

body size (Fig. 2), the amount of lipids stored and the ecological role of the three co-existing *Calanus* spp.

C. finmarchicus is the smallest (Fig. 2 bottom) and is considered an Atlantic species, which is transported to the Arctic by water currents of Atlantic origin (Jaschnov, 1972 ; Conover, 1988). In the southern parts of its distribution *C. finmarchicus* can have multiple generations per year but in the Arctic it has a reported life cycle of 1 year (overwintering stage CV, Fig. 3 top)(Conover, 1988 ; Falk-Petersen *et al.*, 2007). Reproduction in *C. finmarchicus* is fuelled by the phytoplankton bloom (Hirche *et al.*, 1997 ; Niehoff *et al.*, 2002) and is therefore dependent on an early onset of the bloom and a relatively long productive period. The dependence on continuous food supply is why *C. finmarchicus* is confined to the marginal Arctic seas and most likely cannot reproduce in the Arctic proper (Jaschnov, 1970 ; Tande *et al.*, 1985 ; Ji *et al.*, 2012).
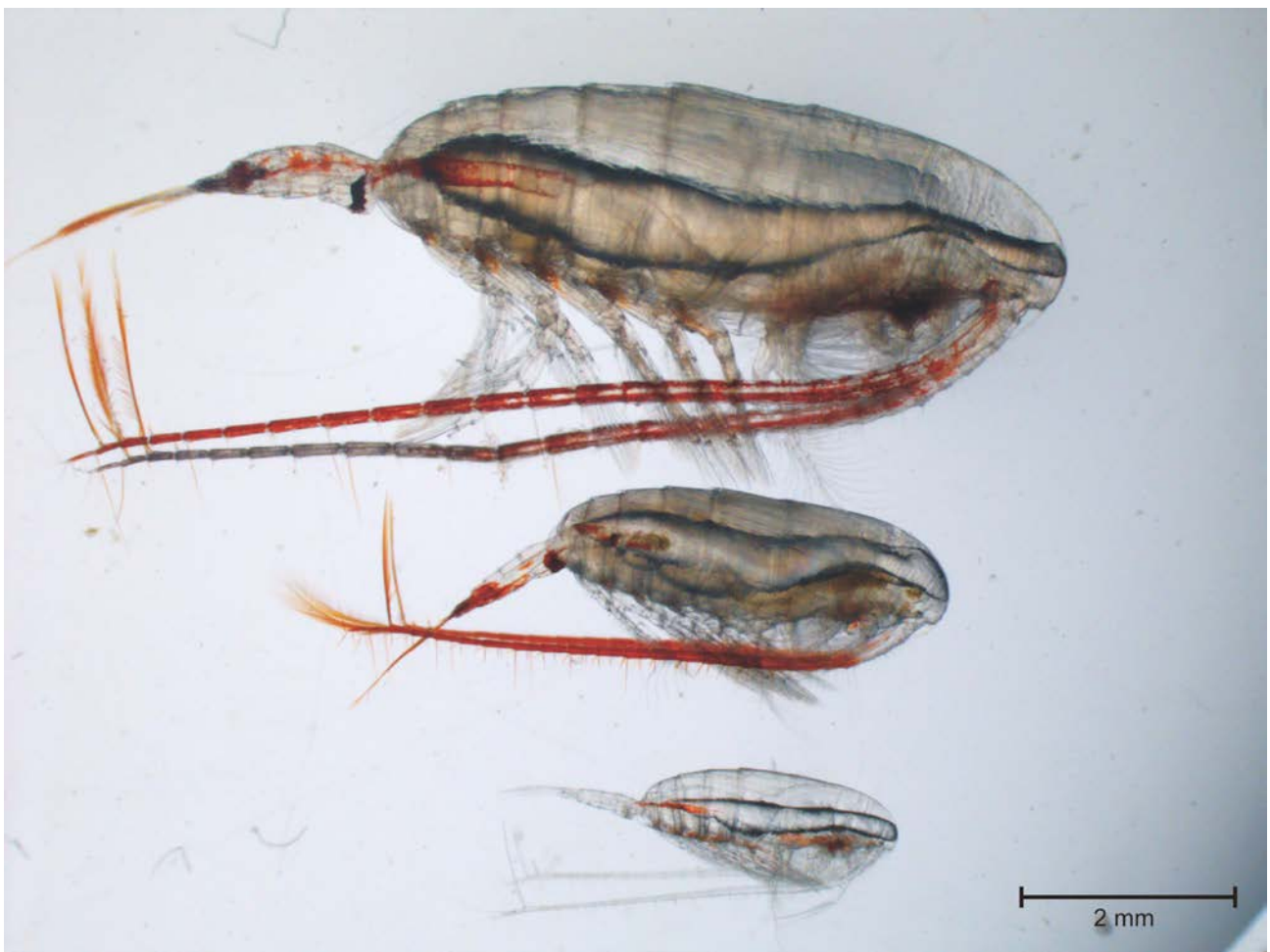
Figure 2. Specimens of (from the top) *Calanus hyperboreus*, *C. glacialis* **and** *C. finmarchicus*. **All display a semi-full lipid sac in the middle of the body cavity. Picture: Malin Daase.**

Calanus glacialis is an endemic Arctic species of intermediate size (Fig. 2 middle) which occurs all over the Arctic shelf seas in seasonal ice covered waters (Jaschnov, 1970 ; Daase *et al.*, 2007 ; Błachowiak-Samołyk *et al.*, 2008 ; Søreide *et al.*, 2008). It is adapted to an environment with high seasonal and interannual variability in food availability and its life cycle can vary between 1-3 years (overwintering stages [C III] C IV-CV) depending on environmental conditions (Fig. 3 middle)(Falk-Petersen *et al.*, 2009 and references within). It uses the ice algae bloom as an early food source to fuel gonad maturation and reproduction but can also start reproduction on internal energy storages (Søreide *et al.*, 2010 ; Daase *et al.*, 2013a). A prolonged life cycle and the higher energy demand of facing the more unpredictable conditions in ice covered seas most likely explain the larger body size and lipid storages of *C. glacialis* compared to *C. finmarchicus*.

The largest of the three *Calanus* species, *C. hyperboreus* (Fig. 2 upper), is an Arctic deep-water species which has its centre of distribution in the deep Arctic and Greenland Sea basin (Hirche, 1991 ; Mumm *et al.*, 1998). Life history strategies of *C. hyperboreus* reflect adaptations to survive extreme variations in food abundance as they can be found in areas with long lasting ice cover. Gonad maturation and egg production are independent of external food supply but are entirely fuelled by the large lipid reserves (Melle and Skjoldal, 1988 ; Hirche and Niehoff, 1996). The life cycle can take up to 5 years (overwintering stages CIII – CV, Fig. 3 lower, review in Falk-Petersen *et al.* (2009)) as *C. hyperboreus* invest more energy in producing large lipid storages than in faster development to survive long periods of limited food supply.
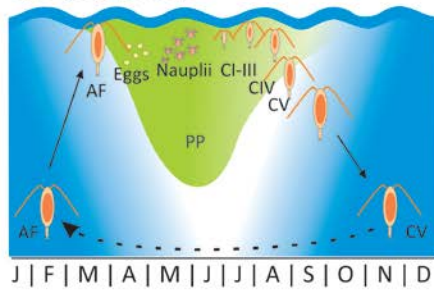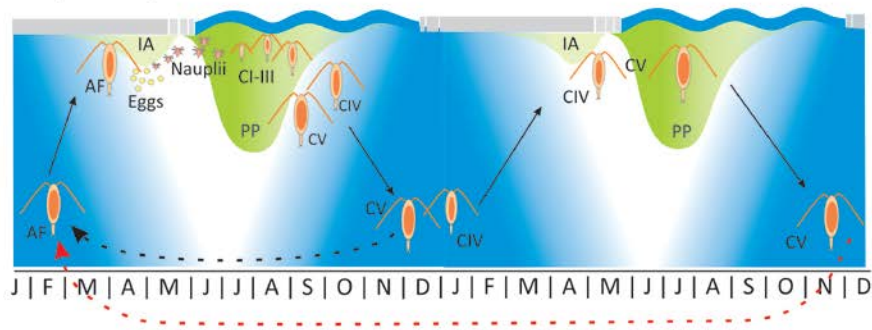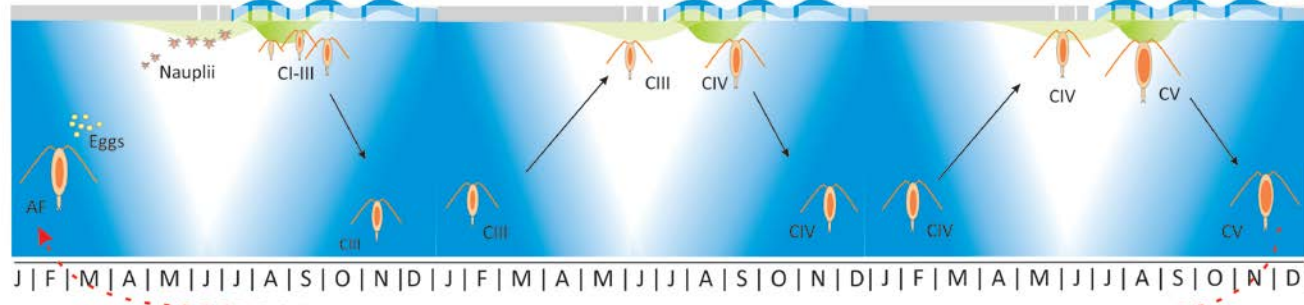
Figure 3. Model of *Calanus* spp. life cycles. Top: One year life cycle as commonly displayed by *C. finmarchicus* in ice-free waters; middle: 1-2 year life cycle as commonly displayed by *C. glacialis*, bottom: multi-year life cycle as commonly displayed by *C. hyperboreus*. IA ice algae; PP phytoplankton; CI-CV copepodite stage C I to C V; AF adult female. Solid black arrows: ontogenetic seasonal migration; hatched red and black arrows connect the cycle. Illustration: Malin Daase.

Stay or migrate?

The pronounced seasonality in food availability is also believed to be the proximate explanation for the distinct ontogenetical vertical migration often recorded in high latitude *Calanus* spp. The older overwintering stages typically stay in deeper water layers in a state of dormancy during the dark, unproductive period and move up to the euphotic zone for spawning and grazing at the onset of the spring bloom (Conover, 1988 ; Vinogradov, 1997). Younger copepodite stages (C I – C III) are usually confined to the surface layers, where they actively feed on the phytoplankton bloom (Fig. 3).

Over the course of the light period the *Calanus* spp. community does not stay uniformly at a specific depth. Variability in depth distribution of zooplankton throughout the season has been attributed to light conditions at a certain depth (Miller *et al.*, 1991) which in turn affects food availability (Unstad and Tande, 1991 ; Hirche, 1996) and the ability of visual predators to detect their copepod prey (Fiksen and Carlotti, 1998 ; Bagøien *et al.*, 2001). In addition to the variation in the total depth range in which a *Calanus* spp. population resides, parts of the population might also engage in diel vertical migration (DVM) at certain times of the year. While conducting DVM, individuals migrate vertically in the water column twice a day, usually upwards at dusk and downwards at dawn. This behaviour is generally explained as a means of avoiding predators in the photic zone (Hays, 2003 ; Ringelberg, 2010). It is a trade-off between the need for herbivorous zooplankton to feed in the euphotic zone and the risk of falling prey to visual predators, thus they avoid predators by descending to darker water layers during day and ascending again to feed in the dark of night. While this is an easy to grasp concept in temperate regions, where differences in the light regime between day and night exist all year round, the situation is less clear in the regions of midnight sun and polar night, with constant light and constant darkness, respectively, for several months at end (Błachowiak-Samołyk *et al.*, 2006 ; Cottier *et al.*, 2006 ; Berge *et al.*, 2014)

See the signs – *Calanus* as climate indicator

Due to tight bonds with specific water masses, *Calanus* spp. are considered biological indicators of these oceanographic features and are as such an important tool in studying fluctuations in the climate system (Daase *et al.*, 2007 ; Falk-Petersen *et al.*, 2007 ; Trudnowska *et al.*, 2012). While of general interest for decades, this has drawn increased attention in line with the growing focus on the effects of global climate change, which is believed to be rapid and pronounced in the Arctic (Post *et al.*, 2009). It has been predicted that, in the wake of global warming, Atlantic water will protrude further into Arctic domains, expanding the distribution of its associated *C. finmarchicus* northwards, potentially replacing the presently dominant *C. glacialis* (Reygondeau and Beaugrand, 2011 ; Wassmann *et al.*, 2011). For the North Atlantic a pole-wards shift of temperate species *C. helgolandicus* coinciding with a decrease of the sub-Arctic *C. finmarchicus* has already been documented (Beaugrand *et al.*, 2009). A displacement of *C. glacialis* by *C. finmarchicus* can potentially influence Arctic marine food webs. For example, several studies (Karnovsky *et al.*, 2003 ; Stempniewicz *et al.*, 2013) have shown that Little Auks prefer the Arctic species *C. glacialis* and *C.*

hyperboreus rather than the Atlantic congener *C. finmarchicus*, probably because of their generally larger size and higher mean lipid content. However, so far the ability of *C. finmarchicus* to survive and colonize the Arctic Ocean is hampered by short growing seasons and low temperatures, and model predictions suggest that even if water temperatures increase 2°C or the growth season is prolonged by two weeks, conditions (food availability, length of growth season, circulation patterns) will not become favorable enough to allow *C. finmarchicus* to penetrate further north (Ji *et al.*, 2012)

Some aspects of *Calanus* spp. as one of the key elements in the Arctic ecosystem, together with methodological approaches to assess its importance are highlighted in the following discussion of the six papers included in this thesis.

Objectives

The overall objective of this thesis is to evaluate the role of *Calanus* spp. as a key element of the high Arctic ecosystem.

To address this main objective, six papers are included in this thesis which focus on different aspects of the Arctic *Calanus* complex: species identification (**paper 1**), *Calanus* spp. as prey (**paper 2, 3, 4**) and variability in *Calanus* spp. distribution (**paper 2-6**).

More specifically, the following objectives were addressed:

1) Species distinction

To understand life history strategies and to accurately monitor and predict changes in *Calanus* species composition and distribution it is imperative to be able to distinguish between the species with good confidence. How well do the established morphological identification methods compare to genetic methods? (**paper 1**)

2) *Calanus* as prey

How does a planktivorous predator with strong preference for *Calanus* spp. prey adapt to the variability in *Calanus* distribution? (**paper 2, 3**)

What is the variability in the energetic value of the various *Calanus* species and stages and how can this be estimated? (**paper 3, 4**)

3) *Calanus* distribution patterns

What is the variability in the geographical distribution of the co-occurring *Calanus* spp. on a larger scale (**paper 2 & 5**) and smaller scale (**paper 3**)?

To which extent do the copepodite stages of these species perform diel vertical migration (DVM) and what is the geographical and seasonal variability in DVM (**paper 5, 6**)?

Study area and the physical environment

All papers in this thesis are based on data collected around the Norwegian archipelago of Svalbard. Most samples were taken in fjords along the western and northern coast of Svalbard, except for **paper 5** which also includes data from the shelf north of Svalbard and one sample off the continental shelf in ice covered waters north-east of Svalbard (Fig. 4).
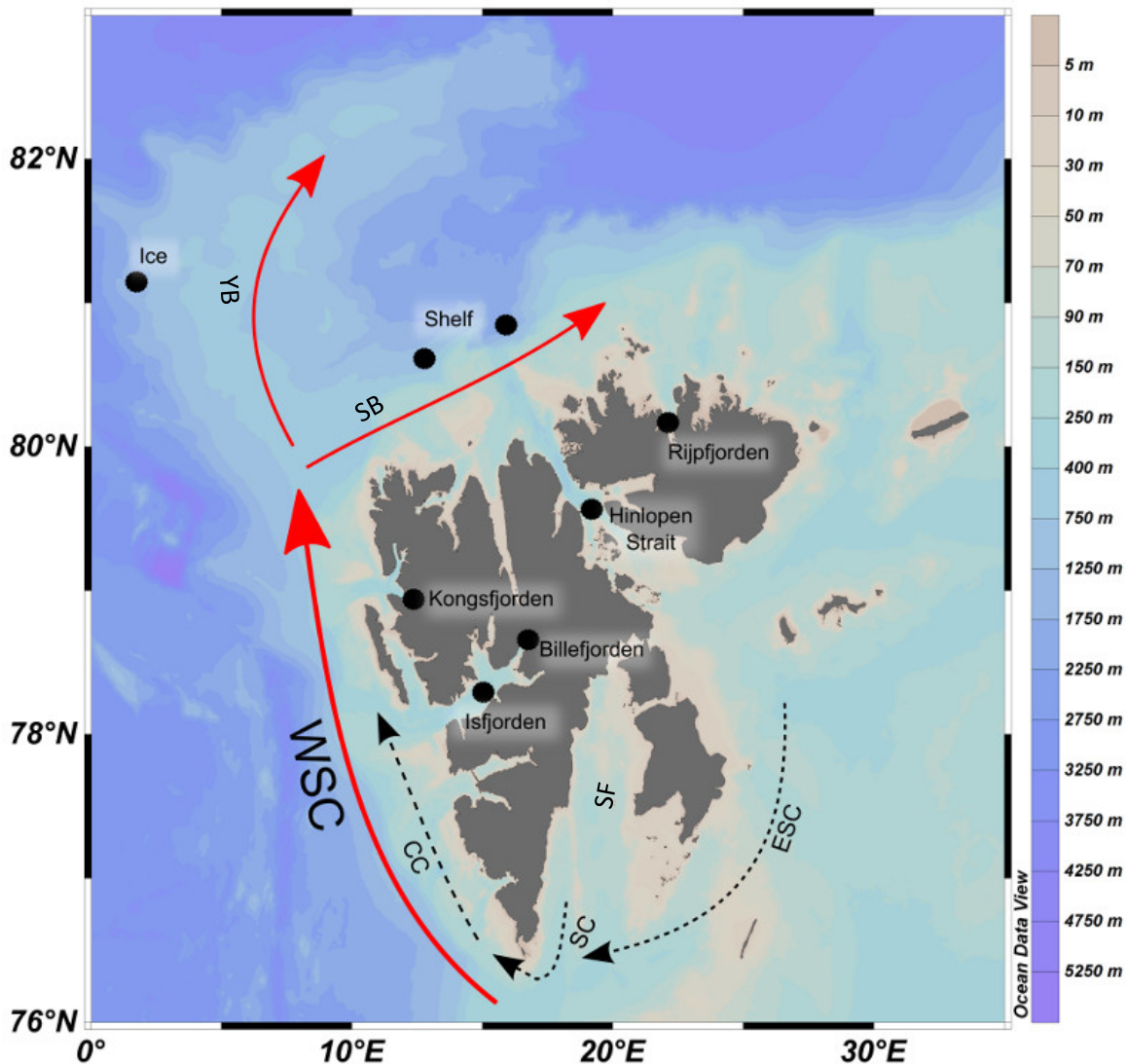
Figure 4. Map of Svalbard with main current system. Dots mark sampling sites of all papers, except paper 4 for which copepods were picked opportunistically at all stations. WSC: West Spitsbergen Current; ESC: East Spitsbergen Current; SC: Sørkapp Current; CC: Coastal Current; YB: Yermark Branch; SB: Svalbard Branch, SF: Storfjorden. Modified after Daase *et al.* (2008).

The two main features defining the water system around Svalbard are the transport of warm Atlantic water from the south along the western coast and the transport of cold Arctic water from north-east along the eastern side of Svalbard (Fig. 4). Atlantic water originating from the North Atlantic Current continues northwards along the Svalbard coast as West Spitsbergen Current (WSC)(Blindheim and Østerhus, 2005). North of Svalbard the remaining WSC splits into the Yermark Branch (YB) which continues into the Greenland Sea and the Svalbard Branch (SB) which turns eastward into the Arctic Ocean. The WSC is the

main vector for the inflow of heat into the Arctic Ocean, but the amount of Atlantic water transported in the WSC is subject to high inter-annual variation (Saloranta and Haugan, 2001 ; Walczowski and Piechura, 2006). The existence of the WSC is the reason for a comparably warm marine (and terrestrial) climate in particular on the western but also northern coast of Svalbard.

Cold water originating from the Arctic Ocean is transported southwards towards the Barents Sea in the East Spitsbergen Current (ESC, Fig. 4) (Pfirman *et al.*, 1994). Parts of it merge with water from Storfjorden to form the South Cape Current (SC) which flows around the southern tip of the archipelago. The SC continues northwards on the continental shelf along the west coast as Coastal Current (CC) parallel to the WSC, forming the western end of a distinct frontal system called the Polar Front (Loeng, 1991 ; Pfirman *et al.*, 1994 ; Saloranta and Svendsen, 2001 ; Karnovsky *et al.*, 2003). Due to this front the Atlantic water is normally separated from the west coast, but a variety of effects like wind forcing in the surface layer and front instabilities caused by topographic irregularities can drive the exchange of water masses across the front (Saloranta and Svendsen, 2001 ; Cottier *et al.*, 2007). Thus the fjords of the western coast are affected both by the cold and fresh waters of the CC as well as the warm and more saline WSC, despite the frontal system (Saloranta and Svendsen, 2001 ; Cottier *et al.*, 2007).

The papers presented in this thesis are based on data from locations influenced by both Arctic and Atlantic water masses. Isfjorden and Kongsfjorden are westward facing fjords which receive regular input of Atlantic water. Billefjorden is a northward extension of Isfjorden with a special hydrography with an outer and an inner basin. The outer basin has a maximum depth of 230 m and is separated from Isfjorden by a 80 m deep sill, the inner basin has a maximum depth of 190 m and is separated from the outer basin by a 45 m deep sill (Arnkværn *et al.*, 2005). These features drastically limit water exchange with the rest of the fjord system. Hinlopen is a strait between the two main islands of the Svalbard archipelago where warmer water from the Atlantic-influenced Svalbard Branch meets the colder water of the northern Barents Sea. The shelf station north of Svalbard is at the boundary to the Arctic Ocean, but still affected by the warmer Svalbard Branch flowing along the shelf break. Rijpfjorden is characterized by cold Arctic water and the station to the north-east was located in the marginal ice zone in Arctic water.
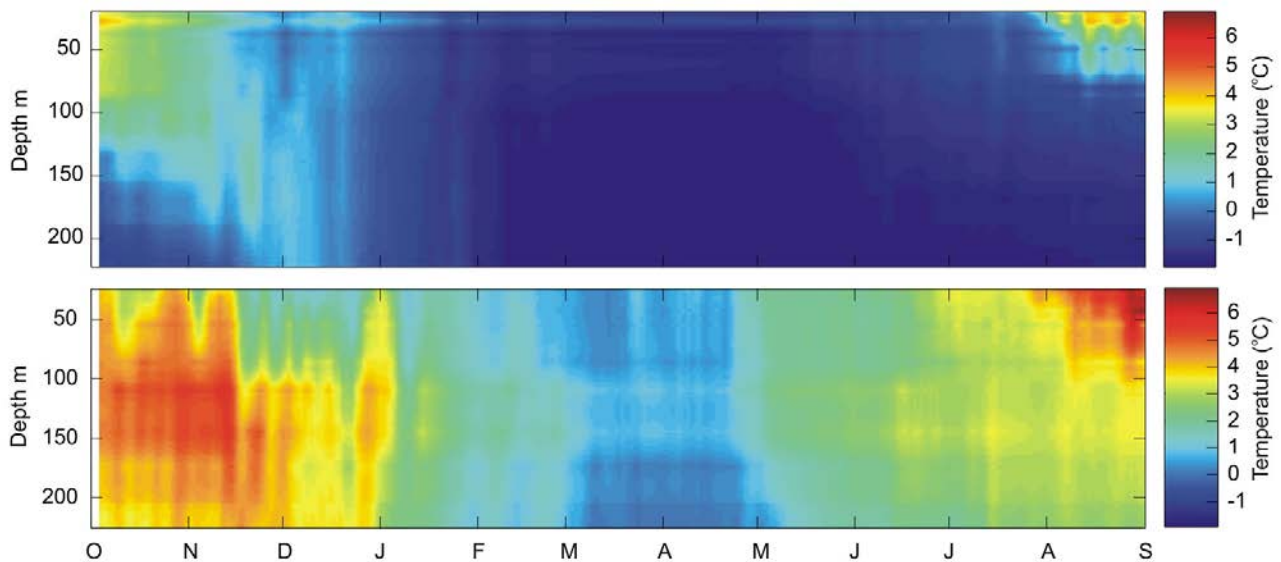
Figure 5: Example of seasonal variation of temperature at an "Arctic" and "Atlantic" type fjord from the study area: Rijpfjorden (upper) and Kongsfjorden (lower). Data recorded by moored observatories (as used in paper 6) from 04 October 2012 to 01 September 2013. Figure from Nahrgang *et al.* (2014)

The temperature data presented in Fig. 5 illustrates the typical regime of a fjord influenced mainly by Arctic water (Rijpfjorden, upper) vs. a fjord influenced mainly by Atlantic water (Kongsfjorden, lower). It is obtained from two moored observatories, similar to the one used in **paper 6**, over the course of an entire year. While Rijpfjorden is covered by sea ice from around December until beginning of July, Kongsfjorden has been free of sea ice for several years now (pers. obs.). In Rijpfjorden the water column is homogenously cold, close to freezing point, from January until July. After sea ice break-up , the surface water warms up to 3 - 5 °C, and some water around 1 - 2 °C penetrates into the fjord. In Kongsfjorden on the other hand, the influx of Atlantic water can be observed almost throughout the year, with water of around five to six degrees penetrating into the fjord at the depth between 50 and 200 m. Even during the coldest period, there is still a core of slightly warmer water present between 100 and 150 m.

While the situation for the Arctic fjord type is more predictable, with an extended period of ice cover and sub-zero water temperatures, the Atlantic fjord type may show strong annual variation, with Fig. 5 (lower panel) reflecting a warm year situation.

Sampling and Methodology - general

Oceanographic data

Two types of CTDs were used to collect oceanographic data, depending on the vessel. On board the R/V Helmer Hanssen (formerly known as R/V Jan Mayen) a ship-board Seabird (Sea-Bird CTD equipped with a Seapoint fluorometer) was deployed routinely whenever sampling took place. During intensive small-boat campaigns (**paper 3**) the hand-held SAIV SD204 and the SD202 were used. None of the CTD data was quality controlled by water sample analysis as is usually done for oceanographic studies but the CTDs have been calibrated regularly, and the three hand-held SAIV CTDs were in addition intercalibrated, which should be sufficient for our purposes.

The vertical migration data in **paper 3** was collected with moored, upward looking 300 kHz acoustic Doppler current profilers.

Zooplankton samples

Zooplankton samples were taken by different brands of WP2 nets or a multiple opening/closing net (Multinet, Hydrobios Kiel), with either 180 µm or 200 µm mesh size (depending on availability) and a mouth opening of 0.25 m^2.. We assumed 100% filtration efficiency in all quantitative net sampling.

Samples for enumeration were stored on a 4% Formaldehyde-in-seawater solution and all individuals in random subsamples of known volume were counted. The samples for image analysis of lipid sac area were kept alive and single individuals were photographed with a digital camera mounted on a stereo microscope. Once photographed individuals were frozen in vials and kept in a -80 C biofreezer until chemical lipid analysis was conducted (**paper 4**). Individuals for genetic analysis were rinsed in distilled water, photographed and stored in 80% Ethanol until analysis.

Sampling area

The sampling areas (dots in Fig. 4) were selected according to the aim of the specific studies. For **paper 1** we selected three fjords influenced by different currents (Kongsfjorden, Rijpfjorden, Billefjorden). Samples for **paper 2** were taken along a transect in Isfjorden, past the little auk colony at Bjørndalen and into Billefjorden, while samples for the high-resolution sampling in **paper 3** were taken on a grid in Isfjorden, just outside the little auk colony at Bjørndalen. For **paper 5**, samples were taken at localities influenced by either Arctic (Shelf, Ice) or Atlantic (Kongsfjorden, Hinlopen) water masses. The moorings for **paper 6** were part of a long term mooring programme in an Atlantic (Kongsfjorden) and Arctic (Rijpfjorden) fjord and samples for **paper 4** were obtained opportunistic from sampling programs at a variety of localities across the Svalbard archipelago.

For specific sampling protocols see the separate material and methods sections in each specific paper.

Results and discussion

Size is not everything – The problem of species determination (paper 1)

To understand life history strategies and to accurately monitor and predict changes in species composition and distribution it is imperative to be able to distinguish between the species with good confidence. In the vast majority of studies in the Arctic (and in four out of six papers in this dissertation) *C. finmarchicus* and *C. glacialis* are determined to species level by the morphological feature prosome length. Size and stage tables, usually based on length frequency analysis of mixed populations of *C. glacialis* and *C. finmarchicus* (to a lesser extent *C. hyperboreus*) have been published for different areas (Jaschnov, 1972 ; Tande *et al.*, 1985 ; Kwasniewski *et al.*, 2003 ; Arnkværn *et al.*, 2005 ; Daase and Eiane, 2007). The tables have been widely used, but the occurrence of large quantities of *C. finmarchicus* in the predominantly Arctic water masses (pers. comm. J. Søreide, M. Daase), suggested that species classification by size may bias observations. In the past decade molecular methods for species determination have become well established. In **paper 1** these methods were used to verify the fit of published length-frequency tables for three of the main sampling localities around Svalbard: Billefjorden, Kongsfjorden and Rijpfjorden.

The results show clearly that *C. glacialis* is frequently misidentified as *C. finmarchicus* when identification is based on prosome length. In total, 26% of *C. glacialis* were misidentified as *C. finmarchicus*, and only 6% the other way round.

Size is one of the plastic traits in zooplankton. It is mainly controlled by developmental time which in turn depends on temperature and food availability (Huntley and Lopez, 1992 ; Campbell *et al.*, 2001). Warmer water masses support a faster development and thus smaller organisms, which has been shown to be true for *C. glacialis* (e.g. Kwasniewski *et al.*, 2003, for Kongsfjorden) and *C. finmarchicus* (Lindeque *et al.*, 2004, in the Irminger Sea). The size distribution varies both in space (Breur, 2003 ; Kwasniewski *et al.*, 2003 ; Lindeque *et al.*, 2004 ; Arnkværn *et al.*, 2005 ; Daase and Eiane, 2007 ; Weydmann and Kwasniewski, 2008, **paper 1**) and time (**paper 1**). This in itself poses a problem. Ideally, one should construct prosome length tables every time samples are taken, as it is unknown a priori if the distribution fits already published size classes. Since this is time consuming it is not always done, instead authors have generalized from size distribution tables that have been established for a certain area, or the tables from areas one assume resemble the hydrographical conditions in the sampled area (e.g. Daase and Eiane, 2007 ; Søreide *et al.*, 2008 ; Rabindranath *et al.*, 2011 ; Daase *et al.*, 2013a ; Daase *et al.*, 2013b; **papers 2 & 3**). Molecular tools to check the validity of prosome length tables have been used in a number of studies, with ambiguous results (Breur, 2003 ; Lindeque *et al.*, 2006 ; Daase and Eiane, 2007 ; Parent *et al.*, 2011). Breur (2003) and Daase and Eiane (2007) conclude that the overlap is not a problem, as the misidentification favours *C.*

finmarchicus and *C. glacialis* alike. However, our study (**paper 1**) concludes that misidentification clearly is one-sided in disfavour of *C. glacialis*. Similar results of large overestimation of *C. finmarchicus* at the expense of *C. glacialis* due to small-sized *C. glacialis* were presented by Lindeque *et al.* (2004) for the Irminger Sea between Greenland and Iceland. For the Canadian Arctic and Atlantic coast, Lindeque *et al.* (2011) also found a large overlap between the two species, but in their case it was mainly caused by large *C. finmarchicus*. Figure 6 illustrates the problem for copepodite stage CV of *C. glacialis* and *C. finmarchicus*, based on some of the most commonly used published size frequency tables for the Svalbard and Barents Sea region in comparison with results from two genetic studies.
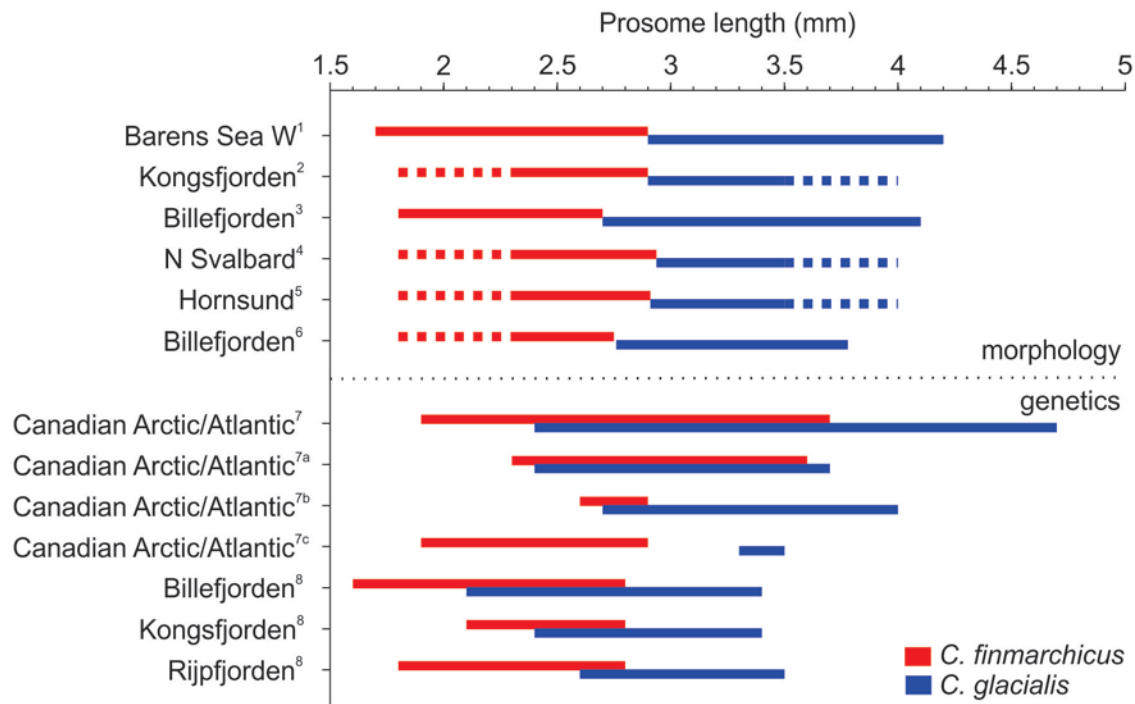
Figure 6. Length range of prosoma length of copepodite stage CV of *Calanus finmarchicus* and *C. glacialis* based on size-frequency analysis (morphology) and genetic analysis (genetics). Broken lines: no minimum/maximum size defined. Reference 7 includes all samples of the entire study, 7 a-c are subsets, 7a : station with largest overlap, 7b: station with largest *C. finmarchicus* minimum: 7c: station with smallest *C. finmarchicus* minimum. References: 1 Tande *et al.* (1985); 2 Kwasniewski *et al.* (2003); 3 Arnkværn *et al.* (2005); 4 Daase and Eiane (2007); 5 Weydmann and Kwasniewski (2008); 6 Breur (2003); 7 Parent *et al.* (2011); 8 Gabrielsen *et al.* (2012)

It is evident that further efforts are needed to evaluate the effect of the size range overlap and that the plasticity of size as a trait needs to be accounted for in future studies. It should be noted that the samples in **paper 1** were not taken randomly across the entire size range, but with focus on the size range where an overlap was suspected. A more systematic approach covering a larger geographic area and the entire size range is needed to assess scale of the misinterpretation.

The perks of long distance travel – bimodal foraging trips of little auks (paper 2)

Many sea birds from the Southern Ocean to the Arctic Ocean feed on zooplankton of various sizes. A particular species of this group, the little auk (*Alle alle*) has been in the focus of the ALKEKONGE research programme, which resulted in 23 publications (see IOPAS (2007) for publication list). The little auk is among the most numerous sea-birds in the archipelago of Svalbard with more than 1 million breeding pairs (Isaksen and Gavrilo, 2000). It feeds preferably on larger copepodite stages of *Calanus glacialis* (Mehlum and Gabrielsen, 1993 ; Karnovsky *et al.*, 2003). The bird's abundance, it's specialization on Arctic zooplankton and it's presumably quick response to changes in prey availability makes it another key species in climate change studies (Stempniewicz *et al.*, 2013).

A successful parenthood requires the allocation of time and energy towards the offspring. This is in particular true for sea birds, which have to meet the high energy demand of the chick during chick rearing period, while also provisioning for self-maintenance. In **paper 2** we studied the foraging behaviour and the prey availability of the little auk. Breeding seabirds, as the little auk, are considered central-place foragers, as they return to a central place after a foraging bout (Elliott *et al.*, 2009). Central place foragers travel a certain distance away from the central place to collect prey in an area where net energy gain is higher than at the central place (Elliott *et al.*, 2009). The bird colony chosen for this study is located in Isfjorden, a fjord characterized by a variable influx of warmer Atlantic water (Berge *et al.*, 2005 ; Cottier *et al.*, 2005), which advects large quantities of the Atlantic copepod species *C. finmarchicus* into the system. With many of the earlier studies on foraging behaviour of little auks focusing on areas where *C. glacialis* is readily available in Arctic water close to the colony (Weslawski *et al.*, 1999b ; Karnovsky *et al.*, 2003), the foraging behaviour of the inhabitants of a colony with less profitable adjacent water masses (i.e. larger amounts of *C. finmarchicus* than *C. glacialis*) was of particular interest. To evaluate what kind of prey is available in the water and what the chicks get served zooplankton was collected in the water column on a transect of four stations across Isfjorden (for the resulting problems of this sampling design, see **paper 3**) and from the gular pouches (a small pouch below the beak) of 24 birds. In addition, some nests were equipped with time loggers, enabling us to obtain a record of the trip times of the nesting parents.

The obtained data revealed two main results: i) Little auks with time loggers attached to their nest had a bimodal foraging strategy, alternating short trips (<5 h) and long trips (>5 h), with a ratio of 5.15 short to one long trip, a behaviour not known from Arctic seabirds before, and ii) the proportion of prey in the gular pouches differed greatly from the proportion found in the sea.

Blue petrels (*Halobaena caerulea*) in the Southern Ocean are known to have a similar bimodal foraging behaviour, caused by the lower energetic value of the food close to the colony and higher quality food

further away. The Blue petrels use the short trips to collect food for the chicks and the longs trips to replenish their own energy reserves with high energy prey (Weimerskirch *et al.*, 2003). We suggest a similar reason for the behaviour of the little auks in the Bjørndalen colony, where the water masses closer to the colony are an unpredictable mixture of Arctic and Atlantic water, while the Arctic water with its energy rich prey is beyond the range of short trips, but within the range of long trips. While this assumption could not be confirmed by the data presented obtained in **paper 2**, recent studies backed our theory by successfully tracking little auks to their foraging sites either with GPS loggers (Jakubas *et al.*, 2012 ; Jakubas *et al.*, 2014) or temperature/depth loggers (Welcker *et al.*, 2009a ; Brown *et al.*, 2012 ; Jakubas *et al.*, 2014). Jakubas *et al.* (2014) show that little auks only conduct long trips during incubation, when there is no chick requiring constant energy supply while subsequently switching to a bimodal pattern when the chick is hatched. During the chick rearing period the birds stayed in the vicinity of the colony on short trips and on long trips they travelled further away. Jakubas *et al.* (2012) showed that little auks returning from long trips weighed significantly more on their return, while they lost the equivalent mass during short trips, supporting the theory that long trips serve self-maintenance. They propose that this pattern is more common among central-place foragers than recognised so far. In summary, recent publications following up on our initially described bimodal foraging pattern theory support the idea that the birds travel to distant sites with more favourable food conditions for self-maintenance during long trips instead of just staying at sea close to the colony for an extended period of time.

We also detected a mismatch between the prey species ratio in the gular pouch relative to the ratio in the sea samples. While the absence of *C. hyperboreus* in the net samples might be explained by birds collecting prey outside Isfjorden at the shelf break during long trips, the absence of *C. glacialis* adult females (AF) in the net samples is harder to explain. Even though they did not contribute large numbers in gular pouches, they were present in most gular pouch samples, but completely absent in the net samples. Possible explanations for this are discussed more in the follow-up **paper 3**.

Finding food – The effects of zooplankton patch size on little auks and sampling design (paper 3)

Zooplankton nets of various diameters, mesh sizes and shapes have been the most commonly used tools to sample the zooplankton community since the pioneering work of systematic zooplankton research by Victor Hensen (Hensen, 1887 ; Wiebe and Benfield, 2003). Hensen disagreed with Ernst Haeckel whether zooplankton is patchily or evenly distributed in the world's oceans (Haeckel, 1890 ; Hensen, 1890 ; Hardy, 1936). This dispute has long since been decided in Haeckel's favour but regardless of the general knowledge about patchiness in the oceans, zooplankton abundance estimates for large areas are often still largely based on single plankton net tows. While this may provide accurate enough estimates for some purposes, in other cases it may be very problematic. The incentive of the study in **paper 3** was to explore patchiness as a possible explanation of the mismatch in species and stage composition between gular pouch contents and sea samples (**paper 2**).

Assessing patchiness - where to sample, where to prey?

The sample design in **paper 2** consisted of four stations along one transect covering Isfjorden. Considering that the fjord system in question is roughly extending 100 km from SW to NE, a transect line with four sampling stations makes this a fairly coarse grid. Available ship time was a limiting factor, as it often is in marine research. The aim of **paper 3** was to assess whether or not patchiness in the zooplankton distribution within the fjord could partly explain the at-sea ratios, and if there were hot-spots where an increased occurrence of larger/more energy rich copepod prey would make it more profitable for little auks to harvest. Furthermore, if patches of that kind exist, what is their extent? At what grid size would one need to sample the area in order to catch the variation caused by patchy distribution? This study increased the sampling resolution in order to assess zooplankton patchiness on a small-to mesoscale. We applied a triangular sampling grid with sampling distances increasing from a few hundred metres to about twenty kilometres between the stations (Fig. 7). At the same time gular pouch samples were obtained from the little auks in the adjacent Bjørndalen bird colony.
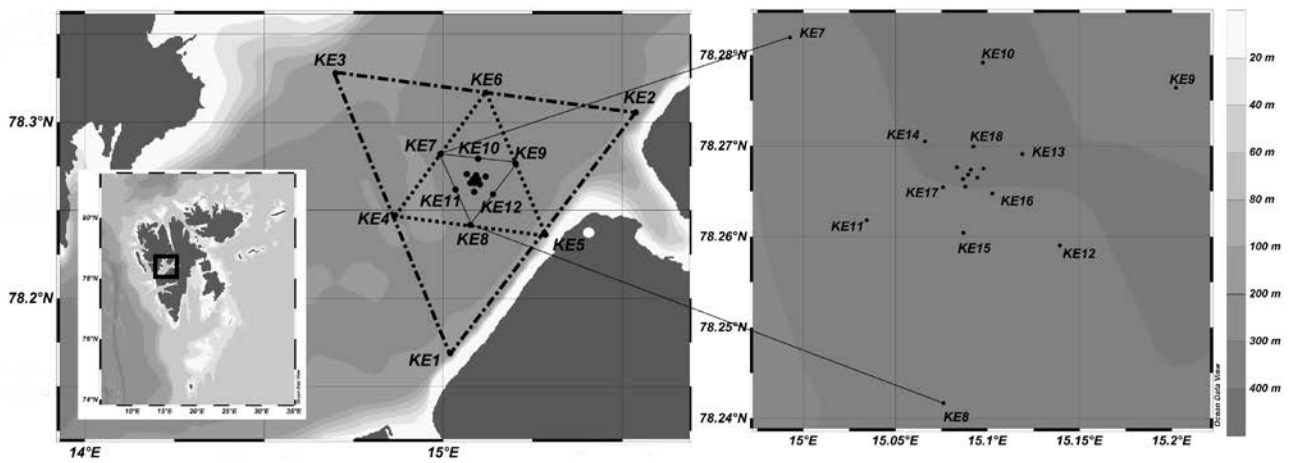
Figure 7. Nested sampling grid and bird colony (white dot). Figure from paper 3.

Both patches in zooplankton distribution (Fig. 3 in **paper 3**) as well variations in the physical properties (Fig. 4 in **paper 3**) were detected in the grid. Spatial autocorrelation analysis of the zooplankton counts revealed patches of size from 0.2 to 1.2 km for older copepodite stages, while no clear pattern was apparent for younger stages. Interesting here is not only that we found a patch on a fairly small scale, but also the range of the variation in total biomass (between 16 and 115 mg m^{-3}) and abundances at the grid stations (Table 2 in **paper 3**).

We converted the observed abundances of copepod species and copepodite stages relevant as prey for little auks into equivalent energy in kJ to compare the potential energy content of different parts of the sampling grid. At the station with the lowest abundances the energy content reached only 1.3 kJ m^{-3} while at the station with the highest abundances it was roughly 16 times more (20.8 kJ m^{-3}). This variation must be very important for planktivorous predators such as the little auk. With the energy demand of an *Alle alle* chick ranging between 100 and 350 kJ d^{-1} (Konarzewski *et al.*, 1993 ; Wojczulanis *et al.*, 2006 ; Welcker *et al.*, 2009b) a parenting little auk would have to invest considerably more time and energy to collect enough food for their offspring in low abundance areas versus high abundance patches. One should therefore expect that the birds do actively search for patches of high prey abundance, and probably even depend on the occurrence of these patches.

The location and existence of patches is not only relevant for planktivorous animals, they also need to be considered by researchers. **Paper 3** shows that a sampling grid in this particular area should have maximum two kilometres distance between sampling sites to catch the small-to-mesoscale variability of zooplankton abundance close to the bird colony. Due to the logistical and financial constraints of zooplankton net sampling, the use of automated equipment like a video plankton recorder would be highly beneficial for this kind of predator-prey studies.

Selecting food – ruler vision or patch detection?

Still unaccounted for is the mismatch of the prey ratio in the gular pouches of the little auks and the ratio of the potential prey in the sea. While we could demonstrate patches with generally higher zooplankton abundance in the vicinity of the little auk colony in Bjørndalen, we were not able to find a location in the sampling grid that resembled the species composition in the gular pouches.

This phenomenon reported both here and in the previous paper has been described previously (Golovkin *et al.*, 1972 ; Bradstreet, 1982 ; Karnovsky *et al.*, 2003) but remains unexplained. In our study, *C. finmarchicus* CIV were dominant in the net samples, but were almost absent in the gular pouches. We did show the existence of small scale patches, but we did not know where the birds we sampled had been feeding. This is a general problem with all studies based on capture of live birds at their nesting sites: it is easy to obtain a gular pouch sample and see what they have collected, but difficult to know where the prey was collected. With new miniaturized GPS loggers it has become possible to check where they have been. But to sample the exact place and depth where they actually foraged is not doable in practice. In our case, the birds may even have been feeding in patches with a different species composition outside our sampling grid. In addition, they might be able to feed selectively. Data presented here and by others (Bradstreet, 1982 ; Weslawski *et al.*, 1999a ; Weslawski *et al.*, 1999b) indicate that little auks rarely prey on food items smaller than 2.5 mm. It should be fair to assume that little auks use prey size as a measure of what to pick and what not, thus not choosing prey by "species". It has also been suggested that they might conduct whale-like filter feeding (Harding *et al.*, 2009). I would argue that this is highly unlikely for two reasons. Firstly, as this kind of feeding would be rather indiscriminate it would be difficult to explain why there are no smaller prey items in the gular pouch and secondly, because of the small diameter of the beak, the bird would have to swim very slow in order to filter water and not just push it away (compare towing speed of small diameter fine-mesh phytoplankton net versus large diameter large-mesh zooplankton net).

It is not known how the size discrimination could be achieved, but one suggestion has been that they use the white spot above the eye (Fig. 8) as a ruler (Jørgen Berge pers. comm.). Brown *et al.* (2012) found that diving little auks spent most of their dive at a certain depth when collecting food. One could imagine that they find patches of high zooplankton abundance both in the horizontal

Figure 8. Little auk displaying the white «Berge-spot» above the eye-lid. Photo credit Geir Johnsen.

and vertical dimensions (Stempniewicz *et al.*, 2013) and consecutively select which item to pick by matching the potential prey item with the "Berge-spot". This theory is highly speculative and further studies should take the anatomy of little auk vision into consideration.

Whatever the mechanism of prey selection may be, the rigorous discrimination against smaller sized items indicates that little auks will be negatively affected by a possible decrease in large prey. A change in climate conditions with an increase in warmer Atlantic water in the Arctic domain and a possible decrease in prey size across all species, as discussed in **paper 1**, could have an equally negative effect as a regime shift to a dominance of a smaller copepod species (*C. finmarchicus*). Recent studies have demonstrated the negative effect of Atlantic dominated waters on chick growth time (Jakubas *et al.*, 2013) and survival of adult little auks (Hovinen *et al.*, 2014). This illustrates why little auks can be used as indicators for secondary climate change effects and should continue to be monitored also in the future, after the "ALKEKONGE" project has ended.

What's in it for me? – Size determines energy content (paper 4)

In **paper 2** we used very coarse measures to argue for a substantial increase in energy content ("The oil sac grows 2.8 times when the prosome length increases from 2.5 to 3.5 mm…") and cite Falk-Petersen *et al.* (2007) with the statement that a CV of *C. glacialis* has a lipid weight 10 times higher than *C. finmarchicus* and *C. hyperboreus* 25 times higher. A more accurate calculation of the increase of energy content with increase in prosome length was needed to assess what size-selective predators such as little auks gain by their prey size discrimination. **Paper 4** explores a quick and easy method to estimate energy content of copepods independent of species and copepodite stage without the hassle of chemical analysis of single individuals. The three *Calanus* congeners store most of their energy in a conspicuous lipid sac and have a very similar lipid composition (Kattner and Hagen, 1995 ; Lee *et al.*, 2006). Several methods using measurements of the lipid sac size as proxy for energy content are available (see table 1, **paper 4**), but none of them are valid for all three *Calanus* spp. To get a general relationship between energy content and its main determinant, the lipid sac, we selected specimens only by lipid sac size, independent of copepodite stage and species.

We measured lipid sac area on digital images and correlated the area with actual lipid measurements by gas chromatography performed on individuals. We found a strong relationship between lipid sac area and total lipid as well as total wax ester content (Fig. 3 in **paper 4**). The resulting equation can be used to convert lipid sac area to total lipid or wax esters. We also published an equation to estimate total lipid by dry weight, which is more inaccurate but might be useful in situations where pictures are not available. The equations are applicable for the three co-occurring *Calanus* spp.

The methodology described here has been successfully applied in several other studies since (e.g. Aubert *et al.*, 2013 ; Daase *et al.*, 2013b ; Zarubin *et al.*, 2014) which all have a focus on variability in individual lipid content.

The ups and downs in life – ontogenetical and diel vertical migration of copepods (paper 5 & 6)

Autumn (paper 5)

The summer situation of the zooplankton community in the Arctic Ocean and the Svalbard fjords is important for the chick recruitment of little auks (Jakubas *et al.*, 2013 ; Hovinen *et al.*, 2014), and has been surveyed for a long time. However less is known about the whereabouts and activities of the copepods during the rest of the year, in particular during winter. In **paper 5** we looked into the vertical distribution and diel vertical migration of the dominant herbivorous zooplankton species at different locations around Svalbard, and in **paper 6** we focus on the question if diel vertical migration (DVM) might exist even in the pitch dark polar night.

DVM has been claimed to be the largest synchronized movement of biomass on Earth (Hays, 2003) occurring in all the world's oceans as well as in freshwater. But in many ways, the Arctic Ocean is different from other oceans, in particular with regards to the much stronger seasonality (polar night vs. midnight sun). The four mesozooplankton species (the three *Calanus* congeners and the omnivorous *Metridia longa*) investigated in **paper 5** comprise the main part of the mesozooplankton community in terms of biomass in the Arctic (Smith and Schnack-Schiel, 1990), thus these should be the ones most relevant for DVM in the Arctic.

We did not find any clear signals of synchronous DVM in *Calanus* spp., even though the study took place around the autumn equinox with distinct day and night. Older and larger copepodite stages of the planktivorous species are mostly located further down in the water column. We also found a south-north gradient in developmental progress with higher abundances of older stages at the more southern locations. In contrast to the *Calanus* spp. did *Metridia longa* show DVM behaviour.

This could probably indicate that the seasonality in the Arctic has a much larger effect on the life strategies of herbivorous zooplankton than daily variations in illumination. During midnight sun, DVM as means of predator avoidance is obviously meaningless, and in the autumn the specimens which are well fed have probably descended to depth for hibernation already, while those which are still close to the surface cannot afford to conduct DVM because they still need to gain more energy reserves for overwintering. One can also explain the south-north gradient with seasonality. A "spring" situation with phytoplankton bloom occurs later in the year the further North one travels, thus a population at the northernmost station will be

in an earlier stage of ontogenetical development (more younger stages) than a population at the southernmost station, for which "spring" has been a while ago already (more older stages)(Rabindranath *et al.*, 2011).

Metridia longa on the other hand is an omnivorous species and thus probably less dependent on the seasonal peak of the phytoplankton bloom. By being able to feed all year round, they can afford to engage in DVM during the time of the year when it would gain a positive effect on survival. This is reflected in the lower mortality index we found for *M. longa* than for *Calanus* spp.

It has been suggested that light could be a major factor determining the vertical positioning of pelagic organisms in the water (Pearre, 2003), thus differences in light conditions between sampling stations could be important for understanding variations in vertical distributions. We did get some indication that the vertical range of the depth distribution of most copepodite stages had a positive linear relationship with their mean depth. For a thorough analysis though, we would have needed in-situ light attenuation measurements instead of theoretical approximations and higher resolution horizontal sampling.

Winter (paper 6)

A completely different methodological approach was used to asses if there is DVM in the dark of the polar night (**paper 6**). Instead of deploying zooplankton nets and consecutively retrieving them and counting the individuals of the different species at different depth intervals and times of the day, we deployed acoustic instruments (ADCP, Acoustic Doppler Current Profiler) in continuous measuring mode over the course of an entire year at an ocean observatory. Originally designed to measure the speed of currents by tracing the speed of small particles drifting with the water, it can also be used to look at vertical migrations of particles.

Surprisingly we did find synchronized DVM behaviour of zooplankton throughout most of the polar night at both localities, Kongsfjorden and Rijpfjorden, even at times when variations in light levels were below the detection limit of the human eye. In Kongsfjorden, which was ice free the entire winter, the observed DVM pattern and its depth range is lowest but still detectable in December and January, the darkest months. In Rijpfjorden, which was ice covered, the signal ceased in December, but returned in January, though at a much lower level than at the same time in Kongsfjorden.

The obvious major drawback of the ADCP observations is the fact that the instrument does not give any information on what kind of particle it tracks; it reacts to anything in a certain size range. Therefore, we had automated sediment traps deployed at the same moorings as the ADCP were attached to. The only collected particle that would fit the signal were calanoid copepods, thus one has to consider them as possible migrators. It is also possible that larger species, like krill, which are able to avoid the sediment traps, could have been the source of the signal. Similar to the identity of the migrants, the reason for the migration remains unclear. Irradiance data from the Aurora station at UNIS, recorded by highly sensitive

loggers, show a variation in solar background irradiance even at the darkest days of the polar night. Also, a shift from a 24h (solar) to a 25h (lunar) cycle in the DVM pattern and the absence of DVM during December and overall lower levels in an ice covered fjord point towards light as a trigger. A recent study by van Haren and Compton (2013) questions the effect of background sunlight. They found DVM patterns in zooplankton in the deep sea, below the penetration level of any indirect light, to be consistent with day length. They also point out that the deepest plankton was the first to start upward migration, which is unlikely if triggered by variation in light, which should affect the plankton in the more light exposed higher layers first. As a possible trigger, van Haren and Compton (2013) suggest a precise biochemical clock, which would contradict the change from solar to lunar cycle as observed in our study. One could also think of combined factors, each doing their part in triggering onset of DVM, depending on their strength. Maybe in strong light/dark gradients light levels are a trigger, in absences of light endogenous triggers take over, and during full moon either moonlight and/or variations of gravitational force by sun and moon could affect DVM behaviour.

In conclusion, while synchronized DVM in fact does seem to cease during periods of midnight sun, it seems to continue during the polar night, and in the equally dark deep sea. The triggers are still highly speculative and need more research. From a predator evasion theory point of view, avoidance of water with even the faintest light could reduce the mortality risk, as visual predators are still present in the polar night. During a recent expedition to Kongsfjorden in January, we observed several actively feeding sea birds, which are supposedly visual predators. One could imagine that these birds are able to utilize even low light levels to better differentiate between water and objects in the water. Regular *et al.* (2011) found another seabird, the common murre (*Uria aalge*), a visual predatory seabird, to utilize moonlight for visual predation. During midnight sun on the other hand, DVM as predator avoidance does not make sense, at least it should not be effective against visual predators.

Some concluding thoughts about size, lipids and the future of *Calanus* research

Reliable species identification is alpha and omega for ecological studies that predict a regime shift from an Arctic (*C. glacialis*) to an Atlantic (*C. finmarchicus*) species dominated system. Using prosome length tables may bias observations, but it is still unknown how large the error is in different parts of the Arctic and at different times of the season. Not only would large errors mean that we get a wrong impression of the status quo, but also our ideas of the effects of a possible regime shift may be misleading. Assuming that we currently overestimate the abundance of *C. finmarchicus* over a large geographical area while in reality there is a substantial number of small *C. glacialis* in the system, one can wonder if a regime shift as predicted in Falk-Petersen *et al.* (2007) would really have dramatic implications. Mostly the predicted consequences are based on the assumption that *C. finmarchicus* in general contains less energy in terms of stored lipids than *C. glacialis*. An increase in warmer Atlantic water would favour the abundance of *C. finmarchicus*, which is smaller and contains 10 times less energy per individual than *C. glacialis* (Falk-Petersen *et al.*, 2007). Thus, in a very simplistic view, a system which shifts from a dominance of *C. glacialis* to a dominance of *C. finmarchicus* would support a different type of higher trophic level predators, as prey-size spectrum would change and the energy availability per unit prey would be reduced.

Relating prosome length to lipid sac area (Fig. 9, unpublished data) indicates that "species" per se is not the best measure of available energy in form of lipids. Firstly, there is an apparent maximum lipid content which is species independent and varies with prosome length only. Thus two copepods of different species but same prosome length will have the same apparent maximum lipid content. Secondly, as the lipid sac can have any area from zero to the apparent maximum, with increasing prosome length the range of possible values increases (see Fig. 9: A copepod of 3 mm prosome length can have any lipid sac area between 0 - 1 mm^{-2}, a copepod of 6 mm prosome length any area between $0 - 5$ mm^{-2}). And last, as all copepods increase in prosome length during their ontogenetic development, a copepodite stage CIV will have a lower apparent lipid maximum than a copepodite stage CV of the same species. Thus for the available lipid content it is not important if the particle in the water is named "glacialis" or "finmarchicus", but how large it is. Despite this common sense understanding (a large particle can contain more liquid (i.e. lipid) than small particle) we often operate with the generalized averages for lipid content of a specific copepod species and stage (as in **paper 2**). Two examples might illustrate the point of this argument: Parent *et al.* (2011) show a complete overlap in size of *C. finmarchicus* and *C. glacialis* at one of their stations (Fig. 6, Ref. 7a). Lindeque *et al.* (2006) found "considerable variation in size of *C. glacialis* over its distribution range" as well as "spatial variability in the mean length of *C. finmarchicus*…", also these identifications confirmed by genetic analysis. Size would in these cases be a better predictor of energy content than species and stage, and reliable species identification is of less importance from the functional view of *Calanus* spp. as prey.
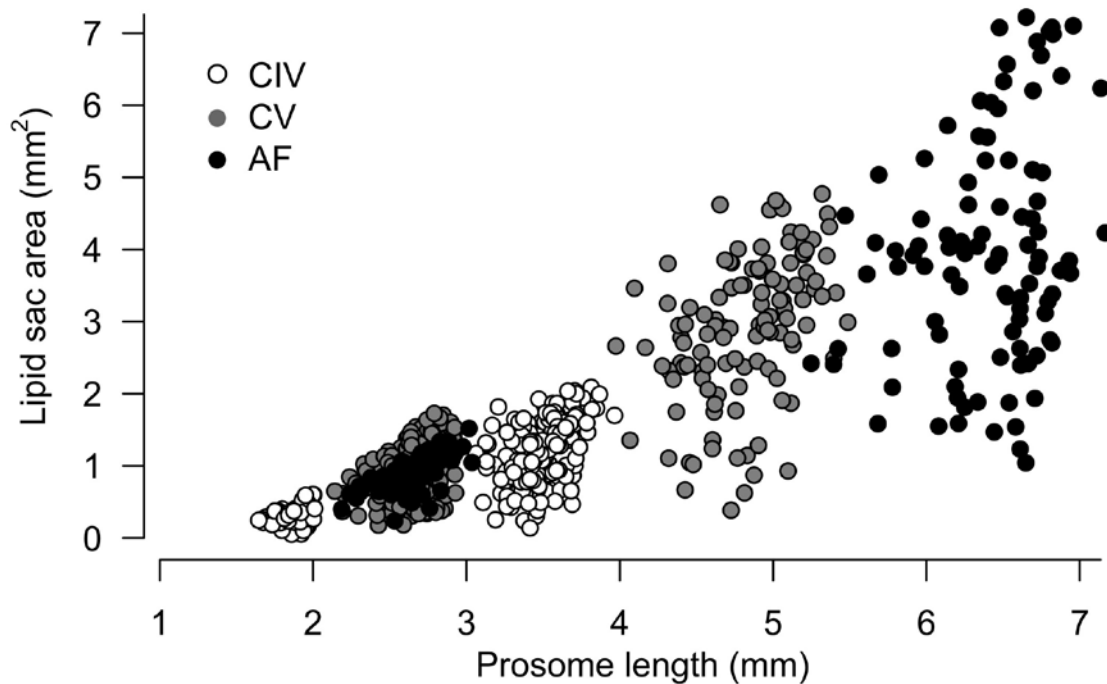
Figure 9. Prosome length and lipid sac area of a pooled sample of ca 800 C. finmarchicus and C. hyperboreus. The data is based on measurements of lipid sac area and prosome length of a mixture of ~800 *C. finmarchicus* and *C. hyperboreus*. *Calanus* spp. was sampled at 12 stations around Svalbard with a 200 µm plankton net between July and October 2010. Measurement of lipid sac area and prosom length were performed according to the method described in paper 4.

The results of **paper 4** (lipid content measured by lipid sac size independent of species), the data of Fig. 9 and the undisputable overlap of species size ranges presented in **paper 1** and other published studies (Lindeque *et al.*, 2006 ; Parent *et al.*, 2011) point to the need for a critical re-evaluation of the suggested *Calanus* regime shift, both of its nature and its potential consequences for higher trophic level.

Among other factors, temperature and developmental time have great impact on the prosome length (Parent *et al.*, 2011). Thus a warming of the Arctic Ocean does not necessarily induce an northward migration of smaller Atlantic species – the smaller Atlantic species might extend their developmental time and grow larger than their average size in the south, or species known to be larger might develop faster and become smaller. The latter is something we possibly observe already in a potentially large number of misidentified small *C. glacialis*, as demonstrated in **paper 1**. It should thus be evaluated for every future study how important it is to be able to distinguish with certainty between species, which (for all practical means) is only possible by using molecular tools.

To be able to predict the future, one has to understand the past – in times of rapid climatic changes, we need to understand how and why the three *Calanus* congeners developed their differences in size and life history to be able to predict future scenarios. Berge *et al.* (2012) recently challenged the general idea of the physical environment as the main factor shaping *Calanus* life history. Instead they argue for predation pressure by large predators in the Arctic, the baleen whales. Could predation by indiscriminately feeding

baleen whales, once numerous on the Arctic shelves, now nearly extinct, be the evolutionary driver favouring smaller and faster growing *C. glacialis* on the shelves? In evolutionary theory (Stearns, 1992) short life cycles and/or higher fecundity as in *C. glacialis* compared to *C. hyperboreus*, can be typical features of species under high predation pressure. We cannot turn back time to answer this question, but we can investigate the *Calanus* spp. community in areas with different selection pressure (e.g. by fish) that exist today. With the help of genetic species determination it could be tested whether a gradient in size of *C. glacialis* correlates with a gradient in predation rates.

In this thesis, several studies compare *Calanus* spp. distributions – between sampling stations or collected by predators vs. their availability at sea (**paper 2, 3, 5**). For all these studies, it would have been advantageous to have an idea how much (if any) impact a potential misidentification could have had on the results. Future studies need to consider this aspect in their sampling design.

While we demonstrated which effect the geographic position of a sampling station can have on the result by hitting or missing a horizontal patch, vertical patchiness can have a major effect as well. In a recent study (Zarubin *et al.*, 2014) nicely illustrated a notable variability in average lipid content in copepods across fine-scale depth ranges, which usually gets integrated in single depth intervals. For **paper 2** & **3** a fine-scale sampling could have added much information on the potential vertical patchiness and in **paper 5** the range of the vertical distribution, which is important for the light preference analysis and the detection of small-scale DVM patterns would have been beneficial for the analysis.

The methodological concerns do not detract from the need to study and understand the Arctic zooplankton communities. The three *Calanus* spp. co-occurring in the waters surrounding Svalbard will continue to spur large research efforts because of their key function as energy rich prey and climatic indicator species.

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Erratum

Figure 4 and the figure text belonging to this figure were unfortunately swapped with an older version in the submitting process. The correct figure and figure text should be:
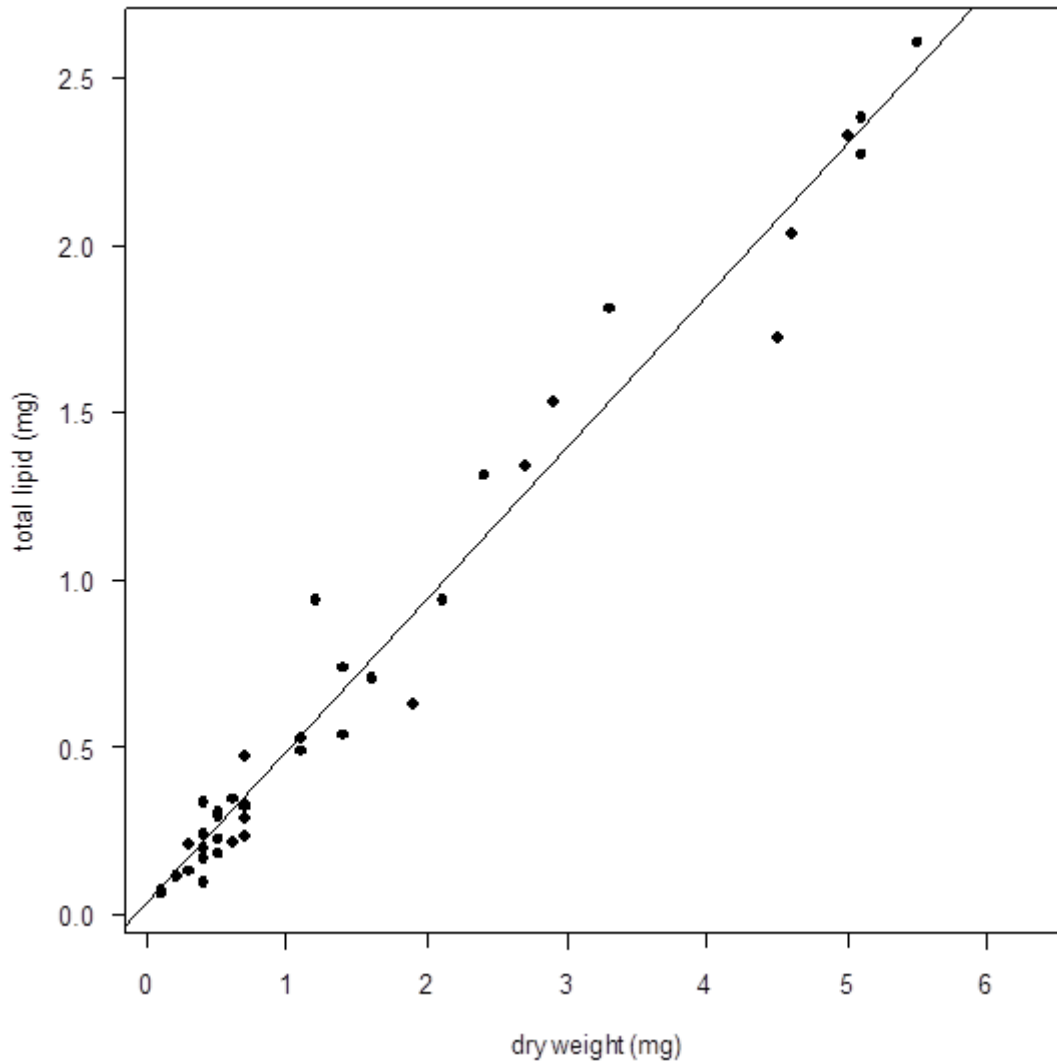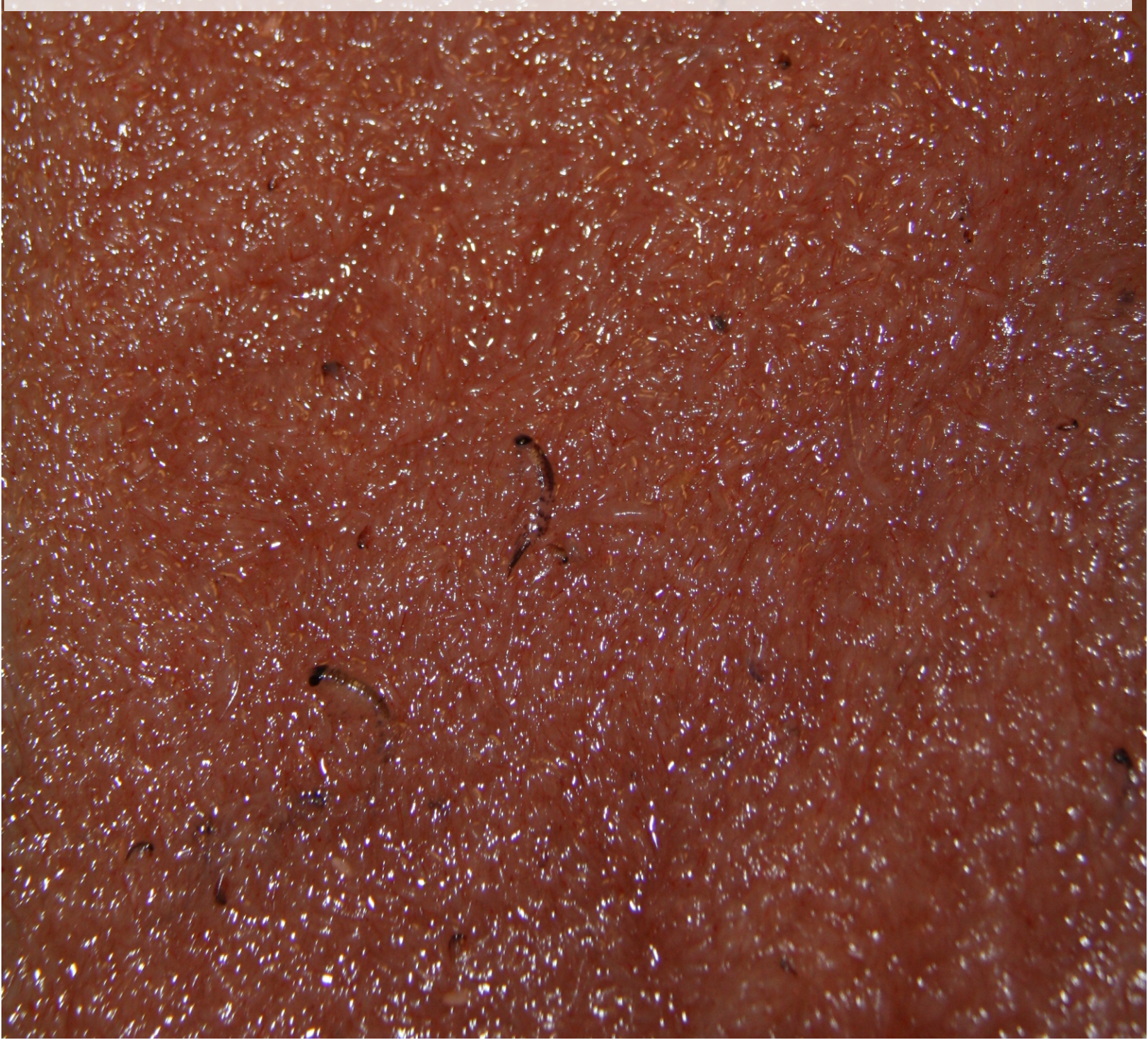

Fig. 4. Correlation between total lipid from gas chromatography and dry weight (entire specimens), n=52, r^2=0.91 P<0.001. Linear regression: TL=0.037 + 0.453DW.

Gabrielsen, T., Merkel, B., Søreide, J., Johansson-Karlsson, E., Bailey, A., Vogedes, D., Nygård, H., Varpe, Ø. and Berge, J. (2012)

Potential misidentifications of two climate indicator species of the marine Arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*

Steen, H., Vogedes, D., Broms, F., Falk-Petersen, S., and Berge, J. (2007)

Little auks (*Alle alle*) breeding in a high Arctic fjord system: Bimodal foraging strategies as a response to poor food quality?

Vogedes, D., Eiane, K., Båtnes, A. S. and Berge, J. (2014)

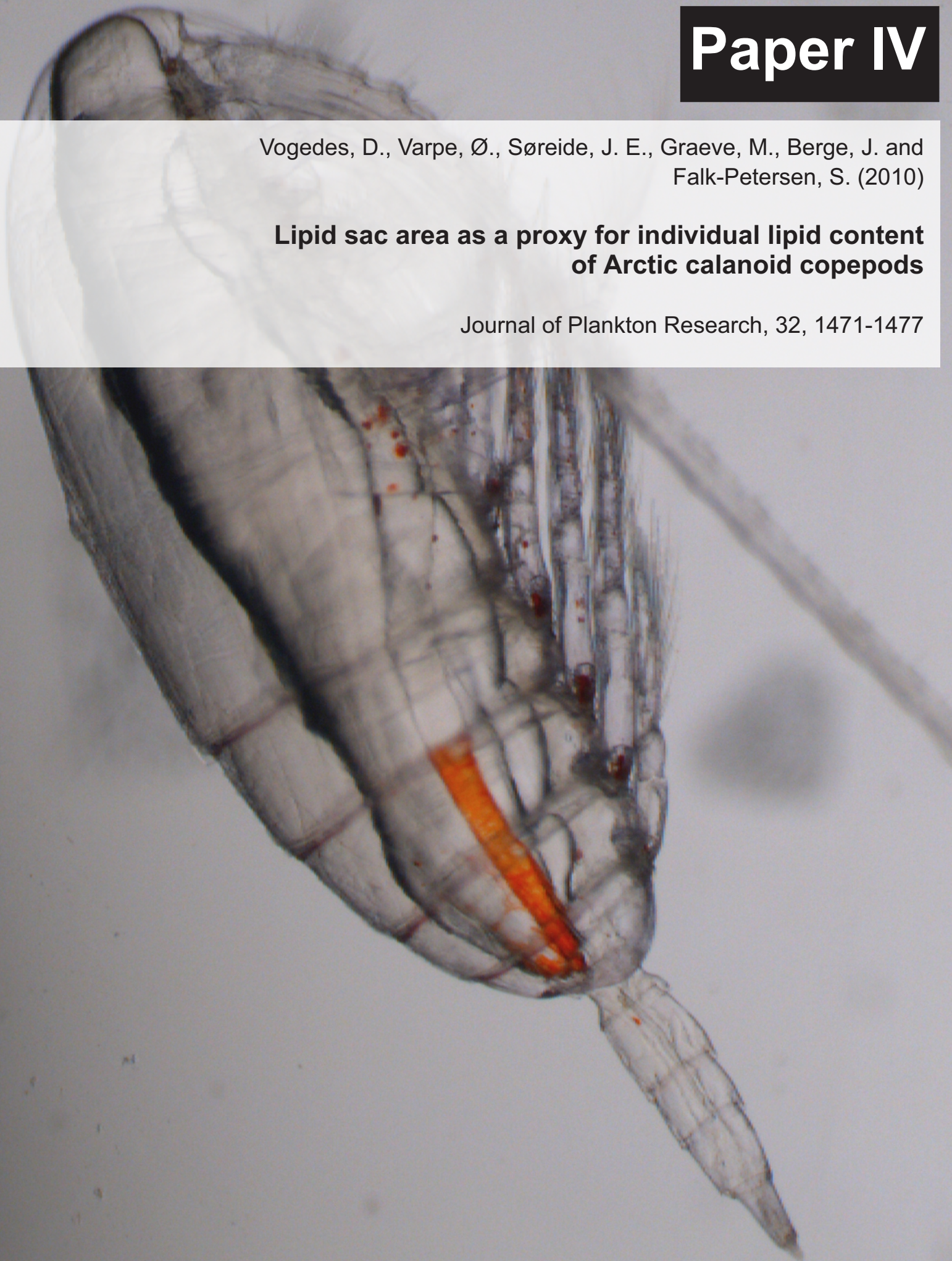# Variability in *Calanus* spp. abundance on fine- to mesoscales in an Arctic fjord: implications for little auk feeding

Vogedes, D., Varpe, Ø., Søreide, J. E., Graeve, M., Berge, J. and Falk-Petersen, S. (2010)

Lipid sac area as a proxy for individual lipid content of Arctic calanoid copepods

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Vertical distribution of *Calanus* spp. and *Metridia longa* at four Arctic locations

Berge, J., Cottier, F., Last, K. S., Varpe, Ø., Leu, E., Søreide, J., Eiane, K., Falk-Petersen, S., Willis, K., Nygard, H., Vogedes, D., Griffiths, C., Johnsen, G., Lorentzen, D. and Brierley, A. S. (2009).

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