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Calanus glacialis – the role of lipids in the life cycle and for the Arctic pelagic food web

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C*alanus glacialis* – the role of lipids in the life cycle and for the Arctic pelagic food web

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Contents

Summary

The Arctic marine ecosystem is characterized by strong seasonality and a short but productive period of primary production in the spring when the ice breaks up. *Calanus glacialis* is one of the key links between primary producers and higher trophic levels, and it is adapted to the strong seasonality by life cycle traits such as; seasonal vertical migration, diapausing, reproduction in the spring and extensive energy storage. The timing of these events will have consequences for the success of *C. glacialis* and also for the energy available at higher trophic levels. The aim of this study was to increase the knowledge about these key life history traits with focus on the role of lipid accumulation, seasonal vertical migration and the transfer of energy from primary producers through *Calanus*, to higher trophic levels, such as seabirds and seals. Lipid accumulation and seasonal vertical migration of *C. glacialis* were studied in the Amundsen Gulf, in the Canadian Arctic (Paper I) and in Svalbard waters (Paper II and III). The transfer of energy to higher trophic levels was studied by comparing the fatty acid composition of predators to that of their prey and by using stable isotope analysis to calculate their trophic level. We analyzed five seabird species from Kongsfjorden; Little auk (*Alle alle*), Brünnich's guillemot (*Uria lomvia*), Black-legged kittiwake (*Rissa tridactyla*), Northern fulmar (*Fulmarus glacialis*) and Glaucous gull (*Larus hyperboreus*) (Paper IV) as well as harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) from the West Ice (Paper V).

The timing of the ascent of *C. glacialis* during spring, the match of reproduction with the primary production as well as the length of the primary production period determines the development of offspring , the overwintering stage the following winter, and hence the length of the life cycle. The shorter the period of primary production, the more important is the match between reproduction and bloom. Ice algae may fuel early maturation of the females and prolong the reproductive period. In the Amundsen Gulf, *C. glacialis* ascended to the surface water in time to feed on the ice algae bloom, but since CIII was the main overwintering stage, the ice algae fuelled development of CIII which could develop to females that possibly could spawn during the summer.

The life history trait of accumulating energy in form of lipids is an adaptation of *Calanus* to the large seasonal and inter-annual fluctuations in food availability, and the lipids represent an effective transfer of energy up the food chain. High levels of the *Calanus* markers 20:1n9 and 22:1n11 in the seabirds Little auk, Black-legged kittiwake and Northern fulmar from Kongsfjorden, Svalbard, indicate that these seabirds are part of the *Calanus* based food web (Paper IV). Harp seals and hooded seals (Paper V) showed considerably overlap in diet, but the fatty acid composition of harp seals originated from a diatom–*Calanus* based food web, while the fatty acids of hooded seals originated from a food web based on dinoflagellates and the prymnosiophyte *Phaeocystis pouchetii*. To conclude, the diatom–*Calanus* food chain is an important driver for the high latitude pelagic arctic food web. The match between timing of primary production, either as ice algae or phytoplankton bloom, and the timing of reproduction of *C. glacialis* is crucial for the accumulation of lipids in *Calanus* may have consequences for the energy available for higher trophic levels.

List of Papers

I. Wold A, Darnis G, Søreide JE, Leu E, Philippe B, Fortier L, Poulin M, Kattner G, Graeve M and Falk-Petersen S (2011) Life strategy and diet of *Calanus glacialis* during the winter-spring transition in Amundsen Gulf, southeastern Beaufort Sea. *Polar Biology* 34:1929-1946.

II. Rabindranath A, Daase M, Falk-Petersen S, Wold A, Wallace MI, Berge J, Brierley AS (2011) Seasonal and diel vertical migration of zooplankton in the High Arctic during the autumn midnight sun of 2008. *Marine Biodiversity* 41:365-382.

III. Wold A, Leu E, Walkusz W and Falk-Petersen S (2007) Lipids in copepodite stages of *Calanus glacialis. Polar Biology* 30: 655-658.

IV. Wold A, Jæger I, Hop H, Geir Wing Gabrielsen GW and Falk-Petersen S (2011) Arctic seabird food chains explored by fatty acid composition and stable isotopes in Kongsfjorden, Svalbard. *Polar Biology* 34:1147-1155.

V. Falk-Petersen S, Haug T, Hop H, Nilssen KT and Wold A (2009) Transfer of lipids from plankton to blubber of harp and hooded seals off East Greenland. *Deep-Sea Research II* 56:2080-2086.

Calanus glacialis CV

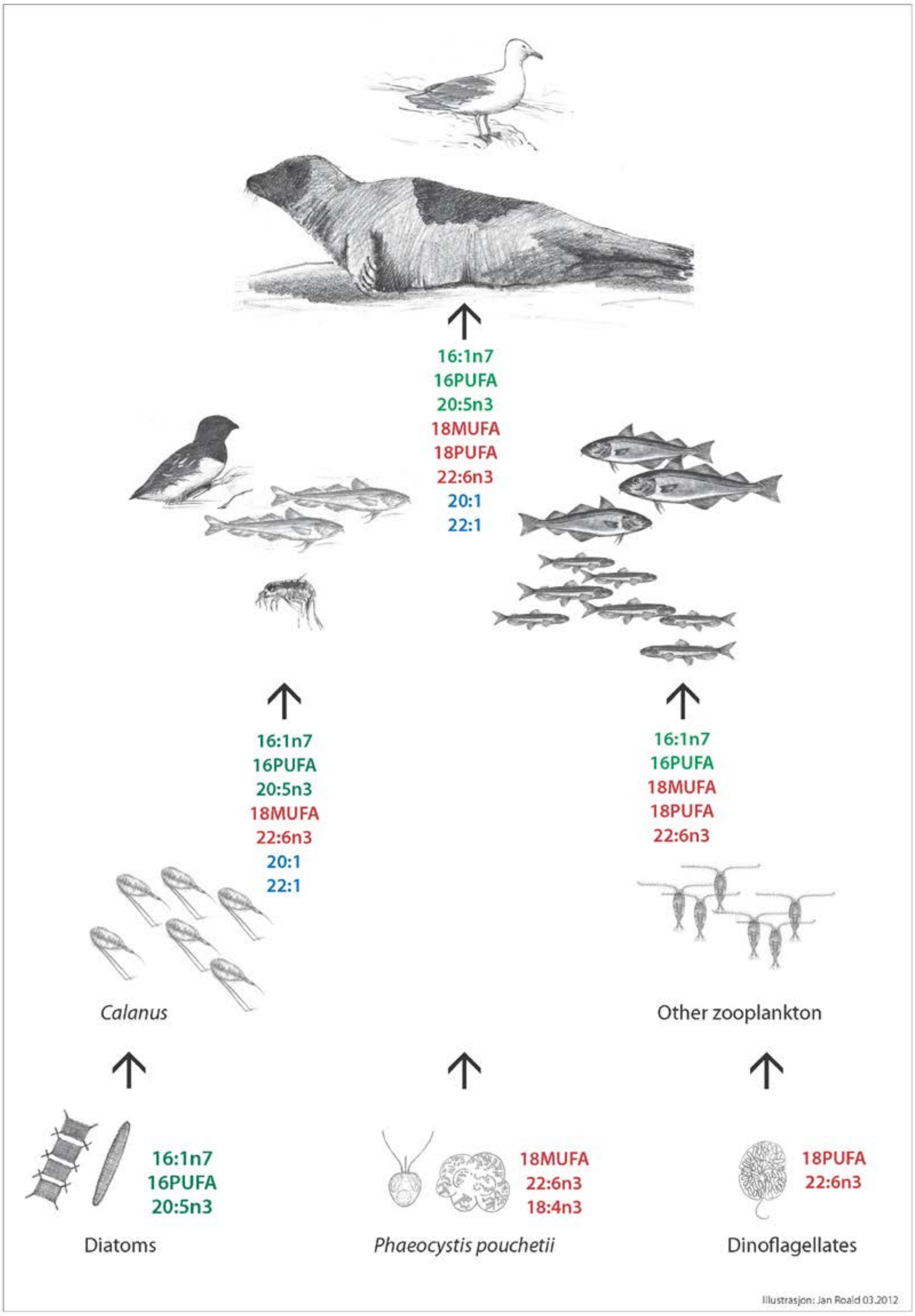
Introduction

Arctic marine ecosystems are characterized by strong seasonal and spatial variability. When light intensity increases during spring, the ice melts and stratification of nutrient-rich water masses lead to a short but prolific period of primary production as both ice algae and pelagic phytoplankton bloom. This short and intensive period of primary production represents the main pulse of energy in the Arctic. The phytoplankton bloom follows the receding ice as it open up, starting in April in the southern parts and as late as September at the furthest North (Zenkevitch 1963; Falk-Petersen et al. 2007). The largest contribution to the overall primary production is from the phytoplankton bloom, while estimates based on *in situ* measurements from the northern Barents Sea suggest that ice algae constitutes 15-22 % of the primary production (Hegseth 1998). Since the ice algal bloom precedes the phytoplankton bloom it represents an early-season food source, which can fuel reproduction and extend the restricted grazing season for herbivorous zooplankton (Leu et al. 2010). In environments with such strong seasonality, grazers (and predators) must synchronise their reproduction and feeding to the seasonally fluctuating food availability. The match-mismatch hypothesis originates from the hypothesis that year-class strength of fish is affected by food availability during critical developmental stages of the larvae (Hjort 1914). Cushing (1974, 1975, 1990) expanded this idea and proposed that the variation of year-class strength of fish depends on the timing of the reproduction in relation to the timing of the phytoplankton and hence copepod recruits, which are the main food for fish during a critical development stage. Even though the match-mismatch hypothesis has been contested, the importance of timing between reproduction and food availability has been supported by several studies (Fortier et al. 1995; Brander et al. 2001; Beaugrand et al. 2003) and the hypothesis has been generalized to encompass the reproductive success of grazers and predators relative to the food availability during critical life stages (Durant et al. 2005; Hipfner 2008). The hypothesis has gained increasing focus in relation to the possible advancement of spring phenology due to climate warming (Ottersen et al. 2001; Beaugrand et al. 2003; Durant et al. 2007), including the potential mismatch between *Calanus* and their prey as a result of potential changes in the sea ice regime and hence primary production (Norrbin et al. 2009; Søreide et al. 2010; Leu et al. 2011). While global warming might disrupt the match between predator and prey, it may at the same time increase primary production and this increase in food abundance might compensate for the asynchrony (Durant et al. 2005).

The *Calanus* species (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*) have successfully adapted to the strong seasonality in food availability, and they are the prime herbivorous comprising >70% of the total zooplankton biomass in the Arctic (Tande 1991; Hirche et al. 1994; Mumm et al. 1998; Auel and Hagen 2002; Søreide et al. 2008). *Calanus* is therefore the key link between primary producers and higher trophic levels (Bradstreet and Cross 1982; Falk-Petersen et al. 1990; Sakshaug 1997). The adaption of the herbivores *C. glacialis* to the highly pulsed food source includes seasonal vertical migration, diapausing (Conover 1988), extensive energy storage (Lee et al. 2006; Falk-Petersen et al. 2009b) and reproduction connected to food availability (Tourangeau and Runge 1991; Madsen et al. 2008; Søreide et al. 2010). The scheduling of these key life history events will have consequences for other activities at other times of the year (McNamara and Houston 2008; Varpe 2012). For example, feeding and lipid accumulation during spring will affect the timing of descent to diapause in the autumn and probably also diapausing depth (Pond and Tarling 2011). These traits have evolved as an adaption to environmental conditions, but are also dependent on the state of the individual organism. The physiological condition of an individual such as energy reserves, size, and parasite load will affect its ability to reproduce, feed, or migrate, and will cause a variation in the strategies observed within and between populations.

One of the main adaptations by *Calanus* to the short but productive feeding season is the rapid conversion of carbon from primary production to energy rich lipid stores, mainly wax esters (Sargent and Henderson 1986; Conover 1988; Atkinson 1998; Lee et al. 2006; Falk-Petersen et al. 2009b). There has been an selective pressure for the efficient biosynthesis of wax esters as lipid stores are important as buffers for the long periods without food, and the variable onset of primary production, encountered in the seasonally ice covered Arctic seas (Falk-Petersen et al. 2009b). The biosynthesis of wax esters is a very effective way to quickly produce large amount of high-energy lipids, since long-chained 20:1 and 22:1 fatty acids and fatty alcohols, which make up a large proportion of the wax esters, contains more energy per unit mass than shorter chained fatty acids and alcohols (Sargent and Henderson 1986). Therefore the carbon fixed by photosynthesis during the Arctic bloom can be transferred as energy rich fatty acids from phytoplankton to top predators within a season (Falk-Petersen et al. 1990). *Calanus* incorporate dietary fatty acids relatively unchanged into their lipid reserves, making it possible to trace lipid energy pathways through the marine food web (Figure 1). The lipids of *Calanus* are relative rich in the essential fatty acids 20:5n3 (eicosapentanoic acid; EPA) and 22:6n3 (docosahexaeonoic acid; DHA) which are exclusively produced by marine algae. These omega 3 (n3) fatty acids are essential for reproduction and growth of all marine organisms (Ackman 1989), and *Calanus* is a key transfer organism of these essential fatty acids from primary producers to higher trophic levels.

As another adaption to the strong seasonality in the Arctic, *Calanus* conduct seasonal vertical migration. *Calanus* descend to greater depths in late summer/autumn where they overwinter as late copepodid stages (CIII-CV) in a state of dormancy. What triggers the entry to and emergency from dormancy is still unknown, but possible cues include: photoperiod, temperature, ambient food concentration, accumulation of energy stores or predator pressure. Rey Rassat et al. (2002) proposed that there is a threshold amount of wax esters that is needed to achieve the energetic requirements associated with dormancy for *C. finmarchics.* This hypothesis is supported by observations of “fat” and “thin” *C. finmarchicus* in deep and surface waters respectively (Hassett 2006). Scott et al. (2000) also suggested that *C. glacialis* will descend to overwintering depth when they have accumulated enough lipids. Recent studies have indicated that not only the amount of lipids, but also the relative amount of PUFAs in the wax ester influence the transition from liquid to solid phase of the wax ester at depth and hence increase their density and therefore influence the diapausing depth of calanoid copepods (Pond and Tarling 2011; Clark et al. 2012). It is therefore likely that the amount of accumulated lipids, and maybe specifically the proportion of PUFAs in the wax esters, affects the timing of descent to overwintering depth for *Calanus*. The timing of the ascent from overwintering depth, relative to the timing of the primary production affects the reproductive success of *Calanus* and hence influences its abundance and availability as prey for larger zooplankton, fish larvae, fish and seabirds. The timing of ascent of *C. glacialis* has been found to be coupled the onset of ice algal bloom (Søreide et al. 2010). The presence of larger predators such as zooplankton and planktivorous fish might represent a driving force on the timing of ascent and descent of *Calanus*. For *C. finmarchicus*, early ascent and spawning reduces the exposure to the migrating Norwegian spring spawning herring (*Clupea harrengus*) in the Norwegian Sea (Kaardtvedt 2000). The predation pressure from herring on large copepodid stages during summer might also represent a driving force for the early descent of *C. finmarchicus* in these areas.



Illustrasjon: Jan Roald 03.2012

Figure 1. Transfer of the main fatty acid trophic markers (FATMs) through a marine Arctic food web

The timing of the reproduction is tightly coupled to their ascent from diapauses. *C. glacialis* has been observed to spawn early in the season when internal lipid reserves (capital breeding) and/or ice algae (income breeding) fuel the maturation of gonads and egg production (Smith 1990; Tourangeau and Runge 1991; Niehoff et al. 2002; Hirche and Kosobokova 2003; Madsen et al. 2008; Søreide et al. 2010). However the peak egg production rate often coincides with high pelagic chlorophyll-*a* concentration later in the season (Tande et al. 1985; Hirche and Bohrer 1987;

Kosobokova 1993; Hirche and Kwasniewski 1997; Kosobokova 1998; Kosobokova 1999; Kosobokova and Hirche 2001; Niehoff et al. 2002; Hirche and Kosobokova 2003). This indicates a long-term spawning potential for *C. glacialis* which can take different turns depending on the environmental conditions. Laboratory experiments have demonstrated that *C. glacialis* females are able to conserve their reproductive capacity for at least 7 months (Hirche 1989), and they are responding rapidly when fed after starvation (Hirche 1989; Madsen et al. 2008). Maximum egg production rates have been observed to last for up to two months when conditions are favourable (Hirche and Kwasniewski 1997). In the White Sea, *C. glacialis* females have been observed to live for a second year after spawning with the potential to spawn twice (Kosobokova 1999). This flexibility in reproductive strategy is most likely a response to the variable environmental conditions encountered, and might be one of the reasons for the success of this species on the Arctic shelves.

The high abundance and energy content of the *Calanus* species makes them a valuable food source for local predators such as larger carnivorous zooplankton (Falk-Petersen et al. 2000a; Falk-Petersen et al. 2001), sympagic amphipods like *Gammarus wilkitzkii* (Scott et al. 2001) and Arctic pelagic fish such as polar cod (*Boreogadus saida*) (Orlova et al. 2009). It is also important food for migrating predators such as the pelagic fish capelin (*Mallotus villosus*) and herring (Bagøien 1999; Kaardtvedt 2000; Orlova et al. 2009) and seabirds feeding on *Calanus* (Karnovsky et al. 2003; Steen et al. 2007). The poleward expansion of pelagic fishes such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) might also increase the predation on *Calanus* in these areas (Renaud et al. 2012). *Calanus* is also indirectly important to migrating seabirds and seals feeding on larger zooplankton and fish that prey on *Calanus* (Nilssen et al. 1998; Haug et al. 2002; Haug et al. 2004). In this thesis I will only discuss the role of *Calanus* for migrating predators such as seabirds and seals. The seasonal vertical movement of *Calanus* up to the surface waters in spring and the rapid accumulation of energy as lipids provide a concentration of energy rich prey in the surface waters in the Arctic during spring and summer. This accumulation of lipid rich prey following the retreat of the ice edge attracts fish, seals, seabirds and whales to travel long distances in order to feed in the Arctic during summer (Sakshaug and Kovacs 2009). The concentration of *Calanus* in the surface waters and the migration of predators facilitate an intense trophic transfer of energy during the Arctic spring and summer (Figure 2). Migrating predators might also transport the energy fixed during the intense productive period in the Arctic to areas further south. One example of such a transport of energy between systems is the huge transport of biomass at a scale of more than $1x10^6$ tons by Norwegian spring spawning herring, which migrates up to the Northern Norwegian Sea and the Barents Sea during summer to prey on the high concentrations of *C. finmarchicus* and returns to the coast for overwintering and spawning (Varpe et al. 2005). Seabirds, seals and whales that migrate to the marginal ice zone during summer will also transport the biomass produced there during the intense production period to areas further south.

The algae-zooplankton interaction forms the basis of the energy flux, and the success at higher trophic level is therefore dependent on synchronization with the pulsed plankton production. The timing of the reproduction and lipid accumulation of *Calanus* may have implication for the amount of energy-rich lipids available to higher trophic levels such as seabirds and seals. The motivation of the present work was to increase the knowledge about these life history traits of *C. glacialis* as one of the key species in the Arctic pelagic food chain, and describe the transfer of energy to higher trophic levels.

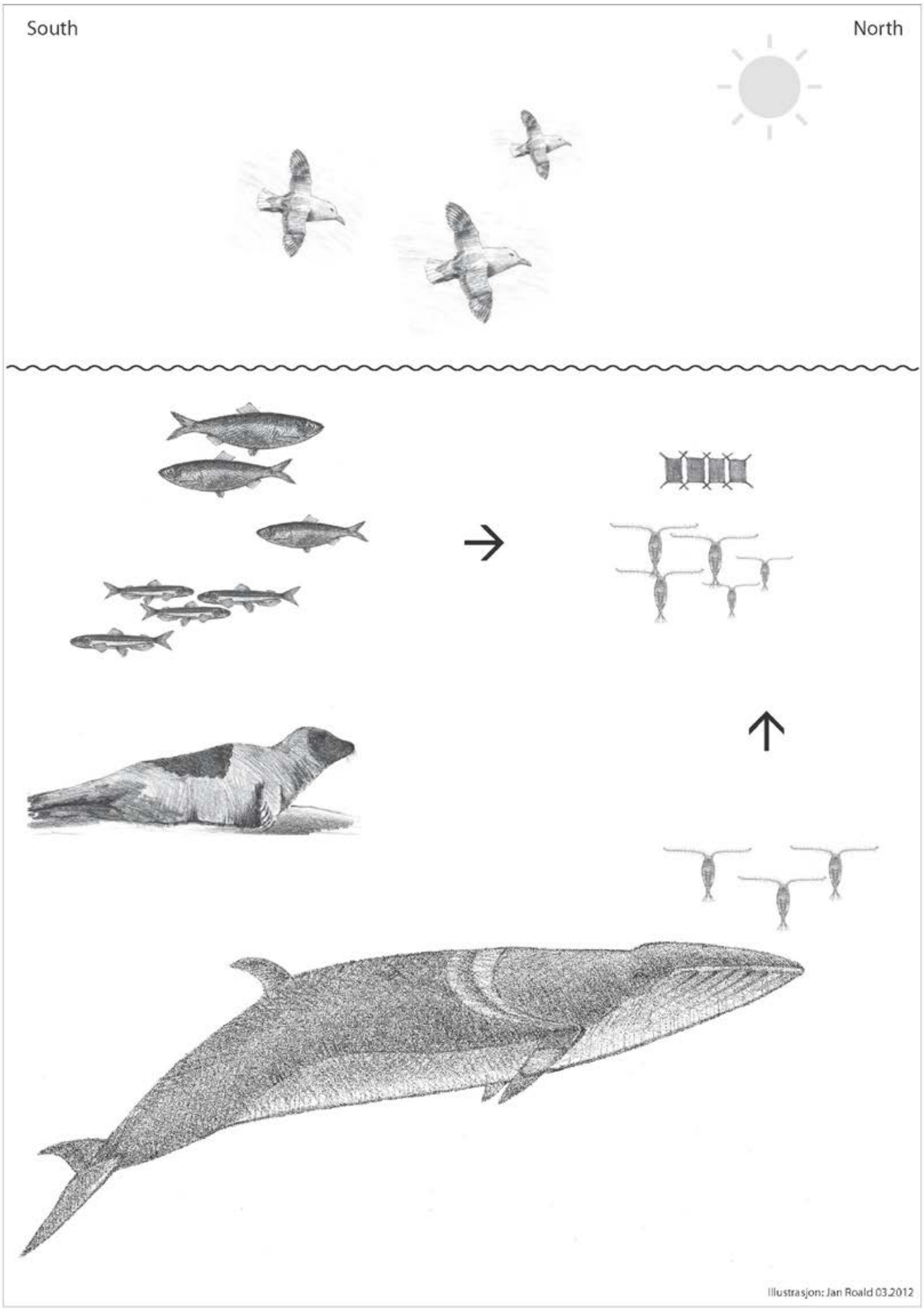


Figure 2. Northward migration of predators and seasonal vertical migration of *Calanus* during Arctic spring and summer

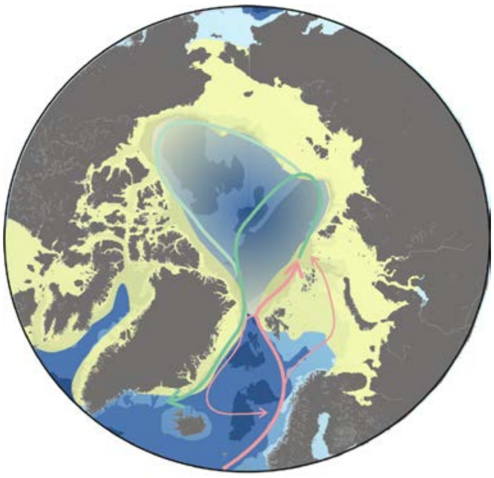
Objectives

The overall aim of this study was to investigate key life history traits of *C. glacialis* such as reproduction and lipid accumulation and the role the lipid accumulation plays for the transfer of energy from primary producers to higher trophic levels in the Arctic food web.

Specific objectives were:

1. To investigate how ice cover and food availability affect life history traits in *C. glacialis*
    a. How does regional and seasonal variability in ice cover and timing of ice algae and phytoplankton blooms affect seasonal vertical migration and overwintering stage? (Papers I and II)
    b. How does variability in timing and extent of ice algal bloom in spring affect reproduction and population development in *C. glacialis*? (Paper I)
2. To determine how fatty acids provided by ice algae and phytoplankton bloom are accumulated by *C. glacialis* (Papers I and III)
3. To evaluate the role lipid accumulation in *C. glacialis* has for the energy transfer to higher trophic levels
    a. How can fatty acid and stable isotope analysis elucidate food sources and trophic levels of seabirds and seals? (Papers IV and V)
    b. Which role does *Calanus* play in the diet of Arctic seabirds and seals? (Papers IV and V)

Box 1 *Calanus glacialis*



Distribution

Calanus glacialis has its main distribution (indicated in yellow) in the relatively shallow Arctic shelf seas, such as the northern Barents Sea, the east and west Greenland shelf, Baffin Bay, the Canadian Archipelago, the northwest coast of North America, the Siberian shelf and the White Sea (Jaschnov 1970; Hirche and Kwasniewski 1997; Kosobokova et al. 1998; Lischka et al. 2001; Head et al. 2003). The distribution is often related to the distribution of cold Arctic or polar waters masses (Daase et al. 2007).

Life cycle

Calanus glacialis is primarily herbivorous and energetic reserves may fuel reproduction and development during early spring (Lee et al. 2006; Falk-Petersen et al. 2009b). However, spawning success seems to depend on additional input from either ice algae or phytoplankton (Niehoff et al. 2002; Søreide et al. 2010). The gonad morphology of *C. glacialis* is preconditioned for exploiting seasonally high food supply allowing frequent spawning and high clutch sizes, which results in high egg production rates (Niehoff 2007). This copepod can spawn as early as March/April and as late as August/September, depending on the sea-ice conditions that largely determine the onset of the algal growth season (Søreide et al. 2010).

Calanus glacialis overwinters at the shelf at 2-400 m depth and has a life-cycle of 1-3 years (Falk-Petersen et al. 2007). It is capable of developing from eggs to wax ester-rich CIII and CIV within a single year (Scott et al. 2000). The increase in body mass and lipid reserves as it develops further from CIV to CV is unlikely to be achieved in a single year, except under favourable conditions. Thus, development from CIV to CV probably occurs in two year-old *C. glacialis.* Under more unfavourable conditions, *C. glacialis* may however develop to CIII in the first year and then to CIV in the second and CV in the third summer. Thus it may take up 3 years to fulfil the life cycle (Tande et al. 1985; Conover et al. 1988; Kosobokova 1999). The large, wax ester-rich CV copepodids overwinter and spawn in their subsequent third- or fourth year. A 1-2 year life- cycle is found in Svalbard fjords (Arnkvaern et al. 2005), in the northern Barents Sea (Slagstad and Tande 1990; Melle and Skjoldal 1998) and in western Greenland (Madsen et al. 2001). In these areas, parts of the population complete the life-cycle in the first year, but a fraction needs a second year for completion. A 1-year cycle is suggested for *C. glacialis* in the Greenland Sea (Smith 1990) and in the Davis Strait (Huntley et al. 1983), and a 2-year cycle in the White Sea (Kosobokova 1999).

Analyses of fatty acids and stable isotopes – potential and limitations

Fatty acid trophic markers

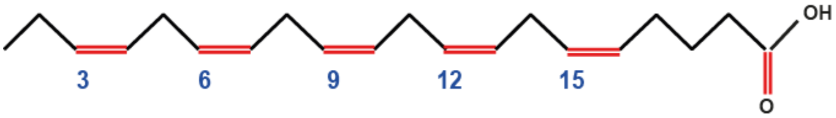
The conservative structure of fatty acids, and for some fatty acids their unique origin have made them a useful tool to study food web structure (Dalsgaard et al. 2003; Iverson et al. 2004; Budge et al. 2006; Iverson 2009). Fatty acids are generally not degraded during digestion, unlike proteins and carbohydrates which are easily broken down. Most biosynthesis of fatty acids occur in primary producers and some herbivorous (e.g. *Calanus*), while organisms at higher trophic levels are generally limited in their capability to synthesize or modify fatty acids. The characteristic fatty acids produced at the bottom of the food chain are called fatty acids trophic markers (FATM) and represent signals that can be incorporated largely unchanged and transferred up the food chain (Dalsgaard et al. 2003). Characteristic FATMs are mainly 16:1n7, 16 PUFAs and EPA from diatoms; 18 PUFAs and DHA from autotrophic dinoflagellates; 18 MUFAs, 18:4n3 and DHA from *Phaeocystis pouchetii*; 16:0, 18:1 and DHA from heterotrophic dinoflagellates and ciliates; while 20:1n9 and 22:1n11 are formed *de novo* by *Calanus* (Table 1, Figure 1). However, the fatty acid composition of phytoplankton also depends on environmental conditions such as temperature, light and nutrients. Fatty acids typical for one group is also present in other groups, but generally in lower amounts. The fatty acid structure is explained in Box 2 and the synthesis of fatty acid in marine algae and calanoid copepods are shown in Box 3. Generally, only plants are able to synthesis (n3 and n6) polyunsaturated fatty acids (PUFA) which are essential constitutes of all heterotrophic organisms (Sargent and Henderson 1986). The relative amount of a FATM in a predator can say something about the base of its food web. Animals have a large capacity to store lipids for short or long term energy demands. Thus ingested fatty acids accumulate in a predator, and analyses of the fatty acids composition can give information about its diet over time.

Table 1. Fatty acid trophic markers (FATM) of phytoplankton (Bacillariophyceae, Dinophyceae and Prymnesiophyceae), bacteria, protozoan, *Calanus*, terrestrial matter and decaying phytoplankton.

Classes	**Typical fatty acids**	**Reference**
Diatoms (Bacillariophyceae)	16:1n7 & 20:5n3 (EPA) 16PUFA	(Dalsgaard et al. 2003) (Mayzaud et al. 1990)
Ice associated diatoms	16:4n1	(Falk-Petersen et al. 1998)
Dinoflagellate (Dinophyceae)	18PUFA (18:4n3 & 18:5n3) 22:6n3 (DHA)	(Reuss and Poulsen 2002) (Dalsgaard et al. 2003)
Prymnesiophyceae (*Phaeocystis pouchetii*)	18 MUFA (18:1n9, 18:1n7) 22:6n3 (DHA) 18:4n3	(Dalsgaard et al. 2003) (Reuss and Poulsen 2002) (Sargent et al. 1985)
Bacteria	Odd & branched chain FA 18:1n7/18:1n9 Iso+anteiso 15:0/16:0	(Budge et al. 2001) (Volkman et al. 1980) (Mancuso et al. 1990)
Protozoan	16:0 & 18:0 18PUFA 22:6n3 (DHA)	(Lund et al. 2008) (Klein Breteler et al. 1999) (Klein Breteler et al. 2004)
Calanus	C20 & C22 MUFA/MUFA-OH	(Sargent and Henderson 1986)
Terrestrial matter	18:2n6 18:2n6+18:3n3	(Napolitano et al. 1997) (Budge et al. 2001)
Decaying phytoplankton	Phytol (fatty alcohol)	(Falk-Petersen et al. 2000a)

Box 2 Fatty acid structure

Fatty acids are composed of a chain of carbon atoms with associated hydrogen atoms, most commonly in even-numbered chains of 14-24 C-atoms. The chains can have 0-6 double bonds with a terminal methyl ($-CH_3$) and terminal carboxyl (-COOH) unit. Fatty acids are named by their carbon number: number of double bonds and location of double bond nearest the terminal methyl group (nx). All other double bond are separated with one single methylene ($-CH_2$) group in between. For example, the polyunsaturated fatty acid 20:5n3 (EPA) has the 5 double bonds with the first double bound at the 3rd C-atom after the methyl group.



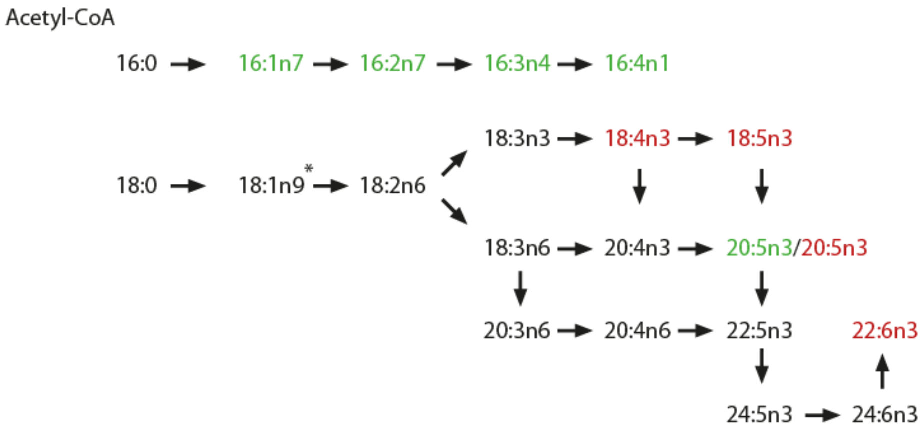
Saturated fatty acid (SAFA) = fatty acid without any double bonds
Monounsaturated fatty acid (MUFA) = fatty acid with one double bond
Polyunsaturated fatty acid (PUFA) = fatty acid with two or more double bond

The turnover rate of individual fatty acids can be species-specific and are often linked to the metabolic condition and reproductive status of the organism (Dalsgaard et al. 2003; Graeve et al. 2005). Feeding experiments with ^{13}C labelled diatom culture have shown incorporation of fatty acids within a week for copepods (Graeve et al. 2005). These experiments also showed that the sum of fatty acids and fatty alcohols biosynthesized *de novo* in copepods were similar to the corresponding fatty acids of the algae except for polyunsaturated fatty acids EPA and DHA, which were higher in copepods than in algae and therefore most likely selectively retained. The similarity of fatty acid and fatty alcohol composition between copepods and algae in this experiment supports that the non-algal fatty acids and alcohols, such as 20:1 and 22:1, are probably synthesized from non-lipid material such as proteins and carbohydrates (Graeve et al. 2005). Since the fatty acids are selectively incorporated or utilized for metabolic and reproductive purposes, the method of using FATM for tracing the food source is most relevant during the feeding period when animals are building up their lipid reserves. At higher trophic levels, we expect the whole-body fatty acid signature of fish to turn over in about 3 weeks (Kirsch et al. 1998). For seals, whales and birds, the turnover time is less certain, but a feeding study with captured harp seals showed that the fatty acids of the diet was apparent in the seals within 1-2 weeks. In general it is accepted that blubber fatty acid can reflect a dietary shift in as little as a month (Budge et al. 2008). The fatty acid composition of a predator lipid store has three metabolic sources: (1) unmodified dietary fatty acids that are directly deposited, (2) dietary fatty acids that are modified, and (3) fatty acids deriving from *de novo* synthesis in the animal. Fatty acids are usually esterified to backbone molecules forming lipids such as triacylglycerol, wax ester and polar lipids (Box 4). Fatty acids are released from their esterified lipid during digestion and modification of fatty acids can be done by elongation (adding 2 carbon units) and desaturation (adding double bonds), but are restricted to saturated fatty acids (SAFA) and monounsaturated fatty acids (MUFA) (Cook 1991). These modifications typically only occur when the animal is consuming a low-fat diet, which is seldom the case in the Arctic. In marine mammals and seabirds unmodified fatty acids are therefore the largest contributor to the lipid stores, but there will always be a small portion fatty acids derived from modification and de *novo* synthesis. Therefore the predator fatty acid composition will never exactly match that of the prey (Budge et al. 2006). The method is also limited in assessing the exact prey if diverse prey with similar fatty acid profiles are eaten, which is often the case. Nevertheless, it will provide some information about the base of the food web of the predator and give information about the diet over time. The method will supplements traditional methods such as stomach and gular pouch analyses or direct observations that are restricted to the hatching and breeding season.

Box 3 Fatty acid synthesis in marine algae and calanoid copepods

Marine algae

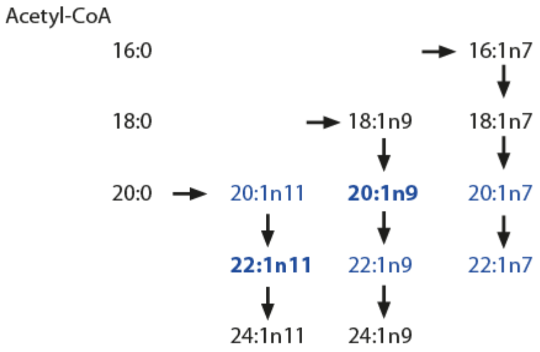
Fatty acids are biosynthesized in the chloroplasts of plants which are the main providers of (n3 and n6) PUFAs, even though some protists and invertebrates also are able to do so. Oleic acid (18:1n9) is the precursor of all n3 and n6 PUFAs. Primary producers possess enzymes, which enable them to insert double-bindings forming 18:2n6 and then 18:3n3 or 18:3n6. The fatty acid 18:3n6 may be converted further to 20:4n6 (AA), 20:5n3 (EPA) and 22:6n3 (DHA). DHA can also be produced via C24 PUFA intermediates. These pathways are typical for dinoflagellates, which often have high levels of 18:4n3, 18:5n3, EPA and DHA. An alternative pathway is the desaturation of 16:0 to 16:1n7 and further desaturation to C16 PUFA, with 16:4n1 constituting the final desaturation product. This biosynthetic pathway is characteristic of diatoms, in which 16:1n7 and C16 PUFA are major fatty acids together with EPA. Fatty acids are mainly esterified to glycolipids constituting the membranes of the cells, whereas polar lipid and triacylglycerol are minor components. Glycolipids are particularly rich in n3 PUFAs while triacylglycerol generally has higher levels of SAFA and MUFA. The fatty acid composition is both species-specific and influenced by environmental conditions such as temperature, light and nutrients. Lower water temperatures result in an increase in the level of unsaturation (increased PUFAs). The impact of light is more ambiguous and more species specific. High levels of nutrients support exponential growth where carbon is allocated into growth and cell division and not lipid storage (triacylglycerol). Hence the phytoplankton has high proportion of glycolipids (PUFAs) during this phase.



* Oleic acid = precursor of all n3 and n6 PUFAs
Bacillariophyceae (diatoms)
Dinophyceae (dinoflagellates) and Prymnesiophyceae (*Phaeochystis pouchetii*)

Calanoid copepods

The *de novo* syntheses of long-chained MUFA are typically for Calanoid copepods like *Calanus*. The fatty acid 16:0 is the precursor for the n7-fatty acids, 18:0 for the n9-fatty acids and 20:0 for the n11-fatty acids. The fatty acids 20:1n9 and 22:1n11 constitute the largest fraction of these long-chained MUFAs in *Calanus*. A considerable amount of the 20:1 and 22:1 MUFAs are also reduced to alcohols during the formation of wax ester.



Modified after Dalsgaard et al. 2003

In our present work we have used fatty acids qualitatively to examine differences in the fatty acids composition of different seabird species (Paper IV) and seal species (Paper V) by use of multivariate methods such as principal component analysis (PCA) and correspondence analysis (CA). The interpretation of the results has focused on the FATM in order to distinguish certain food sources. Because marine lipids include many fatty acids (30-40), multivariate statistical methods are most suitable to cover the information in the data. However, bivariate techniques are also useful to inspect differences between specific fatty acids. Multivariate techniques have been used to examine trophic interactions and spatial and temporal differences among species or groups of animals in several studies (Iverson et al. 1997; Falk-Petersen et al. 2000a; Scott et al. 2000; Dahl et al. 2003; Mayzaud et al. 2003). A limitation with this method is that fatty acids originating from primary producers become more ubiquitous as the trophic level increases and it becomes increasingly complicated to trace FATM as more trophic levels that are involved. In a seabird species like Black-legged kittiwake, preying on both zooplankton and fish, one cannot distinguish whether high levels of 20:1n9 and 22:1n11 are due to high input of *Calanus* or fish that have been eating *Calanus*. Despite these limitations, quantitative fatty acid analysis is a useful method to detect dietary differences and trophic interactions, and has recently been used in several studies of seabirds (Dahl et al. 2003; Iverson et al. 2007; Käkelä et al. 2007; Karnovsky et al. 2008; Wang et al. 2009) and seals (Kirsch et al. 2000; Falk-Petersen et al. 2004; Tucker et al. 2009a). By combining FATM, stomach content analysis and knowledge about the ecology of the animals, one can determine what the important food source for predators is over time.

It is possible to estimate the proportion of diet items in a consumer's diet by using consumer fatty acid composition together with a comprehensive database of the fatty acid signature of potential prey species and accounting for consumer's fatty acid metabolism. This method is referred to as quantitative fatty acid signatures analysis (QFASA), and uses a statistical model to compute the combination of prey fatty acid signatures with the best match with fatty acid profile of the predator, after accounting for predator's fatty acid metabolism (Iverson et al. 2004). The method requires a comprehensive database of the fatty acid composition of all prey species and controlled feeding experiments should be conducted in order to account for the lipid metabolism of the predator. The QFASA has been used in studies of seabirds (Iverson et al. 2004; Iverson et al. 2007; Williams et al. 2009; Käkelä et al. 2010; Wang et al. 2010), seals (Nordstrom et al. 2008; Tucker et al. 2009a) and polar bears (Thiemann et al. 2009), but in this study we have used fatty acids qualitatively to examine differences in fatty acids composition of different seabird species as described above.

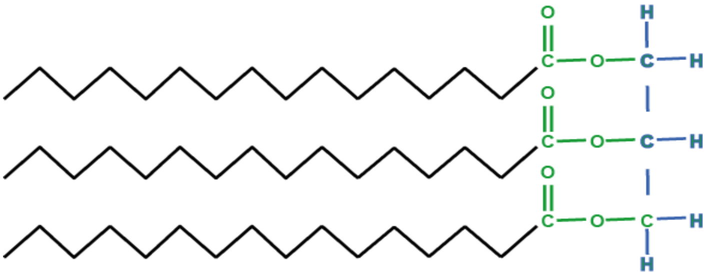
Methods used in present studies

Fatty acids were analysed of whole individuals of *C. glacialis*, of muscle of the seabirds and of the inner blubber of the seals. The inner blubber of seals was used since this is metabolically active tissue and reflects the recent diet (Best et al. 2003; Olsen and Grahl-Nielsen 2003). The lipid analyses were done at UNILAB Analyse, Tromsø. In addition one set of the samples in Paper I was analyzed at Alfred Wegner Institute (AWI), Bremerhaven. The methods used differ slightly, but in general the procedure was as follows. The total lipid was extracted in chloroform: methanol following the method of Folch (1957). Each sample was supplemented with a known amount of the fatty acid 21:0 as internal standard except for Paper I where 23:0 or no internal standard was used, and an acid-catalyzed transesterification was carried out. For *C. glacialis* (Paper I and III) the fatty acid and fatty alcohol composition were analysed for neutral lipids and polar lipids separately while for seals and seabird diet (Paper IV and V) the analyses were done on the total lipid. Fatty acid methyl esters and free alcohols were analysed by gas chromatography. The fatty acids were identified and quantified using a ChemStation software package (Agilent) and results were given as percentages. Details of the methods can be found in Papers I, III, IV and V.

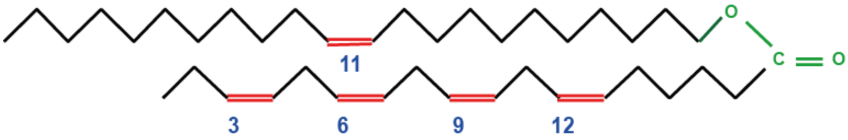
Box 4 Lipid classes

Fatty acids seldom exist in free form and are usually esterified to a backbone molecule. Any lipid containing an esterified fatty acid is called an acyl lipid. Triacylglycerols represent a common storage lipid and make up the majority of lipid in adipose tissue of fish, blubber of seabirds and mammals. Wax ester is another important storage lipid in marine organism, and consists of a fatty acid esterified to a fatty alcohol instead of to a glycerol molecule. Wax ester is important for some species, e.g. *Calanus* which store almost all their energy as was ester (Sargent 1976) and some fish such *Benthosema glaciale* (Falk-Petersen et al. 1986a) and *Lumpenus maculates* (Falk-Petersen et al. 1986b). Another common acyl unit is the phospholipid, which consists of two fatty acids esterified to a glycerol molecule that also contains a polar derivative. Polar lipids are structural components of all cell membranes and have specialized functions. Polar lipid is relatively robust to dietary changes and not a good indicator of diet. The esterified fatty acid of triacylglycerol and polar lipid are hydrolyzed during digestion in seabirds and mammals and then re-esterified during deposition into adipose tissue or blubber. A slightly more complicated process occurs for prey containing wax ester. When a wax ester is metabolized, it is first hydrolyzed to fatty acid and fatty alcohol. Enzymes oxidize the fatty alcohol to corresponding fatty acid. The fatty acids are then esterified into triacylglycerol, which is deposited. Therefore, a predator will store fatty acids as triacylglycerol even if it consumes a diet high in wax ester. The opposite occurs in animals that are able to store energy as wax ester. A fatty acid consumed is reduced to the corresponding fatty alcohol, which is then incorporated into wax ester for storage.

Triacylglycerol



Wax ester



Stable isotopes

Similar to the fatty acid analysis, the stable isotope composition of a consumer provides information of the food assimilated over time and is therefore less dependent on short-term variation in feeding. The naturally occurring stable isotopes ratios of carbon ($\delta^{13}C={}^{13}C/{}^{12}C$) and nitrogen ($\delta\ {}^{15}N={}^{15}N/{}^{14}N$) of living organisms provide a time-integrated measure of the organism's trophic position and have the potential to track energy flows through the food webs (Hobson and Welch 1992; Hobson et al. 1995; Post 2002; Petursdottir et al. 2008). A consumer is typically enriched in ^{15}N by 3-4‰ relative to its diet, while ^{13}C undergoes relatively little fractionation (<1‰) with trophic level (TL) (Minagawa and Wada 1984; Peterson and Fry 1987; Hobson and Welch 1992). The $\delta^{15}N$ values are therefore a tool for determining TLs, while $\delta^{13}C$ provides information about the carbon source of the organism if the available carbon sources have distinct $\delta^{13}C$ values (Post 2002). Large ranges in $\delta\ {}^{13}C$ values for both Ice- pelagic organic matter (POM) and pelagic-POM have been reported, but generally ice- POM is 2-10 ‰ more enriched than pelagic-POM (Hobson et al. 1995; Søreide et al. 2006a; Tamelander et al. 2006). The variation in $\delta\ {}^{13}C$ can be related to poorly representative POM for autotrophic biomass (Søreide et al. 2006a), but there will always be a variation also in "pure" autotrophic biomass due to difference in nutrient sources (new vs. regenerative), concentration and uptake growth rates (Tamelander et al. 2009). In our studies we have used the $\delta^{15}N$ values to calculate TL and $\delta^{13}C$ to track the carbon source of ice- POM vs. pelagic-POM. The TL of a consumer organism is calculated as the difference between the $\delta^{15}N$ of a consumer and of the food web baseline assuming a constant fractionation factor between TLs according to the following equation:

$$TL = \alpha + \frac{\delta^{15}N_{consumer}/\delta^{15}N_{base}}{\Delta N} \qquad \text{Equation 1}$$

$$\propto = trophic\ level\ and\ \Delta N = trophic\ enrichment\ factor$$

The use of this equation has two critical assumptions that are connected: the use of correct baseline value ($\delta^{15}N_{base}$) and correct trophic enrichment factor (ΔN). Problems with separating live autotrophic phytoplankton from detritus and heterotrophic microplankton limit the possibility to obtain a pure sample at the first trophic level, and often samples of particulate organic matter (POM) represent the first TL. The trophic enrichment factor ΔN, is an estimate of the averaged increase in $\delta^{15}N$ per trophic level. Vander Zanden and Rasmussen (2001) suggest that ΔN is more variable for primary producers than for primary consumers. Therefore using primary consumers ($\lambda=2$) instead of primary producers ($\lambda=1$) reduces the error in estimation. Another challenge using $\delta^{15}N$ to calculate TL is the uncertainty about the time needed for the isotope composition of a consumer tissue to reach equilibrium with that of the diet (i.e., turnover time) (O'Reilly et al. 2002).

Although stable isotopes are widely used in marine ecology, no common technique for sample preparation has been agreed upon. This complicates meta-analyses of results from studies using different sample preparation methods. Since the amount of lipids vary largely in Arctic herbivorous zooplankton (Kattner and Hagen 2009) and lipids are depleted in ^{13}C compared to proteins and carbohydrates (van Dongen et al. 2002), the lipids cause a variation in $\delta^{13}C$ values, especially in animals with high lipid content such as Arctic zooplankton. In some studies, lipids have been extracted prior to analysis in order to minimize the variation. Several different lipid extraction methods have been used, and a comparison of the different methods has been done by (Søreide et al. 2006b). This study concluded that in general there was little variation in $\delta^{13}C$ between samples using different extraction method, except for in animals that were rich in lipids.

The model used to calculate TL assumes that all nitrogen assimilated by a consumer is derived from the same source, which is a simplification since consumers have access to several sources of nitrogen. If primary producers are used as a baseline a two-source mixing model can be used as a better approximation (Post 2002; Søreide et al. 2006a). Despite these uncertainties, stable isotope models have been widely used to study the trophic interactions of marine food webs in the Canadian Arctic (Hobson and Welch 1992), the Beaufort Sea (Iken et al. 2005), North Open Water Polynya (Hobson et al. 2002) and the northern Barents Sea and Greenland Sea (Hop et al. 2002a; Søreide et al. 2006a; Tamelander et al. 2006), and have provided useful information about trophic interactions in these systems.

Methods used in present studies

The ratios between heavy and light isotopes (13C/12C or 15N/14N) were measured by Micromass Optima, Isotope Ratio Mass Spectrometer at Institute for Energy Technology (IFE), Kjeller, Norway. Stable isotope abundances are expressed as the deviation from standards in part per thousands (‰) according to the following equation:

$$\delta X = \left[\left(R_{sample}/R_{standard}\right)\right] \times 1000 \qquad \text{Equation 2}$$

$X = {}^{13}C$ or ${}^{15}N$ and R = corresponding ratio ${}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$

Standards for ^{13}C and ^{15}N are calibrated against PeeDee Belemnite (Vienna) and atmospheric nitrogen respectively (IAEA-N-1 and IAEA-N-2). The samples were prepared according to the method described by Søreide (2006b), with removal of lipids and carbonates in order to reduce sample variability. The TL of a consumer organism was calculated according to equation 1. We used the trophic enrichment factor ΔN=3.4‰ determined for the European Arctic (Søreide et al. 2006a), and *Calanus* representing primary consumers (TL=2) was used as the baseline. A mean δ^{15}N = 8.5‰ of all three *Calanus* species for all seasons combined (Søreide et al. 2006a) was used in the seal study (Paper IV), while a mean δ^{15}N=6.7‰ for all three *Calanus* species from Kongsfjorden in spring/summer was used in the seabird study (Paper V).

Study areas

The study areas included the southern Beaufort Sea, Kongsfjorden, and different locations in the Fram Strait (Figure 1). The *Calanus* data originates from the Amundsen Gulf and Franklin Bay in the southern Beaufort Sea in the Canadian Arctic (Paper I) and from the north and west coast of Svalbard (Paper II and III). The seabirds (Paper IV) were collected in Kongsfjorden at the west coast of Svalbard, while the seals (Paper V) were sampled in the open drift ice along the east coast of Greenland from the Fram Strait to the Denmark Strait north west of Iceland. The sampling locations are all north of the Arctic Circle and have strong seasonality in incident solar radiation with 2-4 month of midnight sun and 2-4 months of polar night (Figure 3).

The Amundsen Gulf bridges the Beaufort Sea to the Canadian Arctic Archipelago. The waters of the region typically comprise the Polar Mixed Layer (salinity<31.6; 0-50m the Pacific halocline (salinity of 32.4-33.1; 50-200m) and the Atlantic water mass layer (salinity >34;>200m) (Carmack and MacDonald 2002). Along the inner shelf region, seasonal sea ice begins to form in October and ice normally consolidates in December. In early April, a land fast ice bridge typically forms south of the Banks Island and up to the continent. In May-June, breakup begins and the polynya enlarges to form the Cape Bathurst polynya complex at the entrance of Amundsen Gulf. Satellite data indicate large inter-annual variability in the extent and persistence of open water regions (Arrigo and van Dijken 2004). Land fast ice might not consolidate every year and the ice cover can remain mobile throughout the winter, promoting a more rapid ice breakup during spring. Franklin Bay is a shallow Bay (<250m) south of the Amundsen Gulf that experience long ice cover and is usually not ice-free before mid July.

The Svalbard area is influenced by the inflow of warm Atlantic water from south and the flow of cold Arctic water and drift ice from the north east (Falk-Petersen et al. 2000b; Rudels et al. 2004). The West Spitsbergen Current (WSC) which is the main flow of Atlantic water into the Arctic Ocean runs along the west coast of Svalbard and the transport Atlantic water and heat which shapes local conditions (Walczowski and Piechura 2011). There is a high inter-annual variability in the strength of the WSC and the inflow of Atlantic water into the Arctic (Saloranta and Haugan 2001), with progressive warming of the WSC since 2004. The temperature and salinity at the core of Atlantic Water reached the highest observed values in 2006 (Walczowski and Piechura 2007). In addition, Svalbard waters are often modified by local oceanographic processes (e.g. freshwater run-off, wind driven circulation and cooling). Kongsfjorden is located at the western coast of Svalbard and is influenced both by inflow of Atlantic water from WSC and of Arctic water from the coastal current (Hop et al. 2002b; Svendsen et al. 2002), and there is a high inter-annual variation in the inflow of Atlantic water (Svendsen et al. 2002; Cottier et al. 2005). Kongsfjorden used to have fast-ice cover in winter, but a large inflow of Atlantic water during winter 2005-06 (Cottier et al. 2007) switched the system into a warmer state without almost any fast-ice cover during the following four winters. However, in the winter of 2011 fast-ice again covered the fjord for 3 months.

The East Greenland Current, which originates in the Arctic Ocean and flows south along the east coast of Greenland brings cold, low salinity water to the area of the Greenland Sea north of Iceland (Bourke et al. 1988). These ice covered areas are referred to as West Ice, and represent an important area for hooded and harp seals during breeding and moulting season (Haug et al. 2007).

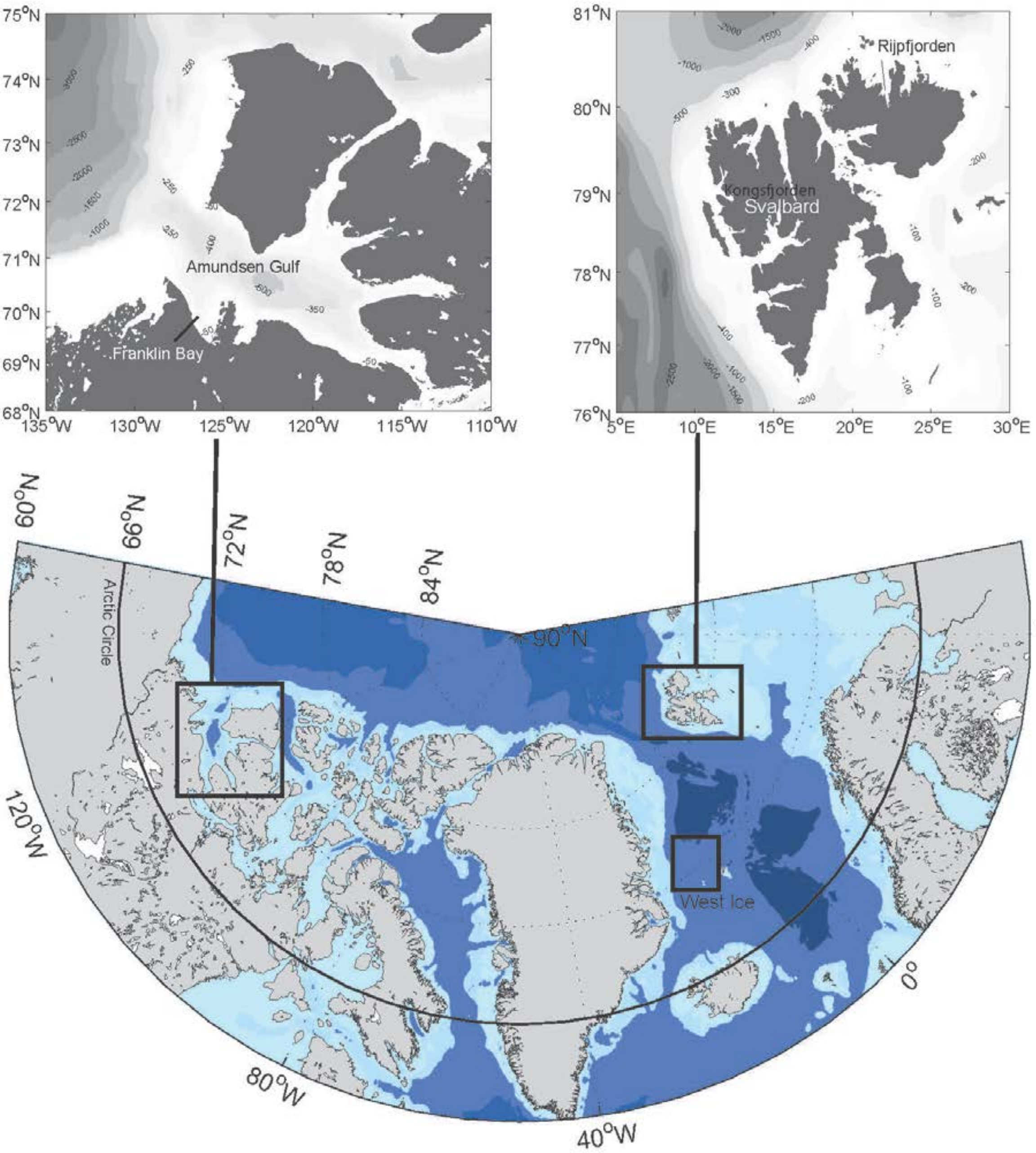


Figure 3. Study areas: Amundsen Gulf, Franklin Bay, Kongsfjorden and West Ice.

Sampling strategy

Calanus glacialis

Data covering an entire year or even just the entire reproduction period of *C. glacialis* is scarce (Kosobokova 1999; Madsen et al. 2001; Søreide et al. 2010), since the field season in the Arctic is usually restricted to the more accessible summer season. Paper I was part of a large interdisciplinary study, the Circumpolar Flaw Lead Study (CFL) that involved the overwintering of CCGS *Amundsen* in the Beaufort Sea, enabling a long sampling period (January – July) with the core sampling during March and April. The aim of overwintering with the CCGS *Amundsen* was to freeze-in in the flaw lead (polynya) for the winter, which would enable repeated sampling at one location. Due to unusual ice conditions during the winter 2008, with moving ice and open leads (Barber et al. 2010), the ship had to relocate several times, resulting in a wider sampling area than initially planned. Nevertheless, the sampling sites were within the area described as polynya assemblage zooplankton (Darnis et al. 2008). In Paper II, six stations at the north west of Svalbard were used in order to investigate the effect of different ice cover, water masses and state of the primary production on the vertical migration of *Calanus*. Rjipfjorden (RF) and ice station (ICE) were "bloom" stations with pronounced fluorescence maxima at approximately 30 m depth. The shelf station (SH) was ice-free and had a pronounced fluorescence at 30 m. Marginal Ice Zone (MIZ) and Shelf break (SHB) stations were sampled in leads and broken ice cover and the fluorescence also peaked around 30 m depth, but was weaker than at RF, ICE and SH. In contrast, Kongsfjorden (KF) had a more late-season condition with the pelagic phytoplankton bloom having culminated 2-3 months prior to sampling. The Amundsen Gulf represents an open shelf system as does the shelf area north of Svalbard, Kongsfjorden is an open fjord system, while Rjipfjorden is a relative closed system.

Seabirds

Seabirds are an integral part of the food web of Kongsfjorden. Due to their role as predators; they can be important indicators of changes at lower trophic levels (Barrett et al. 2007; Iverson et al. 2007). Therefore, a comprehensive coverage of the diet of the main seabird species in Kongsfjorden reveals important information for understanding the local ecosystem. This is a follow-up study of the publications by Dahl et al. (2003) and Jæger et al. (2009), which partly investigated the diets and trophic levels of seabirds breeding in the Kongsfjorden area. The following species have been investigated: Little auk (*Alle alle*), Brünnich's guillemot (Uria lomvia), Black-legged kittiwake (*Rissa tridactyla*), Northern fulmar (*Fulmarus glacialis*) and Glaucous gull (*Larus hyperboreus*).

Seals

Harp seal (*Phoca groenlandica*) and hooded seal (*Cystophora cristata*) co-occur in the drift ice waters of the Greenland Sea during breeding and moulting in March–June (Sergeant 1991; Folkow et al. 1996; Haug et al. 2000; Potelov et al. 2000). Information from satellite tagging indicate that they might co-occur in the Greenland Sea pack ice also outside the breeding and moulting period (Folkow et al. 1996; Folkow et al. 2004). This was further confirmed during the research surveys in September-October 1999 and February-March 2001. The aim of these research cruises was to assess the feeding habits of harp and hooded seals in the Greenland sea during the period July-February, i.e. outside the breeding season, which is an intense feeding period (Kovacs and Lavigne 1986; Nilssen et al. 2000).

Results and discussion

Seasonal vertical migration and overwintering stage

The timing of the ascent during spring, the match of reproduction with the primary production as well as the length of the primary production period will determine how far the offspring will develop during the season, and what will be the overwintering stage the following winter, and hence the length of the life cycle. The shorter the period of primary production, the more important is the match between reproduction and bloom, while a longer period of primary production will allow for development also if part of the reproduction did not match the peak spring bloom. A two year life-cycle will minimise the risk from predation an individual will experience before contributing to the next generation, but cause greater pressure to achieve sufficient energy reserve to fuel overwintering and egg production the following spring. A three year life-cycle will allow individuals more time to accumulate energy reserves, but increase the predation pressure and reduce the likelihood to survive and reproduce. In a variable environment with a short productive season, a short life cycle may result in large inter-annual variations, as the population might boom in good years and crash in bad years. A longer life cycle will give the population an increased ability to withstand bad years even though the overall production of the population is lower.

Seasonal vertical migration is a strategy that allows the copepods to exploit favorable conditions in surface water during spring and summer, and minimize the exposure to predators by descending to deep waters during the unproductive period. In the deep waters they enter a state of dormancy, characterized by reduced metabolism and arrested development rates (Hirche 1996). I refer to this state of dormancy as “diapauses”, which is considered to be a physiological state of dormancy, even though it is not sure that all individuals enter the same level of diapausing state. The timing of emerging from diapause and ascending to surface waters, relative to the timing of bloom periods in the spring, is critical for the population dynamics of *C. glacialis*. In the Amundsen Gulf the first pulse of primary production was the ice algal bloom starting in early April, which was succeeded by the pelagic phytoplankton bloom starting in early May as the ice broke up. June was a phase of relatively low productivity, but a coastal upwelling event in July transported nutrient-rich deep waters resulting in a sudden burst in the subsurface chlorophyll (Forest et al. 2011; Tremblay et al. 2011). The phytoplankton blooming during those events appears to have been primarily composed of large diatoms (Ardyna et al. 2011; Terrado et al. 2011). *C. glacialis* started to ascend to the surface waters by the end of March, and by the end of April, during the peak of the ice algal bloom, the main part of the population was in the surface waters (Figure 5 in Paper I). During summer (May-July) *C. glacialis* was located in the upper 50 m, and in the beginning of August they had descended to deeper waters. Our result is in accordance with previous work showing that the *Calanus* ascent to the surface prior to the onset of ice algal or pelagic phytoplankton bloom (Søreide et al. 2010). *C. glacialis* overwintered mainly as CIII and CIV in 2007-08 (Figure 4). This could indicate that environmental conditions did not allow for part of the population to develop further than CIII in the first year, and a two-three year life cycle might be common in this area. However, the previous year (2007) was a special year in the Amundsen Gulf with regard to the record low ice cover (NSIDC 2011), and a large-scale upwelling event resulted in a massive phytoplankton bloom late in the season (Tremblay et al. 2006; Mundy et al. 2009). These conditions might have resulted in a longer growth season for *C. glacialis* in 2007, enabling CIV to develop to females that spawned late in the season (July) instead of overwintering as CIV and CV. The recruits of such an additional reproduction period late in the season of 2007 would barely have had the time to develop beyond CIII before diapause, which could explain the high proportion of CIII in the overwintering population 2007-2008.

In the study from Svalbard waters (Paper III), the depth distributions of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* were compared between six stations with different ice cover and bloom scenarios, but here I will focus on the depth distribution of *C. glacialis*. At the bloom stations (RF and ICE), the ice cover had just recently broke up, and young (CI-III) *Calanus* stages were present in the upper 50 m, indicating that they were actively feeding (Figure 5). In contrast, at the late season station (KF), which had not been ice covered and most likely had an early pelagic phytoplankton bloom, *C. glacialis* showed a bimodal depth distribution with CIV and CV at the bottom, while smaller stages as well as CV remained in the surface waters, most likely feeding on the “autumn” phytoplankton bloom (Figure 5).

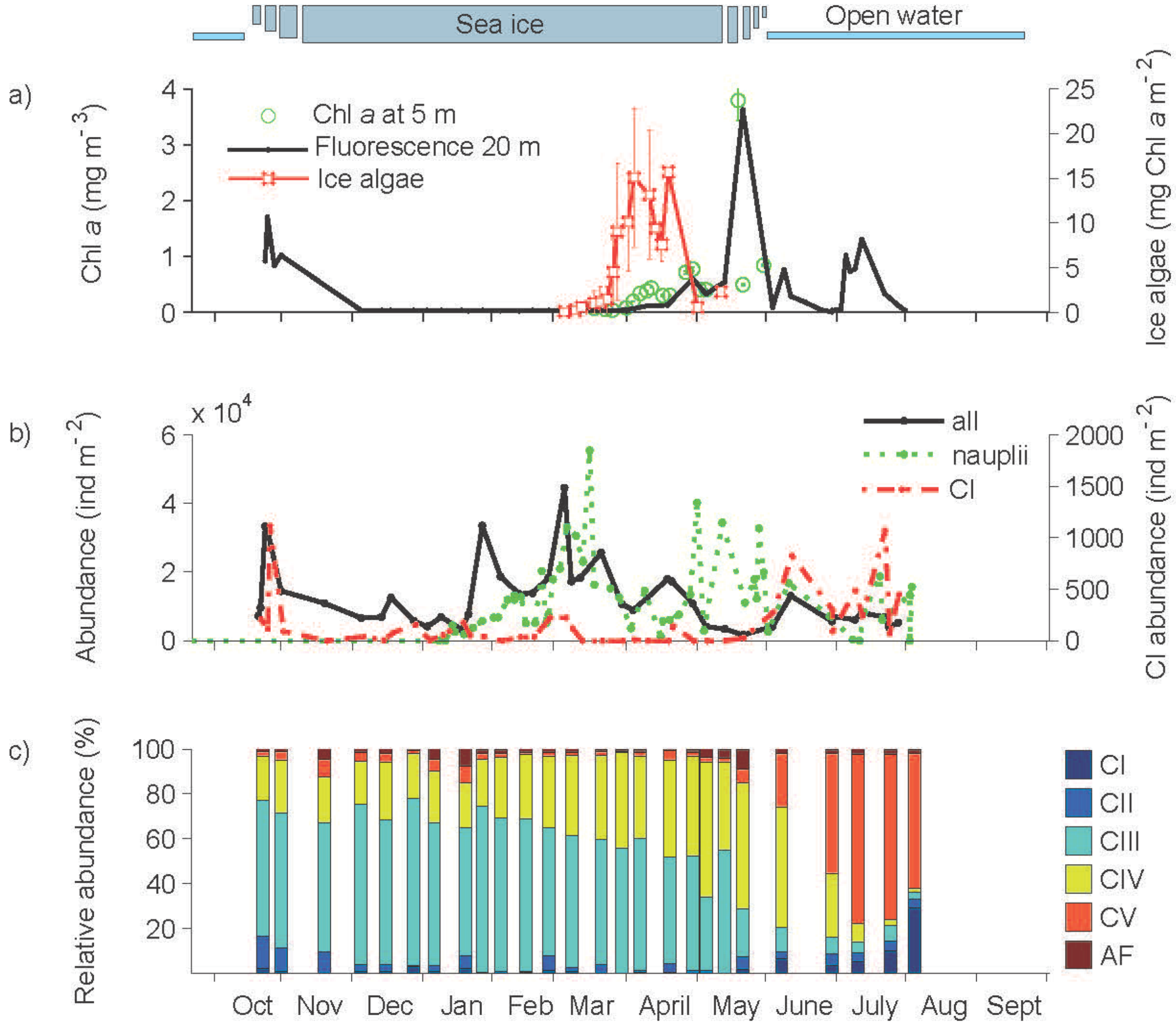


Figure 4. Time series of a) phytoplankton and ice algae chlorophyll-*a* concentration; b) abundance of *Calanus* nauplii, copepodid stage CI and total population of *C. glacialis*; c) stage composition of *C. glacialis* in the Amundsen Gulf in 2007-2008. Note that the first peak of *Calanus* nauplii prior to the ice algal bloom is *C. hyperboreus* nauplii. The figure is modified after Wold et al. 2011 (Paper I).

This bimodal distribution could be due to the fact that the “fat” CIV and CV that had filled up their lipid reserves earlier in the season had already descended to overwintering depth, while the “thin” copepodids were still actively feeding in the surface waters building up their lipid reserves. This could indicate that it is the amount of wax ester (storage lipids)that triggers the descent to diapause (Rey-Rassat et al. 2002; Hassett 2006). Our results indicate that CV and CIV were the main overwintering stages in Kongsfjorden, and that *C. glacialis* fulfilled its lifecycle within 1-2 years, with a large part of the population developing to CV already during the first year, which is in agreement with Scott et al. (2000) and Kwasniewski et al. (2003). Studies from other areas also concluded that CIV and CV were the main overwintering stages for *C. glacialis*, indicating a 1-2 year life cycle as seen in the Barents Sea (Melle and Skjoldal 1998; Hirche and Kosobokova 2011), Svalbard fjords (Arnkvaern et al. 2005; Walkusz et al. 2009; Søreide et al. 2010) and Disco Bay, West Greenland (Madsen et al. 2001).

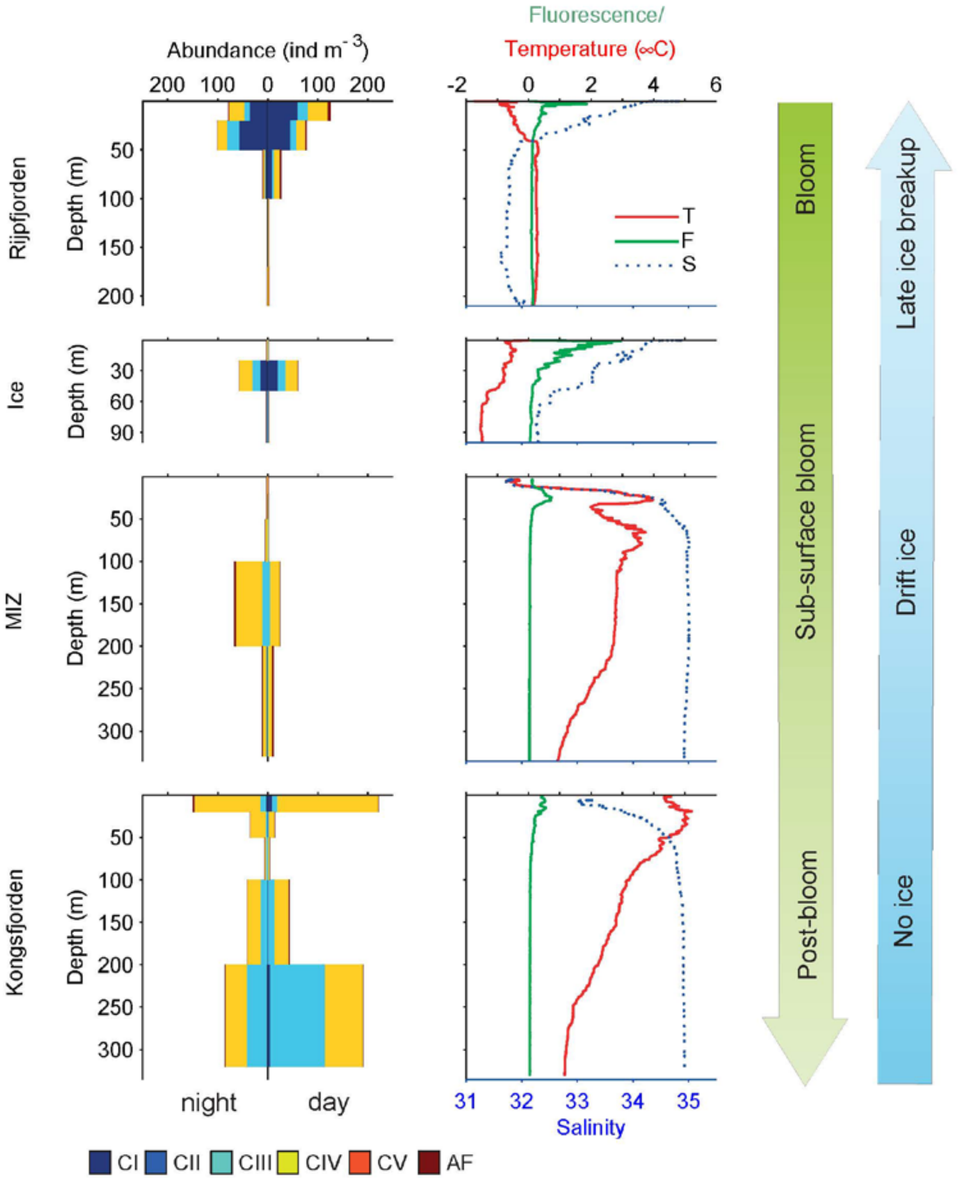


Figure 5. Depth distribution of *Calanus glacialis* at stations with different ice scenarios and bloom situations in Svalbard waters in August. The figure is modified after Rabindranath et al. 2011 (Paper II).

Reproduction and population development

Timing of the reproduction is one life history trait of crucial importance for the success of *Calanus* population, and subsequently it can affect the production of the entire *Calanus*-dominated pelagic food web. In Amundsen Gulf (Paper I), *C. glacialis* started to spawn at the peak of the ice algal bloom. However, since CIII-IV were the main overwintering stages in 2007-08, the energy from ice algae was likely more important for the development of CIII and CIV, than for reproduction that year. There was a small increase in the abundance of CI in beginning of June (Figure 4), which was likely offspring from eggs spawned in April during the ice algal bloom, assuming the development time from eggs to CI to be approx. 50 days (Daase et al. 2011). Then there was a second and larger peak in abundance of CI in beginning of July, suggesting that the main spawning for the *C. glacialis* population occurred in May during the pelagic bloom (Figure 4). This may indicate a delayed development, where only part of the population manages to spawn in spring, while the rest of the overwintering population starts to spawn later in summer. Alternatively spawning early in the season may be done by those CV that had overwintered and developed into females during early spring, while the other spawning event in late summer was due to CIII and CIV that had overwintered and developed to AF during the spring and summer as discussed above. Observations of large numbers of females (up to 1400 ind. m^{-2}) in the surface waters right underneath the sea ice in Franklin Bay in July indicate the potential of a late spawning in this area (Hop et al. 2011). Franklin Bay is different from the Amundsen Gulf polynya since it is covered with fast-ice until July, and the development of *C. glacialis* is likely delayed there compared to the polynya.

These results show the plasticity in reproductive strategy and the long-term spawning potential of *C. glacialis* population, and are in accordance with previous studies concluding that *C. glacialis* might spawn prior to the spring bloom (Hirche and Kattner 1993; Niehoff et al. 2002; Hirche and Kosobokova 2003; Plourde et al. 2005), with ice algae fuelling the early reproduction (Tourangeau and Runge 1991; Søreide et al. 2010), but that the peak in egg production often coincides with the peak in pelagic chlorophyll-*a* concentration later in the season (Kosobokova and Hirche 2001). Life history models show that early spawned eggs have the highest relative contribution to the population recruitment at high latitudes (Varpe et al. 2007), suggesting that offsprings from early recruitments have a better chance to develop to viable overwintering stage during a season. However, if the bloom occurs late, the importance of early spawned eggs for the recruitment decreases relative to later spawned eggs (Varpe et al. 2009). The difference in developmental time will affect the production of the population since a population that develops to CV within one year and reproduces the following year will provide more biomass available for higher trophic levels than a population that uses three years to fulfil its lifecycle. Successful growth and development of a late-summer spawning may be more likely in the Amundsen Gulf than around Svalbard, due to the more southern location. A longer period of sufficient incident light levels in combination with possible upwelling events might provide favourable conditions for primary production events until late in the season, and thus enough food for late-summer spawned *C. glacialis* to develop to CIII or CIV and overwinter.

Figure 6 compares the observations of the life cycle of *C. glacialis* from the Amundsen Gulf with those of *C. glacialis* population from other high Arctic locations with different environmental settings. Kongsfjorden represents an ice free environment with only one major bloom event in spring. Data from Seuthe et al. (2011) from two years of ice-free winters (2006 and 2007) in Kongsfjorden showed that CI dominated the population by the end of May in 2006 and in mid May in 2007. Assuming that the development time from eggs to CI is approx. 40 days at water temperatures encountered during spring in Kongsfjorden (0-1^{o}C) (Corkett et al. 1986), spawning occurred already in mid March prior to the pelagic phytoplankton bloom. This shows that in Kongsfjorden during ice-free winters, *C. glacialis* spawns prior to the phytoplankton bloom, most likely fuelled by internal lipid reserves. However, the development of the population differed between these two years with rapid development in 2006 when there was an early phytoplankton bloom and late development in 2007 when the phytoplankton bloom occurred later in the spring (Seuthe et al. 2011). Rijpfjorden represents a fast-ice environment where the ice retreats late in the season, and there is a short and intense period of pelagic primary production. Studies by Søreide et al. (2010) and Leu et al. (2011) from Rjipfjorden have shown that *C. glacialis* spawns during the ice algal bloom. *C. glacialis* was able to complete its life cycle in 1-2 year and reached high biomass of the population in autumn when it reproduced during the ice algal bloom and the gap between reproduction and pelagic phytoplankton bloom matched the development time from egg to the first feeding stage (Søreide et al. 2010). However, a mismatch in the timing of the first feeding nauplii and the pelagic phytoplankton bloom resulted in much lower biomass (Leu et al. 2011).

Calanus glacialis is able to fulfil its life cycle in 1-2 years both in areas without ice cover and a long primary productive season (Kongsfjorden), and in areas with long ice cover and a short pelagic bloom (Rjipfjorden). In environment without ice cover and only one major phytoplankton bloom in the spring, a capital breeding strategy would allow the offspring to take full advantage of this one bloom. In environments with longer period of ice cover and both ice algal and phytoplankton blooms, income breeding fuelled by the ice algal bloom would be necessary for the offspring to develop during the short pelagic bloom. The ice algal bloom would therefore be increasingly important with higher latitudes and longer duration of the ice cover, since a short ice-free season would not enable both reproduction and development to viable overwintering stages. Early reproduction has the risk of mismatch between food supply and the first feeding stages, but a match would enable a longer period for the offspring to reach the overwintering stage and a shorter life-cycle (Varpe et al. 2007), which could result in high biomass of the population. In the Amundsen Gulf, it is likely that *C. glacialis* spawned later in the season fuelled by the pelagic phytoplankton blooms. The success of such a late reproduction would depend on an extended primary productive season and is therefore restricted to more southern location with a longer period of incoming solar radiation allowing bloom events later in the season.

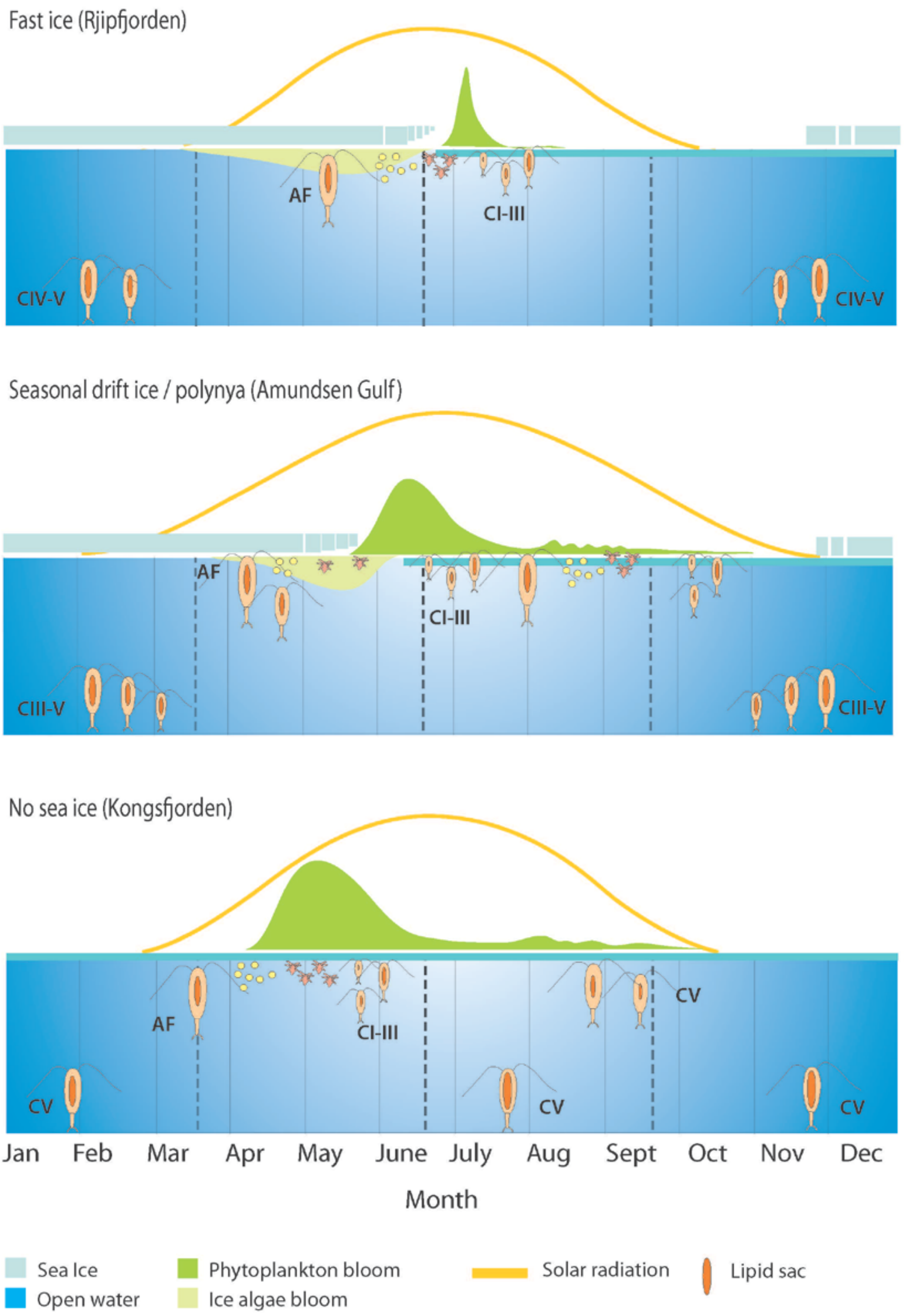


Figure 6. *Calanus glacialis* life-cycle under different sea-ice and primary production scenarios: (a) Fast ice scenario with prolonged ice cover during winter, ice algal bloom preceding the pelagic phytoplankton bloom during spring (Rjipfjorden); (b) Polynya with seasonal ice cover, ice algae, pelagic phytoplankton bloom during spring (Amundsen Gulf) (c) No ice cover during winter and a longer pelagic primary production period in summer (Kongsfjorden). The dotted lines indicate the equinox and solstice.

Fatty acid trophic markers

Arctic spring blooms, taking place in cold nutrient-rich waters, are likely to support alga of high nutritional quality with regard to fatty acid composition, e.g. high levels of PUFAs (Søreide et al. 2010; Leu et al. 2011). These fatty acids, which are nutritionally important for the organisms, can also provide information as fatty acid trophic markers (FATM). *Calanus* spp. are mainly storing energy as wax esters during diapause, and hence have high levels of the long chained fatty acids and fatty alcohols 20:1 and 22:1 in winter, and increased levels of fatty acids derived from phytoplankton during the spring (Falk-Petersen et al. 2009b). Increased amounts of fatty acids derived from phytoplankton are therefore an indication about when they start to feed, as well as what they are eating. *C. glacialis* females from Amundsen Gulf (Paper I) had high neutral lipid (mainly wax esters) content and high proportions of the energy-rich 20:1 and 22:1 fatty acids and fatty alcohols during winter (Figure 7). These observations indicate low utilization of lipids during diapause, which is in accordance with previous studies (Hagen and Auel 2001; Lee et al. 2006). There was a relative decline in the long-chained fatty acids and fatty alcohols 20:1 and 22:1, and an increase in the diatom markers (16:1n7, C16 PUFAs and EPA) in females during the winter-spring transition. Females near the surface had a higher portion of the diatom markers than deep-dwelling females in April, indicating that they were grazing on the available ice algae. Stable isotope measurements (δ^{13}C, δ^{15}N), also reflected the onset of herbivorous feeding on the onset of the ice algal bloom in beginning of April, in accordance with Forest et al. (2011). The proportion of the essential fatty acids EPA and DHA were higher in females than in CIV, and they decreased in the females in April while the other diatom FATMs increased, indicating that these essential fatty acids were used for egg production (Sargent and Falk-Petersen 1988).

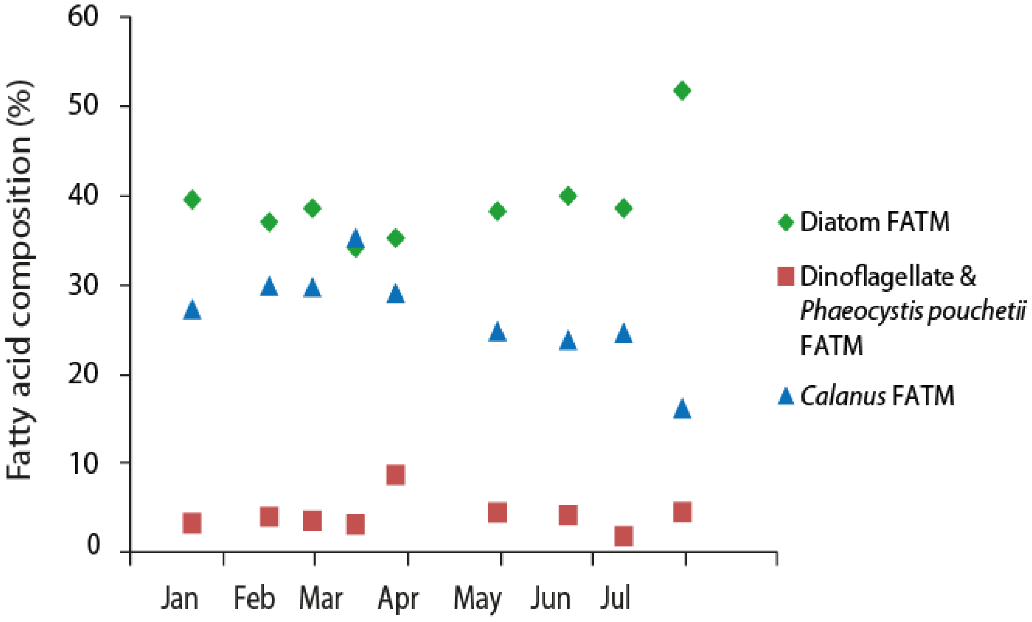


Figure 7. Selected fatty acid markers (% of total fatty acid) of *Calanus glacialis* females in the Amundsen Gulf (January-July 2008) showing the diatom markers (16:1n7, 16 PUFAs and EPA), dinoflagellates markers (16PUFA, 18 PUFA and DHA), the *de novo* synthesized fatty acids 20:1 and 22:1.

The diatom FATMs dominated in the *C. glacialis* females throughout the season, reflecting the high diatom production in these areas. The western Canadian Arctic has a higher silicate concentration than the European Arctic due to influence of silicate-rich Pacific water, which can support diatom production throughout the season. Both ice algal diatoms and pelagic diatoms are characterized by the same fatty acids (16:1n7, C16 PUFA and EPA). However, ice algae are more enriched in ^{13}C than phytoplankton, making it possible to trace ice algal versus phytoplankton carbon sources by investigating δ^{13}C values of the consumers (Søreide et al. 2006a). In March and April, *C. glacialis* had δ^{13}C values closer to the C isotope signature of ice algae than phytoplankton.

In Kongsfjorden 2003 (Paper III) the spring bloom peaked in April and the phytoplankton was in a post bloom situation in May, with a biomass peak at 50-60m consisting mainly of *P. pouchetii* (Leu et al. 2006). Diatoms were still present in the surface waters but in decreasing amounts and flagellates became increasingly important (Leu et al. 2006). However, the high content of diatom markers in *C. glacialis* indicates that diatoms were a major part of their diet earlier in the season. *Calanus glacialis* utilized the phytoplankton spring bloom to build up its lipid reserves, mainly wax esters, and it also incorporated essential fatty acids such as EPA and DHA, especially into the polar lipids. Wax esters were the dominant lipid class of all stages (CII-AF) ranging from 34 % of total lipid in CII to 60 % in CIII-CV. In the earlier stages, 16:1n7 and 16:0 fatty acids and alcohols were the main components, while in the older stages the long-chained 20:1n9 and 22:1n9, synthesized *de novo* by *Calanus*, dominated reflecting that these fatty acids are major part of the wax esters (Figure 8). In the polar lipid fraction of *C. glacialis*, EPA and DHA were present in high amounts, and especially DHA was more abundant than what was reported from the Amundsen Gulf (Paper I). This could reflect higher proportion of dinoflagellates and *P. pouchetii* in the phytoplankton assemblage in Kongsfjorden than in Amundsen Gulf. Scott et al. (2002) found even higher levels of DHA and slightly lower levels of EPA in samples from the autumn in Kongsfjorden when dinoflagellates and protozoan were likely more important prey for *Calanus* than during the spring.

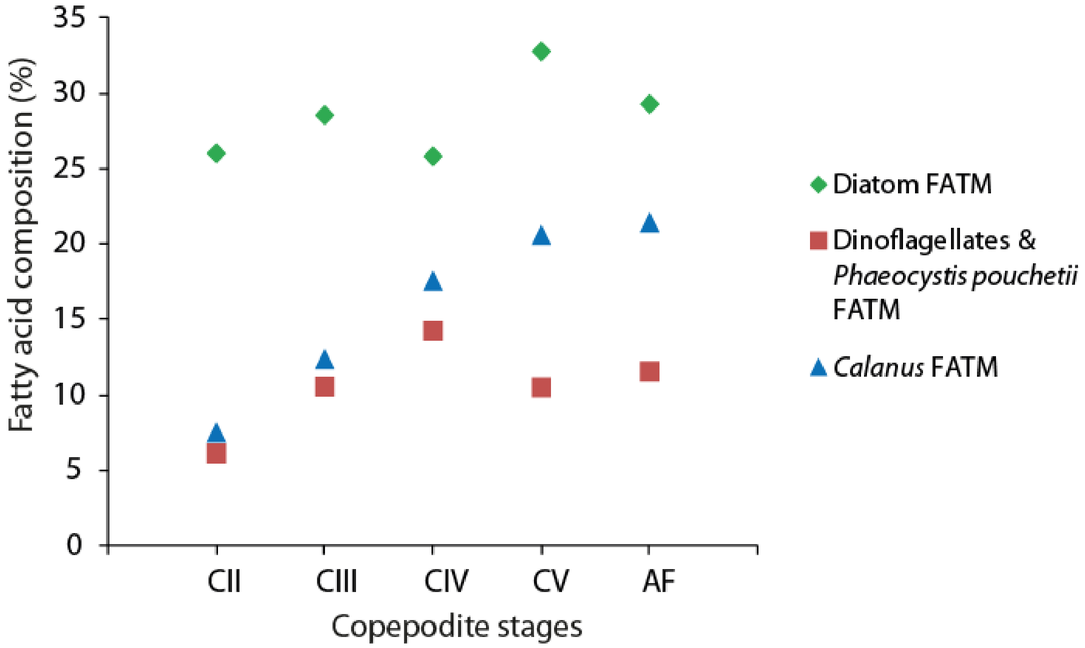


Figure 8. Selected fatty acid markers (% of total fatty acid) of different *Calanus glacialis* CII-AF in Kongsfjorden in May 2003, showing the diatom markers (16:1n7, 16 PUFAs and EPA), dinoflagellates markers (16PUFA, 18 PUFA and DHA) and the *de novo* synthesized fatty acids 20:1 and 22:1.

Our fatty acid analysis show that *C. glacialis* is mainly preying on ice algae and pelagic phytoplankton diatoms during spring. This is in accordance to previous studies of the fatty acid composition (Tande and Henderson 1988; Scott et al. 2002; Søreide et al. 2010), as well as in grazing experiments (Eilertsen et al. 1989; Hansen et al. 1996; Pasternak et al. 2002; Saunders et al. 2003; Swalethorp et al. 2011). However, the importance of protozoans in the copepod diet has recently got increased attention (Klein Breteler et al. 1999; Broglio et al. 2003; Calbet and Saiz 2005; Campbell et al. 2009; Saiz and Calbet 2011; Seuthe et al. 2011). A review on marine calanoid copepod feeding by Saiz and Calbet (2011) concluded that dinoflagellates and ciliates are important contributors to copepod diet in areas with low primary production, such as much of the world's oceans. However, in productive areas and periods, such as the Arctic spring, diatoms are the main part of copepod diets (Saiz and Calbet 2011). Grazing experiments from Disko Bay (Levinsen et al. 2000) and from the Chuckchi and Beaufort Sea (Campbell et al. 2009) showed that during spring, phytoplankton (mainly diatoms) were the selected food for *C. glacialis*, while later in the season, protozoans were the preferred food for *C. glacialis* that were still feeding in the surface water. Protozoans feed on a large variety of microbes, micro-, pico- and nanoplankton including diatoms, resulting in a diverse fatty acid composition, but a general trend is high levels of 16:0, 18:1 and DHA (Klein Breteler et al. 1999; Broglio et al. 2003; Klein Breteler et al. 2004; Chu et al. 2008; Lund et al. 2008).

In this study, we conclude that diatoms are the main food of *C. glacialis* both during the ice algal and pelagic phytoplankton bloom, and the role of diatoms is even more pronounced in the Amundsen Gulf due to influence of silicate-rich Pacific water than in Svalbard waters. The ice algal and phytoplankton bloom periods represent the main grazing periods for *C. glacialis* when the energy is transferred from primary production into the large lipid reserves in *Calanus*.

Lipid transfer to higher trophic levels

The Barents Sea and Svalbard waters support large stocks of marine mammals, and some of the world's largest seabird colonies (Sakshaug and Kovacs 2009). The northward migration of the large stock of pelagic fish, seabirds and mammals follows the spring/summer ice edge bloom with the mass occurrence of *Calanus* in the surface waters (Falk-Petersen et al. 1990; Varpe and Fiksen 2010). The aim of Paper IV was to increase the understanding of the diet and trophic levels of the most common seabirds in Kongsfjorden; Little auk, Brünnich's guillemot, Black-legged kittiwake, Northern fulmar and Glaucous gull. In Paper V we look at the transfer of lipids from plankton to blubber of harp and hooded seals off East Greenland. The fatty acid composition of the muscle of seabirds and blubber of seals were determined and compared with that of their prey species based on the principal of FATM. The trophic position of the seabirds and seals were also determined based on stable isotopes.

In Kongsfjorden, Little auk, Black-legged kittiwake and Northern fulmar had high levels of the *Calanus* markers 20:1 and 22:1, indicating that these seabirds are part of the *Calanus* based food web (Figure 9). Little auk were at a lower trophic level (TL = 3.3) than Black-legged kittiwake (TL = 4.0) and Northern Fulmar (TL = 4.2), indicating that it most likely preys directly on *Calanus* while the *Calanus* markers in the two other species are more likely obtained indirectly through a diet of larger amphipods, krill or pelagic fish such as polar cod or capelin. Levels of 20:1 and 22:1 were much lower in Brünnich's guillemot which is a pursuit diver feeding on fish and amphipods deeper in the water column, closer associated to the benthic food web. Larger variation in the fatty acid composition of Glaucous gull indicate a more diverse diet compared to the other seabirds, which is consistent with being an opportunistic feeder and generalist with a diverse diet of zooplankton, fish, adult birds, chicks, eggs, carrion and offal (Erikstad 1990; Anker-Nilssen et al. 2000). The high levels *of Calanus* FATM in Little auk correspond well to previous diet studies based on stomach content (Mehlum and Bakken 1994; Karnovsky et al. 2003). Little Auk is known to prey specifically on larger stages of *C. glacialis and C. hyperboreus* (Steen et al. 2007), and might therefore be especially vulnerable to changes in abundance and distribution of *C. glacialis*, and that could affect their distribution related to nesting sites and their reproductive success. Large inflow of Atlantic water into Kongsfjorden during winter 2005-06 (Cottier et al. 2007) switched the system into a warmer state and the following four winters no fast-ice cover settled. This resulted in a shift to more Atlantic dominated zooplankton community with *C. finmarchicus* being more abundant than *C. glacialis* (Falk-Petersen pers. comm.). This might have forced especially Little Auk to fly longer distances (e.g. ice edge northwest of Svalbard) to find aggregations of lipid-rich *C. glacialis* and *C. hyperboreus* (Karnovsky et al. 2010). Levels of *Calanus* FATM were relatively high in Northern fulmar but lower than previously reported from Kongsfjorden (Dahl et al. 2003). However, the seabirds analysed by Dahl et al. (2003) were sampled in 1997 while the birds in our study were sampled in 2005 and 2006, which were warmer years, especially 2006. Larger zooplankton species such as *Themisto libelulla* and *Thysanoessa* spp., as well as pelagic fish like polar cod and capelin are likely important prey for Northern fulmar. *T. libellula* is more abundant in Arctic water masses typical in cold years, while *Thysanoessa* spp. is closer linked to Atlantic water, typical for warm years. The abundance of polar cod and capelin is also highly variable between years (Hop and Gjøsæter submitted). This variance in the abundance of the main prey species of Northern fulmar could be reflected in the fatty acid signatures of the seabirds sampled in different years.

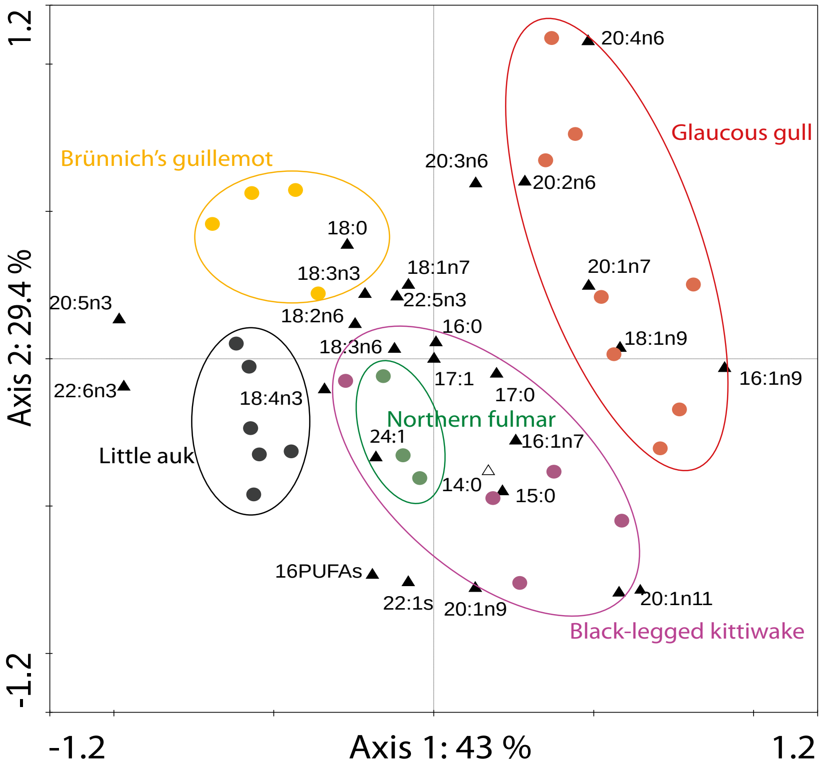


Figure 9. PCA showing the distribution of fatty acids of the seabirds; Little auk, Brünnich's guillemot, Northern fulmar, Black-legged kittiwake and Glaucous gull in Kongsfjorden during summer. Modified after Wold et al. 2011 (Paper IV).

The seabirds in Kongsfjorden are likely to encounter two different feeding scenarios; (1) a cold Arctic water influenced fjord with ice cover in winter dominated by Arctic species such as *C. glacialis*, *T. libelulla* and polar cod and (2) a warm Atlantic water-influenced fjord without ice cover in winter, as seen during 2006-10, with a zooplankton assemblage dominated by Atlantic species such as *C. finmarchicus* and krill. The last scenario is similar to the situation in the fjords of Northern Norway (Falk-Petersen et al. 1982; Falk-Petersen 1984). The first scenario will be more favourable for species such as Little auk, which is dependent on the larger stages of *C. glacialis* and *C. hyperboreus* (Steen et al. 2007). The other seabirds feeding on both zooplankton and fish such as; Black-legged kittiwake, Brünnich's guillemot and Northern fulmar, would be expected to do well in both scenarios. However, the populations of Black-legged kittiwake and especially Brünnich's guillemot have declined in many areas in Svalbard for the last ten years most likely die to food availability in the summer (MOSJ 2012).

Harp seal and hooded seal co-occur in the drift ice waters of the Greenland Sea during breeding and moulting in March–June (Sergeant 1991; Folkow et al. 1996; Haug et al. 2000; Potelov et al. 2000), but they might also occur in the Greenland Sea pack-ice outside the breeding and moulting season and Hooded seals appear to be present in this area approximately 40 % of the year (Haug et al. 2007). Harp and hooded seals have distinct seasonal variation in their blubber thickness with maximum thickness in autumn and winter and minimum in spring and summer (Rasmussen 1960; Nilssen et al. 1997). This reflects that the energy produced during the Arctic spring bloom is transferred mainly as fatty acids up through the food chain during summer and autumn and end up as energy stores in top predators such as seals in the autumn and winter which is catabolised during reproduction the following spring and early summer. The fatty acid composition revealed that harp seals are more associated with pelagic prey than hooded seals (Paper V). The fatty acid profile of harp seals originated from diatoms (16:1n7 and EPA) and the presence of 16:4n1 might be due to input of ice algae, which associate species to the ice-edge ecosystem (Figure 10). In contrast, the fatty acids of hooded seals originated from dinoflagellates and *P. pouchetii* (18:1n9 and DHA), which tend to be more important in an open Atlantic water ecosystem. However, dinoflagellates and *P. pouchetii* blooms are also reported at Arctic shelf areas (Leu et al. 2006; Degerlund and Eilertsen 2010). Hooded seals caught around Jan Mayen and Denmark Strait had high levels of *Calanus* FATM (up to 25%), probably due to capelin which is known to be an important part of their winter diet in these areas (Haug et al. 2004; Haug et al. 2007). The fat seals also had higher levels of *Calanus* FATM indicating the importance of *Calanus* at the base of the food chain of these seal species. The fatty acid results are in accordance with stomach content analyses from the same area showing that pelagic crustaceans (amphipods and krill) were the most important prey for harp seals, whereas the hooded seal diet was characterized by the squid *Gonatus fabricii* , polar cod and capelin (Haug et al. 2004). The difference in diet might also be a result of different foraging depths with harp seal known to be a pelagic feeder at the continental shelf (Folkow et al. 2004) while hooded seal is a deep diver associated with the continental shelf edge and deep ocean (Folkow and Blix 1999; Folkow et al. 2004). This difference in foraging habitats is also reflected in studies from the northwest Atlantic (Lawson et al. 1995; Hammill and Stenson 2000; Kapel 2000; Tucker et al. 2009b). Stable isotope analyses showed that both species are true carnivores at the top of the food web, with hooded seals being slightly higher in the food web than harp seals.

The relevance of fatty acid analyses as an indication of seal diet has been debated by Grahl-Nilsen et al. (2011), who criticized the relevance of previous studies since either they were done on captive animals (Kirsch et al. 2000) or on predator and prey collected at different areas (Falk-

Petersen et al. 2004; Falk-Petersen et al. 2009a; Tucker et al. 2009a). Grahl-Nielsen et al. (2011) compared the inner and the outer blubber of harp seals and of potential prey species collected simultaneously, and concluded that the weak relationship between the fatty acids of the inner blubber and that of the prey suggested that the fatty acid composition of the inner blubber was mainly determined by the metabolism rather than the fatty acid composition of the prey. However, the results showed that *T. libellula*, *Thysanoessa* spp., Polar cod and Arctic cod were the species with fatty acids most similar to that of the inner blubber of harp seals, which is similar to our results. Since the seals most likely have a mixed-diet and a diet varying during the season, the fatty acid profile of the seals will be a mixture of the fatty acid profiles of the prey over time in addition to changes due to metabolism.

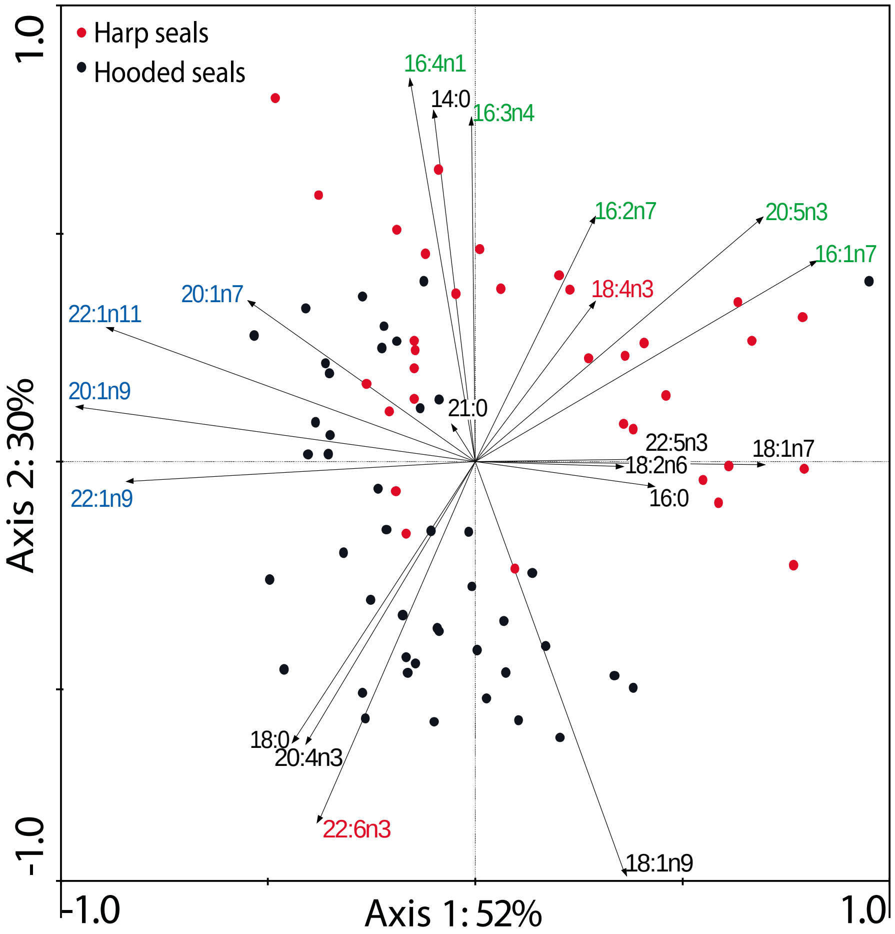


Figure 10. PCA showing the distribution of fatty acids of harp seals (*Phoca Groenlandica*) = red circles, and Hooded seals (*Cystophora cristata*) = black circles. Modified after Falk-Petersen et al. 2009 (Paper V).

Conclusions

1. The annual light cycle and the extent and thickness of ice and snow cover control the onset and duration of ice algal and phytoplankton blooms, and regulate the life cycle of *C. glacialis*. Life cycle events of *C. glacialis* such as ascent from overwintering depth, reproduction and lipid accumulation are scheduled in order to utilise this short and intense period of primary production, which occurs as the ice opens up in the spring. The ice algal bloom may fuel early maturation and prolong the reproductive period of *C. glacialis*, or fuel the growth and development from overwintering CIII and CIV, making it possible to develop to females that could spawn during the summer (Paper I). The seasonal vertical distribution of *C. glacialis* is determined by the progression of the bloom. *C. glacialis* descends to deeper waters earlier in the season in area with an early break up of ice and an early phytoplankton bloom than in areas with a persistent ice cover and late phytoplankton bloom (Paper II).
2. The ice algae bloom mainly consists of diatoms which produce PUFAs that are of high nutritional quality and important for growth and reproduction of *C. glacialis*. A relative increase in the PUFAs derived from diatoms in *C. glacialis* females in the early spring in the Amundsen Gulf (Paper I), indicates that they were feeding on available ice algae. Diatoms were the main food source for *C. glacialis* throughout the season in Amundsen Gulf. In Kongsfjorden (Paper III) *C. glacialis* utilized the phytoplankton spring bloom to build up its lipid reserves, mainly as wax esters, and it also incorporated essential fatty acids such as EPA and DHA into its lipid reserves. The long-chained *de novo* synthesized 20:1n9 and 22:1n9 fatty acids dominated in the older copepodid stages. The role of ice algae for the reproduction of *C. glacialis* becomes increasingly more important at higher latitudes and in areas with long duration of the ice cover, such as Rjipfjorden,due to shorter period of sufficient incoming solar irradiance. A reduction in sea ice as seen in Kongsfjorden will lead to an earlier pelagic primary production during spring and likely several smaller primary production events later in the season.
3. The diatom – *Calanus* food chain is an important driver for the high latitude pelagic arctic food web. High levels of the *Calanus* markers 20:1n9 and 22:1n11 in the seabirds Little auk, Black-legged kittiwake and Northern fulmar from Kongsfjorden, Svalbard, indicate that these seabirds are part of the *Calanus* based food web, while Brünnich's guillemot and Glaucous gull were not so closely linked to the *Calanus* food chain (Paper IV). Little auk occupied the lowest trophic level followed by Brünnich's guillemot, Black-legged kittiwake, Glaucous gull and Northern fulmar. Harp seals and hooded seals (Paper V) showed considerably overlap in their diet, but the fatty acid composition of harp seals originated from a diatom-*Calanus*–based food web. The fatty acids of hooded seals originated from dinoflagellate and *P. pouchetii*-based food web.
4. The life history trait of accumulating energy in form of lipids is an adaptation of *Calanus* to the large seasonal and inter-annual fluctuations in food availability and the physical environment. The lipids represent an effective transfer of energy up the food chain. The match between primary productions, either as ice algae or phytoplankton bloom, and the reproduction of *C. glacialis* is therefore crucial for the accumulation of lipids in *Calanus* and hence also for the energy available to higher trophic levels.

References

Ackman RG (1989) Marine Biogenic Lipids, Fats and Oils. CRC Press, Boca Raton.

Anker-Nilssen T, Bakken V, Strøm H, Golovkin AN, Biankii VV, Tatarinkova IP (2000) The status of the marine birds breading in the Barents Sea Region. The Norwegian Polar Institute Report Series, vol 113. The Norwegian Polar Institute, Tromsø.

Ardyna M, Gosselin M, Michel C, Poulin M, Tremblay JE (2011) Environmental forcing of phytoplankton community structure and function in the Canadian High Arctic: contrasting oligotrophic and eutrophic regions. Mar Ecol-Prog Ser 442:37-57.

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

Arrigo KR, van Dijken GL (2004) Annual cycles of sea ice and phytoplankton in Cape Bathurst polynya, southeastern Beaufort Sea, Canadian Arctic. Geophys Res Lett 31:8 L08304.

Atkinson A (1998) Life cycle strategies of epipelagic copepods in the Southern Ocean. J Mar Syst 15:289-311.

Auel H, Hagen W (2002) Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. Mar Biol 140:1013-1021.

Bagøien E (1999) Predatory impact on evertebrates and fish on overwintering *Calanus*. University of Oslo, Oslo

Barber DG, Asplin MG, Gratton Y, Lukovich JV, Galley RJ, Raddatz RL, Leitch D (2010) The International Polar Year (IPY) Circumpolar Flow Lead (CFL) System Study: Overview and the Physical System. Atmos-Ocean 48:225-243.

Barrett RT, Camphuysen K, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Hüppop O, Leopold MF, Montevecchi WA, Veit RR (2007) Diet studies of seabirds: a review and recommendations. ICES J Mar Sci 64:1675-1691.

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426:661-664.

Best NJ, Bradshaw CJA, Hindell MA, Nichols PD (2003) Vertical stratification of fatty acids in the blubber of southern elephant seals (*Mirounga leonina*): implications for diet analysis. Comp Biochem Phys, A 134:253-263.

Bourke RH, Weigel AM, Paquette RG (1988) The westward turning branch of the West Spistbergen Current. J Geophys Res (C Oceans) 93:14065-14077.

Bradstreet MSW, Cross WF (1982) Trophic relationship at high Arctic ice edge. Arctic 35:1-12.

Brander KM, Dickson RR, Shepherd JG (2001) Modelling the timing of plankton production and its effect on recruitment of cod (*Gadus morhua*). ICES J Mar Sci 58:962-966.

Broglio E, Jonasdottir SH, Calbet A, Jakobsen HH, Saiz E (2003) Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. Aquat Microb Ecol 31:267-278.

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: A primer on analysis and interpretation. Mar Mamm Sci 22:759-801.

Budge SM, Parrish CC, McKenzie CH (2001) Fatty acid composition of phytoplankton, settling particulate matter and sediments at a sheltered bivalve aquaculture site. Mar Chem 76:285-303.

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divoky GJ (2008) Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157:117-129.

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

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

Carmack EC, MacDonald RW (2002) Oceanography of the Canadian shelf of the Beaufort Sea: a setting for marine life. Arctic Suppl 55:29-45.

Chu FLE, Lund ED, Podbesek JA (2008) Quantitative significance of n-3 essential fatty acid contribution by heterotrophic protists in marine pelagic food webs. Mar Ecol-Prog Ser 354:85-95.

Clark KAJ, Brierly AS, Pond DW (2012) Composition of wax ester is linked to diapause behaviour in *Calanus finmarchicus* in a sea loch environment. Limnol Oceanogr 57:65-75.

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, Bedo AW, Herman AW, Head EJH, Harris LR, Horne EPW (1988) Never trust a copepod - some observations on their behavior in the Canadian Arctic. B Mar Sci 43:650-662.

Cook HW (1991) Fatty acid desaturation and chain elongation in eucariotes. In: Vance DE, Vance J (eds) Biochemistry of lipids, lipoproteins and membranes. Elsevier Science, New York, pp 141-169.

Corkett CJ, McLaren IA, Sevigny JM The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* (Jaschnov) and *C. hyperboreus* (Kroyer) with comment on the equiproportional rule. In: Schriever G, Schminke HK, Shih CT (eds) Proceedings of the second international Conference on Copepoda, Ottawa, Canada, 1986. The National Museum of Canada, pp 539-546

Cottier F, 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

Cottier FR, MacLachlan S, Howe J (2005) Rapid shifts in Arctic marine climate: observations and archives in a Spitsbergen fjord. Ocean Challenge 14:16-23.

Cushing DH (1974) The natural regulation of fish populations. In: Harden Jones FR (ed) Sea Fisheries Research. Elek Science, London, pp 399-412.

Cushing DH (1975) Marine Ecology and Fisheries. Cambridge University Press, Cambridge.

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249-263.

Daase M, Søreide JE, Martynova D (2011) Effects of food quality on naupliar development in *Calanus glacialis* at subzero temperatures Mar Ecol-Prog Ser 429:111-124.

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. J Plankton Res 29:903-911.

Dahl TM, Falk-Petersen S, Gabrielsen GW, Sargent JR, Hop H, Millar R-M (2003) Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar - a trophic study from an Arctic fjord. Mar Ecol-Prog Ser 256:257-269.

Dalsgaard J, St. John M, Gerard K, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:227-318.

Darnis G, Barber DG, Fortier L (2008) Sea ice and the onshore-offshore gradient in pre-winter zooplankton assemblages in southeastern Beaufort Sea. J Mar Syst 74:994-1011.

Degerlund M, Eilertsen HC (2010) Main species characteristics of phytoplankton spring blooms in NE Atlantic and Arctic Waters (68–80° N). Estuar Coast 33:242-269.

Durant JM, Hjermann DO, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecol Lett 8:952-958.

Durant JM, Hjermann DO, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271-283.

Eilertsen HC, Tande KS, Taasen JP (1989) Vertical distributions of primary production and grazing by *Calanus glacialis* Jaschnov and *Calanus hyperboreus* Kroyer in Arctic Waters (Barents Sea). Polar Biol 9:253-260.

Erikstad KE (1990) Winter diets of 4 seabird species in the Barents sea after a crash in the capelin stock. Polar Biol 10:619-627.

Falk-Petersen I-B, Falk-Petersen S, Sargent JR (1986a) Nature, origin and possible roles of lipid deposits in *Maurolicus muelleri* (Gmelin) and *Benthosema glaciale* (Reinhardt) from Ullsfjorden, Northern Norway. Polar Biol 5:235-240.

Falk-Petersen S (1984) Growth of the Euphasiids, *Thysanoessa inermis*, *Thysanoessa raschii* and *Meganyctiphanes norvegicus* in a Subarctic fjord, Northern Norway. Can J Fish Aquat Sci 42:14-22.

Falk-Petersen S, Falk-Petersen IB, Sargent JR (1986b) Structure and function of an unusal lipid storage organ in the arctic fish *Lumpenus maculatus* Fries. Sarsia 71:1-6.

Falk-Petersen S, Hagen W, Kattner G, Clarke A, Sargent J (2000a) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. Can J Fish Aquat Sci 57:178-191.

Falk-Petersen S, Haug T, Hop H, Nilssen KT, Wold A (2009a) Transfer of lipids from plankton to blubber of harp and hooded seals off East Greenland. Deep Sea Res (II Top Stud Oceanogr) 56:2080–2086.

Falk-Petersen S, Haug T, Nilsen 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, Hop H, Budgell WP, Hegseth EN, Korsnes R, Løyning TB, Ørbæk JB, Kawamura T, Shirasawa K (2000b) Physical and ecological processes in the marginal ice zone of the northern Barents Sea during the summer melt period. J Mar Syst 27:131-159.

Falk-Petersen S, Hopkins CCE, Sargent J (1990) Trophic relationship in the pelagic Arctic food web. In: Barnes M, Gibson RN (eds) Trophic relationship in the marine environment. Aberdeen University Press, Aberdeen, pp 315-333.

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

Falk-Petersen S, Sargent JR, Henderson J, Hegseth EN, Hop H, Okolodkov YB (1998) Lipids and fatty acids in ice algae and phytoplankton from the Marginal Ice Zone in the Barents Sea. Polar Biol 20:41-47.

Falk-Petersen S, Sargent JR, Hopkins CCE, Vaja B (1982) Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: Lipids in Euphasiids *Thysanoessa raschi* and *T. inermis* during spring. Mar Biol 68:97-102.

Falk-Petersen S, Sargent JR, Kwasniewski S, Gulliksen B, Millar R-M (2001) Lipids and fatty acids in *Clione limacina* and *Limacina helicina* in Svalbard waters and the Arctic Ocean: trophic implications. Polar Biol 24:163-170.

Falk-Petersen S, Timofeev S, Pavlov V, Sargent JR (2007) Climate variability and possible effects on Arctic food chains. The role of *Calanus*. In: Ørbæk JB, Tombre T, Kallenborn R, Hegseth EN, Falk-Petersen S, Hoel AH (eds) Arctic-alpine ecosystems and people in a changing environment. Springer Verlag, Berlin, pp 147-166.

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for isolation and purification of total lipides from animal tissue. J Biol Chem 226:497-509.

Folkow LP, Blix AS (1999) Diving behaviour of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. Polar Biol 22:61-74.

Folkow LP, Mårtensson PE, Blix AS (1996) Annual distribution of hooded seals (*Cystophora Cristata*) in the Greenland and Norwegian Sea. Polar Biol 16:179-180.

Folkow LP, Nordøy E, Blix AS (2004) Distribution and diving behaviour of harp seals (*Phagophilus groenlandicus*) from Greenland sea stock. Polar Biol 27:281-298.

Forest A, Tremblay JE, Gratton Y, Martin J, Gagnon J, Darnis G, Sampei M, Fortier L, Ardyna M, Gosselin M, Hattori H, Nguyen D, Maranger R, Vaque D, Marrase C, Pedrós-Alió C, Sallon A, Michel C, Kellogg C, Deming J, Shadwick E, Thomas H, Link H, Archambault P, Pipenburg D (2011) Biogenic carbon flows through the planktonic food web of the Amundsen Gulf (Arctic Ocean): A synthesis of field measurments and inverse modeling analyses. Prog Oceanogr 91:501-511.

Fortier L, Ponton D, Gilbert M (1995) The match mismatch hypothesis and the feeding success of fish larvae in ice-covered southeastern Hudson Bay. Mar Ecol-Prog Ser 120:11-27.

Graeve M, Albers C, Kattner G (2005) Assimilation and biosynthesis of lipids in Arctic *Calanus* species based on 13C feeding experiments with a diatom. J Exp Mar Biol Ecol 317:109-125.

Grahl-Nielsen O, Haug T, Lindstrøm U, Nilssen KT (2011) Fatty acid in harp seal blubber do not necessarily reflect their diet. Mar Ecol-Prog Ser 426:263-276.

Hagen W, Auel H (2001) Seasonal adaptations and the role of lipids in oceanic zooplankton. Zoology 104:313-326.

Hammill MO, Stenson GB (2000) Estimated prey consumption by harp seals (*Phoca groenlandica*) , hooded seals (*Cystophora groenlandica*), grey seals (*Halichoerus grypus*) and harp seals (*Phoca vitulina*) in Atlantic Canada. J Northwest Atl Fish Sci 26:1-23.

Hansen B, Christiansen S, Pedersen G (1996) Plankton dynamics in the marginal ice zone of the central Barents Sea during spring: Carbon flow and structure of the grazer food chain. Polar Biol 16:115-128.

Hassett RP (2006) Physiological characteristics of lipid-rich "fat" and lipid-poor "thin" morphotypes of individual *Calanus finmarchicus* C5 copepodites in nearshore Gulf of Maine. Limnol Oceanogr 51:997-1003.

Haug T, Nilssen KT, Corkeron P, Lindblom L (2002) Diets of harp and hooded seals in drift ice waters along the coast of Greenland. NAMMCO Sci Pub. Reykjavik.

Haug T, Nilssen KT, Lindblom L (2000) First independent feeding of harp seal (*Phoca groenlandica*) and hooded seal (*Cystophora cristata*) pups in Greenland Sea. NAMMCO Sci Pub 2:29-39.

Haug T, Nilssen KT, Lindblom L (2004) Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. Polar Res 23:35-42.

Haug T, Nilssen KT, Lindblom L, Lindstrom U (2007) Diets of hooded seals (*Cystophora cristata*) in coastal waters and drift ice waters along the east coast of Greenland. Mar Biol Res 3:123-133.

Head EJH, Harris LR, Yashayaev I (2003) Distribution of *Calanus* spp. and other mezooplankton in the Labrador Sea in relation to hydrography in the spring and summer (1995-2000). Prog Oceanogr 59:1-30.

Hegseth EN (1998) Primary production of the northern Barents Sea. Polar Res 17:113-123.

Hipfner JM (2008) Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. Mar Ecol-Prog Ser 368:295-304.

Hirche HJ (1989) Egg production of the copepod *Calanus glacialis* - Laboratory experiments. Mar Biol 103:311-318.

Hirche HJ (1996) Diapause in the marine copepod, *Calanus finmarchicus* - A review. Ophelia 44:129-143.

Hirche HJ, Bohrer RN (1987) Reproduction of the Arctic copepod *Calanus glacialis* in Fram Strait. Mar Biol 94:11-17.

Hirche HJ, Hagen W, Mumm N, Richter C (1994) The Northeast Water Polynya, Greenland Sea. 3. Mesozooplankton and Macrozooplankton. Distribution and production of dominant herbivorous copepods during spring. Polar Biol 14:491-503.

Hirche HJ, Kattner G (1993) Egg production and lipid content of *Calanus glacialis* in spring: indication of a food-dependent and food-independent reproductive mode. Mar Biol 117:615-622.

Hirche HJ, Kosobokova K (2003) Early reproduction and development of dominant calanoid copepods in the sea ice zone of the Barents Sea - need for a change of paradigms? Mar Biol 143:769-781.

Hirche HJ, Kosobokova KN (2011) Winter studies on zooplankton in Arctic seas: the Storfjord (Svalbard) and adjacent ice-covered Barents Sea. Mar Biol 158:2359-2376.

Hirche HJ, Kwasniewski S (1997) Distribution, reproduction and development of *Calanus* species in the Northeast Water in relation to environmental conditions. J Mar Syst 10:299-317.

Hjort J (1914) Fluctuation in the great fisheries of Northern Europe viewed in light of biological research. Rapp p-v Réun Cons Int Explor Mer 20:1-228.

Hobson KA, Ambrose Jr. WG, Renaud PE (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol-Prog Ser 128:1-10.

Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon J-M, Fortier M (2002) A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: Implications for evaluating trophodynamics and the flow of energy and contaminants. Deep Sea Res (II Top Stud Oceanogr) 49:5131-5150.

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high-arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol-Prog Ser 84:9-18.

Hop H, Borgå K, Gabrielsen GW, Kleivane L, Skaare JU (2002a) Food web magnification of persistent organic pollutants in poikilotherms and homeotherms from the Barents Sea. Environ Sci Technol 36:2589-2597.

Hop H, Gjøsæter H (submitted) Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) in relation to water masses and sea ice conditions. Mar Biol Res.

Hop H, Mundy CJ, Gosselin M, Rossnagel AL, Barber DG (2011) Zooplankton boom and ice amphipod bust below melting sea ice in the Amundsen Gulf, Arctic Canada. Polar Biol 34:1947-1958.

Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalczuk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S-Å, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002b) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167-208.

Huntley M, Strong KW, Dengler AT (1983) Dynamics and community structure of zooplankton in the Davis Strait and northern Labrador Sea. Arctic 36:143-161.

Iken K, Bluhm BA, Gradinger R (2005) Food web structure in the Arctic Canada Basin: evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Polar Biol 28:238-249.

Iverson SJ (2009) Tracing aquatic food webs using fatty acids: from qualitative indicators to quantitative determination. In: Arts M, Brett TM, Kainz M (eds) Lipids in Aquatic Ecosystems. Springer-Verlag, New York, pp 281-307.

Iverson SJ, Field C, Bowen WD, Blanchard W (2004) Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecol Monogr 74:211-235.

Iverson SJ, Frost KJ, Lowry LF (1997) Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Mar Ecol-Prog Ser 151:255-271.

Iverson SJ, Springer AM, Kitaysky AS (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. Mar Ecol-Prog Ser 352:235-244.

Jæger I, Hop H, Gabrielsen GW (2009) Biomagnification of mercury in selected species from an Arctic marine food web in Svalbard. Sci Total Environ 407:4744-4751.

Jaschnov VA (1970) Distribution of *Calanus* species in the seas of the Northern Hemisphere. Internationale Revue der Gesamten Hydrobiologie 55:197-212.

Kaardtvedt S (2000) Life history of *C. finmarchicus* in the Norwegian Sea in relation to planktivourous fish. ICES J Mar Sci 57:1819-1824.

Käkelä A, Furness RW, Kelly A, Strandberg U, Waldron S, Käkelä R (2007) Fatty acid signatures and stable isotopes as dietary indicators in North Sea seabirds. Mar Ecol-Prog Ser 342:291-301.

Käkelä R, Käkelä A, Martinez-Abrain A, Sarzo B, Louzao M, Gerique C, Villuendas E, Strandberg U, Furness RW, Oro D (2010) Fatty acid signature analysis confirms foraging resources of a globally endangered Mediterranean seabird species: calibration test and application to the wild. Mar Ecol-Prog Ser 398:245-258.

Kapel F (2000) Feeding habits of harp and hooded seals in Greenland waters. NAMMCO Sci Pub 2:50-64.

Karnovsky N, Harding A, Walkusz W, Kwasniewski S, Goszczko I, Wiktor J, Routti H, Bailey A, McFadden L, Brown Z, Beaugrand G, Gremillet D (2010) Foraging distributions of little auks

Alle alle across the Greenland Sea: implications of present and future Arctic climate change. Mar Ecol-Prog Ser 415:283-293.

Karnovsky NJ, Hobson KA, Iverson S, Hunt Jr. GL (2008) Seasonal changes in diets of seabirds in the North Water Polynia: a multiple indicator approch. Mar Ecol-Prog Ser 357:291-299.

Karnovsky NJ, Kwasniewski S, Weslawski JM, Walkusz W, Beszczynska-Möller A (2003) Foraging behavior of little auks in a heterogeneous environment. Mar Ecol-Prog Ser 253:289-303.

Kattner G, Hagen W (2009) Lipids in marine copepods: Latitudinal characteristics and perspective to global warming. In: Arts M, Brett TM, Kainz M (eds) Lipids in Aquatic Ecosystems. Springer, New York, pp 257-280.

Kirsch PE, Iverson SJ, Bowen DW, Kerr SR, Ackman RG (1998) Dietary effects on the fatty acid signature of whole Atlantic cod (*Gadhus morhua*). Can J Fish Aquat Sci 55:1378-1386.

Kirsch PE, Iverson SJ, Bowen WD (2000) Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (*Phoca groenlandica*). Physiol Biochem Zool 73:45-59.

Klein Breteler WCM, Koski M, Rampen S (2004) Role of essential lipids in copepod nutrition: no evidence for trophic upgrading of food quality by a marine ciliate. Mar Ecol-Prog Ser 274:199-208.

Klein Breteler WCM, Schogt N, Baas M, Schouten S, Kraay GW (1999) Trophic upgrading of food quality by protozoans enhancing copepod growth: role of essential lipids. Mar Biol 135:191-198.

Kosobokova K, Hansen H, Hirche HJ, Knickmeier K (1998) Composition and distribution of zooplankton in the Laptev Sea and the adjacent Nansen Basin during summer, 1993. Polar Biol 19:63-76.

Kosobokova KN (1993) Reproduction and fecundity of the White Sea copepod *Calanus glacialis* in experimental conditions. Okeanologiya 33:392-396.

Kosobokova KN (1998) New data on the life cycle of *Calanus glacialis* in the White Sea (based on seasonal observations of its genital system development). Oceanology 38:347-355.

Kosobokova KN (1999) The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. Polar Biol 22:254-263.

Kosobokova KN, Hirche HC (2001) Reproduction of *Calanus glacialis* in the Laptev Sea. Polar Biol 24:33-43.

Kovacs KM, Lavigne DM (1986) *Cystophora Cristata*. Mammalian Species 258:1-9.

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.

Lawson JW, Stenson GB, McKinnon DG (1995) Diet of harp seals (*Phoca groenlandica*) in nearshore waters of the northwest Atlantic during 1990-1993. Can J Zool 73:1805-1818.

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

Leu E, Falk-Petersen S, Kwasniewski S, Wulff A, Edvardsen K, Hessen DO (2006) Fatty acid dynamics during the spring bloom in a high Arctic fjord: importance of abiotic factors vs. community changes. Can J Fish Aquat Sci 63:2660-2779.

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

Leu E, Wiktor J, Soreide JE, Berge J, Falk-Petersen S (2010) Increased irradiance reduces food quality of sea ice algae. Mar Ecol-Prog Ser 411:49-60.

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

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.

Lund ED, Chu FLE, Harvey E, Adlof R (2008) Mechanism(s) of long chain n-3 essential fatty acid production in two species of heterotrophic protists: *Oxyrrhis marina* and *Gyrodinium dominans*. Mar Biol 155:23-36.

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.

Madsen SJ, Nielsen TG, Tervo OM, Söderkvist J (2008) Importance of feeding for egg production in *Calanus finmarchicus* and *C. glacialis* during the Arctic spring. Mar Ecol-Prog Ser 353:177-190.

Mancuso CA, Franzmann PD, Burton HR, Nichols PD (1990) Microbial community structure and biomass estimates of methanogenic Antarctic lake ecosystem as determined by phospholipid analyses. Microbial Ecol 19:73-95.

Mayzaud P, Boutoute M, Alonzo F (2003) Lipid composition of the euphausiids *Euphasia vallentini* and *Thysanoessa macrura* during summer in the Southern Indian Ocean. Antarct Sci 15:463-475.

Mayzaud P, Claustre H, Augier P (1990) Effect of variable nutrient supply on fatty acid composition of phytoplankton grown in an enclosed experimental ecosystem. Mar Ecol-Prog Ser 60:123-140.

McNamara JM, Houston AI (2008) Optimal annual routines: behaviour in the context of physiology and ecology. Philos Trans R Soc B-Biol Sci 363:301-319.

Mehlum F, Bakken H (1994) Seabirds in Svalbard (Norway): status, recent changes and management. Seabirds on Islands Threats, Case Studies and Action Plans, Birdlife Conservation Series. BirdLife International, Cambridge.

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.

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and relation between ^{15}N and animal age. Geochim Cosmochim Acta 48:1135-1140.

MOSJ (2012) Miljøovervåkning Svalbard og Jan Mayen - MOSJ. http://mosj.npolar.no/.

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.

Mundy CJ, Gosselin M, Ehn J, Gratton Y, Rossnagel A, Barber D, Tremblay J-É, Palmer M, Arrigo KR, Darnis G, Fortier L, Else B, Papakyriakou T (2009) Contribution of under-ice primary production to an ice-edge upwelling phytoplankton bloom in the Canadian Beaufort Sea. Geophys Res Lett 36:10.1029/2009GL038837.

Napolitano GE, Pollero RJ, Gayoso AM, MacDonald BA, Thompson RJ (1997) Fatty acids as trophic markers of phytoplankton blooms in the Bahia Blanca estuary (Buenos Aires, Argentina) and in Trinity Bay (Newfoundland, Canada). Biochem Syst Ecol 25:739-755.

Niehoff B (2007) Life history strategies in zooplankton communities: The significance of female gonad morphology and maturation types for the reproductive biology of marine calanoid copepods. Prog Oceanogr 74:1-47.

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.

Nilssen KT, Ahlqvist I, Harbitz A, Haug T, Lindblom L (1998) Feeding habits of harp seals (*Phoca groenlandica*) during summer in Svalbard waters. Population Biology:1-21.

Nilssen KT, Grotnes PE, Haug T, Potelov V (1997) Seasonal variation in body condition of adult Barents Sea harp seals (*Phoca groenlandica*). NAMMCO Sci Pub 2:9-27.

Nilssen KT, Pedersen O-P, Folkow LP, Haug T (2000) Food consumption estimates of the Barents Sea harp seals. NAMMCO Sci Pub 2:9-28.

Nordstrom CA, Wilson LJ, Iverson SJ, Tollit DJ (2008) Evaluating quantitative fatty acid signature analysis (QFASA) using harbour seals *Phoca vitulina richardsi* in captive feeding studies. Mar Ecol-Prog Ser 360:245-263.

Norrbin F, Eilertsen HC, Degerlund M (2009) Vertical distribution of primary producers and zooplankton grazers during different phases of the Arctic spring bloom Deep Sea Res (II Top Stud Oceanogr) 56:1945-1958.

NSIDC (2011) National Snow and Ice Data Center. Arctic Sea Ice News and Analyses, updated frequently. http://nsidic.org/arcticseaicenews/index.html.

O'Reilly CM, Heckey RE, Cohen AS, Plisnier PD (2002) Interpreting stable isotopes in food webs: Recognizing the role of time averaging at different trophic levels. Limnol Oceanogr 47:306-309.

Olsen E, Grahl-Nielsen O (2003) Blubber fatty acids of minke whales: stratification, population identification and relation to diet. Mar Biol 142:13-24.

Orlova EL, Dolgov AV, Rudneva GB, Oganin IA, Konstantinova LL (2009) Trophic relations of capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*) in the Barents Sea as a factor of impact on the ecosystem. Deep Sea Res (II Top Stud Oceanogr) 56:2054-2067.

Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. Oecologia 128:1-14.

Pasternak A, Riser CW, Arashkevich E, Rat'kova T, Wassmann P (2002) *Calanus* spp. grazing affects egg production and vertical carbon flux (the marginal ice zone and open Barents Sea). J Mar Syst 38:147-164.

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annual Revue of Ecological Systems 18:293-320.

Petursdottir H, Gislason A, Falk-Petersen S, Hop H, Svavarsson J (2008) Trophic interactions of the pelagic ecosystem over the Reykjanes Ridge as evaluated by fatty acid and stable isotope analyses. Deep Sea Res (II Top Stud Oceanogr) 55:83-93.

Plourde S, Campbell RG, Ashijan CJ, Stockwell DA (2005) Seasonal and regional patterns in egg production of *Calanus glacialis*/*marshallae* in the Chukchi and Beaufort Seas during spring and summer, 2002. Deep Sea Res (II Top Stud Oceanogr) 52:3411–3426.

Pond DW, Tarling GA (2011) Phase transitions of wax esters adjust buoyancy in diapausing *Calanoides acutus*. Limnol Oceanogr 56:1310-1318.

Post DM (2002) Using stable isotopes to estimate trophic positions: models, methods, and assumptions. Ecology 83:703-718.

Potelov V, Nilssen KT, Svetochev V, Haug T (2000) Feeding habits of harp (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) during late winter, spring and early summer in the Greenland Sea. NAMMCO Sci Pub 2:40-49.

Rasmussen B (1960) Om klappmyssbestanden i det nordlige Atlanterhav. Fisken og Havet 1:1-23.

Renaud PE, Berge J, Varpe Ø, Lønne OJ, Nahrgang J, Ottesen C, Hallanger I (2012) Is the poleward expamsion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*? Polar Biol.

Reuss N, Poulsen LK (2002) Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. Mar Biol 141:423-434.

Rey-Rassat C, Irigoien X, Harris R, Carlotti F (2002) Energetic costs of gonad development in *Calanus finmarchicus* and *C. helgolandicus*. Mar Ecol-Prog Ser 238:301-306.

Rudels B, Jones PE, Schauer U, Eriksson P (2004) Atlantic sources of Arctic Ocean surface and halocline waters. Polar Res 23:181-208.

Saiz E, Calbet A (2011) Copepod feeding in the ocean: scaling patterns, composition of their diet and the bias of estimates due to microzooplankton grazing during incubations. Hydrobiologia 666:181-196.

Sakshaug E (1997) Biomass and productivity distributions and their variability in the Barents Sea. ICES J Mar Sci 54:341-350.

Sakshaug E, Kovacs KM (2009) Introduction. In: Sakshaug E, Johnsen G, Kovacs KM (eds) Ecosystem Barents Sea. Tapir, Trondheim.

Saloranta TM, Haugan PM (2001) Interannual variability in the hydrography of Atlantic water northwest of Svalbard. J Geophys Res (C Oceans) 106:13931-13943.

Sargent J, Henderson RJ (1986) Lipids. In: Corner EDS, O'Hara SCM (eds) The biological chemistry of marine copepods. Clarendon Press, Oxford, pp 491-531.

Sargent JR (1976) The structure, metabolism and function of lipids in marine organisms. In: Malins DC, Sargent JR (eds) Biochemical and biophysical perspectives in marine biology. Academic Press, London, pp 149-212.

Sargent JR, Eilertsen HC, Falk-Petersen S, Taasen JP (1985) Carbon assimilation and lipid production in phytoplankton in northern Norwegian fjords. Mar Biol 85:109-116.

Sargent JR, Falk-Petersen S (1988) The lipid biochemistry of calanoid copepods. Hydrobiologia 167:101-114.

Saunders PA, Deibel D, Stevens CJ, Rivkin RB, Lee SH, Klein B (2003) Copepod herbivory rate in a large arctic polynya and its relationship to seasonal and spatial variation in copepod and phytoplankton biomass. Mar Ecol-Prog Ser 261:183-199.

Scott CL, Falk-Petersen S, Gulliksen B, Lønne OJ, Sargent JR (2001) Lipid indicators of the diet of the sympagic amphipod *Gammarus wilkitzkii* in the Marginal Ice Zone and in open waters of Svalbard (Arctic). Polar Biol 24:572-576.

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.

Sergeant DE (1991) Harp seals, man and ice. Can Spec Publ Fish Aquat Sci 114:1-153.

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

Slagstad D, Tande KS (1990) Growth and production dynamics of *Calanus glacialis* in an Arctic pelagic food web. Mar Ecol-Prog Ser 63:189-199.

Smith SL (1990) Egg production and feeding by copepods prior to the spring bloom of phytoplankton in the Fram Strait area of the Greenland Sea. Mar Biol 106:59-69.

Søreide JE, Falk-Petersen S, Hegseth EN, Hop H, Carroll ML, Hobson KA, Blachowiak-Samolyk K (2008) Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. Deep Sea Res (II Top Stud Oceanogr) 55:2225-2244.

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006a) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Oceanogr 71:59-87.

Søreide JE, Leu E, Berge J, Graeve M, Falk-Petersen S (2010) Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Global Change Biol 16:3154-3163.

Søreide JE, Tamelander T, Hop H, Hobson KA, Johansen I (2006b) Sample preparation effects on stable C and N isotope values: a comparison of methods in Arctic marine food web studies. Mar Ecol-Prog Ser 328:17-28.

Steen H, Vogedes D, Broms F, Falk-Petersen S, 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.

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

Swalethorp R, Kjellerup S, Dunweber M, Nielsen TG, Moller EF, Rysgaard S, Hansen BW (2011) Grazing, egg production, and biochemical evidence of differences in the life strategies of

Calanus finmarchicus, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. Mar Ecol-Prog Ser 429:125-144.

Tamelander T, Kivimae C, Bellerby RGJ, Renaud PE, Kristiansen S (2009) Base-line variations in stable isotope values in an Arctic marine ecosystem: effects of carbon and nitrogen uptake by phytoplankton. Hydrobiologia 630:63-73.

Tamelander T, Renaud PE, Hop H, Carroll ML, Ambrose JWG, Hobson KA (2006) Trophic relationships and pelagic-benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. Mar Ecol-Prog Ser 310:33-46.

Tande KS (1991) *Calanus* in north norwegian fjords and in the Barents Sea. Polar Res 10:389-407.

Tande KS, Hassel A, Slagstad D (1985) Gonad maturation and possible life cycle strategies in *Calanus finmarchicus* and *Calanus glacialis* in the northwestern part of Barents Sea. Paper presented at the 18th European Marine Biology Symposium, Oslo,

Tande KS, Henderson RJ (1988) Lipid composition of copepodite stages and adult females of *Calanus glacialis* in Arctic waters of the Barents Sea. Polar Biol 8:333-339.

Terrado R, Medrinal E, Dasilva C, Thaler M, Vincent W, Lovejoy C (2011) Protist community composition during spring in an Arctic flaw lead polynia. Polar Biol 34:1797-1801.

Thiemann GW, Iverson SJ, Stirling I (2009) Using fatty acids to study marine mammal foraging: The evidence from an extensive and growing literature. Mar Mamm Sci 25:243-249.

Tourangeau S, Runge JA (1991) Reproduction of *Calanus glacialis* under ice in spring in Southeastern Hudson Bay, Canada. Mar Biol 108:227-233.

Tremblay J-E, Bélanger S, Barber DG, Aspelin M, Martin J, Darnis G, Fortier L, Gratton Y, Link H, Archambault P, Williams WG, Philippe B, Gosselin M (2011) Climate forcing multiplies biological productivity in the coastal Arctic Ocean. Geophys Res Lett 38:L18604.

Tremblay JE, Michel C, Hobson KA, Gosselin M, Price NM (2006) Bloom dynamics in early opening waters of the Arctic Ocean. Limnol Oceanogr 51:900-912.

Tucker S, Bowen WD, Iverson SJ, Blanchard W, Stenson GB (2009a) Sources of variation in diets of harp and hooded seals estimated from quantitative fatty acid signature analysis (QFASA). Mar Ecol-Prog Ser 384:287-302.

Tucker S, Bowen WD, Iverson SJ, Stenson GB (2009b) Intrinsic and extrinsic sources of variation in the diets of harp and hooded seals revealed by fatty acid profiles. Can J Zool 87:139-151.

van Dongen BE, Schouten S, Sinninghe Damsté JS (2002) Carbon isotope variability in monosaccharides and lipids of aquatic algae and terrestrial plants. Mar Ecol-Prog Ser 232:83-92.

Vander Zanden MJ, Rasmussen JB (2001) Variation in delta N-15 and delta C-13 trophic fractionation: Implications for aquatic food web studies. Limnol Oceanogr 46:2061-2066.

Varpe Ø (2012) Fitness and phenology: annual routines and zooplankton adaptions to seasonal cycles. J Plankton Res (Horizons) DOI: 10.1093/plankt/fbr108.

Varpe Ø, Fiksen Ø (2010) Seasonal plankton-fish interactions: light regime, prey phenology, and herring foraging. Ecology 91:311-318.

Varpe Ø, Fiksen Ø, Slotte A (2005) Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. Oecologia 146:443-451.

Varpe Ø, Jørgensen C, Tarling GA, Fiksen Ø (2007) Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. Oikos 116:1331-1342.

Varpe Ø, Jørgensen C, Tarling GA, Fiksen Ø (2009) The adaptive value of energy storage and capital breeding in seasonal environments. Oikos 118:363-370.

Volkman JK, Eglinton G, Corner EDS (1980) Stereols and fatty acids of marine diatom *Biddulphina sinensis*. Phytochemistry 19:1809-1813.

Walczowski W, Piechura J (2007) Pathways of the Greenland Sea warming. Geophys Res Lett 34.

Walczowski W, Piechura J (2011) Influence of the West Spitsbergen Current on the local climate. Int J Climatol 31:1088-1093.

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

Wang SW, Hollmen TE, Iverson SJ (2010) Validating quantitative fatty acid signature analysis to estimate diets of spectacled and Steller's eiders (*Somateria fischeri* and *Polysticta stelleri*). J Comp Physiol B 180:125-139.

Wang SW, Iverson SJ, Springer AM, Hatch SA (2009) Spatial and temporal diet segregation in northern fulmars *Fulmarus glacialis* breeding in Alaska: insights from fatty acid signatures. Mar Ecol-Prog Ser 377:299-307.

Williams CT, Iverson SJ, Buck CL (2009) The effects of diet and caloric restriction on adipose tissue fatty acid signatures of tufted puffin (*Fratercula cirrhata*) nestlings. J Comp Physiol B 179:711-720.

Zenkevitch L (1963) Biology of the Seas of the USSR. Georg Allen and Unwin, London.

Paper I

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