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Lipids and diapause in *Calanus* spp. in a high-Arctic fjord: state-dependent strategies?

Tracking lipids through the polar night

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Abstract:

Calanus copepods *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* are keystone species in the Arctic marine ecosystem, constituting 70-90% of the zooplankton biomass. In high latitudes, the growing season is short and unpredictable, and the winter long and unproductive. These species have adapted flexible life histories, lipid accumulation, and a state of deep-water diapause to survive. Winter ecology is not well studied in the high-Arctic due to the difficulty of logistics. This study presents a high-resolution year-long time series of hydrological data, *Calanus* spp. stage composition, depth distribution and lipid content in a high-Arctic, seasonally ice covered fjord in Svalbard. The timing of descent to and ascent from diapause was of interest, specifically with regards to differences due to copepodite stage, prosome length, and lipid content. *C. glacialis* dominated the *Calanus* community and stages CIV and CV entered diapause. Females and males molted and ascended early 4 and 6 months before the spring phytoplankton bloom, respectively. Large, lipid-rich individuals molted and ascended first. Females reproduced in April, when there was nearly no food available, thus exhibiting capital breeding fueled by lipid stores. Descent to deep water began already in July, with the largest and most lipid rich individuals descending first.

Words: 200

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Introduction

Calanus copepods are keystone species in the Arctic marine ecosystem, constituting 70-90% of the zooplankton biomass in the Arctic (Blachowiak-Samolyk et al., 2008; Conover, 1988; Daase and Eiane, 2007; Falk-Petersen et al., 1999; Hirche, 1991; Jaschnov, 1970; Kwasniewski et al., 2003; Madsen et al., 2001; Tremblay et al., 2006). As the dominant herbivores in Arctic waters (Conover and Huntley, 1991; Falk-Petersen et al., 2009; Hop et al., 2006; Søreide et al., 2008), they play an essential role in the ecosystem by converting phytoplankton sugars into energy-rich wax esters upon which the upper levels of the Arctic marine food chain rely (Falk-Petersen et al., 1990). These wax esters comprise the majority of *Calanus*' considerable lipid reserves, which can be 50-70% of their dry weight (Lee et al., 2006; Sargent and Falk-Petersen, 1988; Scott et al., 2000). In addition to being a key energy storage which allows their survival in the harsh climate of the Arctic, these lipids also make *Calanus* species valuable prey to predators including seabirds, fish, and whales (Dale and Kaartvedt, 2000; Falk-Petersen et al., 1990; Karnovsky et al., 2003; Rogachev et al., 2008), species which are ecologically, economically, and culturally important.
The three *Calanus* species present in Arctic waters are *C. finmarchicus* (Gunnerus, 1765), *C. glacialis* (Jaschnov, 1955), and *C. hyperboreus* (Krøyer, 1838) *(Conover and Huntley, 1991; Daase and Eiane, 2007; Hirche, 1991; Søreide et al., 2008)*. These species are morphologically very similar, but differ in their size (*C. finmarchicus* being the smallest, and *C. hyperboreus* the largest), life spans and distributions, though they can co-occur (Conover, 1988; Falk-Petersen et al., 2009). *C. finmarchicus* is an Atlantic species with centers of distribution in the Norwegian Sea and Laborador Sea, though it can be brought up into the Arctic Ocean with Atlantic water as it submerges under Arctic waters along the shelf margin (Conover, 1988; Falk-Petersen et al., 2009). *C. glacialis* is distributed along the Arctic shelf seas and *C. hyperboreus* has the center of its distribution in the deep waters of the Arctic seas (Conover, 1988). Though much is known of the life history of copepods in boreal waters and the low-Arctic, less is known of the dynamics of these key species in the high-Arctic (Arnkvaern et al., 2005).

The high Arctic presents the marine ecosystem with unique challenges, including seasonal extremes of solar irradiance, sea ice for up to 10 months per year, and water temperatures near the freezing point of seawater(-1.8°C).These contribute to a seasonal pattern in Arctic seas consisting of a short growing season dependent upon sea ice, stratification and light, followed by a long, dark and unproductive winter (Conover and Huntley, 1991). As sea ice breaks up in spring, solar irradiance finally reaches the surface waters, where it promotes stratification of nutrient-rich water and facilitates a short burst of high primary productivity, in the form of phytoplankton which become available for zooplankton grazers *(Falk-Petersen et al., 2009)*. Ice break up is dependent on variable climatic conditions and consequently there is considerable interannual variability in the timing and magnitude of the spring phytoplankton bloom (Durbin et al., 2003; Heide-Jørgensen et al., 2007; Sameoto and D, 2001). In order to deal with the sporadic and extremely short-lived food supply and harsh environmental conditions, *Calanus* copepods in the Arctic have adopted a strategy of lipid accumulation and seasonal, ontogenic migration to deep waters, where they overwinter in a state of suspended development and highly reduced metabolism called diapause (Hagen and Auel, 2001; Hirche, 1996; Lee et al., 2006). This allows them to endure starvation in the unproductive winter season by relying on large lipid reserves and a low metabolism at depth (Jonasdottir, 1999). The copepods then ascend in

spring to surface waters to reproduce and exploit the abundant food supply of the spring phytoplankton bloom.

Calanus eggs hatch and develop through six naupliar stages (NI to NVI) and five pre-adult copepodite stages (CI to CV) and finally, the adult stage CVI, either male (CM) or female (CF) (Lee et al., 2006) Growth and development is dependent upon temperature and food availability (Campbell et al., 2001a; Campbell et al., 2001b; Fiksen and Carlotti, 1998). In the older stages, CIII, CIV and CV, copepodites accumulate large quantities of lipids in their lipid sacs (Hygum et al., 2000) and have the potential to enter diapause. For *C. finmarchicus*, a species which typically has a life span of one year, the main overwintering stage is CV (Arnkvaern et al., 2005; Falk-Petersen et al., 2009). *C. glacialis* has a typical life span of 1-2 years, and the main overwintering stages are CIV and CV *(Arnkvaern et al., 2005; Falk-Petersen et al., 2009; Kosobokova, 1999)*. C.hyperboreus has the longest potential life span, ranging 1-5 years, and can enter diapause as CIII, CIV and CV *(Falk-Petersen et al., 2009, and sources within)*.

Diapause depth is usually between 200m and 2000m, depending on ocean bathymetry and species, with *C. finmarchicus* and *C. hyperboreus* diapausing up to several thousand meters depth (Auel et al., 2003; Falk-Petersen et al., 2009; Heath, 1999; Heath et al., 2000; Østvedt, 1955; Visser and Jonasdottir, 1999) and *C. glacialis* in shallower shelf seas (Arnkvaern et al., 2005; Kosobokova, 1999). The diapause depth is likely also influenced by finding the depth of the neutral buoyancy of the copepod's lipids at a given temperature and pressure (Dale et al., 1999; Lee et al., 2006; Visser and Jonasdottir, 1999) and potentially by the presence of predatory fish (Bagøien et al., 2001; Dale et al., 1999). In diapause, the copepods are mostly quiescent (although alert and capable of rapid escape responses) (Miller and Tande, 1993), they do not feed or move their intestine, the gut-epithelium morphology changes (Dahms, 1995) , and there is a reduction in the molting hormones ecdysteroids in *C. finmarchicus* (Johnson, 2004). Metabolism is highly reduced, but still continues on a low level, around 15-30% of the normal, surface-dwelling CV respiration rate (Hirche, 1983, 1989; Miller et al., 1991) Benefits of diapause also include darkness and immobility, likely providing protection from predators which are reliant on visual or mechanical cues and low parasite loads (Bagøien et al., 2001; Dale et al., 1999; Kaartvedt, 1996, 2000; Miller et al., 1991).

Life History Flexibility

Phenology is especially important in highly seasonal environments (Hagen and Auel, 2001; Hansen et al., 2003; Varpe, 2007; Varpe et al., 2009). As the periods of food supply are short and sporadic in the Arctic, the success of *Calanus* populations depends upon the temporal match of their reproduction to their food supply, the phytoplankton and ice algae blooms (Falk-Petersen et al., 2009; Hagen and Auel, 2001; Hirche and Kosobokova, 2003; Søreide et al., 2010). Timing reproduction such that feeding nauplii stages (NIII or later) and young copepodites occur at the beginning of the bloom may result in the best utilization of a bloom for the developing generation (Irigoien, 2004). However, consideration of other factors which also vary around the timing of the spring bloom, such as predation pressure, has been shown in life history models to affect the fitness of offspring produced at different times in relation to the spring bloom(Varpe, 2007; Varpe et al., 2009). Eggs produced too late in the season may not reach an overwintering stage before the onset of winter(Varpe, 2007).

Reproductive strategy

The three *Calanus* species exhibit different reproductive strategies to cope with the different seasonal environments of their main distributions (Falk-Petersen et al., 2009; Hagen and Auel, 2001; Hirche and Kosobokova, 2003; Hirche and Kwasniewski, 1997; Niehoff et al., 2002). For *C. finmarchicus*, which is adapted to seas with a predictable annual spring bloom, complete gonad development and egg production are dependent upon ingested food (Diel and Tande, 1992; Hagen and Auel, 2001; Harris et al., 2000; Niehoff et al., 2002; Plourde and Runge, 1993; Runge, 1985). *C. glacialis*, whose range is the seasonally ice-covered Arctic seas, is adapted to the possibility of variable spring bloom timing, reliant on ice breakup timing. Accordingly, *C. glacialis* is able to reproduce either before the spring bloom, relying solely on lipid reserves or utilize the bloom to reproduce at a higher rate while feeding (Hirche and Kattner, 1993; Kosobokova, 1999; Smith, 1990). Lastly, *C. hyperboreus* , which lives primarily in ice-covered waters, reproduces in the deep in the absence of food in late winter, maturation and egg production being fueled entirely by stored lipid (Conover and Siferd, 1993; Hirche and Niehoff, 1996).

The Arctic *Calanus* species therefore exhibit a diversity of reproductive strategies (Falk-Petersen et al., 2009; Hagen and Auel, 2001; Lee et al., 2006) representing both income and capital breeding. Income breeding refers to reproduction based on concurrent food intake, whereas capital breeding describes reproduction based on stored resources (Jönsson, 1997; Lee et al., 2006). Copepods may exhibit different strategies at different times, possibly dependent upon the lipid storage state of the individual (Varpe et al., 2009) and environmental conditions.

Diapause

Diapause plays a crucial role for *Calanus* in surviving in unpredictable environments (Dahms, 1995). Diapause is flexible in its phenology, ontogenic onset, and duration, allowing for a plastic life history strategy. For these reasons, *Calanus* is able to survive and reproduce over large geographic ranges and in environments with large interannual variability (Hind et al., 2000; Johnson, 2004; Miller et al., 1991; Planque et al., 1997). *Calanus* copepods are able to produce several generations during one year before reentering diapause (Østvedt, 1955; Varpe and Fiksen, 2010), indicating that diapause is a dynamic response to environmental conditions). The timing of the diapause state also shows variability, potentially matching the local conditions. The phenology of *C. finmarchicus* arousal from dormancy and peak of reproduction varies by several months across its entire North Atlantic range(30-80°N, 80-90°E), likely reflecting differences in the spring bloom timing along a latitudinal gradient (Arashkevich et al., 2004; Hind et al., 2000; Johnson et al., 2008; Planque and Batten, 2000; Planque et al., 1997; Speirs et al., 2006). Johnson (2004) found similar variation in diapause initiation in *C. pacificus* in the waters off southern California. Proximate populations can also exhibit differences in dormancy timing by several months, if the hydrography of the areas shows stark differences (Johnson et al., 2008).

Life span

In addition to variability in diapause phenology, the life history strategies, or the stages at which diapause occurs, of *Calanus* copepods show considerable flexibility as well, varying between sites and between years *(Falk-Petersen et al., 2009; Madsen et al., 2001)*. The life span depends on local conditions

for feeding, growth and development possible during the summer period (dependent on food availability, water temperature, and the length of the food availability) (Arashkevich et al., 2004; Tande, 1991). Often, life spans are longer in higher latitudes. At some sites at lower latitudes in the Norwegian Sea, several generations can be produced within one summer, whereas at other sites with lower growth potential, younger stages enter diapause at the end of summer, and the life span becomes multiannual *(Arashkevich et al., 2004; Arnkvaern et al., 2005; Falk-Petersen et al., 2009; Scott et al., 2000)*. For example, *C. glacialis* has a 2 year life cycle in the White Sea and the high north (Arnkvaern et al., 2005; Kosobokova, 1999; Scott et al., 2000; Søreide et al., 2010) and an annual life cycle south of the polar front (Conover, 1988). The ability to extend the life span by entering diapause at early stages in years with poor feeding and growth conditions is especially pronounced in *C. glacialis* and *C. hyperboreus*, and gives them an advantage over *C. finmarchicus* in stochastic environments (Arnkvaern et al., 2005; Falk-Petersen et al., 2009; Hagen and Auel, 2001).

Miller et al. (1991) point out that the evolution of phenology to match local environments over broad geographical ranges is a more amenable solution than evolving different temperature and nutritional ranges for the species. This geographical diversity in reproductive strategy, diapause phenology and life span is an adjustable response to the local environment, a manifestation of the "flexible repertoire of behaviors" *Calanus* can use to maximize their fitness in response to an unpredictable environment (Fiksen and Carlotti, 1998). Fiksen (2000), in his models of optimal life history strategies for *C. finmarchicus*, found that a dynamic response to the environment was the only evolutionarily robust trait, and that 'genes' dictating a fixed probability of entering diapause at a given stage soon were dropped from the population (Fiksen, 2000). However, the mechanism by which *Calanus* are able to alter their phenology and life history to a range of habitats is unknown (Arashkevich et al., 2004)

Diapause Triggers

Despite its importance in understanding the population dynamics and phenology of *Calanus* populations (Speirs et al., 2006), the physiological triggers dictating the initiation and termination of diapause are unknown (Heath, 1999; Hind et al., 2000; Hirche, 1996; Miller et al., 1991). Several hypotheses have been set forth. One possibility is photoperiod (Miller et al., 2000), which has been shown to trigger diapause in insects and copepods with resting eggs (Dahms, 1995), and could explain the latitudinal variation in phenology. However, photoperiod has not been shown to instigate diapause in *Calanus*, in either the field or in experiments (Hind et al., 2000; Johnson, 2004; Johnson et al., 2008; Miller et al., 1991; Niehoff and Hirche, 2005). Several studies have shown that the period in which *Calanus* CV copepods enter diapause stretches from before the summer solstice , when daylengths are increasing, through the autumn equinox , a period when daylengths are decreasing (Johnson, 2004; Niehoff and Hirche, 2005). Furthermore, control of ascent by photoperiod is highly unlikely due the extremely low light levels in the overwintering habitats of *C. finmarchicus* at depths of over 1000m and in the high north, when ascent occurs during or near the end of the polar night (Hind et al., 2000). *C. finmarchicus* is a deep water species, and therefore is used to diapausing in 1000m, supposedly without environmental cues for ascent, whereas *C. glacialis* is a fjord and coastal species, and therefore potentially could get some light cues for ascent at relatively shallow diapause depths. Finally, the intrapopulation asynchronicity of diapause ascent also indicates that the trigger is not solely an environmental cue (Heath, 1999; Thorisson, 2006).

An alternate explanation of diapause timing, especially arousal, is that of an endogenous timer, or an internal clock, possibly controlled by the endocrine system (Dahms, 1995; Miller et al., 1991). In his experiment on *C. finmarchicus* done in complete darkness, Harris (1963) found that there was an "intrinsic rhythm of activity" which produced diurnal, vertical migrations throughout the year, except for the winter months of November-January, when all activity stopped (Harris, 1963). Østvedt (1955) suggested that *C. finmarchicus* overwintering in the dark of 1000m may need to respond to the cue of gonad development rather than photoperiod for diapause arousal (Hirche, 1996; Østvedt, 1955). Irigoien (2004) and Johnson (2004) suggest an analog to the insect hormone methyl farnesoate as potential hormonal cues, but a diapause-regulating hormone has not been identified yet in *Calanus*.

Modeling diapause timing in *Calanus finmarchicus* at four distant sites, both coastal and oceanic, from 57°N to nearly 70°N, in the NW Atlantic, (Hind et al., 2000) concluded that entry into diapause was controlled by food limitation and the termination of diapause came about after normal development, at a slowed, temperature-dependent rate, progressed throughout the winter. They suggested that at the point of molting from CIV to CV, a copepod would assess food availability and, if it was low, the CV would enter diapause. Thus, geographical differences in phenology may be a reflection of differential bloom dynamics, and timing of diapause entry could change interannually depending on food conditions. However, this is dependent upon the ability of the older copepodite stages to interpret food availability. High lipid storage is necessary before entering diapause and therefore waiting until stage CIV detects low food concentrations may be risky, as CVs may face both starvation and high predation risk in surface waters (Johnson, 2004; Kaartvedt, 2000; Varpe et al., 2009). Furthermore, as Speirs et al. (2006) pointed out, there are often individuals descending to diapause early in the summer, while phytoplankton food concentrations are still high, which seems to invalidate the food-limitation hypothesis. The idea that diapause duration is dependent upon a slow, but ongoing, development over winter is supported by Hirche (1983), who found that *C. finmarchicus* CVs took progressively less time to molt into adults in the lab after sampling as the winter progressed.

Role of Lipids in Diapause and Life History

Recently, more focus has been put on the role of lipids in controlling the diapause state (Fiksen, 2000; Fiksen and Carlotti, 1998; Hassett, 2006; Ingvarsdóttir et al., 1999; Irigoien, 2004; Jonasdottir, 1999; Maps et al., 2010; Miller et al., 2000; Pepin and Head, 2009; Rey-Rassat et al., 2002; Saumweber, 2006) and reproductive strategy (Lee et al., 2006; Varpe et al., 2009). A state-dependent control of diapause would help explain the intrapopulation variability in diapause timing as well as the geographic variability. Irigoien (2004) and Maps (2010) propose a lipid-accumulation hypothesis where both diapause initiation and termination are controlled by a copepod's lipid status. Indeed, lipid accumulation may control the levels of diapause-regulating hormones, as many hormones are fatty acid or cholesterol derivatives (Irigoien, 2004).

The minimum lipid level required for entry into diapause should support metabolism throughout the winter, the ascent migration, molt to adult and the beginning of gonad maturation (Arashkevich et al., 2004; Irigoien, 2004; Rey-Rassat et al., 2002) as these processes often occur before the bloom, in low food conditions (Hirche and Kattner, 1993). For *C. finmarchicus*, a species whose final gonad maturation and egg

production is dependent on ingested food, this minimum amount of lipids may be sufficient. It has therefore been suggested that descent to diapause in *C. finmarchicus* is reliant upon reaching a threshold of lipid reserves (Irigoien, 2004; Johnson et al., 2008; Maps et al., 2010), an estimated 70ug, or 25-50% of dry weight of a CV (Jonasdottir, 1999; Rey-Rassat et al., 2002). Those individuals that did not reach the threshold at the end of the summer would remain in the surface, facing predation and starvation over winter (Hassett, 2006; Irigoien, 2004).

For *C. glacialis* and *C. hyperboreus* , which often use lipids to mature and produce eggs before the bloom, more lipid than this minimum would be necessary in order to fuel these energy-costly processes (Hirche and Bohrer, 1987; Lee et al., 2006). The amount of "surplus" lipid a copepod has after diapause and molt may affect its reproductive strategy (Lee 2006), where greater lipid stores allow for the production high-fitness, capitally bred eggs independent of the spring bloom (Varpe 2009). Early eggs produced before the phytoplankton bloom are important for high-latitude copepods (Hagen and Schnack-Schiel, 1996) and have been shown to have higher fitness than those produced later (Varpe, 2007). Individuals with low lipids may not be able to produce eggs before the bloom, and must wait until food is available. In this way, lipid accumulation before diapause may affect reproductive strategy and timing the next spring. Diapause descent timing therefore involves a tradeoff between lipid accumulation and predation risk, which is higher in surface waters (Kaartvedt, 2000; Varpe et al., 2009).

Arousal from diapause could also be lipid-mediated, with a lower limit potentially triggering ascent in *C. finmarchicus* (Hirche, 1996; Irigoien, 2004; Miller et al., 1991; Saumweber, 2006; Visser and Jonasdottir, 1999). Metabolism of lipid reserves does occur during diapause, with estimates ranging from ~5% reduction (Jonasdottir, 1999) to 50% (Arashkevich et al., 2004) over the winter period for *C. finmarchicus* . Saumweber et al. (2006) estimated potential diapause lengths for *Calanus finmarchicus* based upon body length, lipid reserves and water temperature, with warmer temperatures resulting in shorter diapause durations due to faster metabolism of lipid reserves. For *C. glacialis*, having high lipids may allow females to molt early and produce eggs females before the phytoplankton bloom. As Maps et al. (2010) point out, it is possible that descent is lipid- mediated and ascent is triggered by a different cue.

Mismatch Potential

Polar regions are expected to experience the effects of global warming more acutely than lower latitudes (IPCC 2007). The physical environment of the Arctic is already changing rapidly, a phenomenon most starkly evident in the current decline of Arctic sea ice (Arrigo et al., 2008; Comiso and Josefino, 2006; Comiso et al., 2008; Parkinson et al., 2008). The last decade has shown significant quickening in the rate of loss of Arctic sea ice extent, both in winter and summer (Comiso and Josefino, 2006; Comiso et al., 2008), with an unprecedented low of summer sea ice extent in 2005 and then again in 2007, the last representing an astounding decrease of 23% from the previous year (Arrigo et al., 2008; Comiso et al., 2008; Parkinson et al., 2008) In general, the sea ice extent is the lowest it has been in the last 800 years (Fauria et al., 2010).

Climate change in the Arctic will mean less sea ice, but likely also earlier breakup timing in spring (Hansen et al., 2003; Ingram et al., 1996; Johannessen et al., 2004). The breakup of sea ice strongly affects

the timing of the spring phytoplankton bloom, as the albedo of sea ice prevents up to 90% of photosythetically active radiation (PAR) from penetrating into the surface (Smetacek and Nicol, 2005). Sea ice breakup allows the solar irradiation needed for bloom initiation, so earlier break up timing may result in earlier or more predictable spring blooms (Hansen et al., 2003; Swalethorp et al., in press). However, lack of sea ice may also postpone the bloom due to increased wind-driven mixing of the water column (Melle and Skjoldal, 1998).

Utilizing various reproductive strategies, Arctic *Calanus* spp. attempt to synchronize their reproduction with a short spring bloom (Hagen and Auel, 2001; Lee et al., 2006). If *Calanus* ascends from diapause and reproduces far before the bloom, copepodites may starve before the bloom arrives and egg production may be highly reduced for income breeders such as *C. finmarchicus*. If ascent and reproduction occurs after the bloom, the growing copepodites would have to spend a longer time feeding on a less abundant food supply in the surface, exposing themselves to predation (Cushing et al., 1990; Kaartvedt, 2000; Varpe et al., 2009) . Thus, if the timing of ice breakup shifts to earlier in the spring, it may create a mismatch in timing between the phytoplankton bloom and the ascent and reproduction of *Calanus*, wherein the *Calanus* population ascends too late to fully exploit the phytoplankton bloom (Hansen et al., 2003). This would reduce reproductive success and lower the ability of the next generation to store sufficient lipids for winter. It is unknown whether *Calanus* will be able to alter the timing of its ascent from diapause and reproduction to match an earlier bloom (Hansen et al., 2003; Norrbin et al., 2009). Thus, determining the factors which influence the timing of diapause, ascent, and reproduction are essential in understanding how *Calanus*, and resultantly the whole Arctic marine ecosystem, will respond to the decline of sea ice with climate change.

The Study

This study sought to investigate the seasonal dynamics of *Calanus* with regards to vertical distribution and individual lipid level in a high-Arctic, seasonally ice-covered fjord in Svalbard throughout an entire year (Jul 2008-Aug 2009). *Calanus* community composition and lipid sac volume data were collected by depth, and supplemented with hydrographical data from CTD hauls and a mooring stationed near the sampling site.

Specifically, I looked at the timing of the seasonal descent to and ascent from diapause of different developmental stages in two species of *Calanus* copepods (*C. finmarchicus* and *C. glacialis*). For *C. glacialis*, I investigated how the lipid level of copepodites varied by season, depth, and copepodite stage. Though *Calanus* species have been extensively studied in the summer months and at lower latitudes, little is known about their biology in the long, cold, and dark polar winter due to the logistical difficulty of fieldwork.

The study site was Billefjorden, on the west coast of Svalbard, a protected sill fjord with little advection, making it ideal for population development studies (Arnkvaern et al., 2005). *C. glacialis* dominates the *Calanus* community, comprising 60-80% of the total abundance of *Calanus*, the others being *C. finmarchicus*, 20-30%, and *C. hyperboreus*, 5-20% (Arnkvaern et al., 2005). This study focused on *C. finmarchicus* and *C. glacialis*.

Hypotheses

A) Descent

I hypothesize that the accumulation of sufficient lipid stores for overwintering is the trigger which initiates diapause. Accordingly, larger lipid stores should be found in those individuals which have descended to depth and likely begun diapause, whereas lipid-poor individuals who had not reached the threshold would remain in the surface waters attempting to accumulate lipids. If the threshold theory (Irigoien, 2004; Maps et al., 2010) is correct, individuals which have reached a threshold of lipid: body carbon would be triggered to descend, and the lipid richness in the diapausing habitat would be relatively uniform throughout the population. *C. glacialis*, however, may not follow the lipid threshold theory, as it benefits from surplus lipids, and thus may exhibit a wider range of lipid levels at the onset of diapause. We hypothesize that younger stages will descend later than CVs, remaining in the surface longer to exploit the longest period possible for feeding and developing. Descent will not be synchronous, but occur over a long period, as copepods reach sufficient lipid levels.

B) Ascent

In the spring, I hypothesize that *C. finmarchicus* and *C. glacialis* ascend to the surface before the sea ice breakup and the consecutive phytoplankton bloom, with reproduction timed such that the young copepodite stages co-occur with the phytoplankton bloom. *C. glacialis* may exhibit more of a capacity for capital breeding than *C. finmarchicus*, producing eggs before the onset of the phytoplankton bloom. As life history models predict that eggs produced early have the highest fitness (Varpe et al. 2007), the females with the highest lipids may utilize their reserves to ascend first and produce egg independently of the spring phytoplankton bloom (Varpe et al., 2009). If the length of diapause is dependent upon continued, slow development, the variation in timing of ascent will be similar to the variation in descent timing. However, if it is linked to environmental cues (i.e. photoperiod), the ascent will be more synchronous.

Methods

Study Area

The study was carried out monthly from July 2008 to August 2009, in Billefjorden, a high-Arctic, seasonally ice-covered fjord in Svalbard (78°40'N; 16°40'E). Billefjorden is a side-fjord of Isfjorden, the largest fjord on the west coast of Spitsbergen (Figure1). It is located in the innermost, northeastern part of Isfjorden and is around 30 km long and 5-8km wide. It is a double sill fjord, with an outer sill of about 70m depth protecting a basin of ~230m depth and an inner sill of 50m depth protecting an inner basin of approximately 190m depth (Nilsen et al 2008). Towards the head of the fjord, the fjord branches into two small bays Petuniabukta to the north and Adolfbukta to the south. The sampling site was located in Adolfbukta. A large glacier, Nordenskiöldbreen, a tributary of the Lomonosofonna icecap, meets the fjord at the back of Adolfbukta, providing meltwater and sediment in the summer and autumn. For 6-7 months of the year, Billefjorden is covered with sea ice and its protected, innermost bay, Adolfbukta, remains ice-covered the longest.

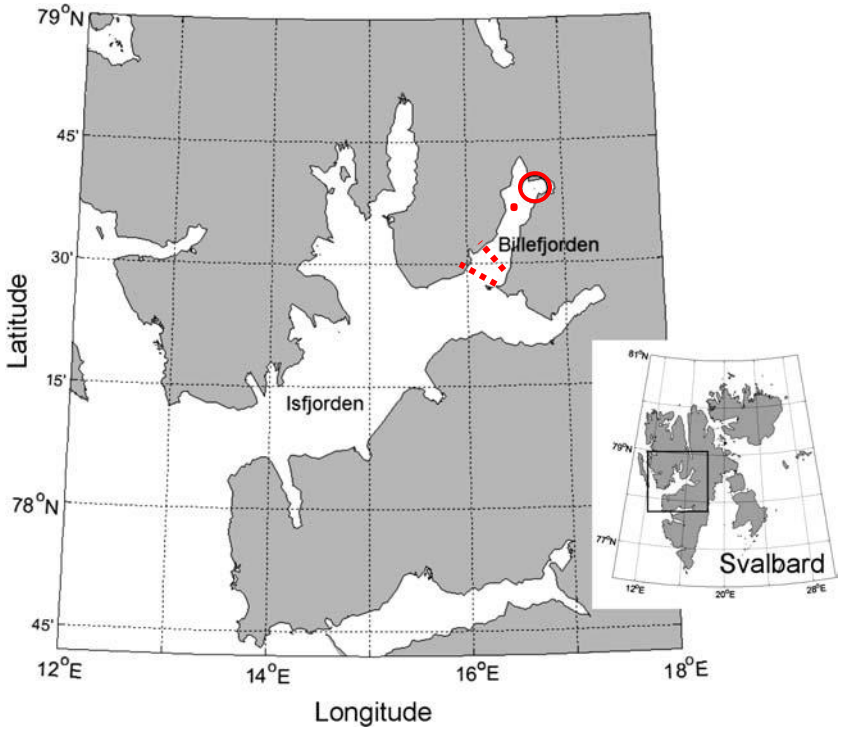

Figure 1**.** Map of Svalbard (inset) with Isfjorden, the largest fjord on the west coast, enlarged. Billefjorden is a side-fjord located in the northeast end of Isfjorden. The mooring and standard CTD sampling station were located in Adolfbukta, encircled in a red circle. The lone red dot indicates the location of the CTD station on June 17th. Red dotted lines indicate the two sills in Billefjorden. Modified from Arnkvaern et al. (2005).

The sills of Billefjorden provide some barrier to advection of outer water masses from Isfjorden. The Atlantic waters of the West Spitsbergen Current and the Arctic waters of the Sorkapp Current both strongly influence the hydrography of fjords along the west coast of Spitsbergen, including Isfjorden (Svendsen et al. 2002, Nilsen at al. 2008). Adolfbukta, the inner basin of Billefjorden, is apparently nearly entirely isolated from this, however (Nilsen et al. 2008, Darelius 2003). This isolation has the basis for previous zooplankton

population development studies in the fjord, which assume that the effects of advection are negligible on the population composition and that chronological observations reflect local population development (Arnkvaern et al 2005).

Sampling Trips

Fifteen sampling campaigns to Adolfbukta were carried out over the course of the study (2008-2009), with a minimum of monthly frequency and higher frequency in spring (Appendix Table 2). Zooplankton sampling was performed from a boat in the summer and autumn (July to December), when the fjord was ice-free, or through a hole sawed in the sea ice (~1m in diameter) when the fjord was ice-covered in winter (January to June). Samples were consistently collected at a site in inner Adolfbukta (39.72' N; 16º 44.34' E)(see Figure 1), with the exception of one sampling date, the 17th of June, 2009. On that date, the sea ice was thinning, with leads forming in Billefjorden. Therefore, samples were taken by boat in a lead in the ice near the middle of Billefjorden, inside the innermost sill but a few kilometers southwest of the typical sampling site. The water depth at this June sampling site was 146m compared to the 180m at the standard sampling site.

Physical Data

CTD casts concurrent with each sampling trip collected water temperature, fluorescence and salinity data at the Adolfbukta site. CTD casts were taken with a SAIV handheld CTD with the exception of two sampling dates, when a Seabird CTD was used (August 26t and September 6th). Both had a mounted fluorometer. The downcast was selected for analysis, with the exception of January 14th, when the downcast failed to record data.

In addition to the CTD casts, a mooring deployed in Adolfbukta from August 2008 to August 2009 provided hydrographic data with high temporal resolution. Six miniloggers measured temperature every 20 minutes at 46m, 56m, 76m, 111m, 126m, and 151m. Four Seabird CTDs (Conductivity Temperature Density instruments) measured conductivity, temperature, pressure, and density every 12 minutes at 19m, 30m, 90m, and 185m. A fluorometer and light sensor measured fluorescence and PAR (photosynthetically active radiation) were measured at 19m every 12 minutes. Water depth was 191m at the site of the mooring, and to avoid foulage by sea ice the uppermost instrument was located at 19m, next to an undersurface buoy. Flourescence was not calibrated with water samples, and thus is a relative measure which was supplemented with more detailed phytoplankton data collected at the zooplankton sampling site concurrently by L. Kuckero (2009). More information on the mooring can be found from J. Berge (UNIS, Svalbard). Though the mooring site was not exactly the same as the zooplankton and CTD sampling site, the mooring was within 2km of the sampling site in the same deep basin of Adolfbukta, with similar water depth (~185m). The bay has been shown to be relatively homogenous, stable and unaffected by advective currents (Darelius 2003), and it is assumed that the mooring represents the hydrological conditions at the sampling site.

MATLAB 7.3.0 R2006b (The MathWorks, Inc.) and Microsoft Excel 2007 (Microsoft Corporation) were used for physical data analyses and graphing. The seawater library toolkit 2.0.1 (CSIRO, Phil Morgan 1993)

for MATLAB was used to calculate seawater densities from mooring miniloggers and CTDs. All measurements from mooring instruments (temperature, salinity, density, PAR, fluorescence) were averaged by day. Temperature, salinity, and density measurements were then transformed into 7-day running averages for contour graphs. The minilogger at 76m was removed from analyses, as its measurements were consistently below -2C, and below CTD cast measurements at the same time and depth by 1-2C. The CTD salinity measurements from 36m were also discarded, as they were consistently>5 below similar measurements from CTD casts and unexpectedly low (~29) compared to the surrounding waters.

CTD cast data were interpolated in 1 meter depth sections, measurements from <0.2m were discarded, and the downcast was selected for analysis, with the exception of January, when the upcast was selected. On March 23 and 30, the CTD ceased to function below ~30m so only the upper water column was measured.

Satellite pictures from NASA and the Norwegian Meteorological Institute (polarview.met.no) were used to determine the date of sea ice freeze-up and break-up in Adolfbukta.

Zooplankton Sampling

Depth-stratified samples of zooplankton was either collected by a Multi Plankton Sampler (MPS, Hydrobios) or a WP2 closing net (Hydrobios), towed vertically at the depths: 20-0m, 50-20m, 100-50m, and 175-100m. Both nets had an opening of 0.25m^2 and a mesh size of 200 µm. Live zooplankton samples for lipid sac analysis were taken from two depth strata: surface, 50-0m, and deep, 175-100m. When the MPS was used, the two automatically-taken samples from 20-0m and 50-20m were combined to comprise the 50-0m sample. The MPS net was towed at a speed of approximately 1m/s by winch on board ship, and the WP2 was towed by hand or snowmobile at a similar speed when on sea ice. The zooplankton community samples were preserved in a 4% formaldehyde-sea water solution, buffered with borax, shortly (< 30 min, with the exception of one sampling trip November 4, when formalin was added 12h after sampling) after collection. In order to store the live samples at near-in situ temperatures, samples were transported back to the lab in large (~50L) buckets with false bottoms in the autumn and in 1L thermos bottles stored inside a thermal isolation chest in the winter, when air temperatures were often less than -15°C. They were transferred to a cold lab (~1-4°C) within hours of sampling ad kept in large buckets (2 -50L, depending on the density of the sample).

Zooplankton Community Analysis

For the enumeration of the *Calanus* community (N1-Adult), samples with abundant zooplankton were counted in subsamples of 5ml (from 250-500mL) until a minimum of 100 *Calanus* were counted per sample. Subsamples were taken using a large-mouthed pipette. Samples with few individuals were counted in their entirety. The developmental stage and prosome length was recorded for each of the counted individuals, prosome length at 16x or 20x being measured with the eyepiece ruler (precision: +/-0.05mm, calibrated to with a 2mm calibration slide) on a Leica dissecting microscope. A few samples were photographed and their prosome length measured digitally (see Lipid Sac Analysis methods). The volume of water sampled was calculated using the area of the net opening and the theoretical vertical distance the net

was towed. For density calculations, the volume of water sampled was calculated using the area of the net opening and the theoretical vertical distance the net was towed.

The three *Calanus* species have very similar morphologies, and have traditionally been separated into species by prosome length ranges at given developmental stages (Kwasniewski et al. 2003; Breur, 2003; Arkvaern et al. 2005). This length-based classification has been shown to vary depending on the fjord in which the zooplankton community is sampled (Kwasniewski et al., 2003; Arkvaern et al., 2005). The classifications determined by Arnkvaern et al. (2005) which were specifically generated from data on *Calanus* in Billefjorden were the most accurate for this study of that which could be found in the literature, though new genetics data (*Gabrielsen* et al., unpublished data) and prosome length distributions measured in this study were used to determine new classifications.

Lipid Sac Analysis: Transport and Imaging

The measurement of the lipid sacs of *Calanus* individuals was accomplished through digital image analysis of pictures of live copepods, as described in Vogedes etal (2010). When alive, the large lipid sac of *Calanus* copepods is clearly visible through their transparent exoskeleton. After death, however, this exoskeleton soon becomes opaque, and it is impossible to measure the lipid sac size with this method. Thus, the samples for lipid sac analysis were transported alive back to the laboratory at temperatures as close to *in situ* as possible (-2C<T<1C in winter, ~<5C in summer) and processed in the cold lab (~1-4°C) within two days after capture, mostly within one day. The live copepod samples were filtered into 200ml of seawater for subsampling, which was done with a large-mouthed pipetter. Subsamples were processed one by one until approximately 100 *Calanus* CIV, CV, CF (female), or CM (male) had been photographed. *Calanus* CIV, CV, CF, and CM individuals were gently picked out of the subsample using feather forceps and placed in a single droplet of seawater on a Petri dish. Thus immobilized on their side, a picture was taken from the lateral view. Pictures were taken with a high resolution camera (Sony HDR-HC7) mounted on the eyepiece tube of a Leica dissecting microscope. To enable measurement of the pictures, a calibration slide (2 mm or 1.5 mm diameter) was photographed at each magnification.

Lipid Sac Analysis: Image Analysis

Image analysis was performed in the free image analysis software "ImageJ" (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/, 1997-2008). The perimeter of the lipid sac was manually traced in the program, producing both a perimeter measurement and an area of the lipid sac, seen laterally. The prosome length was also measured. Using the calibration slide picture, the program calibrated all measurements from pixels to micrometers. Prosome length and developmental stage were used to determine the species according to the same method as for the community analyses. The lipid sac area data were transformed into total lipid values using the equation presented by Vogedes et al. (2010):

Eq. 1 $TL = 0.197A^{1.38}$ TL=total lipid (mg), A=lipid sac area (mm^2)

This method has been shown to be an accurate, fast, cheap, and non-destructive alternative to gas chromatography analyses in the quantification of the amount of total lipid and wax ester stored in individual *Calanus* copepods. Vogedes et al. (2010) found a high correlation between the lipid sac area and both the total lipid (r^2=0.94) and the wax ester content (r^2 = 0.95) (all data ln-transformed), as determined by gas-chromatography . Wax ester comprises the majority of *Calanus* lipids (Lee et al., 2006). Total lipid is presented in this study. There was no significant difference between the prosome lengths measured from digital images used in lipid sac analysis and those measured under the stereomicroscope for community quantification(est=-0.0033, t=-0.431, df=10598, p=0.666).

Condition Factor

To get a measure of lipid state which could be compared between copepods of different length, a condition factor was calculated which scaled total lipid to prosome length. Condition factors, which scale weight to length, can be used for comparing the body condition, fatness, or nutritional status of individuals of different lengths. Condition factor is a measure which has been developed in fisheries science over a century ago (Froese, 2006; Fulton, 1904; LeCren, 1951; Nash et al., 2006). The classic measure is Fulton's Condition Factor (Fulton, 1904; Ricker, 1975):

Eq. 2 $K = \frac{W}{L^3}$ where K= Fulton's condition factor, W= body weight, L=body length.

The Fulton condition factor has been adapted and utilized in zooplankton studies to evaluate copepodite condition in *Acartia clause* and *A. hudsonica* (Durbin and Durbin, 1978; Durbin et al., 1992) and *Calanus finmarchicus (Campbell et al., 2001b)*.

However, the standard practice of multiplying the length by the power of 3, the "cube-law", has been questioned by many, as reviewed by Froese (2006). LeCren (1951) altered Fulton's condition factor by introducing the modern "relative condition factor", which measures the deviation of an individual from the average predicted weight for its length, rather than the deviation from the "ideal growth" predicted from the cube law. Relative condition factor (K_{rel}) is defined as:

Eq. 4 $K_{rel} = W / aL^b$

where the parameters *a* and *b* come from the logarithmic weight - length relationship:

Eq. 5 $W = aL^b$

Though the factor *b* averages to be roughly equal to 3 for most fish species, there is significant variability between species, sexes, and stages (Froese, 2006), and thus is should be calculated for each weight-length relationship.

In this study, relative lipid condition factors were calculated from Eq. 4 (LeCren 1951), where weight was given as total lipid (mg) and length was given as prosome length (mm). The parameters a and b were determined from linear models fit to ln-transformed total lipid and prosome length data, using the logarithmic equivalent of Eq. 4:

Eq. 6 $$\ln W = \ln a + b \ln L$$

Models were fit individually for *C. glacialis* stages CIV, CV, CF, and CM, and thus the parameters used in the condition factors are stage-specific. Thus, the condition factors are relevant for comparison of condition within stage but not between different stages. A larger condition factor is taken to indicate better condition as it measures lipid content based on prosome length. Values over 1 are of higher condition than expected by the model, whereas those below 1 have a lower than expected condition.

Statistics

All statistic analyses were done with R-statistical environment (Version 2.9.2, www.r-project.org). Graphs were made using the graphics package "ggplot2". Least-squares regressions were performed to test for significant changes in total lipid levels or condition factor with time. Differences in total lipid, prosome length, and condition factor between surface and deep habitats and between sampling trips were tested using t-tests and pairwise t-tests with Holm corrections to control for multiple testing.

Results

Physical Data: hydrography, sea ice

Billefjorden was covered with fast ice continually from the beginning of January 2009 to the end June 2009. Frazil ice was observed in Adolfbukta, in inner Billefjorden, as early as the 4th of November, but satellite images indicate that fast ice froze in the fjord between the 23rd December 2008 and 2nd January 2009 (Figure 3). Ice break-up in Adolfbukta occurred once, between the 28th of June and 3rd of July (Figure 3). The ice was blown out of the fjord within a few days.

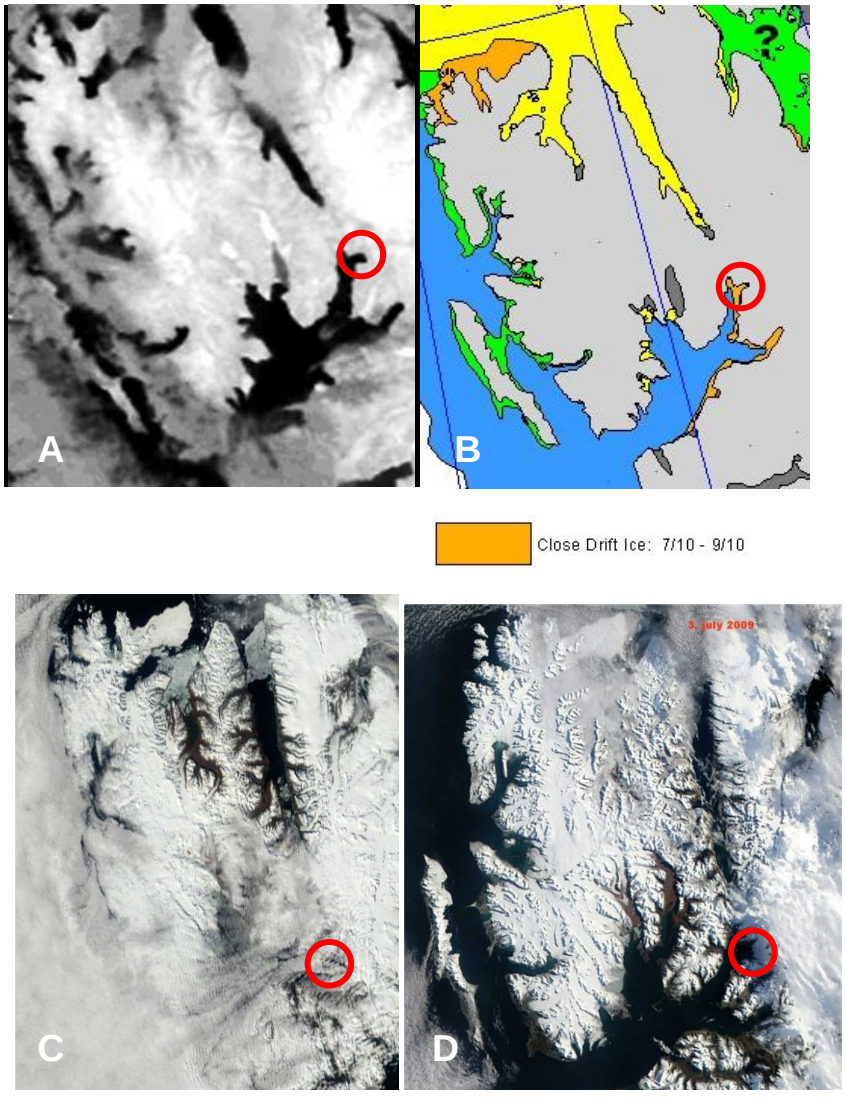

Figure 2. Satellite pictures (A,C, D) and compiled ice charts (B) for northwest Svalbard, showing the timing of sea ice cover and break up in Adolfbukta, Billefjorden during the winter of 2008-2009. Adolfbukta, Billefjorden is encircled with a red circle. The photo from December 23, 2008, (A), shows Billefjorden being ice-free, though on January 2, 2009, Adolfbukta is covered by 70-90% ice. The photos from June 28, 2009(A) and July 3, 2009(B) 2009 indicate the date of sea ice break up in Adolfbukta to be between those two dates. Sea ice cover in Adolfbukta, and most of Billefjorden, is complete on June 28th (C), but the fjord is ice free on July 3rd (D). Satellite pictures A, C, and D are from NASA, ice chart (B) from polarview.met.no.

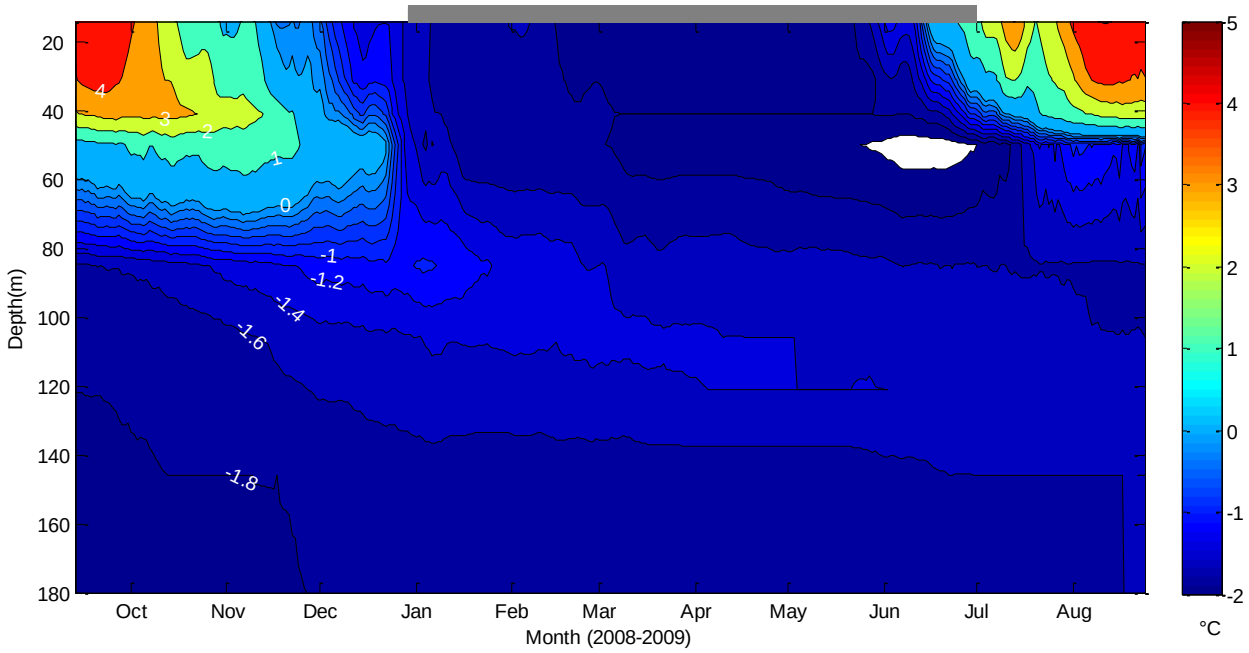

Figure 3. Temperature (°C) of the water column in Billefjorden, calculated from mooring CTDs and miniloggers situated at 19m, 30m, 46m, 56m, 90m, 111m, 126m, and 185m. Values are 7-day running averages. The grey bar indicates the period with sea ice cover.

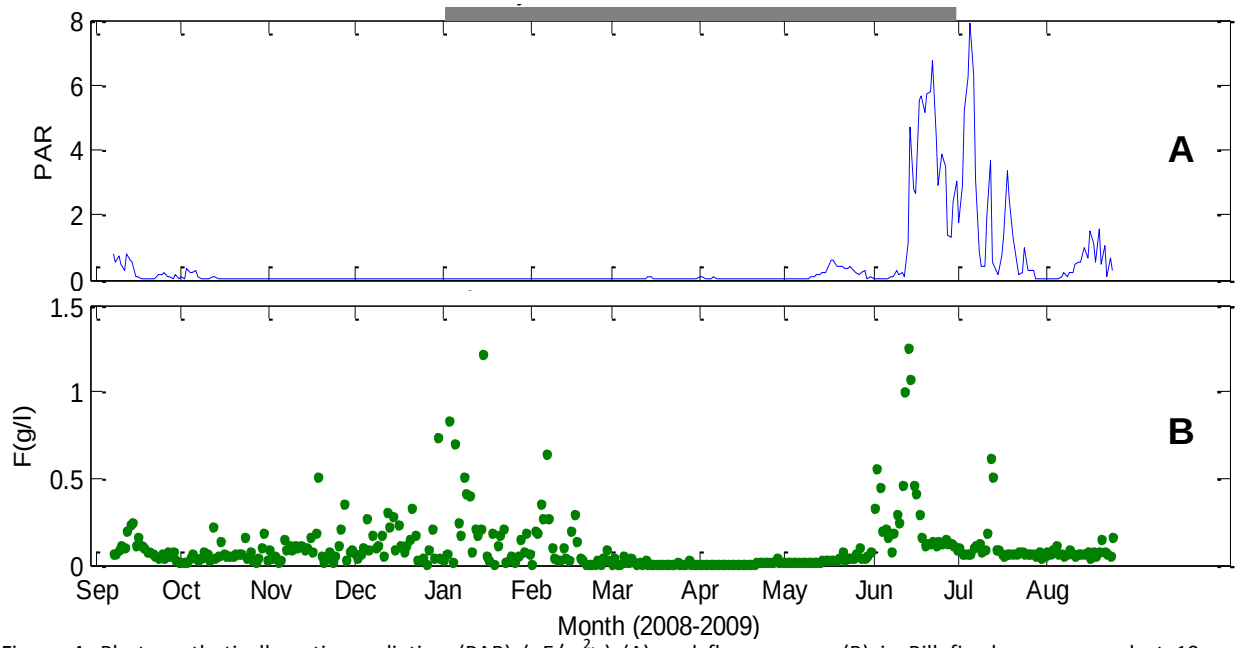

Figure 4. Photosynthetically active radiation (PAR) (µE/m^2·s) (A) and fluorescence (B) in Billefjorden, measured at 19m on the Adolfbukta mooring for one year (2008-2009). The grey bars indicate the period with sea ice cover.

Though ice break-up occurred at the end of June (Figure 4), warm water was evident under the ice before then. Beginning June 13th a temperature increase was observed at 19m on the mooring (Figure 4) and the June 17th CTD cast shows warm water to a depth of 47m and surface water of 1°C (Figure 8). Though the June 17th CTD cast was taken in an open lead at a slightly different site than the other CTDs, the mooring data supports the finding that by 13-17th of June, two weeks before ice break-up, warming was present in the surface waters. Interestingly, PAR measured at 19m from the mooring, increased sharply on June 14th (Figure 11a), earlier than the ice break-up date indicated by the satellite images and personal observations.

Two weeks before ice break up, June 13-17th, fluorescence measured at 19m on the mooring peaked (Figure 4b), which corresponds closely to first peak in PAR measured at the same depth, on June 14th (Figure 4a). From personal observations on June 17th, the ice was thin, with very little snow cover and many melt holes.

Species Determination

The similarity in morphology of the *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* is such that they are often determined to species based on defined ranges of prosome length (Kwasniewksi, Arnkvaern, Daase and Eiane). These prosome length boundaries are most often based on fitting overlapping distributions to a length frequency (MIX analysis) and have been found to vary geographically (Kwasniewksi, Arnkvaern, Daase and Eiane). Arnkvaern etal 2005 have published prosome ranges based on length frequency distributions for the three *Calanus* species in Billefjorden, and these were to be used in this study. However, in a genetic investigation of *C. glacialis* and *C. finmarchicus* from Billefjorden, Gabrielsen et al. (unpublished data) found that only 2 of 107 female *Calanus* copepodites from Billefjorden over a range of prosome lengths were *C. finmarchicus*, though 35 would have been assigned as *C. finmarchicus* according to Arnkvaern et al (2005). This is an overestimation of *C. finmarchicus* females of 1950%. Therefore, genetics data from Gabrielsen etal (unpublished data) were used to reevaluate the prosome length boundaries suggested by Arnkvaern etal (2005). The prosome length distributions gathered in this study (**Figure 5**), gathered both from individuals used in lipid sac analyses and for community analyses, added to the understanding of the relative abundances of the three *Calanus* species in Billefjorden and provided a large sample size (n= 11345) to give stronger support through genetically-supported MIX analyses for determining morphological species cutoffs from multimodal length distributions.

This study uses new prosome length cutoffs for differentiating between *C. finmarchicus* and *C. glacialis* (Table 1). For stages CIV-CF, *Gabrielsen* etal 's (in press) genetics data was used to determine prosome length boundaries between *C. glacialis* and *C. finmarchicus*. For a given stage, the proportion of copepods that were genetically determined to be *C. glacialis* and *C. finmarchicus* at a given prosome length(divided into 0.1mm bins) was multiplied by the frequency of that prosome length in the natural population. In this way, it was possible to determine cutoff sizes between *C. finmarchicus* and *C. glacialis* which would result in equal numbers of both species being misidentified, thus cancelling each other out. MIX analyses (MIX v3.0,MacDonald and Green 1988), supported with genetics data, were also performed for all stages and supported the cutoffs determined for CIV-CF (Figure 5, Table 1). For CIV and CV, the prosome length was slightly bimodal, with the mode representing the larger *C. glacialis* individuals being substantially larger than that of *C. finmarchicus* (Figure 5). MIX analysis determined that the proportion of *C. glacialis* for CIV and CV was 81% and 89% respectively (Appendix Table 1). Females and males showed a more unimodal distribution (Figure 5). Genetics data on females showed that 2 of the 107 females tested were *C. finmarchicus*, so a cutoff was determined (Table 1). Nonetheless, the proportion of the females which were *C. glacialis* was 0.8%. Genetics data was lacking for males, and the distribution was normal, producing only estimations of one species in the MIX analysis. These are presented in this study as *Calanus* sp. males.

The length distributions of young stages (CI-CIII) were slightly different than the older stages (Figure 5). Stage CIII showed bimodality in length distribution, though, the mode representing *C. finmarchicus* was larger (68%) than that of *C. glacialis* (27%). For CI and CII, no clear bimodality was present (Figure 5). Using Arnkvaern's boundaries, there was a dominance of *C. finmarchicus* in both CI and CII, and very few *C. glacialis*. *C. hyperboreus* was present primarily as young stages CI-CIV, with a few females.

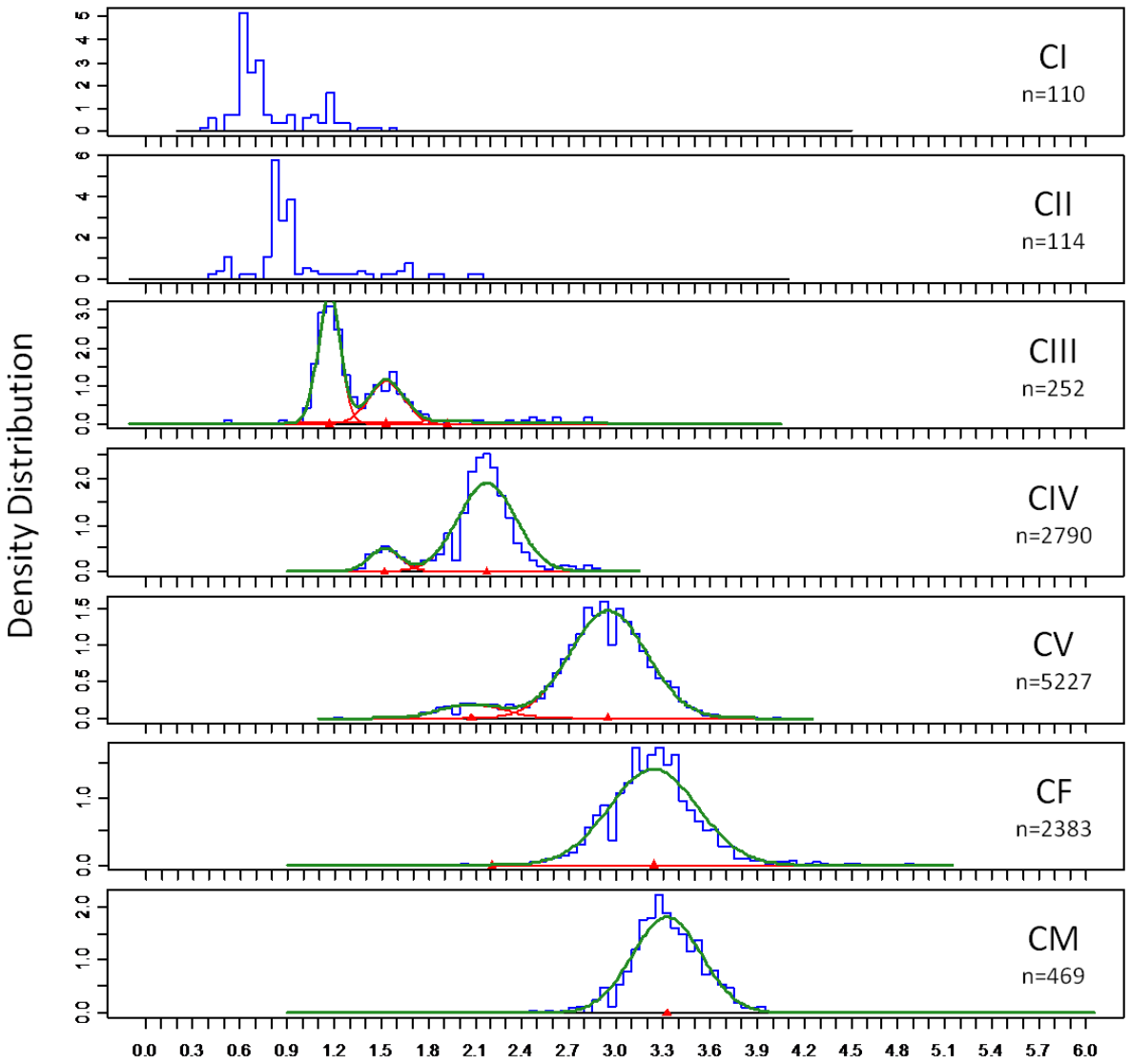

Figure 5. Prosome length density distribution of all *Calanus* copepodite stages (CI-CV, females (CF) and males (CM)) with length frequency analysis (MIX analysis). Length measurements are combined from both lipid analysis and formalin sample data from Billefjorden, 2008-2009. Sample sizes for each stage are given; total n= 11345. For CIV-CF, genetics data (*Gabrielsen* et. al., unpublished) was included as conditional data in the MIX analyses.

Table 1. Prosome lengths used for species determination for *Calanus finmarchius, C. glacialis,* and *C. hyperboreus* in Billefjorden, Svalbard. Values in bold for this study are new and based on genetics data and MIX analysis from *Gabrielsen* et al. (unpublished) and this study. Values not in bold are the same as Arnkvaern etal 2005.

	This study			Arnkværn et al. 2005		
	C. finmarchicus	*C. glacialis*	*C. hyperboreus*	*C. finmarchicus*	*C. glacialis*	*C. hyperboreus*
CI	na	na	>0.92	<0.8	0.8 - 0.92	>0.92
CII	na	na	>1.49	<1.13	1.13 - 1.49	>1.49
CIII	na	na	>1.99	<1.47	1.47 - 1.99	>1.99
CIV	**≤1.80**	**1.81** - 2.9	≥3 (spine)	<2.1	2.1 - 2.9	≥3 (spine)
CV	**≤2.40**	**2.41** - 4.1	>4.1 (spine)	≤2.7	2.7 - 4.1	>4.1 (spine)
CF	**≤2.60**	**2.61-**	(spine)	≤3	>3	
CM	na	na	na			

Calanus Community Composition

C. glacialis was the most abundant *Calanus* species, comprising between 24-90% of the entire *Calanus* community (Figure 6). *C. finmarchicus* comprised 0.5-27% and *C. hyperboreus* comprised 0.4-74%. The relative abundance of the three species varied greatly by stage (Appendix Table 1). Due to the low abundance of *C. finmarchicus*, *C. glacialis* results will be presented first, and *C. finmarchicus* results will be presented last. Lipid data will only be presented for *C. glacialis*.

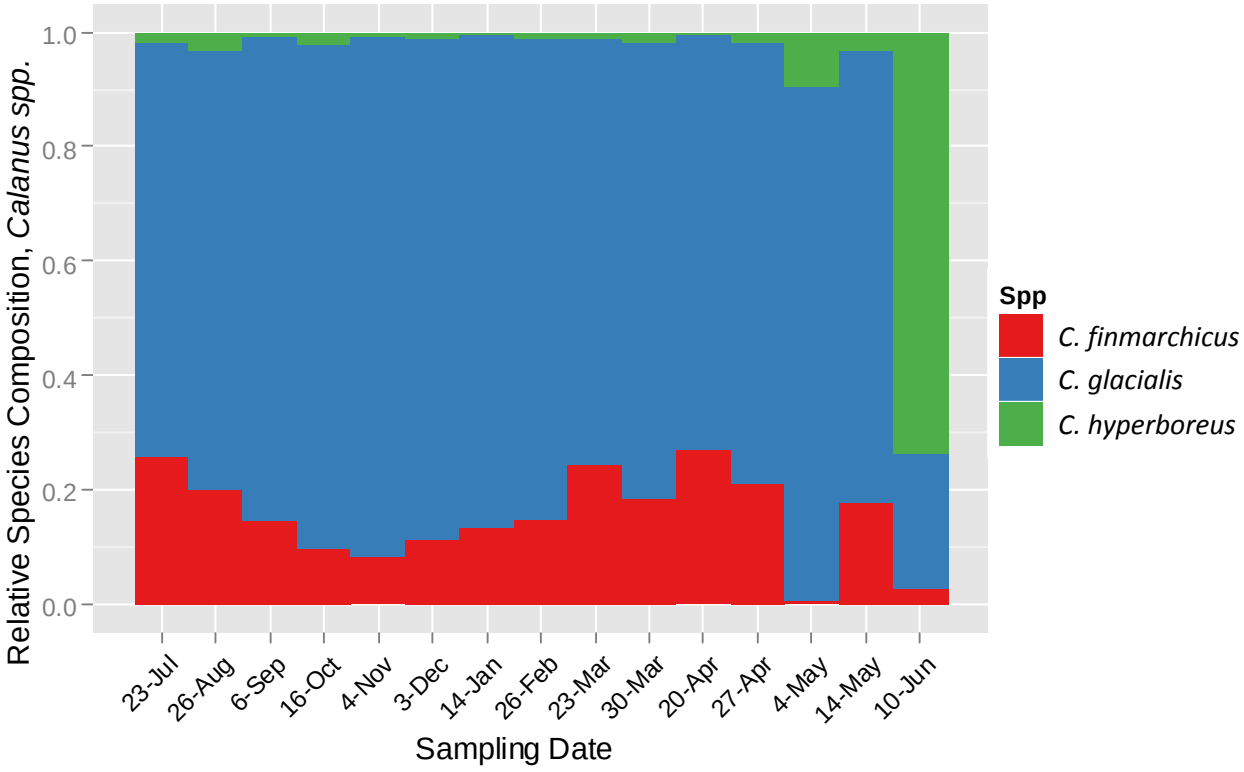

Figure 6. Relative abundance of *C. finmarchicus*, *C. glacialis*, and *C.hyperboreus*. All copepodite stages are included (CI-CF) except males, which were not determined to species.

C. glacialis was dominated by stage CV from late summer 2008 to January (**Figure 7**). From January on, females increase in relative abundance, but the total abundance of *C. glacialis* declines sharply. *C. finmarchicus* was dominated by stage CIV through the winter (from October to May), with young stages comprising approximately half of the population in July 2008 and August 2009 (**Figure 8**). The total abundance of *C. finmarchicus* also declined over the study period.

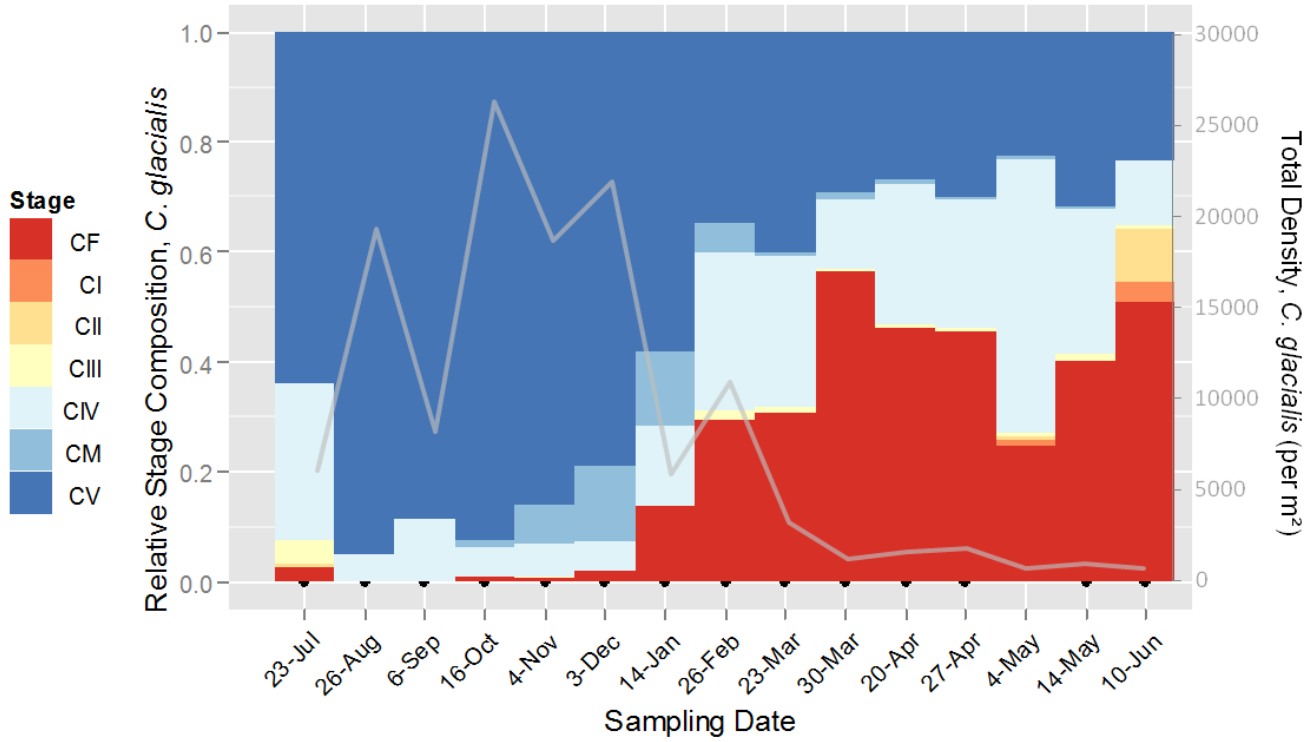

Figure 7. Relative copepodite stage composition and total *C. glacialis* density in Billefjorden 2008-2009. Stage composition is represented by colored bars, with proportion noted on the left-hand y-axis. Density (line, scale on right y-axis) is presented in indiv. m^{-2} and includes all stages of *C. glacialis*.

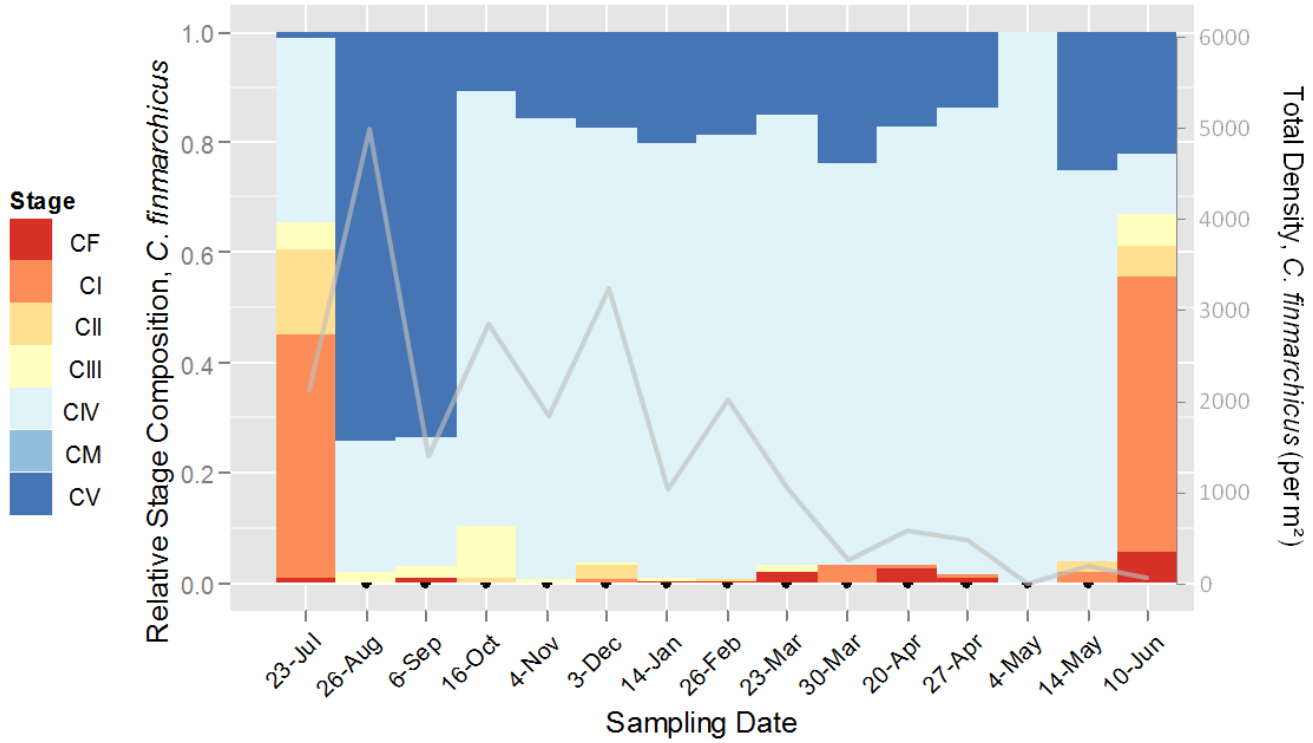

Figure 8. Relative copepodite stage composition and total density of *C. finmarchicus* in Billefjorden 2008-2009. Stage composition is represented by colored bars, with proportion noted on the lefthand y-axis. Density (line, scale on right y-axis) is presented in indiv. m^{-2} and includes all stages of *C. finmarchicus*.

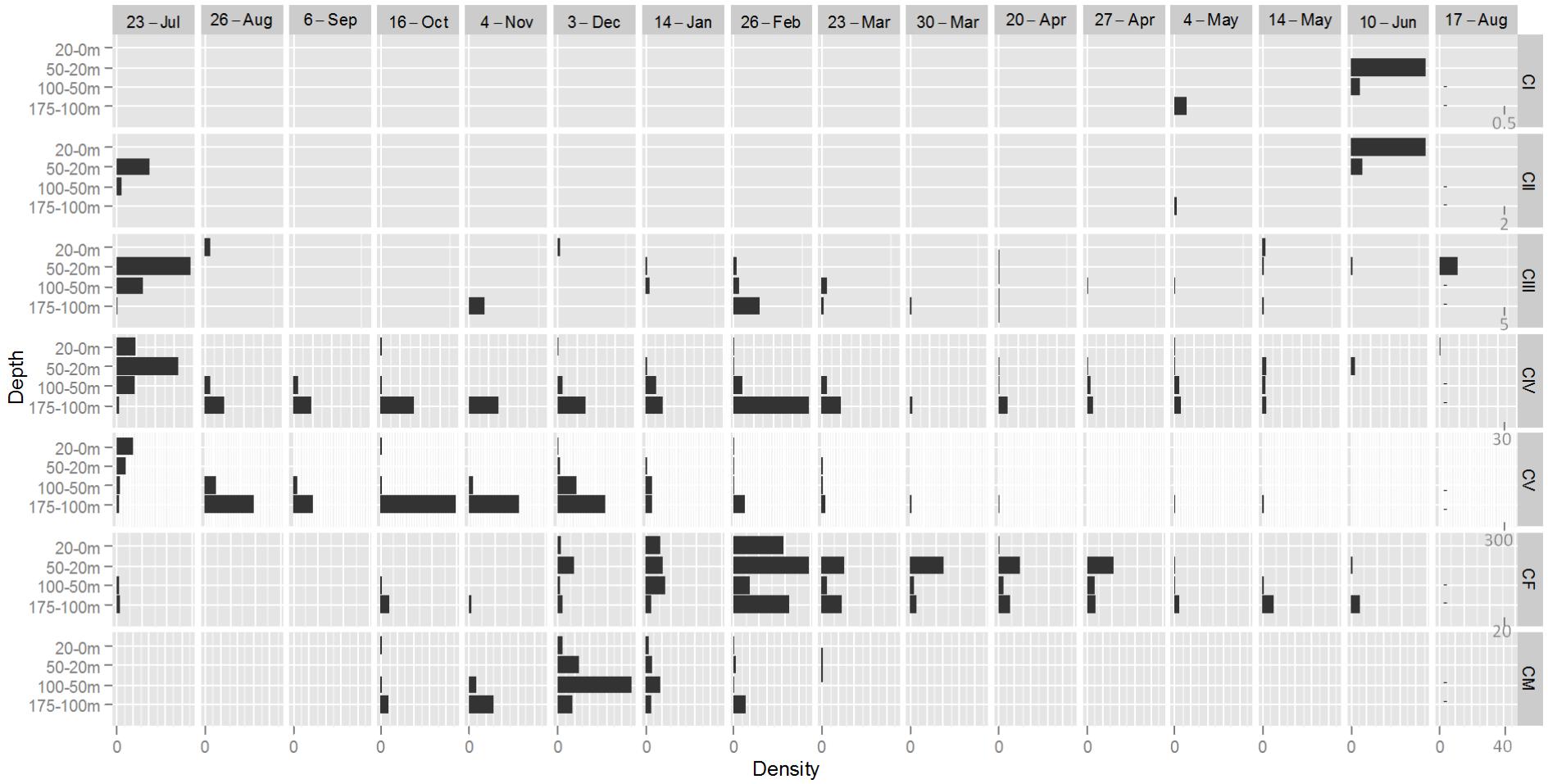

Figure 9. The depth distribution and density (indiv. m^{-3}) of *C. glacialis* stages CI-CF and *Calanus* sp. males in Billefjorden through the year 2008-2009. Scales for the x-axis are stage-specific and are noted at the end of each row; each white line represents an interval of 10 indiv. m^{-3}. Dashes in the August 17 sampling date indicate that the two deepest samples were not counted. The values represented here are found in Appendix Table 3.

Seasonal Depth Distribution

Calanus glacialis densities varied between 0.2 and 334 individuals m^{-3}, with peak abundance in the water column in October 2008, at 25380 individuals m^{-2} (Figure 9).

Stage CV

During the autumn of 2008, *C. glacialis* CVs descended to depth between July 23rd and August 26th. A few individuals had already descended to diapause by the first sampling trip (July 23, 2008), evidenced by the presence of stage CV copepodites in the deepest layer (Figure 9). However, at this time, the majority of the CV copepodites were in the upper 50m (Figure 9). By August 26th, nearly all CVs were in the deepest sample, 175-100m (Figure 9). The density of CVs in the deep increased from July to October, peaking at 297m^{-3} in the 175-100m layer. After December, densities of CVs in the deep declined sharply from between 50-300 indiv. m^{-3} (in August to November) to <50 indiv. m^{-3} (February to March), and nearly zero after March 23rd for the remainder of the sampling period (Figure 9, Appendix Table 3). CVs were found predominantly in the deepest layer from August 2008 to March 2009.

C. glacialis CIVs were consistently less abundant than CVs. Similar to CVs, they descended from the upper waters (concentrated in the 50-20m stratum) in July of 2008 to the deeper layers by the end of August, remaining there through May (Figure 9). Their density peaked at 47m^{-3} in the 175-100m sample in February (Figure 9, Appendix Table 3).

Adults

After being nearly absent from the water column from August to November, *C. glacialis* females showed a distinct arrival midwinter, appearing for the first time in the water column on December 3 (Figure 9). Densities were low, but congregated above 100m with a peak of 5.3m^{-3} at 50-20m (Figure 9). Densities of females increased throughout the water column by January 14, and peaked on February 26, with high densities in the upper 50m (23.4 indiv.m^{-3} at 50-20m; 14.9 indiv. m^{-3} at 20-0m) and in the deep (20.2 indiv. m^{-3} at 175-100m) (Figure 9, Appendix Table 3). Moderate densities remained from March 23 to April 27, though very few to no females were found in the surface 20-0m. In general from December to late April, females were consistently found in the highest numbers in the 50-20m depth stratum (Figure 9). From the beginning of May (5th) to June 10, female densities were low (<5 indiv. m^{-3}), and most individuals were found in the deep (Figure 9).

Males appeared in the water column before females, first appearing in the deepest layer in October, and peaking in abundance in December in the 100-50m depth stratum (46.1 indiv. m^{-3})(Figure 9), Appendix Table 3). By March, and for the remainder of the sampling period, the number of males in the water column was near zero (Figure 9, Appendix Table 3).

Young Stages

Young copepodite stages of *C. glacialis* (CI-CIII) had low densities, and CI and CII were present only in a short period (Figure 9). CI and CII individuals appeared in early May and peaked at densities <4m^{-3} in June at 50-20m (CI) and 20-0m (CII) (Figure 9, Appendix Table 3). CIII was present nearly year-round in low densities, with highest densities in the upper 50m in July 2008 and August 2009 (Figure 9, Appendix Table 3).

Lipids

In all, 3397 *Calanus* were photographed for lipid analysis. Of these, 2880 had lipid sacs which were able to be measured, and 517 were excluded from analysis due to a poorly visible or broken lipid sac, often due to a dead individual.

Stage CV

The seasonal trends in lipid contents of *C. glacialis* CV copepodites differed considerably between those in the surface and those in the deep. The highest lipid levels were found in the deep-dwelling CVs in July of 2008 (mean TL=0.50mg, SE=0.02, n=72). Lipid levels were also high in September 2008 and again at the end of the sampling period, August 2009 (Figure 10). Strangely, the sampling trips on September 6 and August 26, 2008 showed significantly lower lipid levels than the high lipid levels in the previous and subsequent sampling trips. Those trips (August 26 and September 6) were not significantly different from one another ($p= 0.40$), but both were significantly different from the sampling trip before (July 23) and after (September 26) (both $p<0.01$), which were themselves not significantly different from one another ($p=1$) (pairwise t-tests with Holm correction). Overall, during the time when densities of CVs were increasing in the deep (July-October), the average lipid level declined slightly (slope: -0.0023, intercept: 0.52, $p<0.01$, df=350). From November to January, when adults appeared in the highest numbers, the lipid content also shows a significant decrease (slope= -0.00086, intercept=0.38, $p<0.01$, df=256)(Figure 10). From January to June 2009, low numbers of CVs in the deep show relatively stable lipid distributions (Figure 10). The lipids of those in the surface increased significantly from July to October (slope= 0.0016, intercept= 0.075, $p<0.01$, df=68), when total lipid peaked at an average of 0.27mg (SE=0.02, n=36). Total lipid was lowest in CVs in the surface in summer (July and August 2008, August 2009) and in spring (March-June 2009).

To understand the role of lipids in the decision of a copepodite to remain in the surface or descent to diapause, the intrapopulation variability of lipid content for *C. glacialis* CVs was examined with regards to depth in the water column (Figure 10). The lipid content of the *C. glacialis* CV copepodites in the deep was consistently greater, on average, than in those in the surface (Figure 10) throughout the whole year (ANOVA (estimate= -0.15484 SE=0.00894, t=17.320, $p< 0.01$). In the beginning of descent to diapause (July 23), there was a strong distinction between the lipids of CV copepodites in the surface and the deep, with significantly higher lipids in the deep than in the surface (t-test, t=18.33, df= 59, $p <0.01$) (Figure 10,Table 2). For the following three sampling trips, there continued to be higher lipid levels in the deep than in the surface, though not significant on September 6th (t-tests: August 26th: t-stat= 3.52, p= 0.04, df= 14; September 6th: t-stat=2.65, p= 0.40, df=6; September 23rd: t-stat=16.29, df=206, $p <0.01$) (Figure 10, Table 2). A similarly strong pattern was present at approximately the same time of year, one year later (August 2009) (t-test, August: t= 12.04, $p<0.01$, df=116) (Figure 10, Table 2). However, from October to June, there was considerable, if not total, overlap between the lipid distributions of the CVs in surface and deep communities (Figure 10). With the exception of the March 23rd sampling trip, when deep and surface lipids differed significantly (t-test: t-stat=3.65, $p<0.01$, df=10), the lipid content of CVs in the deep and surface did not differ significantly during this period (Table 2).

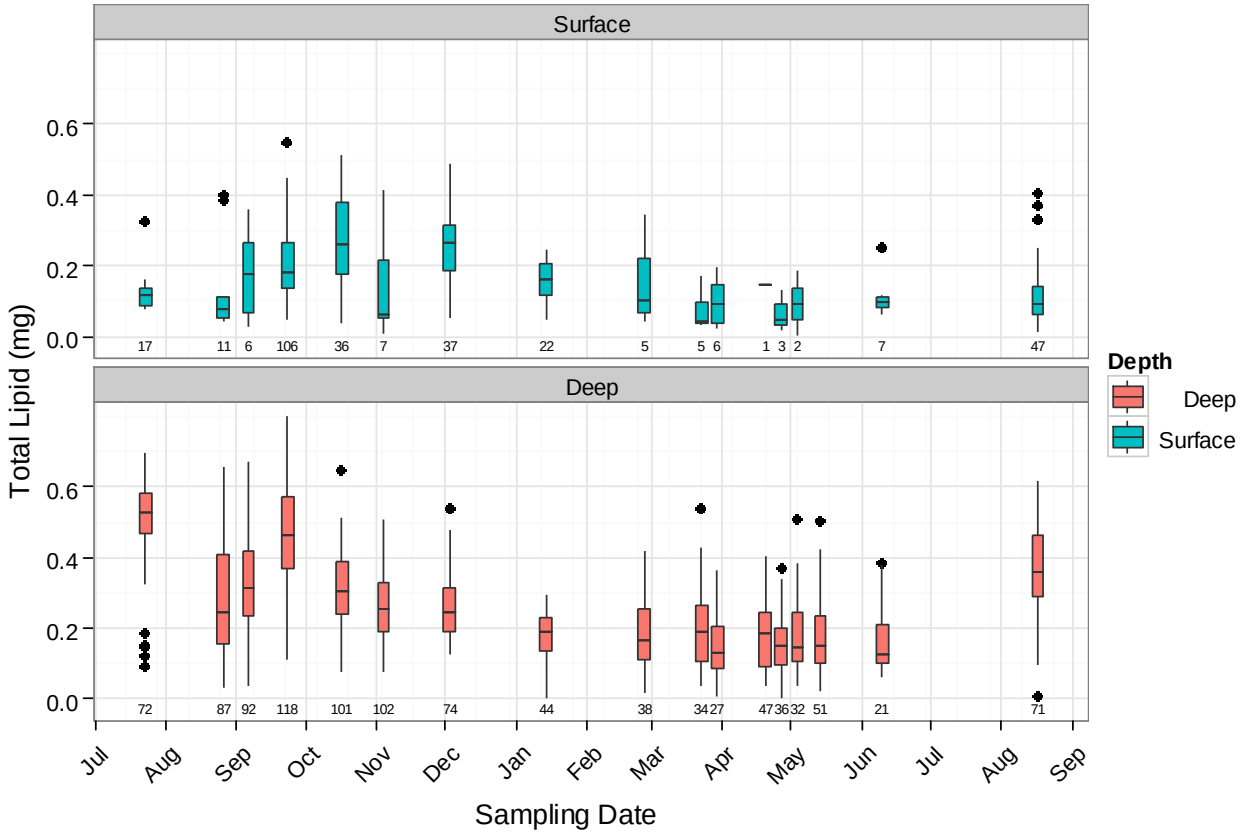

Figure 10. Total lipid seasonal trends for *C. glacialis* CV for surface and deep samples. Upper and lower box levels indicate the 25% and 75% quantiles, the middle line indicates the median, and the whiskers indicate the range of the inter-quartile range (IQR, the middle 50% of data). Outliers are displayed as points. Sample size is indicated below the box.

Stage CIV

The seasonal trends in lipid contents of *C. glacialis* CIV were less marked than CV. The highest lipid levels in CIVs in the deep were in November 2008 (mean TL= 0.07mg, SE= 0.01, n= 6) (Figure 11). For the autumn period of 2008, August to October, lipids in the surface CIVs declined and those in the deep increased (Figure 11). Generally, lipid levels were stable for both surface and deep communities through the year (Figure 11).

The lipid distributions of *C. glacialis* CIVs did not differ between surface and deep as starkly as with the CVs (Figure 11, Table 2). The lipids of the surface and deep populations differed significantly on only two sampling dates, October 2008, and May 4, 2009 (t-tests: October: t= 3.42, p= 0.04, df= 16; May: t= 4.79, p<0.01, df= 40) (Figure 11). Generally, the lipid level of the CIVs in the deep was similar to that of the CIVs in the surface (t-tests in Table 2, Figure 11).

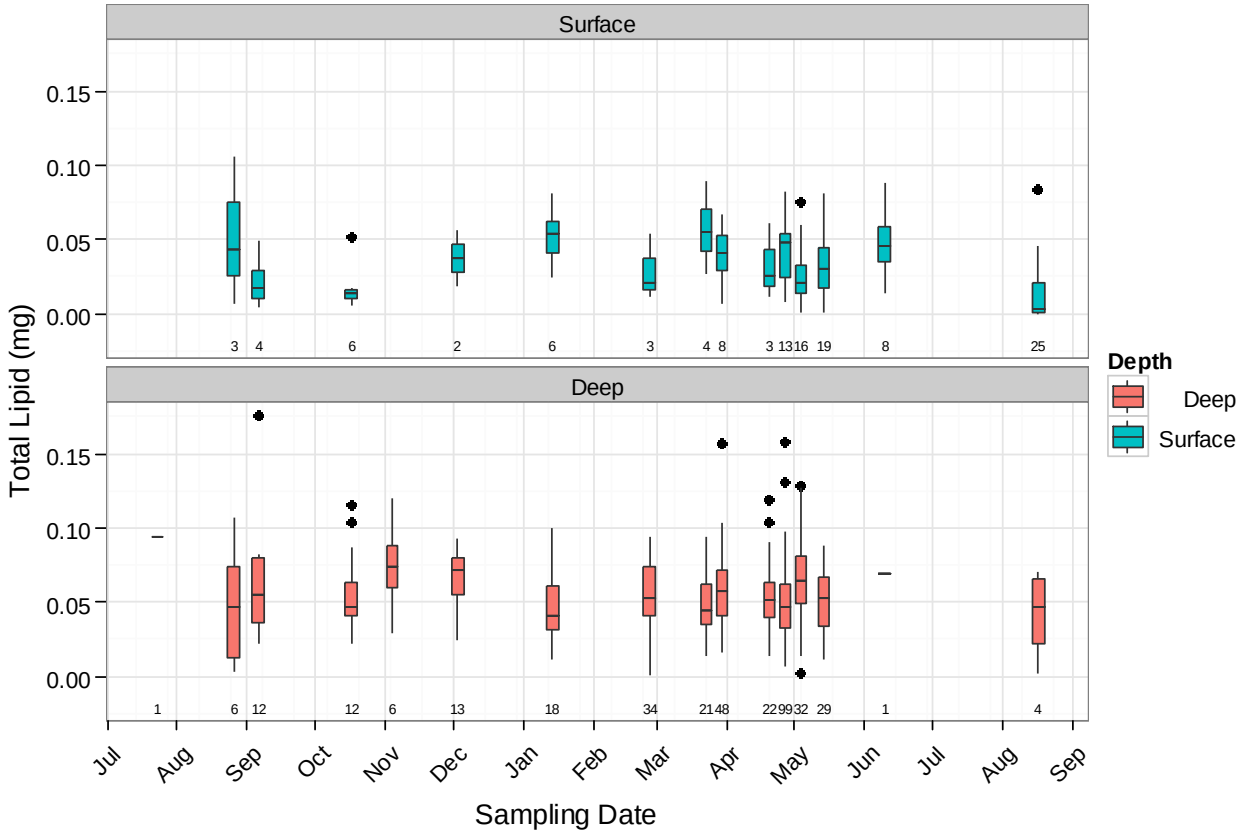

Figure 11. Total lipid seasonal trends for *C. glacialis* CIV for surface and deep samples. Boxplot statistics as in Figure 10. Sample sizes are below each box.

Females

The highest total lipid levels were found as females first appeared in the water column, in December, in the surface (mean=0.30mg, SE=0.02, n=18) (Figure 12, Table 3). In the deep at this sampling date, only one female individual was found, also of high lipid (TL=0.25). After its initial peak at 0.30mg in December, female lipids declined sharply in the surface waters (Figure 12), falling to an average of 0.06mg (SE=0.04, n=3) on on May 14th (Figure 12). This decline in lipids over time for the females in the surface waters (December to May) was significant (slope=-0.0013, intercept=0.50, $p < 0.01$, df=390). In the deep, the average lipid content of females also decreased over time, but the decline was not as steep nor did it reach as low levels as the surface females. From an average of 0.24mg (SE=0.03, n=13) in January, female lipid content in the deep declined to 0.18mg in June (SE=0.01, n=37), a slight, but significant, decline (slope=-0.00043, intercept=0.32, $p < 0.01$, df=294) (Figure 12). The distribution of total lipid content in *C. glacialis* females varied significantly between surface and deep populations for four sampling trips, March 23rd, March 30th, April 20th and April 27th, with the surface population having lower lipids than the deep population (Figure 12) (t-tests in Table 4).

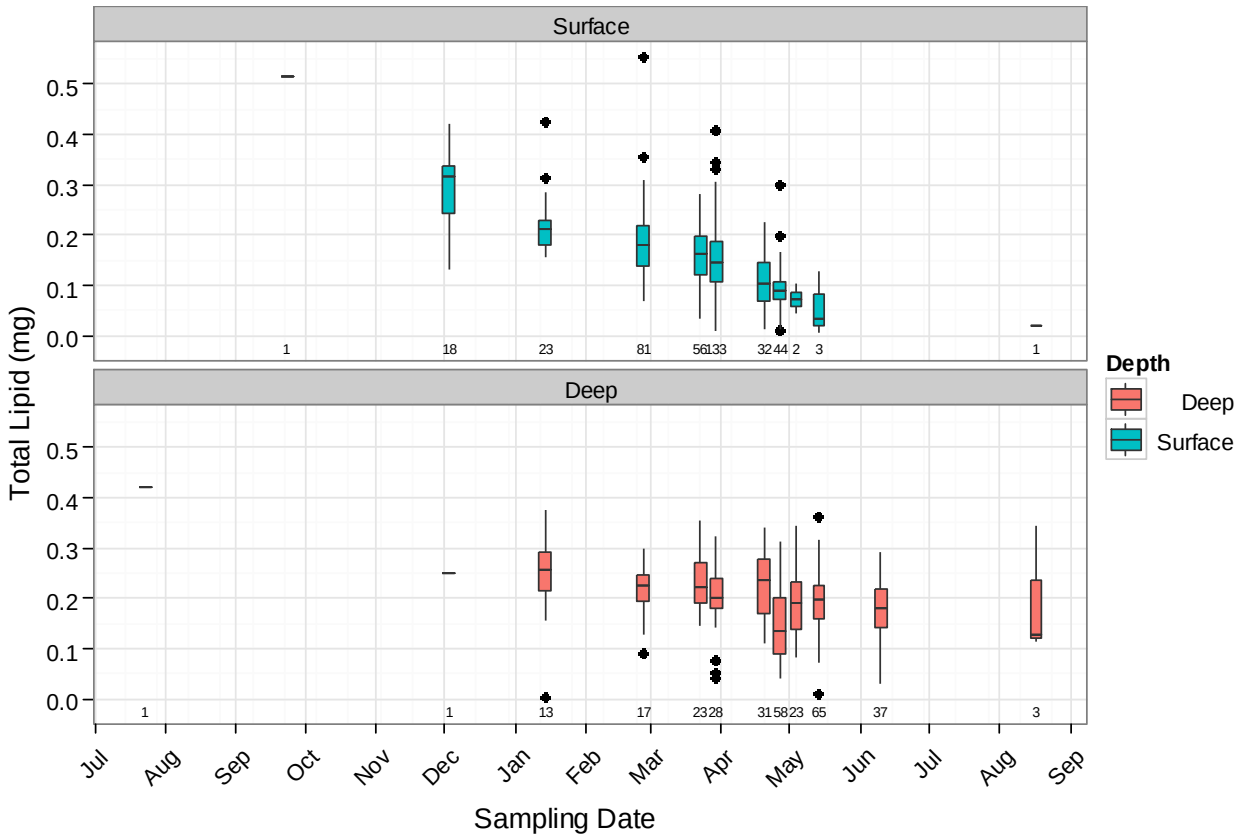

Figure 12. Total lipid seasonal trends for *C. glacialis* females (CF) for surface and deep samples. Boxplot statistics as in Figure 10. Sample sizes are below each box.

Males

The total lipid content of males showed a decline with time in both the surface and deep (Figure 13). The decline was steeper in the surface than the deep (surface: slope=-0.0025, intercept=0.79, p <0.01, df=74; deep: slope=-0.0022, intercept=0.73, p <0.01, df=33). The highest average total lipid was found in the earliest males to appear in the water column, in October in the deep (mean= 0.51mg, SE=0.02, df=8) (Figure 12). The distribution of total lipid content in *Calanus* sp. males did not vary significantly between surface and deep populations for any sampling trip (Figure 13, t-tests in Table 4).

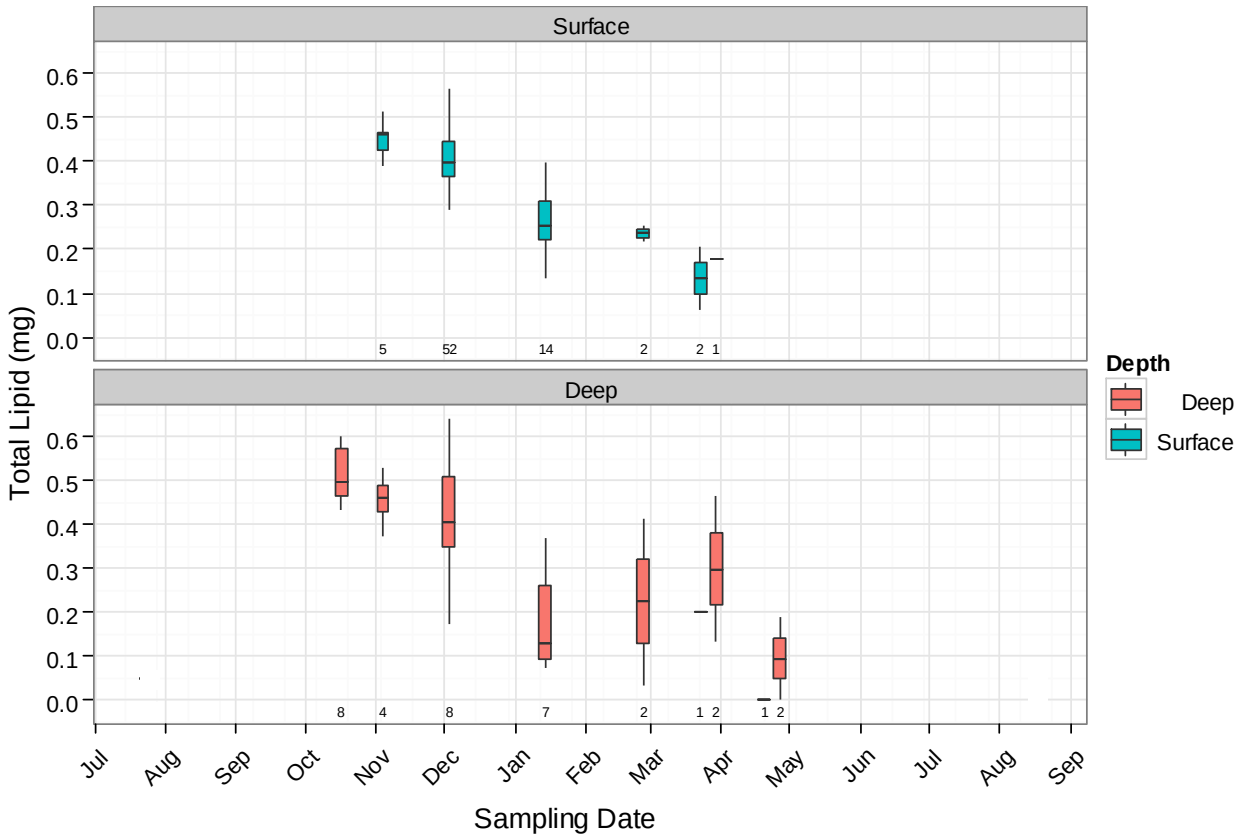

Figure 13. Total lipid seasonal trends for *Calanus* sp. males (CM) for surface and deep samples. Boxplot statistics as in Figure 10. Sample sizes are below each box.

Prosome Lengths

Stages CV and CIV

The mean prosome length of the CV and CIV copepodites also varied throughout the year. The highest prosome lengths for CVs were found in the deep in the early period of descent, a trend which was true for both the summer of 2008 (July 23rd) and 2009 (August 17th) (Figure 14). High CV prosome lengths were also found in the deep in September 2008, though, similar to the trend in total lipids the prosome lengths in the August 26th and September 6th trips are lower than the trips before and after. Following this peak in September, prosome length for CVs in the deep showed no trends over winter and through spring. Prosome length was significantly larger in deep-dwelling CVs than those in the surface in late summer 2008 (July and September 23rd) and 2009 (August 17th) (t-tests in Table 4). There were no seasonal trends in the prosome lengths of the CVs in the surface, or in CIVs in the deep or surface (Figure 14).

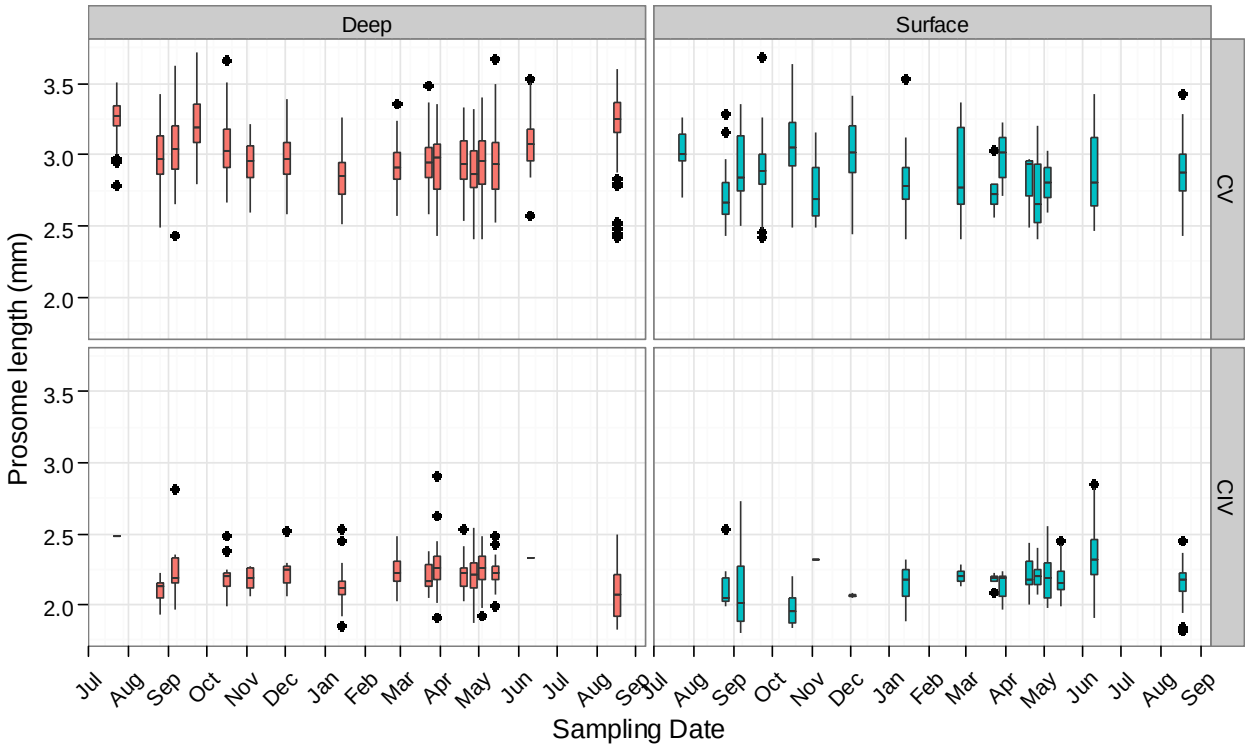

Figure 14. Prosome length seasonal trends for *C. glacialis* CIV and CV for surface and deep samples. Red boxes are deep samples, blue boxes are surface samples. Boxplot statistics as in Figure 10. Sample sizes per sampling date are as indicated in total lipid graphs (Figure 10, Figure 11) and in Table 2.

Stages CF and CM

The prosome lengths of females were longest in those which molted and appeared first in the water column, in December (Figure 15). From January to the end of May, female prosome lengths were relatively constant in both the deep and surface, changing only in June, when the prosome length was lower in the surface and higher in the deep (Figure 15). Male prosome length declined significantly in both the surface and the deep with time (surface: slope=-0.0027, intercept=3.77, $p < 0.01$, df=74; deep: slope=-0.0019, intercept=3.71, $p < 0.01$, df=33) (Figure 15). Prosome length was not significantly different between deep and surface-dwelling individuals for either males or females on any sampling date (Table 4).

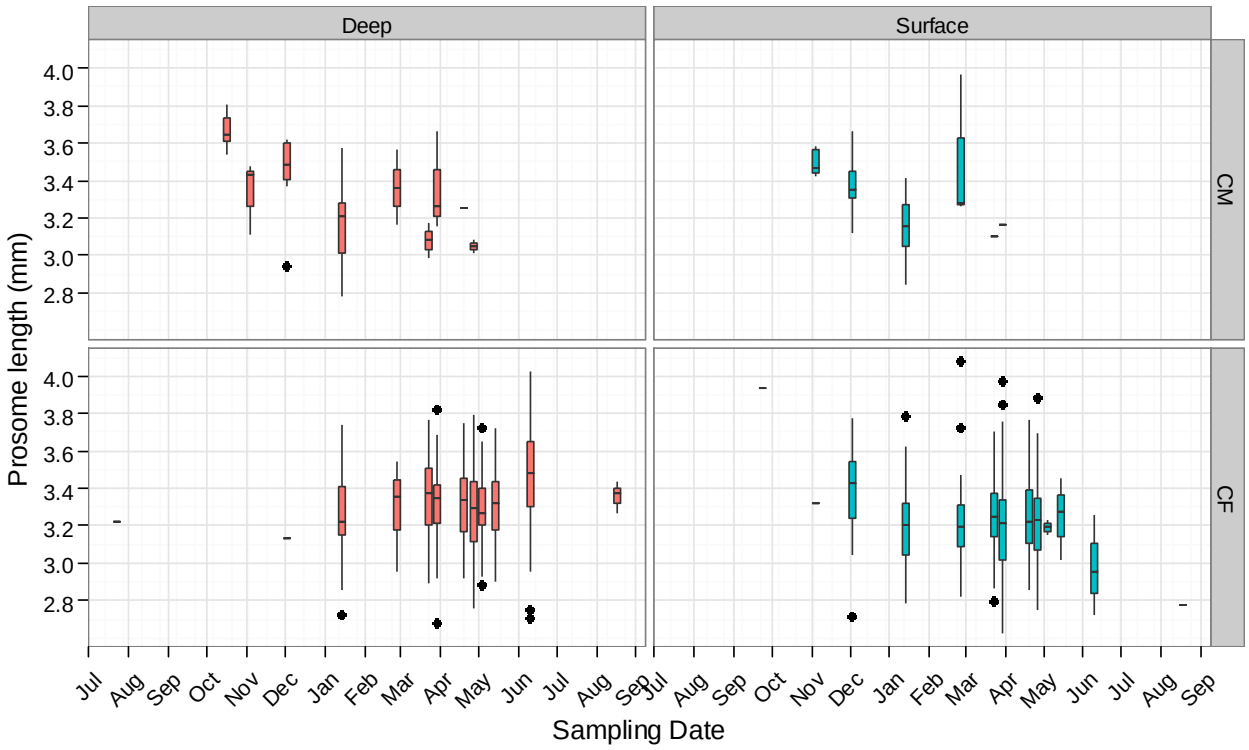

Figure 15. Prosome length seasonal trends for *C. glacialis* females (CF) and *Calanus* sp. males (CM) for surface and deep samples. Red boxes are deep samples, blue boxes are surface samples. Boxplot statistics as in Figure 10. Sample sizes per sampling date are as indicated in total lipid graphs (Figure 12, Figure 13) and in Table 3.

Condition Factor

The relationship between prosome length and total lipid differed considerably by stage (Figure 16) for *C. glacialis* CIV-CF and *Calanus* sp. males. Linear models for each stage were fit to ln-transformed PL and TL data in order to calculate a stage-specific condition factor (Figure 17).

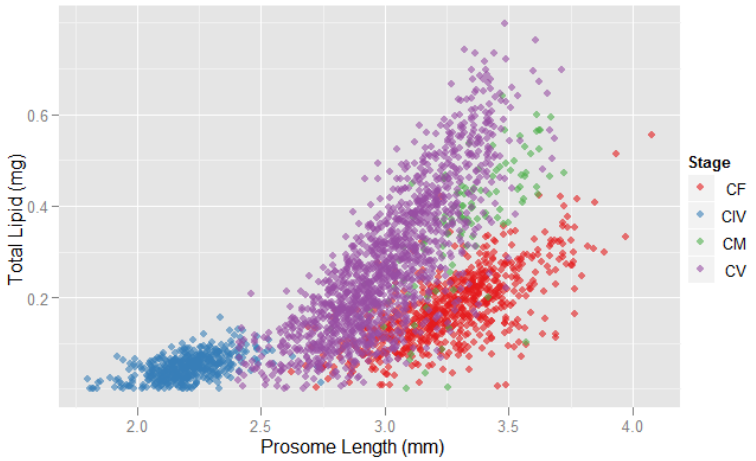

Figure 16. The relationship of total lipid to prosome length for large stages of *C. glacialis* (CIV- CF) and *Calanus* sp. males. Total lipid has been calculated from lipid sac area measurements according to Vogedes etal 2010.

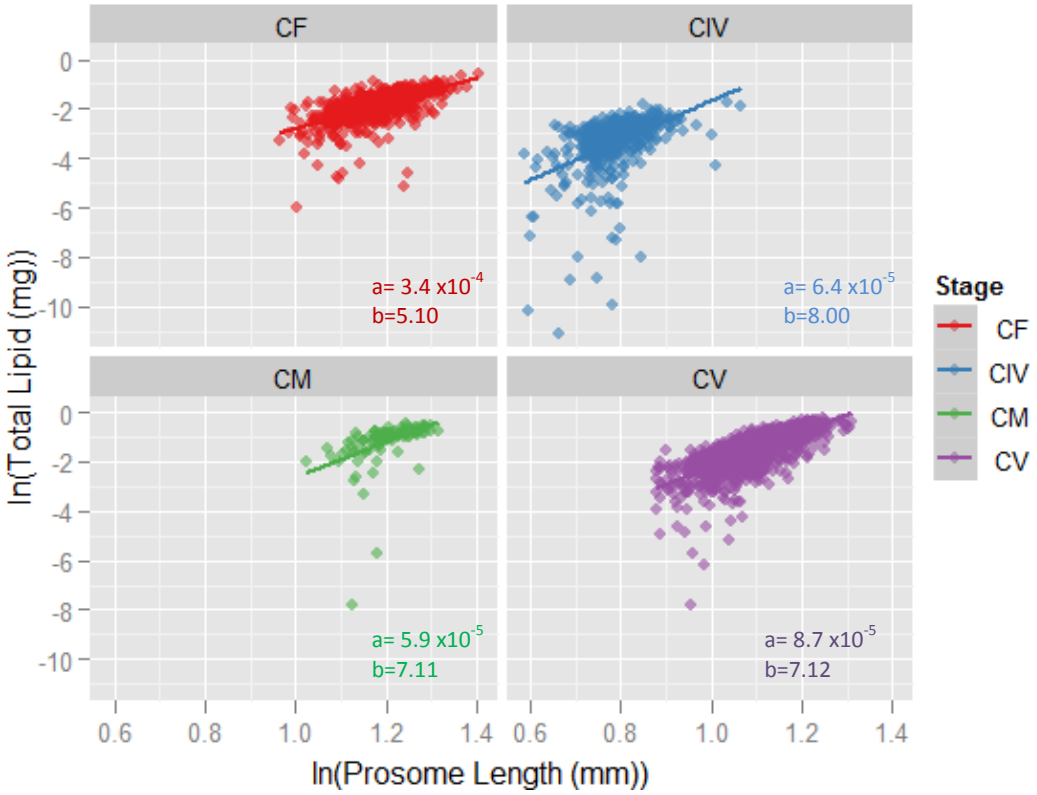

Figure 17. Linear models fit to ln-transformed total lipid and prosome length data, for large stages of *C. glacialis* (CIV- CF) and *Calanus* sp. males. Total lipid has been calculated from lipid sac area measurements according to Vogedes etal 2010. The parameters a and b of the weight-length equation ($\boldsymbol{W = aL^b}$, Eq. 5) are derived from the linear models and are presented in each box. The parameter a was calculated as $e^{intercept}$ and b as the slope. These parameters were used in calculating stage-specific condition factors. Lines represent the prediction of the linear model on ln-transformed data.

Stage CV

A lipid condition factor was calculated which adjusted the total lipid value for the prosome length according to the relative condition factor of LeCren (1951) (Eq. 4). Parameters used in the condition factor were calculated for each stage from linear models fit to ln-transformed data (Figure 16, Figure 17). By accounting for the effect of varying prosome length throughout the season, the relative lipid storage condition of the copepods became more clear (Figure 18). There was a significant difference in the lipid condition factor between CVs in the surface and the deep in July, late September and October (t-tests in Table 4, Figure 18). Though the mean condition factor in August and early September followed this trend (higher in the deep), the difference was not significant (t-tests in Table 4). After October, there was no difference between the lipid condition of the CVs in the surface and deep, but the difference appeared again strongly the next summer, in August 2009, and once in the spring, April 27 (t-tests in Table 4).

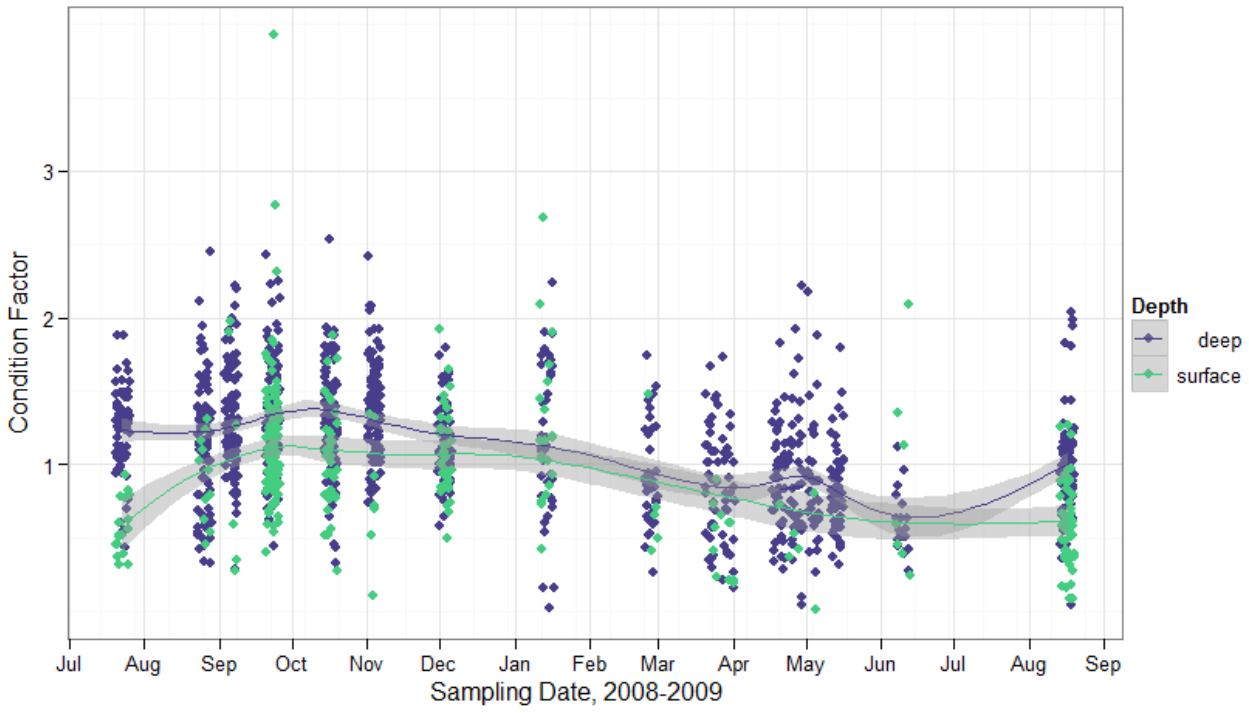

Figure 18. Condition factor for CV *C. glacialis* in surface (50-0m, green dots) and deep (175-100m, blue dots). Lines are predictions from loess smoothing. Shaded area indicates the 95% confidence interval.

Average condition factors in the deep were highest in the late summer, averaging 0.291 (SE=0.017, n=470) from July-October, 0.206 (SE=0.023, n=258) from November to February, when adult stages were at peak abundances, -0.144 (SE=0.024, n=248) during spring (March-June), and 0.009 (SE=0.042, n=71) in August 2009. In the surface waters, the lipid condition factor of CVs increased from July (mean=0.428, SE=0.05, n=17) to late September (mean=0.167, SE=0.043, n=106) (slope=0.0059, intercept=-0.41, $p<0.01$, df=174), nearly reaching the level of the condition of CVs in the deep (Figure 18). By December, the mean condition factor of surface and deep populations were not significantly different(t-tests in Table 4).

The condition factor of the deep-dwelling CV population was relatively constant through the period were densities of CVs were increasing in the deep (July-October), and did not change significantly with time (slope=0.00051, intercept=0.25, p=0.42, df=468)(Figure 18). However, from November to February, however, as adult densities peaked, the condition factor of CVs decreased significantly with time (slope=-0.0035, intercept=0.78, p<0.01, df=256). Condition factor continued to decrease in CVs in the deep through spring (March to June), but at a lower rate (slope=-0.0022, intercept=0.51, p=0.04, df=246).

Stage CIV

In general, the condition factor of CIVs in both the surface and deep increased slightly from July to January, decreased during spring and then diverged by late summer 2009 (Figure 19). The condition factor of CIVs did not vary significantly between deep and surface-dwelling individuals at any sampling period throughout the whole year (t-tests in Table 4) (Figure 19)In August of 2009, the few CIVs captured in the deep showed a higher condition factor than those in the surface, but the sample size was low.

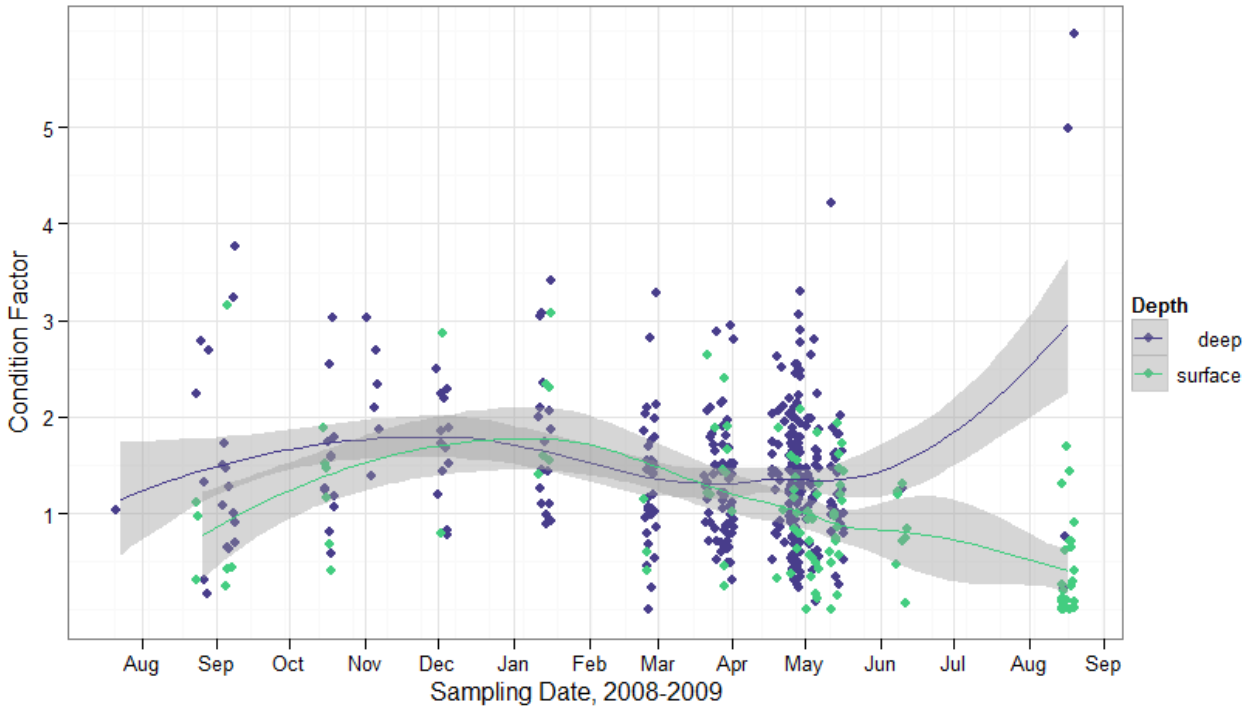

Figure 19. Condition factor for CIV *C. glacialis* in surface (50-0m, green dots) and deep (175-100m, blue dots). Lines are predictions from loess smoothing. Shaded area indicates the 95% confidence interval.

Females

The condition factor of female copepodites was highest in the beginning of their molting (December), and declined through the spring, most steeply in the surface. Though of similar condition factor in December and February, females in the surface had significantly lower condition factors than those in the deep on March 23rd, April 20th and April 27th, as the spring progressed (t-tests in Table 4).

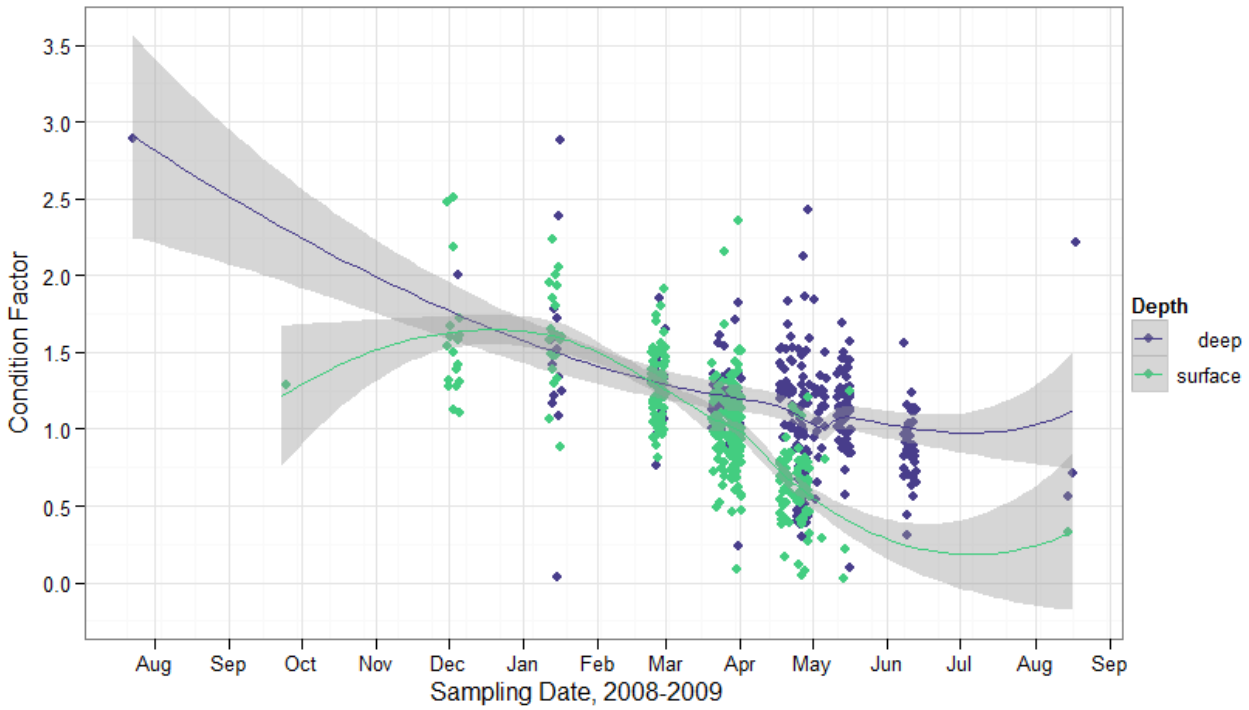

Figure 20. Condition factor for female *C. glacialis* in surface (50-0m, green dots) and deep (175-100m, blue dots). Lines are predictions from loess smoothing. Shaded area indicates the 95% confidence interval.

Males

The condition factor of males was highest in November and December, at the peak of their molting (December), and declined through the spring (Figure 21). The condition factor never varied significantly between surface and deep-caught males (t-tests in Table 4), though, with the exception of November, males in the surface had slightly higher condition factors than those in the deep.

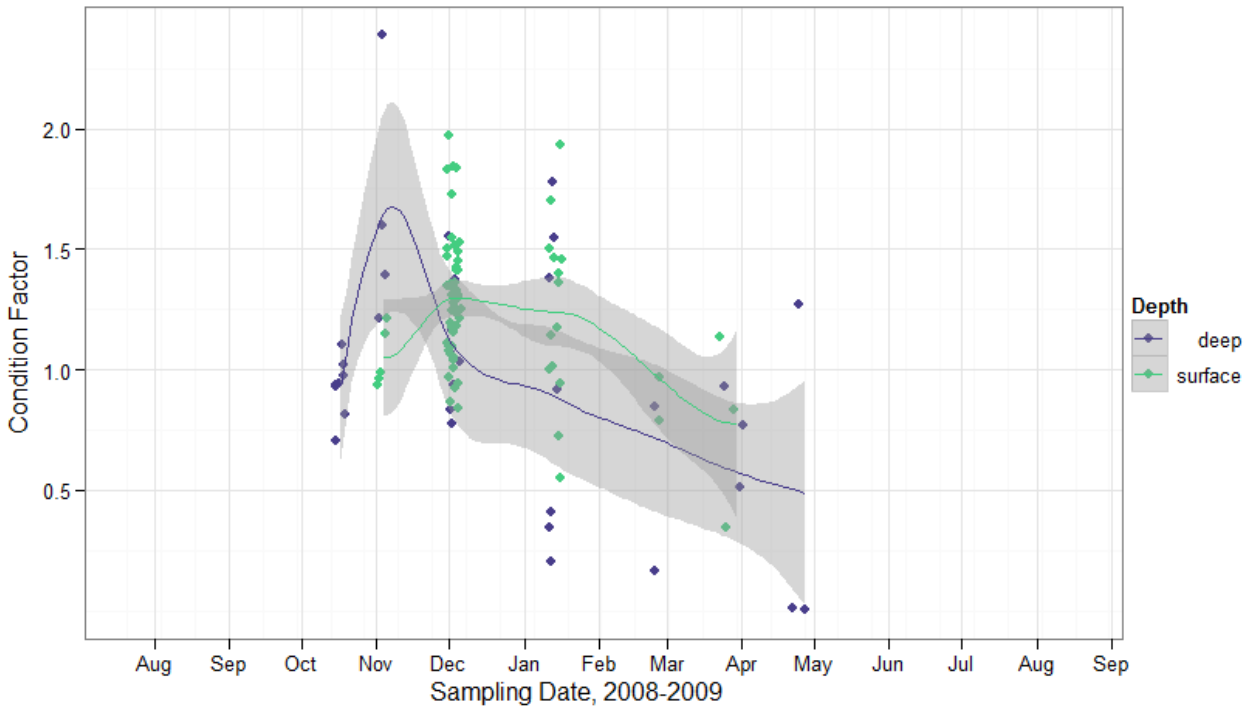

Figure 21. Condition factor for *Calanus* sp. males in surface (50-0m, green dots) and deep (175-100m, blue dots). Lines are predictions from loess smoothing. Shaded area indicates the 95% confidence interval.

C. finmarchicus

C. *finmarchicus* CVs descended from the mid depths (100-20m) in July to below 100m by late August 2008, showing similar descent timing as *C. glacialis* CVs (Figure 22). The maximum density of CVs in the deep was 30 indiv. m^{-3} in August 2008 (Figure 22, Appendix Table 4). The majority of the CVs were in the deep from August to November (**Figure 22**). However, from December to February, CVs were distributed almost evenly throughout the entire water column (**Figure 22**). From the March 30 sampling date and on, there were very few *C. finmarchicus* CVs in the water column (**Figure 22**).

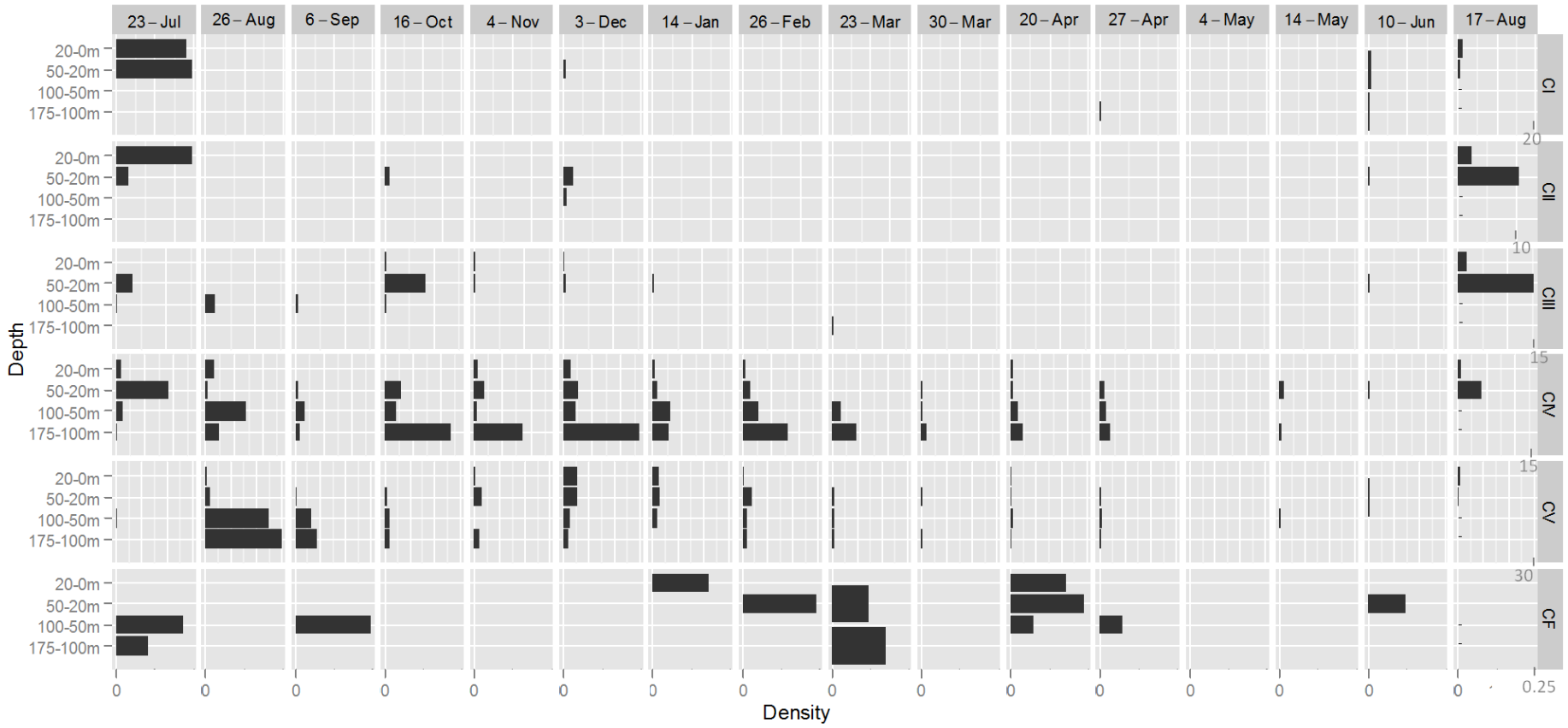

Figure 22. The depth distribution and density (indiv. m^{-3}) of *C. finmarchicus* stages CI-CF Billefjorden through the year 2008-2009. Scales for the x-axis are stage-specific and are noted at the end of each row; each white line represents an interval of 10 indiv. m^{-3}. Dashes in the August 17 sampling date indicate that the two deepest samples were not counted. The values represented here are found in Appendix Table 4.

Table 2. Total lipid (mg) in *C. glacialis* CIV and CV. Total lipid values were calculated from lipid sac area values using a equation in Vogedes etal. 2010. Mean, standard error and degrees of freedom are given. Dates when a particular stage was not found are not presented.

Stage	Date	Surface			Deep		
		mean	SE	n	mean	SE	n
CIV	23-Jul-08	-	-	0	0.09	-	1
	26-Aug-08	0.05	0.03	3	0.05	0.02	6
	6-Sep-08	0.02	0.01	4	0.06	0.01	12
	16-Oct-08	0.02	0.01	6	0.06	0.01	12
	4-Nov-08	-	-	0	0.07	0.01	6
	3-Dec-08	0.04	0.02	2	0.07	0.01	13
	14-Jan-09	0.05	0.01	6	0.05	0.01	18
	26-Feb-09	0.03	0.01	3	0.05	0.00	34
	23-Mar-09	0.06	0.01	4	0.05	0.00	21
	30-Mar-09	0.04	0.01	8	0.06	0.00	48
	20-Apr-09	0.03	0.01	3	0.06	0.01	22
	27-Apr-09	0.04	0.01	13	0.05	0.00	99
	4-May-09	0.03	0.01	16	0.06	0.01	32
	14-May-09	0.03	0.01	19	0.05	0.00	29
	10-Jun-09	0.05	0.01	8	0.07	-	1
	17-Aug-09	0.01	0.00	25	0.04	0.02	4
CV	23-Jul-08	0.13	0.01	17	0.50	0.02	72
	26- Aug -08	0.13	0.04	11	0.28	0.02	87
	6-Sep-08	0.18	0.05	6	0.33	0.01	92
	23-Sep-08	0.21	0.01	106	0.47	0.01	118
	16-Oct-08	0.27	0.02	36	0.31	0.01	101
	4-Nov-08	0.15	0.06	7	0.27	0.01	102
	3-Dec-08	0.26	0.02	37	0.26	0.01	74
	14-Jan-09	0.16	0.01	22	0.18	0.01	44
	26-Feb-09	0.15	0.06	5	0.18	0.01	38
	23-Mar-09	0.08	0.03	5	0.20	0.02	34
	30-Mar-09	0.10	0.03	6	0.15	0.02	27
	20-Apr-09	0.15	-	1	0.19	0.01	47
	27-Apr-09	0.07	0.03	3	0.16	0.01	36
	4-May-09	0.09	0.09	2	0.18	0.02	32
	14-May-09	-	-	0	0.18	0.01	51
	10-Jun-09	0.11	0.02	7	0.17	0.02	21
	17-Jun-09	0.15	0.02	5	-	-	0
	17-Aug-09	0.12	0.01	47	0.36	0.02	71

Table 3. Total lipid (mg) in *C. glacialis* CF and *Calanus* sp. CM. As in Table 2.

Stage	Date	Surface			Deep		
		mean	SE	n	mean	SE	n
CF	23-Jul-08	-	-	0	0.42	-	1
	23-Sep-08	0.51	-	1	-	-	0
	3-Dec-08	0.30	0.02	18	0.25	-	1
	14-Jan-09	0.22	0.01	23	0.24	0.03	13
	26-Feb-09	0.19	0.01	81	0.21	0.01	17
	23-Mar-09	0.16	0.01	56	0.23	0.01	23
	30-Mar-09	0.15	0.01	133	0.20	0.01	28
	20-Apr-09	0.10	0.01	32	0.23	0.01	31
	27-Apr-09	0.09	0.01	44	0.15	0.01	58
	4-May-09	0.07	0.03	2	0.19	0.01	23
	14-May-09	0.06	0.04	3	0.19	0.01	65
	10-Jun-09	-	-	0	0.18	0.01	37
	17-Aug-09	0.02	-	1	0.20	0.07	3
CM	16-Oct-08	-	-	0	0.51	0.02	8
	4-Nov-08	0.45	0.02	5	0.46	0.03	4
	3-Dec-08	0.41	0.01	52	0.42	0.05	8
	14-Jan-09	0.26	0.02	14	0.18	0.04	7
	26-Feb-09	0.24	0.02	2	0.23	0.19	2
	23-Mar-09	0.14	0.07	2	0.20	-	1
	30-Mar-09	0.18	-	1	0.30	0.17	2
	20-Apr-09	-	-	0	0.00	-	1
	27-Apr-09	-	-	0	0.10	0.10	2

Table 4. T-test results comparing the total lipids and the prosome lengths of *Calanus* copepods in the deep and surface through the year (2008-2009). *C. glacialis* stages CIV- CF (female), and *Calanus* sp. CM (male) are presented. P-values are adjusted using the Holm correction method, and those showing significant differences between surface and deep are set in bold. Only sampling dates with sufficient sample size for a t-test are shown. The direction of difference in the means (Δ) is given as "surface-deep"; if negative, deep individuals have higher values.

		Total Lipid				Prosome Length				Condition Factor			
Stage	Depth	t	p	Δ	df	t	p	Δ	df	t	p	Δ	df
CIV	26-Aug	-0.12	1.00	0.0	3	-0.52	1.00	0.0	7	1.47	1.00	-0.8	7
	6-Sep	2.64	0.22	0.0	12	0.50	1.00	-0.1	3	0.57	1.00	-0.4	4
	16-Oct	3.42	**0.04**	0.0	16	4.10	**<0.01**	-0.2	21	1.15	1.00	-0.3	13
	3-Dec	1.54	1.00	0.0	1	4.95	**0.03**	-0.2	6	-0.12	1.00	0.1	1
	14-Jan	-0.68	1.00	0.0	10	-0.35	1.00	0.0	12	-0.79	1.00	0.3	10
	26-Feb	1.86	1.00	0.0	2	0.72	1.00	0.0	3	2.57	0.84	-0.6	3
	23-Mar	-0.65	1.00	0.0	4	0.67	1.00	0.0	6	-0.99	1.00	0.4	4
	30-Mar	2.19	0.47	0.0	11	3.42	**0.05**	-0.1	13	-0.18	1.00	0.0	8
	20-Apr	1.45	1.00	0.0	3	0.05	1.00	0.0	7	0.79	1.00	-0.4	2
	27-Apr	0.86	1.00	0.0	17	-0.10	1.00	0.0	18	1.22	1.00	-0.2	19
	4-May	4.79	**<0.01**	0.0	40	1.60	1.00	-0.1	22	3.89	0.01	-0.6	37
	14-May	2.85	0.08	0.0	36	1.57	1.00	0.0	44	1.99	0.64	-0.4	45
	17-Aug	1.69	1.00	0.0	3	-0.47	1.00	0.0	6	1.77	1.00	-2.6	3
CV	23-Jul	18.32	**<0.01**	-0.4	59	6.43	**<0.01**	-0.2	31	11.97	**<0.01**	-0.7	34
	26-Aug	3.52	**0.04**	-0.2	14	3.17	0.09	-0.3	13	2.66	0.14	-0.3	16
	6-Sep	2.65	0.40	-0.1	6	0.95	1.00	-0.1	6	0.79	1.00	-0.2	5
	23-Sep	16.29	**<0.01**	-0.3	206	12.19	**<0.01**	-0.3	223	3.40	**0.01**	-0.2	201
	16-Oct	1.65	0.85	0.0	51	-0.40	1.00	0.0	49	3.86	**<0.01**	-0.3	62
	4-Nov	1.89	0.85	-0.1	6	1.82	1.00	-0.2	6	3.30	0.13	-0.6	6
	3-Dec	0.15	1.00	0.0	57	-0.57	1.00	0.0	60	1.46	0.90	-0.1	64
	14-Jan	1.13	1.00	0.0	55	0.47	1.00	0.0	43	-0.61	1.00	0.1	41
	26-Feb	0.50	1.00	0.0	5	0.28	1.00	0.0	5	0.84	1.00	-0.2	5
	23-Mar	3.65	**0.05**	-0.1	10	2.38	0.58	-0.2	6	2.70	0.22	-0.4	7
	30-Mar	1.60	0.85	-0.1	10	-0.82	1.00	0.1	7	3.09	0.09	-0.4	12
	27-Apr	2.54	0.81	-0.1	3	0.46	1.00	-0.1	2	5.37	**<0.01**	-0.5	21
	4-May	0.89	1.00	-0.1	1	0.61	1.00	-0.1	1	1.22	1.00	-0.5	1
	10-Jun	1.69	0.85	-0.1	15	2.29	0.35	-0.2	23	-1.18	1.00	0.3	6
	17-Aug	12.04	**<0.01**	-0.2	116	9.55	**<0.01**	-0.3	152	6.66	**<0.01**	-0.4	111
CF	14-Jan	0.86	0.40	0.0	17	0.59	1.00	0.0	38	-0.58	1.00	0.1	15
	26-Feb	1.72	0.29	0.0	30	2.19	0.30	-0.1	26	0.18	1.00	0.0	21
	23-Mar	4.68	**<0.01**	-0.1	37	2.03	0.34	-0.1	39	3.28	**0.01**	-0.2	63
	30-Mar	3.31	**0.01**	0.0	39	2.78	0.07	-0.1	60	2.46	0.09	-0.1	38
	20-Apr	8.27	**<0.01**	-0.1	57	1.81	0.44	-0.1	84	12.60	**<0.01**	-0.7	59
	27-Apr	4.99	**<0.01**	-0.1	99	0.92	1.00	0.0	91	5.40	**<0.01**	-0.4	92
	4-May	3.68	0.29	-0.1	1	1.90	0.69	-0.1	2	2.26	0.95	-0.6	1
	14-May	3.64	0.24	-0.1	2	0.45	1.00	-0.1	2	1.65	0.95	-0.6	2
	10-Jun	na	na	na	na	3.00	0.44	-0.1	2	na	na	na	na
CM	4-Nov	0.15	1.00	0.0	5	-2.07	0.30	0.1	8	2.26	0.30	-0.6	3
	3-Dec	0.14	1.00	0.0	7	1.02	1.00	-0.1	9	-2.05	0.28	0.2	9
	14-Jan	-1.63	0.55	0.1	9	-0.03	1.00	0.0	20	-1.15	0.57	0.3	8
	26-Feb	-0.06	1.00	0.0	1	-0.46	1.00	0.1	3	-1.06	0.57	0.4	1

Discussion

Hydrographic Conditions, Ice Algae and Phytoplankton Blooms

Adolfbukta was covered with fast ice for six months of the year, from the beginning of January to the beginning of July, which seems to be typical for the fjord (polarview.met.no) (Figure 2). Stratification of temperature and salinity was nearly absent in the water column in the winter, and the transition to an isothermal and isohaline state occurred concurrently with the production of fast ice on the fjord. From January to June, the water column was homogenous and cold (-1.4 to -1.8°C) (Figure 3). Sea ice thickness varied from 72 cm in February to a mean of 100 cm in May and was covered by 5.1 cm to 22.7 cm of snow, the thinnest layer being measured in February (Kuckero, 2009).

Data on ice algae and phytoplankton, taken simultaneously with this study, showed an ice algae bloom on the underside of the sea ice in May (total 65ug /L chl-a, large cells=40ug /L chl-a)(Kuckero, 2009). The ice algae bloom was later, had a shorter duration and lower biomass than has been reported in other fjords on Svalbard (Søreide et al., 2010)

The phytoplankton bloom started in June under melting sea ice (4.4ug /L chl-a at 15m, large cells= 4ug /L chl-a at 15m) (Kuckero, 2009)(Figure 4b). Mooring data show that at that time, PAR also peaked and warm water (0-1°C)) was present down to 20m, two weeks before ice break up. The high temporal resolution of the mooring's hydrographic data supports the finding that the main pelagic phytoplankton bloom occurred in mid June in Billefjorden, as well as indicates a smaller second bloom in mid July. There was no evidence of a late-summer bloom, as expected from theory on Arctic waters (Falk-Petersen et al., 1990). This second bloom occurred concurrent with a convective mixing of the upper water layer, evident in the deterioration of the thermocline at that time (Figure 3), which likely brought a new pulse of nutrients to the surface. In addition to showing the timing of the spring phytoplankton blooms, the fluorometer on the mooring showed several intermittent, unexpected, high fluorescence values during the winter, when low phytoplankton biomass would be expected in the water column due to cold temperatures and lack of solar irradiance due to the polar night and thick sea ice. CTD data (Appendix Figures 6-9) show that there was nearly zero fluorescence in the water column from the beginning of November to the end of March, and Kuckero's (2009) more precise measurements found extremely low chl-a biomass in February: below 0.03 µg/l in the water column and 0.087 µg/l in the sea ice. Thus, the high values of the mooring fluorometer over winter are taken as not indicative of phytoplankton presence. Other moorings deployed on Svalbard have also shown similarly strange winter fluorescence values, however it may be an instrument sensitivity issue when total fluorescence is very low or something trapped in the small chamber where fluorescence is measured (personal communication, J. Søreide). Overall, it appears that there is a near total lack of phytoplankton or ice algae food for copepods food from November to mid-May (Figure 4b, Appendix Figure 9, Kuckero, 2009), with a small ice algae bloom in May and a phytoplankton bloom in mid-June.

Community Composition, Species Determination

New genetic results showed that the morphological species identification guidelines available produced significantly incorrect estimations of *Calanus* species composition, even when using the fjord-specific guidelines calculated by MIX-statistics for Billefjorden *Calanus* by Arnkvaern et al. (2005). This study used new prosome length cutoffs for differentiating between *C. finmarchicus* and *C. glacialis*. *Gabrielsen* et al 's (in press) genetics data was used in conjunction with this study's considerable prosome length sample size (n=11345) in MIX analyses which produced new prosome length boundaries for differentiation *C. finmarchicus* and *C. glacialis* for CIV, CV, and CF. In stages CIII-CV, bimodality was present in the prosome length distribution. Interestingly, the proportion of CVs and CIVs which were *C. glacialis* was high (81% and 89% respectively), but the MIX analysis shows that for CIII, the proportion of *C. finmarchicus* is the highest (68%) (Appendix Table 1). For females and males, the distribution was nearly unimodal. Breur (2003) and (Arnkvaern et al., 2005) also found that separating CF was difficult due to high overlap (40%) between *C. finmarchicus* and *C. glacialis*, and so Arnkvaern et al. reverted to divisions for CV and CF from Madsen etal (2001). However, the genetics data on females showed that only 2 of the 107 females tested were *C. finmarchicus.* Overall in the sampled population, the proportion of the females which were *C. glacialis* was 99.1% and *C. finmarchicus*, 0.08%. Genetics data was lacking for males, and the distribution was very normal, producing only estimations of one species in the MIX analysis. This is highly likely *C. glacialis*, but is presented in this study as *Calanus* sp. males.

The length distributions of CI and CII show no clear bimodality and, when determined to species following (Arnkvaern et al., 2005), show a dominance of *C. finmarchicus*. Either the boundary between *C. finmarchicus* and *C. glacialis* should be significantly lower (as was true for CIV-CF), or the species composition of young stages is different than that of older stages, with *C. finmarchicus* being predominately present as stages CI-CIII and *C. glacialis* being predominantly present as CIV-CM . The lack of good species resolution in the CI-CII stages may be a result of the time of year in which samples were taken. Though there is high temporal resolution over a whole year, the samples do not include mid June to mid July, the likely time of peak *C. glacialis* reproduction in Billefjorden (Arnkvaern *et al*., 2005, this study). With samples from that period included, perhaps a mode of *C. glacialis* would also appear in CI and CII.

Copepod size varies by geographical location due to differences in food availability and quality, water temperature, growth rates, and potentially seeding stock (Arnkvaern et al., 2005; Daase and Eiane, 2007; Kwasniewski et al., 2003). Thus, there may be a potential for the size of *Calanus* to vary interannually within Billefjorden based on environmental conditions and potentially some low-level advection from Isfjorden (Breur, 2003).

For two sampling dates, August 26 and September 6, 2008, *Calanus* species were staged and the species determined according to the prosome length guidelines of Kwasniewski *et al.* (2003), without recording the prosome length. Thus, the densities of the three species presented for these dates are based on a different set of morphological divisions than was used in the rest of the study. As the prosome length dividing lines of Kwasniewski were found to be too large for Billefjorden (*Gabrielsen* et al., unpublished data; this study), the number of *C. finmarchicus* were likely overestimated and *C. glacialis* underestimated for

those two sampling dates. However, the lipid sac data contained exact prosome length measurements, so the species determination for the lipid data is the same for all sampling dates.

Sampling Methods Issues

A steep decline in the population of *C. glacialis* was documented over the course of the winter, with the sharpest decline from December to January (Figure 10). Between these two sampling dates, net type was also switched, from a ship-based MPS net to an ice-based WP2 net. Though mesh size is the same, towing speed (crane vs hand or snow-scooter, potential drift by the boat), and the accuracy of the depth strata may differ between the two techniques. Diapausing *Calanus hyperboreus* have been shown to form highly dense swarms within 1m of the seafloor (Auel et al., 2003), so it is likely that densities in the deepest layer are influenced by exactly how close to the seafloor the net reached. The automatically- closing MPS net was used from September to December, ensures that the sampling strata were taken at correct depths. Thus, the density increases due to descent to diapause are trusted. As for the change to WP2 net in January, CV densities did decrease, but CIV densities did not. As CVs began the peak of their molting at this time, their decrease is likely most attributable to molting, with a neglible net-effect.

In December, samples were taken both at night and day, and the day samples are presented here with the exception of the 20-0m sample, which was from the night. The polar night has begun by December on Svalbard, and PAR was near zero (Figure 4a). Studies on diel vertical migration (DVM) in Billefjorden in late August/early September (A. Bailey et al., unpublished data) showed that even at that time, with some diurnal change in solar radiation, DVM was not present. Therefore, the values of the night 20-0 sample should be representative also of the *Calanus* community in the day. A comparison to densities derived from samples analyzed for lipid sac measurements show that density was similar in the two methods (Appendix Figure 1).

Density calculations are based the volume of water sampled. The volume of water sampled was calculated using the area of the net opening and the theoretical vertical distance the net was towed. Several weaknesses are present in the estimation of the volume of water sampled. Firstly, the nets lacked a depth beacon, and the length of the cable was assumed to be the depth of the net. This assumption may be inaccurate if the cable was not completely vertical in the water column (due to the boat drifting or strong current), such that the real depth of the net was shallower than the theoretical net depth. Additionally, both the multiplankton sampler and WP2 lacked a flowmeter; therefore, in the case of strong water currents or the boat drifting, the net may have sampled water in the horizontal direction also as it was towed up vertically. However, the temporal resolution, especially in the polar night, and time span of this dataset make it a valuable new time series of a high-latitude zooplankton community.

Community and Seasonal Cycle

Calanus glacialis: Descent to Depth

A few individuals had already begun to descend to depth when sampling began in late July 2008. By August, the majority of the population had migrated from the surfaces waters to the deep and had thus likely entered diapause. Density of CVs in the deepest layer, 175-100m, increased from August to October, peaking at 305 indiv. m^{-3} (Figure 10, Appendix Table 3), so it is taken that descent at a low level throughout early autumn.

The diapausing stock of *C. glacialis* was dominated by CVs (86-95 % of individuals in the deep) from September to October (before molting). CIVs comprised 5-11% of the diapausing population at this time. As CVs molted to adults from November to February, their relative proportion of the diapausing animals decreased. CIIIs were present in extremely low numbers intermittently throughout the winter, the highest density being found in the deepest layer in February (2 indiv. m^{-3}). Before molting, in November, CIIIs comprised 0.4% of the population in the deep. The presence of mostly CIVs and CVs in the diapausing population indicates a mix of 1 and 2 year life cycles for *C. glacialis* in Billefjorden, with a dominance of the 1 year life cycle. This fits well with what was found by (Arnkvaern et al., 2005) in Billefjorden and for *C. glacialis* in Rijpfjorden in northern Svalbard (Søreide et al., 2008; Søreide et al., 2010) and in the Barents Sea (Melle and Skjoldal, 1998). However, a 2 year life cycle is also common in the Arctic (Falk-Petersen et al., 2009). Productivity and water temperature affect the generation time of *C. glacialis*, with shorter life spans being found in Atlantic waters within the Barents Sea (Melle and Skjodal 1998) and in seasonally ice-covered waters during favorable ice years (Søreide et al., 2008) . In Rijpforden, a 1-2yr life span as been found for *C. glacialis*, with a higher proportion of CIV overwintering than in Billefjorden (~30%)(Søreide et al., 2010). Despite its extreme environment, Søreide suggests that *C. glacialis* managed a 1 yr life cycle due to the presence of both an ice algae and phytoplankton bloom.

Calanus glacialis: Molt to Adults

Molting from CVs to males began in October, before females, and peaked in December with a peak abundance in the water column of 3501 indiv. m^{-2} (Appendix Table 3). Female molting began in December and peaked in February at 3272 indiv. m^{-2}. Males appeared in October and November in the deep, below 100m, and ascended, concentrating primarily in the 100-50 stratum. Females first appeared in the upper 100m, but showed a distribution throughout the water column, with the highest concentration at 50-20m at their peak in February and throughout the spring until April. Assuming that molted adults would not descend after ascent, the presence of both females and males throughout the water column seems to indicate that molting occurred at depth, before ascent. Male *C. finmarchicus* have been observed to rise to an intermediate layer in the water column, where they mate with females as they ascend up through the layer to the surface (Heath, 1999). A similar mating strategy seems to be occurring in Billefjorden with *C. glacialis*.

Breur (2003) also found males present in Billefjorden in December, though neither Breur nor Arnkvaern *et al.* (2005) had the sampling frequency through winter to show when the females and males peaked. The temporal resolution of sampling in the wintertime in this study gives an idea of the exact timing and overlap of the adult population. Males and females overlapped in the greatest numbers from December to February, but male abundance had dropped sharply by the time female abundance peaked in February

(Figure 10, Appendix Table 3). Molting occurred midwinter, 6 and 4 months before the spring bloom in June, for males and females respectively. The period of female presence in the water column (7 months) was greater than that of males (4.5 months).

Accompanying the initiation of molting of adults was a decrease in density of CVs, from a peak of 305 indiv. m^{-3} in October to 195 indiv. m^{-3} in December to 14 indiv. m^{-3} in February, after the peak molting period of both males and females. From March 30 to June, CV density was extremely low (<5 indiv. m^{-3}), a reduction likely due to a combination of molting and mortality (see Lipid Discussion below). In concurrent sampling in Billefjorden, (Grigor, 2010) found high densities of the predatory chaetognath *Sagitta elegans*, a *Calanus* predator, in the deep throughout the winter. The highest concentrations were found in spring from February to May, at a maximum of 1500 indiv.m^{-3} for +40mm individuals. Thus, predation in the deep may be a significant component of the sharp decrease in CV densities after December.

Calanus glacialis: Reproduction

Female abundance dropped sharply after its peak in February, from 30 indiv. m^{-3} to between 8 and 13 indiv. m^{-3} at 50-20m throughout March and April. By May and June, there were nearly no females in the upper 100m. Interestingly, there were a few in the deep at this time (2-4 indiv. m^{-3}). In two sampling dates in May, when the ice algae bloom occurred in Billefjorden (Kuckero 2009), the total abundance of females in the water column was 5% and 11% of the abundance in February (May 4th and 11th, Table).

From the presence of CI and CII on the June 10th, it is possible to back-calculate egg laying. The water column under the sea ice in spring was homogenous and cold, the upper 80m being below -1.6°. The only published data on naupliar development in *C. glacialis* is from laboratory populations reared at +2°C to +10°C (Corkett etal 1996). In the first study to follow the complete development of *C. glacialis* nauplii at sub zero temperatures similar to those found in *C. glacialis'* natural habitat, Daase et al. (in preparation) found that at -1.2°C, the development time from hatching to CI was 51 days. They also found that the time it takes for an egg to hatch is approximately 8 days at -1.2°C. Thus, in the cold (-1.6°C), food-limited environment of Billefjorden in early spring where these processes may be slow, an estimate of 59 days from egg laying to CI (8d to hatch + 51d development) may apply. To produce CIs by June 10th, an estimated time of egg laying would be around April 12th. CIIs present in June would have perhaps been laid as eggs even earlier, in late March/early April. These dates are later than the reported reproduction in (Arnkvaern et al., 2005), who reported a back-calculated time of egg laying in Billefjorden by *C. glacialis* as "no later than February/March". During the sampling trips closest to the time of egg laying (March 30th and April 20th), female abundance was most concentrated at 50-20m (13.3 and 8.5 indiv. m^{-3}). Egg laying occurred approximately 6 weeks after the peak abundance of females in late February. It takes at least 3-4 weeks for *C. glacialis* females to mature their gonads, dependent on food availability (Tourangeau and Runge, 1991). Food availability in February-April, during the period of gonad maturation and egg laying, was extremely low (Figure 4b).

C. glacialis females likely produced eggs in mid-April while food concentrations were near zero (flourescence<0.1 g l^{-1}, Figure 4b, Appendix Figure 9). Egg production in *C. glacialis* has been shown to be strongly tied to food availability (Hirche and Bohrer, 1987; Hirche, 1989; Hirche and Kattner, 1993), but this

may vary from environment to environment (Conover, 1988). Hirche and Bohrer (1987) found *C. glacialis* females did not produce eggs under dense pack ice in the Fram Strait and ceased to produce eggs after only 3 days of starvation. Some suggest that the linkage between egg production and food abundance in *C. glacialis* makes *C. glacialis* similar to *C. finmarchicus* in its reproductive strategy (Hirche, 1989; Hirche and Bohrer 1987). Others have reported active spawning in *C. glacialis* well before the bloom when food concentrations were extremely low, for example in the Greenland Sea (Smith, 1990). Conover (1988) reports that "in the central Canadian arctic, spawning is initiated under 2 m of seasonal ice in June when chlorophyll may be less than 0.1 ug l^{-1} in the water column, as though in anticipation of the spring flowering (Conover & Harris, unpublished)." Egg production can also be supplemented by food from ice algae before the spring phytoplankton bloom (Hirche and Kosobokova, 2003; Søreide et al., 2010). The decoupling of egg production and food availability would in indicate that *C. glacialis* can also exhibit capital breeding similar to *C. hyperboreus* (Smith, 1990).

The first available food for copepods was in the form of the ice algae bloom in May (Kuckero, 2009). In temperatures below -1°C, *C. glacialis* eggs need about 3 weeks to develop to the first nauplii feeding stage (NIII) (M. Daase & J.E. Søreide unpubl. data). If spawning began in mid-April, the first feeding naupliar stage would have been present at the time of the ice algae bloom, but it's unknown if they could exploit such a resource. Werner and Hirche (2001) reported that *C. glacialis* eggs floated and accumulated densely under spring sea ice in the Barents Sea during an ice algae bloom. The authors suggested that ice algae is probably used as a nursery ground for young larvae. Kuckero (2009) did find a significant proportion of the ice algae bloom to be composed of small cells (3-0.7 µm; 25 ug /L of a total of 65ug /L Chl-a), which may be able to be eaten by naupliar stages.

Compared to previous studies in Billefjorden, the low abundance of females in spring is apparently not out of the ordinary. (Arnkvaern et al., 2005) also found extremely low densities in the spring (April to May), with an approximate *C. glacialis* female abundance of 600 indiv. m^{-2} (their Figure 5). Breur (2003) found similarly low female abundances in spring, reporting a maximum of 810 indiv. m^{-2} in mid-March to 270 indiv. m^{-2} in May (his Figures 10b and 11). Total female abundance in the water column in this study decreased from the peak in February (3272 indiv. m^{-2}) to 651m^{-2} in March to 161-349 indiv. m^{-2} in May. Thus, it appears that the low female abundance in Billefjorden in the spring of 2009 was similar to what it has been in previous years (2001 and 2003).

Young stages of *C. glacialis* (CI-CIII) were of low abundance, and found primarily in July 2008 and June 2009. Maximum abundances of CI-CII were 24 and 61 indiv. m^{-2} in June 2009 and 265 indiv. m^{-2} on August 17th respectively (Appendix Table 3) . This is an order of magnitude lower than the peak abundances of young stages reported by (Arnkvaern et al., 2005), which peaked in mid-June and mid-July at: CI 1700 and 1875 indiv. m^{-2}, CII 3750 and 3400 indiv. m^{-2}, and CIII 1500 and 3400 indiv. m^{-2} (estimations from their Figure 10b and 11). In 2003, Breur reported finding "no evidence of reproduction" in *Calanus* species during his sampling period, which lasted through winter to May, though nauplii abundance showed that it was in the early stages in May. Similar to his experiment, it may have been that the sampling did not capture the peak of reproduction in Billefjorden. In 2001, the peak abundance of *C. glacialis* occurred one month after ice break up (mid July and mid June respectively) (Arnkvaern et al., 2005). Thus, as the ice break up in Adolfbukta

occurred in the beginning of July in 2009, it may be expected that the peak of *C. glacialis* would have occurred in late July/ beginning of August, and was thus not captured with the sampling.

Nonetheless, recruitment of *C. glacialis* seems to be lower than that reported by Arnkvaern *et al.* (2005) for Billefjorden. This may be due to a late ice algae bloom of short duration and low biomass in the spring. In other fjords on Svalbard, ice algae has been shown to fuel early maturation and boost the egg production in *C. glacialis* females such that their offspring overlap with, and can fully exploit, the spring phytoplankton bloom later in the spring (Hirche and Kosobokova, 2003; Søreide et al., 2010). Thick sea ice with a significant snow cover throughout spring may be one reason for the poor ice algae bloom, reducing the light penetration necessary for an under-ice algae bloom. Increased snow cover on sea ice was shown affect *C. glacialis* reproduction in Rijpfjorden, in northern Svalbard by causing a 2 week delay in the spring phytoplankton bloom in 2008 compared to 2007 (Leu et al., in press). As a result, *C. glacialis* reproduction was reduced fivefold compared to 2007, when there was less snow and an earlier ice breakup.

Summary of C. glacialis *development*

C. glacialis produced eggs in early spring, under the sea ice and in the absence of food. This resulted in the first feeding nauplii stages appearing as the ice algae bloom developed in May and CI-CIIs overlaping with the spring phytoplankton bloom. This capital breeding, which uncouples egg production from food availability, is a key arctic adaptation seen in *C. hyperboreus* and *C. glacialis* which allows them to match their offspring to a short growing season(Conover and Huntley, 1991; Falk-Petersen et al., 2009). This strategy requires large lipid stores in order to support early molting, maturation and egg production in nearly complete absence of food.

Comparison to C. finmarchicus

C. finmarchicus is often referred to as an expatriate in the Arctic Ocean, being continually seeded from Atlantic waters pushing north from the Atlantic via the West Spitsbergen Current. In Billefjorden, advection from the Atlantic-influenced Isfjorden is very limited, though it may occur sporadically (Breur, 2003; Darelius, 2003). *C. finmarchicus* nonetheless is found in Billefjorden throughout the year, and constitutes between 63-83% of the young stages and 0.8-13% of older stages (Appendix Table 1). The paradox of the presence of young stages and lack of both females and males indicates that either, 1) the morphological guidelines for species determination need to be altered for CI-CIII, or 2) the young *C. finmarchicus* stages were advected into Billefjorden in early June from Isfjorden. Isfjorden is more dominated by *C. finmarchicus* due to the influence of Atlantic water, so an introduction of water from Isfjorden would likely increase the abundance of *C. finmarchicus* in Billefjorden. Breur (2003) has proposed such an advective event in early spring of 2002 above sill depth, but hydrographic data with a higher temporal resolution are needed to support the theory. The mooring which collected data from 2008-2009 in Billefjorden, in addition to this study's CTD casts, provided such data and gave no indication of an advective event during the sampling period. Thus, using genetics to determine better prosome length divisions for species determination of young *Calanus* stages in Billefjorden is needed for understanding the *Calanus* dynamics of the fjord.

Both *C. finmarchicus* CIVs and CVs were present throughout winter, but were of more equal relative abundance and more evenly distributed throughout the entire water column than were *C. glacialis* CIVs and CVs. The equal presence of CVs and CIVs possibly indicates that significant proportion of *C. finmarchicus* does not manage to complete a life cycle in 1 year, though the number which survive through to their second year appears low (Figure). Falk-Petersen et al. (2009) report only one study where a 2 year life cycle was found for *C. finmarchicus*, near the Canadian archipelago (Longhurst et al., 1984). Breur (2003) interestingly also found *C. finmarchicus* to be distributed throughout the water column, with highest densities at the surface, in December in Billefjorden. Pedersen et al. (1995) also report overwintering *C. finmarchicus* in coastal Norway and the Barents Sea which remained in the upper 100m, but the reason for staying in the surface waters is still unclear. However, due to the lack of light in the polar night and the homogeneity of the cold water, it is possible that some individuals can overwinter with a low metabolism and some measure of predator protection even in surface waters (Conover and Huntley, 1991).

C. finmarchicus is adapted to live in the more predictable environment of the Atlantic (Conover, 1988; Falk-Petersen et al., 2009), where upon molt and ascent females can utilize the spring bloom to complete maturation and to fuel egg production. In Billefjorden, the spring phytoplankton bloom doesn't begin before mid-June. *C. finmarchicus* females would face the challenge of surviving until June without food, after which the offspring produced may arrive after the bloom is already finished, making their development to CV and deposition of enough lipids difficult before the onset of winter around October. The income breeding strategy of *C. finmarchicus* is thus poorly suited to the unpredictable environment of the Arctic, likely explaining its low abundance compared to *C. glacialis* (Arnkvaern et al., 2005; Falk-Petersen et al., 2009).

State: Lipids, Prosome length, Condition factor

Issues with values and sampling

The conversion of lipid sac area to total lipid was calculated using the equation determined by Vogedes et al. (2010), which showed that lipid sac area and total lipid were highly correlated (r^2=0.94 for ln-transformed data). However, their model was based on a sample of three *Calanus* species (C. *finmarchicus*, *C. glacialis*, and *C. hyperboreus*; stages CIV-CF) which had large prosome lengths and lipid sacs (range PL: 2.13-7.01mm ; lipid sac area: 0.388-6.474mm^2), mostly due to the inclusion of *C. hyperboreus* CV and CF. Thus, the TL-lipid sac area conversion calculation created from the upper range of lipid levels may not be as accurate for estimating the TL of low-lipid individuals in this data set (range, this study, PL: ; lipid sac area: $3.6x10^{-4}$-2.755 mm^2).

In two of the 17 sampling trips, sampling technique may have affected the representativeness of the individuals used for lipid analysis. In July 2008, *Calanus* were not subsampled, but randomly sampled, when picked for lipid sac photographing, and thus the subset of the whole sample which was ultimately used for lipid analysis may be skewed in favor of large animals which are easy to see. On September 23, 2008, a WP3 net was used for sampling, which has a mesh size of 500µm instead of the 180µm used on all other sampling

trips. This may mean that the sample contains a disproportionate number of animals from the large end of the size distribution. However, 500µm (0.5mm) is smaller than the smallest copepods which were being sought for lipid analysis (1.5-2.5mm CIV, *C. finmarchicus* and *C. glacialis*), and, considering both deep and surface samples, the range of PL captured on that date was similar to other dates.

CV Lipids

The first *C. glacialis* CVs to enter diapause had already descended by the end of July 2008 and showed the highest average total lipid level and prosome length of the entire sampling year. Both total lipid and prosome length were also high on September 23, after slightly lower values in the intervening sampling dates August 26 and September 6. Similarly high total lipid levels and prosome lengths were found in the deep-dwelling CVs the next summer, August 2009, supporting the hypothesis that the first to descend to diapause are the largest and most lipid rich CVs. However, looking at the condition factors of the diapausing CVs reveals that the relative lipid condition of CVs was consistent throughout the descent period. Thus, it's possible that large animals of good condition descended first, but smaller animals of similarly good condition descended later, reducing the total lipid and prosome length distributions but keeping the mean condition factor in the diapausing population constant.

From the end of summer to early autumn (July-September), CVs in the deep had significantly higher total lipid levels, longer prosome lengths, and higher condition factors than those remaining in the surface (except for non-significance on August 36 and September 6, due perhaps to low sample sizes, Table-). Many studies have shown similar findings, that after the spring bloom, the copepods that have entered diapause have higher lipids and longer prosome lengths than in the surface waters (Heath, 1999; Hirche, 1983; Jonasdottir, 1999; Miller et al., 2000). This is likely because those in the deep have gained sufficient lipids to overwinter and molt to adults the next spring, whereas the surface population is a mixture of CVs which have just molted and thus have little lipid and those which have been feeding and are attempting to accumulating enough lipid.

C. *finmarchicus* has been suggested to descend to diapause upon accumulating a given threshold of lipids (Irigoien, 2004; Maps et al., 2010). Such a threshold would be the minimum lipid required to support metabolism over winter, molting to adult, ascent and the initiation of gonad maturation. Completion of gonad maturation and egg production in *C. finmarchicus* is based on energy gained by feeding during the spring bloom (Diel and Tande, 1992; Hagen and Auel, 2001; Harris et al., 2000; Lee et al., 2006; Niehoff et al., 2002; Plourde and Runge, 1993; Runge, 1985). However, a threshold may be a less beneficial, and thus a less likely, paradigm for *C. glacialis* and *C. hyperboreus* because, as capital breeders, CVs often molt and ascend well before the spring bloom, maturing their gonads and producing eggs using only stored lipids, without feeding. The number of eggs a *C. glacialis* female can produce before the bloom is tied to the amount of additional lipids she has after molting, ascent and maturation. As eggs produced before the bloom may have the highest reproductive fitness (Varpe et al., 2009), *C. glacialis* and *C. hyperboreus* CVs would benefit from gaining as much lipid as possible before entering diapause, rather than descending and leaving abundant food in the surface once they reached a minimum threshold. However, the surface habitat also has higher

predation pressure, so CVs may face a tradeoff of the benefit of gaining supplemental lipids for capital-bred egg production and the danger of predation.

The theoretical lipid threshold for diapause descent is suggested to be a size-dependent measure of lipid (Maps et al., 2010), despite the fact that Rey-Rassat et al. (2002) reports that the amount of lipid required for molting and gonad maturation to be independent of copepod size. Though a threshold of lipids at descent is convenient to model, it is difficult to find in the field. The population in the surface should be below the threshold. In the deep, those individuals which are newly descended should be at the threshold, but those which have been in the deep for some time may no longer have as high lipids as they did upon descent. Thus, there may be more variability in the lipids of individuals found in the deep than there is amongst individuals when they descend. The condition factor of the deep-dwelling population of CVs did not change with time during the descent period (July to September). However, the significant variability within the population at each sampling date does not indicate that the *C. glacialis* individuals in diapause had descended at a specific lipid condition. Thus, no support for a lipid threshold controlling diapause descent was found.

Diapause

The amount of lipid stores used to support a reduced metabolic rate in diapausing CVs has been estimated to be anything from nearly nothing (Jonasdottir, 1999; Miller et al., 2000) to significant losses of up to 50% of the original lipid level at entrance to diapause (Pasternak et al., 2001; Pepin and Head, 2009; Saumweber, 2006) for *C. finmarchicus*. Ingvarsdottir found low respiration rates in diapausing *C. finmarchicus* and estimated the loss of carbon content to be 0.250ugC day^{-1}. For *C. glacialis*, estimated carbon loss during diapause and early gonad maturation is 0.16% body C d^{-1} (Hirche and Kattner, 1993). Søreide et al. (unpublished data), have found that the rate of oxygen consumption in both diapausing and active, feeding *Calanus glacialis* copepodites to be $2.44x10^{-3}$ and 2.17×10^{-2} umol O2 h^{-1} $indiv^{-1}$, respectively, indicating a decrease of respiration of 89%. These preliminary values indicate that the cost of metabolism in diapause is, relative to the active state, low, but perhaps enough to result in significant lipid decreases over a period of many months. Using a temperature-dependent rate of lipid use, potential diapause length can be calculated from lipid stores, depending on the temperature of the overwintering habitat (Ingvarsdóttir et al., 1999; Johnson et al., 2008; Saumweber, 2006). However, determining the rate of lipid use by diapausing animals is not straightforward. Change in the lipid distribution of diapausing CVs is not purely attributable to use of lipids for the maintenance of metabolism, but can also reflect changes in the CV population due to molting of CVs to adults or loss due to mortality (starvation or predation). Molting of the largest CVs first would decrease the average lipid level of the remaining CVs. Mortality of lipid-poor CVs due to starvation may increase the average lipid level, whereas preferential predation of large *Calanus* may reduce the average lipid level. However, the decrease of lipids from the peak (July) to November, the last sampling date before the peak molt of males, may be the best estimate of metabolic use of lipids by CVs. A least-squares regression gives a slope of 0.0023mg total lipid lost $indiv^{-1}$ d^{-1} from July to November(statistics in Results), resulting in a predicted loss of 0.23mg over that 100 day period. From November to February, during the peak period of molting to males and females, the decrease in lipids is -0.00086mg total lipid $indiv^{-1}$ d^{-1}, though this may be more an effect of molting of lipid-rich CVs than metabolism of lipids.

A key component of the lipid threshold hypothesis for diapause initiation is that CVs would only descend to diapause once they have reached a lipid level which is sufficient to cover metabolism overwinter, molting, gonad maturation, and ascent from diapause (Irigoien, 2004; Maps et al., 2010; Rey-Rassat et al., 2002). Irigoien (2004) proposed that finding a significant proportion of the overwintering CV population with lipid levels below the threshold would disprove the hypothesis. The energetic cost of gonad maturation and molting to adult has been estimated to be 70 µgC and 8 µgC, respectively, by Jonasdottir (1999) and collectively as ~70 µgC by Rey-Rassat et al. (2002) for *C. finmarchicus* CV to CF . These lipid requirements are quite consistent and, interestingly, independent of the amount of previous lipid reserves and the length of the individual (Rey-Rassat *et al.* 2002). However, these values only apply to *C. finmarchicus*. Even though the threshold theory of accumulating lipid to a point and then descending, doesn't fit with the reproductive strategy of *C. glacialis*, *C. glacialis* may still have a minimum threshold below which the cue is not signaled to enter diapause. Ingvarsdottir (1999) suggests that it's necessary to have retained a minimum of 51% of the lipids that the CV started diapause with in order for *C. finmarchicus* CVs to be able to molt and ascend, where they will be able to begin feeding. If Ingvarsdottir's (1999) estimation of 51% of the original lipid level that is required at the end of diapause for successful molting and ascent, perhaps this is applicable also for *C. glacialis*. Taking the average lipid level of CVs in the deep in July (0.50mg +/-0.02), 51% of the deep-dwelling CVs are below 50% (0.25mg) in December, when peak molting to males occurs, and 78% are in March, after the peak molting of both males and females. However, *C. glacialis* has a greater tendency towards capital breeding than the income breeder *C. finmarchicus*, and thus, as discussed before, has different energy requirements. In this study, *C. glacialis* molted into males and females 6 and 4 months before the spring bloom, respectively. Thus, the minimum lipid threshold required for successful reproduction after diapause must include not only molting to adult, gonad maturation, and ascent, as *C. finmarchicus* requires, but also energy to maintain metabolism, fully mature their gonads (which, for *C. finmarchicus* is supported by feeding on the bloom, Rey-Rassat et al. 2002), and produce eggs in the absence of food. Thus, even the threshold of ~50% of lipid reserves to be retained by the end of diapause for *C. finmarchicus* would be conservative for *C. glacialis*. During winter, both abundance and total lipid of diapausing CVs decreased sharply between December and January. By January, the average lipid level of diapausing CVs was 0.18mgTL+/-0.01, only 38% of the level at the end of September (0.47mgTL+/-0.01). This decrease may in part be due to molting to males (peak in December) and may also be due to mortality of CVs due to decreasing lipid stores. Indeed, mortality of overwintering CVs due to starvation may represent a significant loss for the emergent population in *C. finmarchicus* (Pasternak et al., 2001; Pepin and Head, 2009). Pepin and Head (2009) found that 23-53% of *C. finmarchicus* CVs overwintering in the Laborador Sea and Newfoundland Shelf did not have sufficient lipid in December to support molting to adult and the initiation of gonad development. They calculated that the loss of 23-53% of the population over 3-6 months would represent an instantaneous mortality rate of 0.008 day^{-1}, which was within or below estimates of CV mortality rates reported by Ohman et al. (2004) for *C. finmarchicus* across the North Atlantic and *C. glacialis* in Billefjorden (0.075 d^{-1} in spring, Arnkvaern et al., 2005).

Adult Lipids

The highest lipid levels were found in the first males and females to molt, in October and December, respectively. These early-molting individuals also had the highest prosome lengths and condition factors, so not only were they large, their lipid content relative to their size was also high. The distribution of males prosome length showed a strong decline with time, a clear indication that the largest individuals molted first. This may be attributable to an earlier molting of *C. glacialis* and later of *C. finmarchicus*, but the unimodality of the CM prosome length distribution points to the presence of only one species, *C. glacialis*. Thus, it's likely that small CVs molt into small CMs after the early molting of large individuals for *C. glacialis*.

To investigate if there is a state-dependence in molting timing, the lipid condition when newly molted should be compared throughout the molting period. However, female lipids decline quickly once molted due to gonad maturation and egg production. It could be assumed that those in the deep are the most recently molted, or "newest", females, as they have yet to ascend. During the peak molting period, December to end of February, the total lipid level of females in the deep (potentially newly molted) was quite consistent (~0.25mg), but lower than the first females to molt (in December) (t-test, $t = -5.33$, $df = 18$, $p<0.01$). A similar trend was seen for the condition factor (t-test, $t = -4.69$, $df = 18$, $p<0.01$). Thus, the first females to molt had significantly more lipids and better condition than the potentially newly-molted females which molted later. Females may benefit from being in the surface waters early, were they are able to opportunistically respond to an early bloom of ice algae or phytoplankton. Eggs produced before the bloom may have the highest fitness in areas with short spring blooms (Varpe, 2007). Lipid rich females, therefore, would be able to support themselves for longer and produce more eggs pre-bloom. Perhaps, if a female has the extra lipid necessary to support reproduction before the bloom, she molts early. If she has low lipid, then molting is delayed in order to wait for the phytoplankton bloom.

After the peak molting period, from March to April, low densities of females were found which were concentrated in the 50-20 stratum. In May however, there were low densities in the deep with very low lipids. ,Though *C. glacialis* females have been shown to have the ability to be iteroparous, to build up lipids again after reproduction for a second overwintering (Kosobokova, 1999), it is unlikely that females would descend again before producing eggs and utilizing the spring bloom to sufficiently rebuild of their own stores. Arkvaern et al. (2005) did not show evidence of iteroparity of *C. glacialis* females in Billefjorden, though they lacked the sampling in the late fall-early winter that would be needed to show it. Either these lipid-poor females in the deep in May are newly molted from lipid-poor CVs, or they have descended from the surface after reproduction, as has been seen with *C. glacialis* in fjords in Norway (Niehoff and Hirche, 2005). This may be a sign of iteroparity, which has been found in *C. glacialis* in the White Sea (Kosobokova, 1999).

While molting midwinter, both males and females must rely on lipid stores to molt and ascend. Following molt, females use considerable energy on the maturation of their gonads (Pasternak et al., 2001; Seuthe et al., 2006). Conversely, Sargent and Falk-Petersen (1988) suggest that the energetic cost of producing male reproductive system is very low for *Calanus* sp. males, but that total lipids nonetheless decrease due to intense physical activity associated with copulation and spermatophore attachment. Often, reproductive processes occur in the absence of food (Arnkvaern et al., 2005; Hirche and Kattner, 1993; Niehoff et al., 2002). Hirche and Kattner (1993) found that, even in the presence of food, *C. glacialis* females can lose up to half of their lipid content during gonad maturation in as little as 17 days. For females, egg production also requires significant lipids (Hirche, 1989; Niehoff et al., 1999). *C. glacialis* eggs contain

0.40/ug C egg^{-1}, and in periods of considerable production ((1274 eggs in 23 d), egg production can consume 5% of body C female $^{-1}$ d $^{-1}$(Hirche, 1989). In the absence of food, *C. glacialis* females can manage to produce eggs, though after two months of starved egg production, Hirche and Kattner (1993) found that the females contained only 13% of their original lipid level. If food becomes available, however, female lipid content may plateau, as egg production is fueled by ingested food (Hirche and Kattner, 1993). Similarly, Martynova and Søreide (in preparation) found that gonad maturation in the absence of food reduced lipid stores by 53% (from 135.3 ug TL to 63.9 ug TL ind^{-1}) after 13 days of starvation. Given food, gonad maturation did not cause a decrease in total lipid. The lipid levels of females in this study showed strong declines throughout the winter and spring, showing a decline from 0.30+/-0.02mg in December to 0.06+/-0.04mg in mid-May (a decline of 0.00044mg TL d^{-1}). No stabilization of lipid levels was seen during the study period, indicating the decline was a function of gonad maturation and egg production in the absence of food. Our data on the decline from March-May (0.16+/-0.01mg to 0.06+/-0.04mg TL) fits well with the decline of *C. glacialis* female lipids reported by Søreide et al. (2010) in Rijpfjorden, in northern Svalbard (~0.160-0.050mg TL). Egg production in the few low-lipid *C. glacialis* females present in May was nearly zero (Søreide and Bailey, unpublished data), indicating that females were likely either spent after producing eggs earlier, fueled by lipid reserves and possibly waiting for the phytoplankton bloom to produce eggs based on ingested food. As Kattner and Hirche (1993) point out, *C. glacialis* has the potential for both capital and income breeding.

Summary

C. glacialis most likely produced eggs under the sea ice and in the absence of food in early spring, utilizing their significant lipid stores for maturation and egg production. This likely resulted in the first feeding nauplii stages appearing as the ice algae bloom developed in May and CI-CIIs overlapping with the spring phytoplankton bloom.

Low recruitment compared to other years may be due to a late and low-biomass sea ice algae bloom, which has been shown to boost reproduction in other Svalbard fjords by fueling egg production before the spring phytoplankton bloom.

By producing eggs well before the presence of food, *C. glacialis* exhibited a capital breeding strategy similar to the polar species *C. hyperboreus*. This capital breeding, which uncouples egg production from food availability, is a key arctic adaptation which allows females to match their offspring to a short period of food availability. This strategy requires large lipid stores in order to support early molting, maturation and egg production in nearly complete absence of food, and a threshold of lipids at which diapause is triggered is an unlikely explanation of diapause entry. Though extra lipid accumulation is a benefit for *C. glacialis* as it supports capital breeding and survival in times of low food, copepodites in the end of summer must these benefits against predation in the surface. Flexibility in life history and diapause gives *C. glacialis* the opportunity to wait for good conditions.

Adults which molted first were the largest and most lipid rich individuals. Perhaps, molt timing is linked to lipids in such a way that, if an individual has surplus lipids for capital breeding it molts early, and if not it remains in diapause, waiting to produce eggs simultaneously with the spring bloom. In general, *C. glacialis* is

well adapted to the unpredictable, pulsed food regime of the Arctic due to this ability to produce eggs even in the absence of food, and also due to its longevity, ability to preserve its reproductive potential through periods of starvation, and rapid mobilization of ovaries and high egg production in the presence of food (Hagen and Auel, 2001; Hirche, 1989; Hirche and Kattner, 1993).

Conclusion

The Arctic marine ecosystem is highly influenced by the sea ice regime and the timing of the spring bloom. In a warming climate, the already apparent recession of sea ice will continue, potentially resulting in an earlier spring phytoplankton bloom (Hansen et al., 2003; Johannessen et al., 2004). The ability of *Calanus* spp. to match their reproduction to the spring bloom is important for the success of their populations. Earlier ice break up and earlier spring blooms may result in a mismatch in the timing of *Calanus* reproduction and food availability if *Calanus* has a fixed phenology (Hansen et al., 2003; Søreide et al., 2010). Norrbin et al. (2009) suggested that *C. glacialis* and *C. finmarchicus* showed the potential to match an early spring bloom which occurred in Svalbard waters in 2006 due to early sea ice retreat. This study's results indicate that lipid-rich individuals molt to adults and ascend early such that they have the potential to either utilize an early food resource for egg production, or produce eggs based on lipid reserves in the absence of food, which will match a late bloom. Thus, surplus lipids allow for flexibility of timing of reproduction. The, large lipid reserves, long life, and potential for both capital and income breeding of *C. glacialis* females may provide the flexibility needed for survival in a changing climate.

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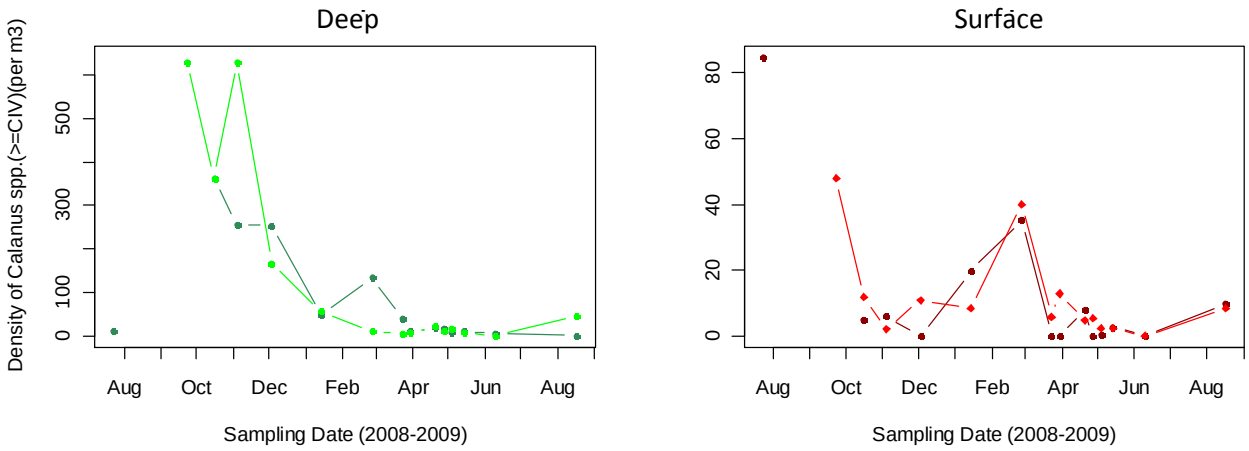
Appendix



Appendix Figure 1. Deep (a) and surface (b) *Calanus* sp. densities, as calculated from samples taken for lipid sac analyses (light green and light red points) and zooplankton community enumeration (dark green and dark red points). For comparison to lipid samples, community sample densities were converted from depth strata 20-0m and 50-20m to 50-0m and only stages (CIV-CF and CM) of all three *Calanus* species are included. Deep samples are from 175-100m; surface are 50-0m. Densities are in indiv. m^{-3},

Appendix Table 1. Species composition, based on the new morphological prosome length cutoffs for species identification for CIV, CV, and CF, and supported by MIX analysis. Stages CI-CIII and *C. hyperboreus* prosome boundaries are kept from Arnkvaern et al 2005. See Table 1 for species determination. *Unimodality of the prosome distribution of males indicates that all are likely *C. glacialis.*

	%			
	C. finmarchicus	*C. glacialis*	*C. hyperboreus*	Total n
CI	62.7	7.3	30.0	110
CII	82.5	7.0	10.5	114
CIII	68.0	27.0	4.9	244
CIV	12.5	80.7	6.8	2790
CV	10.0	89.7	0.2	5227
CF	0.8	99.1	0.1	2382
CM		100*		469

Appendix Table 2. Sampling overview for Billefjorden 2008-2009.

			Sampling Time		Formalin Samples								Lipid Samples				
					Day				Night				Day		Night		
Date	Transport	Net Type	Day	Night	20-0	50-20	100-50	180-100	20-0	50-20	100-50	180-100	50-0	175-100	50-0	175-100	Notes
23-Jul-08	Polarcircle	WP2 Hydro bios	~12:00	na	x	x	x	x	na	na	na	na	x	x	na	na	*
26-Aug-08	*Jan Mayen*	Multinet	13:05	1:20	x	x	x	x	x -	x -	x -	x -	x x	na x	x- x-	x- x-	**
6-Sep-08	*Jan Mayen*	Multinet	11:15	22:15	x	x	x	x	x -	x -	x -	x -	x x	x- x	x- x-	x- x-	**
23-Sep-08	*Viking Explorer*	WP3	14:15	0:45	x	0	0	0	0	0	0	0	x-	x-	x	x	
16-Oct-08	*Viking Explorer*	Multinet	15:20	0:56	x	x	x	x	0	0	0	0	na	na	x	x	
4-Nov-08	*Viking Explorer*	Multinet	13:50	0:10	x	x	x	x	0	0	0	0	na	na	x	x	
3-Dec-08	*Viking Explorer*	Multinet	12:40	0:30	0	x	x	x	x	0	0	0	na	na	x	x	***
14-Jan-09	Snow scooter	WP2 Hydrobios	18:00-19:30	na	x	x	x	x	na	na	na	na	x	x	na	na	
26-Feb-09	Snow scooter	WP2 Hydrobios	12:36-13:05	23:10-0:00	x	x	x	x	0	0	0	0	x	x	na	na	
23-Mar-09	Snow scooter	WP2 Hydrobios	17:00-18:00	na	x	x	x	x	na	na	na	na	x	x	na	na	
30-Mar-09	Snow scooter	WP2 Hydrobios	14:39-15:30	na	x	x	x	x	na	na	na	na	x	x	na	na	
20-Apr-09	Snow scooter	WP2 Hydrobios	15:30-17:00	na	x	x	x	x	na	na	na	na	x	x	na	na	
27-Apr-09	Snow scooter	WP2 Hydrobios	15:30-14:45	na	x	x	x	x	na	na	na	na	x	x	na	na	
4-May-09	Snow scooter	Danish WP2net	14:00-15:10	na	x	x	x	x	na	na	na	na	x	x	na	na	
14-May-09	Snow scooter	Danish WP2net	14:15-15:20	na	x	x	x	x	na	na	na	na	x	x	na	na	
10-Jun-09	Polarcircle/skis/dogs	Danish WP2net	na	20:40-22:08	na	na	na	na	x	x	x	x	na	na	x	x	
17-Jun-09	*Polar girl*	Danish WP2net	12:45	na	0	na	na	na	na	na	na	na	x	na	na	na	
14-Jul-09	Polar cirkel	Danish WP2net	~12:00	na	0	0	0	0	na	na	na	na	na	na	na	na	
17-Aug-09	*Jan Mayen*	Multinet		20:25 (lipid)	x	x	0	0	na	na	na	na	na	na	x	x	

Notes:

*Indivuals picked for lipid pictures not subsampled, so not representative of pop.

**Lipid samples divided in 4 strata: 20-0, 50-20, 100-50, 180-100m

*** Night formalin surface sample presented with daytime samples

Key	
x	Analyzed, presented
x -	Analyzed, not presented
na	No samples taken
0	Sampled, not analyzed

Appendix Table 3. *C. glacialis* copepodite densities from Billefjorden, from four depth strata throughout one year (2008-2009). Density per depth stratum are given are given in indiv. m^{-3}. Abundance in the entire water column is given in indiv. m^{-2}. Samples not counted are indicated by "na".

Stage	Depth(m)	23-Jul	6-Sep	26-Sep	23-Sep	16-Oct	4-Nov	3-Dec	14-Jan	26-Feb	23-Mar	30-Mar	20-Apr	27-Apr	4-May	14-May	10-Jun	17-Aug
CI	175-100	0.0	0.0	0.0	na	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	na
	100-50	0.0	0.0	0.0	na	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	na
	50-20	0.0	0.0	0.0	na	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
	20-0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Water Column	0	0	0	na	0	0	0	0	0	0	0	0	0	8	0	24	na
CII	175-100	0.0	0.0	0.0	na	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	na
	100-50	0.2	0.0	0.0	na	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	na
	50-20	1.1	0.0	0.0	na	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
	20-0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0
	Water Column	40	0	0	na	0	0	0	0	0	0	0	0	0	4	0	61	na
CIII	175-100	0.1	0.0	0.0	na	0.0	1.1	0.0	0.0	2.0	0.2	0.1	0.1	0.0	0.0	0.1	0.0	na
	100-50	2.0	0.0	0.0	na	0.0	0.0	0.0	0.3	0.4	0.3	0.0	0.0	0.2	0.1	0.0	0.0	na
	50-20	5.4	0.0	0.0	na	0.0	0.0	0.0	0.1	0.3	0.0	0.0	0.1	0.0	0.0	0.1	0.1	1.3
	20-0	0.0	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
	Water Column	265	8	0	na	0	80	4	18	174	30	4	12	8	4	12	4	na
CIV	175-100	1.5	10.0	9.6	na	40.5	30.9	36.3	13.5	52.9	17.9	3.3	8.6	6.5	2.8	2.8	0.0	na
	100-50	11.2	3.0	3.2	na	1.0	0.5	6.4	11.7	9.4	5.6	0.9	2.6	4.0	2.3	1.0	0.1	na
	50-20	43.5	0.3	0.1	na	0.1	0.1	2.6	2.1	2.0	0.1	0.4	1.2	2.1	0.1	3.3	2.6	3.2
	20-0	11.4	0.4	0.2	0.6	0.2	0.0	2.0	1.0	1.2	0.0	0.0	0.0	0.0	0.4	0.0	0.0	2.0
	Water Column	2204	916	888	na	3096	2351	3157	1679	4520	1622	310	811	752	337	357	82	na
CV	175-100	8.3	200.0	80.0	na	305.1	204.8	195.2	27.9	45.7	14.1	3.1	4.8	4.6	1.6	3.2	1.4	na
	100-50	17.3	46.0	16.5	na	5.0	17.1	80.6	29.1	4.6	2.2	1.2	0.5	2.4	0.6	0.4	0.4	na
	50-20	34.8	0.5	0.4	na	0.4	1.1	11.8	5.4	4.0	1.6	1.2	0.7	1.6	0.0	0.5	0.7	3.5
	20-0	65.3	1.2	0.4	3.6	0.8	1.2	5.2	3.9	0.8	0.0	0.0	0.2	0.0	0.0	0.0	0.0	1.6
	Water Column	3843	17340	6847	na	23156	16269	#####	3783	3797	1211	329	408	513	149	278	142	na
CF	175-100	1.5	0.0	0.0	na	3.2	1.1	2.1	2.4	22.2	7.8	2.4	4.7	3.9	1.9	4.3	3.7	na
	100-50	0.9	0.0	0.0	na	0.1	0.0	1.3	8.0	6.6	1.9	1.5	2.0	3.4	0.2	0.4	0.2	na
	50-20	0.0	0.0	0.0	na	0.0	0.0	6.5	6.7	29.5	8.9	13.3	8.5	10.7	0.1	0.1	0.5	0.0
	20-0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	5.7	19.6	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
	Water Column	156	0	0	na	244	80	451	892	3272	945	651	717	788	161	349	303	na
CM	175-100	0.0	0.0	0.0	na	4.3	14.9	9.6	3.5	7.2	0.2	0.2	0.1	0.0	0.0	0.1	0.0	na
	100-50	0.0	0.0	0.0	na	0.2	4.8	46.1	9.1	0.6	0.0	0.0	0.1	0.0	0.1	0.0	0.0	na
	50-20	0.0	0.0	0.0	na	0.0	0.0	13.9	4.0	0.9	0.3	0.1	0.3	0.1	0.0	0.0	0.0	na
	20-0	0.0	0.0	0.0	0.0	0.2	0.0	3.0	2.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	na
	Water Column	0	0	0	na	336	1360	3501	878	602	22	16	16	4	4	4	0	na

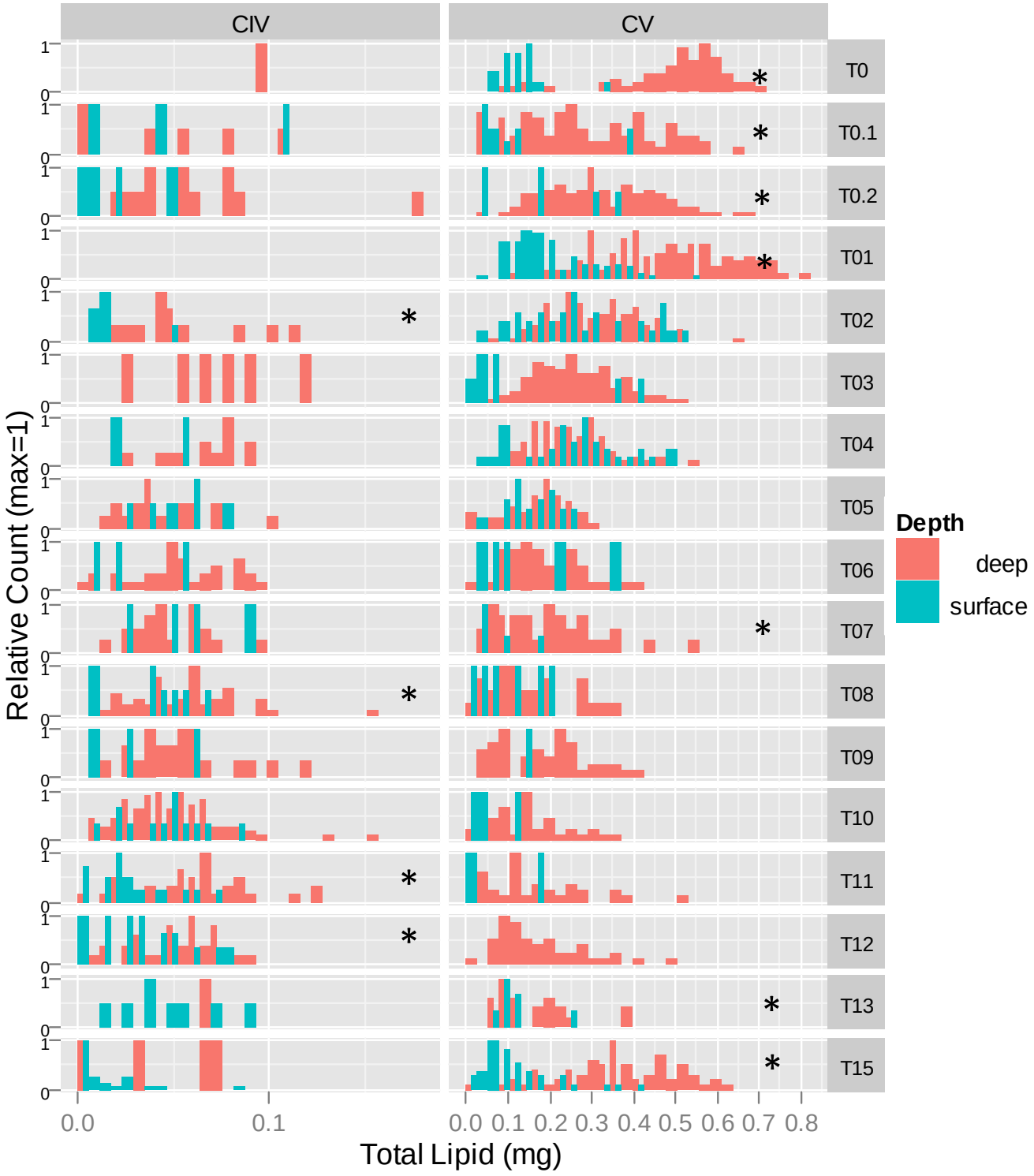
Appendix Table 4. *C. finmarchicus* copepodite densities from Billefjorden, Svalbard, from four depth strata throughout one year (2008-2009). Density per depth stratum are given are given in indiv. m^{-3}. Abundance in the entire water column is given in indiv. m^{-2}. Samples not counted are indicated by "na".

		23-Jul	26-Sep	6-Sep	23-Sep	16-Oct	4-Nov	3-Dec	14-Jan	26-Feb	23-Mar	30-Mar	20-Apr	27-Apr	4-May	14-May	10-Jun	17-Aug
CI	175-100m	0	0	0	na	0	0	0	0	0	0	0.1	0.1	0.1	0	0.1	0.2	na
	100-50m	0	0	0	na	0	0	0	0	0	0	0	0	0	0	0	0	na
	50-20m	19.6	0	0	na	0	0	0.7	0	0	0	0	0	0	0	0	0.7	0.5
	20-0m	18.0	0	0	3.8	0	0	0	0	0	0	0	0	0	0	0	0	1.2
	Water Column	947	0	0	na	0	0	21	0	0	0	8	4	4	0	4	34	na
CII	175-100m	0.056	0	0	na	0	0	0	0	0	0	0	0	0	0	0.1	0	na
	100-50m	0.078	0	0	na	0	0	0.6	0	0.1	0	0	0	0	0	0	0	na
	50-20m	2.2	0	0	na	0.9	0	1.6	0	0	0	0	0	0	0	0	0.1	10.4
	20-0m	13.1	0	0	3.8	0	0	0	0	0	0	0	0	0	0	0	0	2.4
	Water Column	335	0	0	na	28	0	81	0	4	0	0	0	0	0	4	4	na
CIII	175-100m	0	0	0	na	0	0	0	0	0	0.2	0	0	0	0	0	0	na
	100-50m	0.157	2.0	0.5	na	0.3	0	0	0	0	0	0	0	0	0	0	0	na
	50-20m	3.3	0	0	na	8.3	0.3	0.5	0.1	0	0	0	0	0	0	0	0.1	15.2
	20-0m	0	0	0	4.6	0.2	0.2	0.2	0	0	0	0	0	0	0	0	0	1.6
	Water Column	106	100	27	na	268	12	18	4	0	14	0	0	0	0	0	4	na
CIV	175-100m	0.112	5.0	1.6	na	0	1.1	5.3	0.7	1.3	0.4	0.1	0.1	0.3	0	0.1	0	na
	100-50m	0.235	14.0	3.5	na	3.2	0.3	0.6	0	0.5	0.1	0	0.4	0.4	0	0	0	na
	50-20m	6.5	0.5	1.2	na	5.6	3.6	2.8	0.3	1.2	0	0.4	0.1	0.1	0	0.3	0	5.6
	20-0m	0	3.2	0	5.4	0.2	1.4	1.2	0	0.6	0	0	0.6	0	0	0.2	0	0.4
	Water Column	216	1155	329	na	332	229	539	57	169	32	20	39	47	0	20	0	na
CV	175-100m	0	30.0	8.8	na	2.1	2.1	2.1	0	2.0	1.0	0.4	0.5	0.3	0	0.3	0	na
	100-50m	0.5	25.0	6.4	na	2.2	0.3	2.6	1.7	2.0	1.2	0.2	0.8	0.8	0	0.5	0	na
	50-20m	0	1.9	0.5	na	1.1	3.2	5.3	2.6	3.7	0.9	0.7	0.5	0.3	0	0.1	0.4	0.5
	20-0m	0	0.4	0.4	1.6	0	0.6	5.4	2.4	0.8	0	0	0.6	0	0	0	0	0.8
	Water Column	27	3564	1004	na	300	281	556	211	370	157	63	102	67	0	51	15	na
CF	175-100m	0.112	0	0	na	0	0	0	0	0	0.2	0	0	0	0	0	0	na
	100-50m	0.235	0	0.27	na	0	0	0	0	0	0	0	0.1	0.1	0	0	0	na
	50-20m	0	0	0	na	0	0	0	0	0.26	0.1	0	0.3	0	0	0	0.1	0
	20-0m	0	0	0	0	0	0	0	0.2	0	0	0	0.2	0	0	0	0	0
	Water Column	20	0	13	na	0	0	0	4	8	18	0	16	4	0	0	4	na

Appendix Table 5. *C. glacialis* and *C. finmarchicus* densities and abundance from 17 sampling dates in Billefjorden, Svalbard, from four depth strata (in m^{-3}) and for the whole water column (in m^{-2}). All copepodite stages (CI-CF) are included, with the exception of males, which could not be determined to species.

	C. glacialis				
	175-100m	100-50m	50-20m	20-0m	Water column (m^{-2})
23-Jul-08	11.4	31.5	84.9	76.7	6453
26-Sep-08	210.0	49.0	0.8	2.0	18264
6-Sep-08	89.6	19.7	0.5	0.6	7735
23-Sep-08	na	na	na	4.2	na
16-Oct-08	348.8	6.0	0.5	1.0	26496
4-Nov-08	237.9	17.6	1.2	1.2	18780
3-Dec-08	233.6	88.3	20.9	9.0	22742
14-Jan-09	43.8	49.0	14.2	10.6	6591
26-Feb-09	122.8	21.0	35.8	21.6	12378
23-Mar-09	39.9	10.0	10.6	0.0	3808
30-Mar-09	8.9	3.6	14.9	0.0	1293
20-Apr-09	18.2	5.0	10.5	1.0	1948
27-Apr-09	15.0	10.0	14.4	0.0	2061
4-May-09	6.5	3.2	0.3	0.4	662
14-May-09	10.4	1.8	4.0	0.2	995
10-Jun-09	5.1	0.7	5.0	2.4	641
17-Aug-09	na	na	8.0	3.6	na

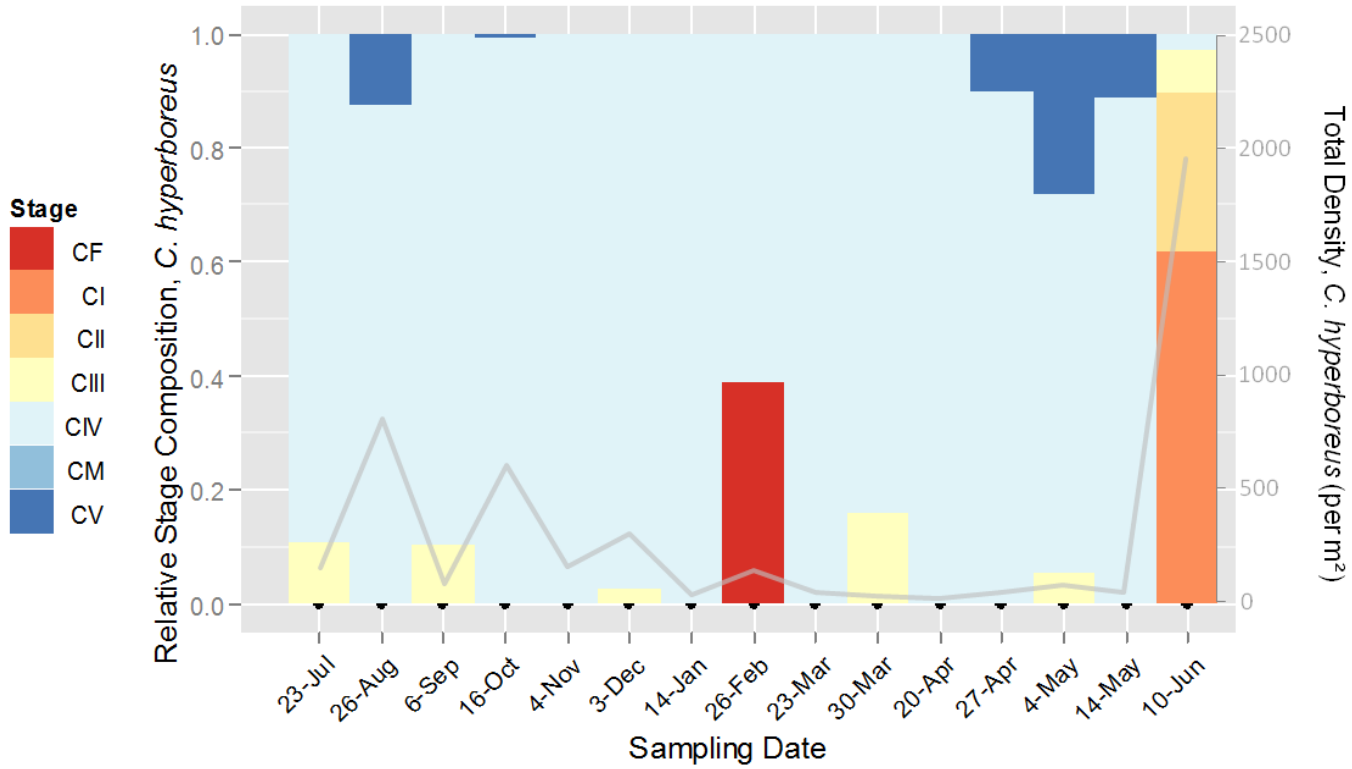
	C. finmarchicus				
	175-100m	100-50m	50-20m	20-0m	Water column (m^{-2})
23-Jul-08	0.3	1.3	31.6	31.0	1650
26-Sep-08	35.0	41.0	2.4	3.6	4819
6-Sep-08	10.4	10.7	1.7	0.4	1373
23-Sep-08	na	na	na	19.2	na
16-Oct-08	2.1	5.7	15.9	0.4	928
4-Nov-08	3.2	0.5	7.1	2.2	523
3-Dec-08	7.5	3.8	10.9	6.8	1215
14-Jan-09	0.7	1.7	3.0	2.5	279
26-Feb-09	3.3	2.5	5.1	1.4	567
23-Mar-09	1.7	1.3	1.0	0.0	222
30-Mar-09	0.6	0.2	1.0	0.0	90
20-Apr-09	0.6	1.3	0.9	1.4	161
27-Apr-09	0.6	1.3	0.4	0.0	121
4-May-09	0.0	0.0	0.0	0.0	0
14-May-09	0.5	0.5	0.4	0.2	78
10-Jun-09	0.2	0.0	1.4	0.0	63
17-Aug-09	na	na	32.3	6.4	na



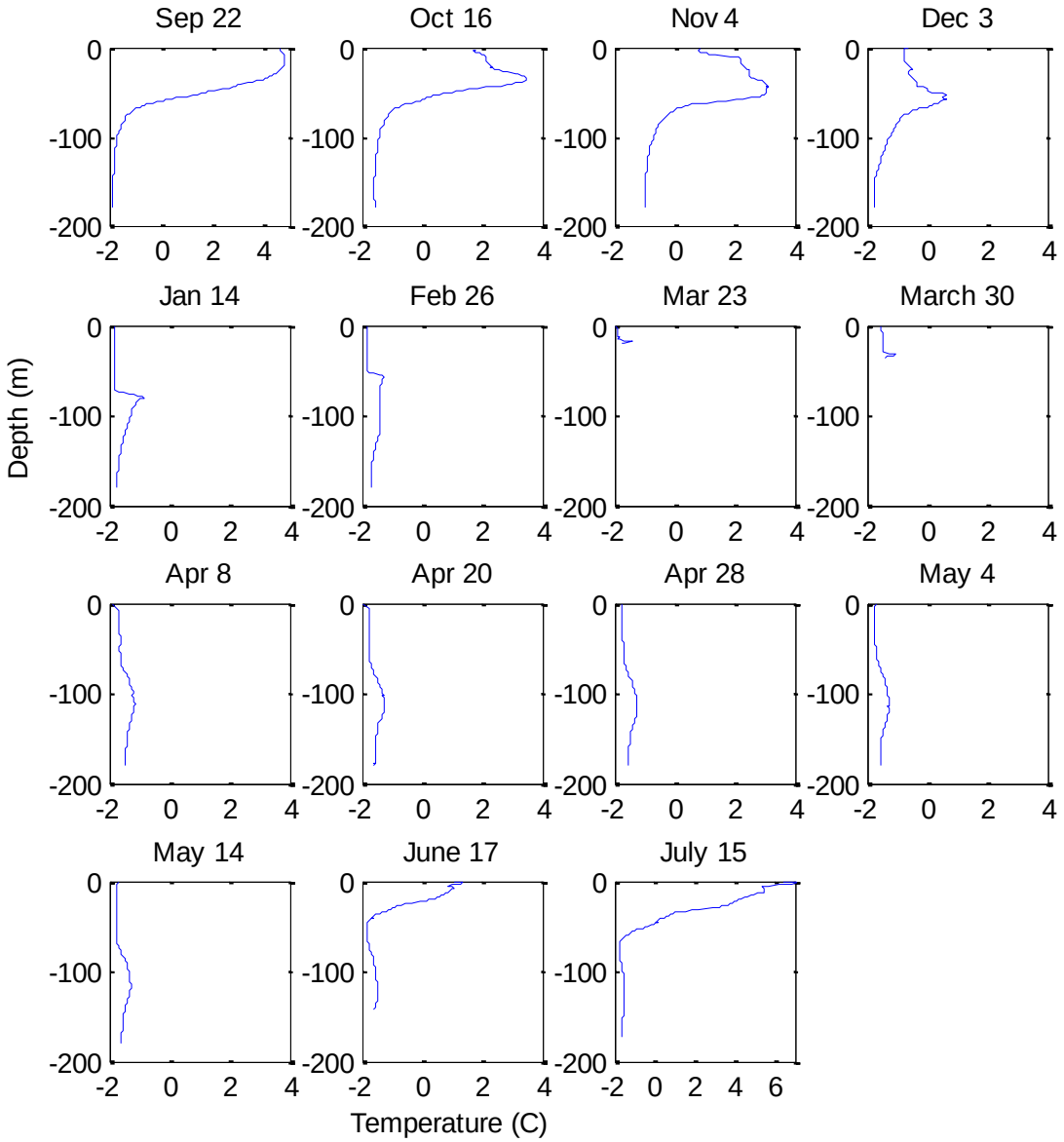
Appendix Figure 2. Distributions of total lipid in deep and surface for *C. glacialis* CIV and CV. Asterisks indicate a significant difference in the distribution of total lipid between the surface and deep populations.

Appendix Figure 3. Distributions of total lipid in deep and surface for *C. glacialis* females and *Calanus* sp. males. Asterisks indicate a significant difference in the distribution of total lipid between the surface and deep populations.

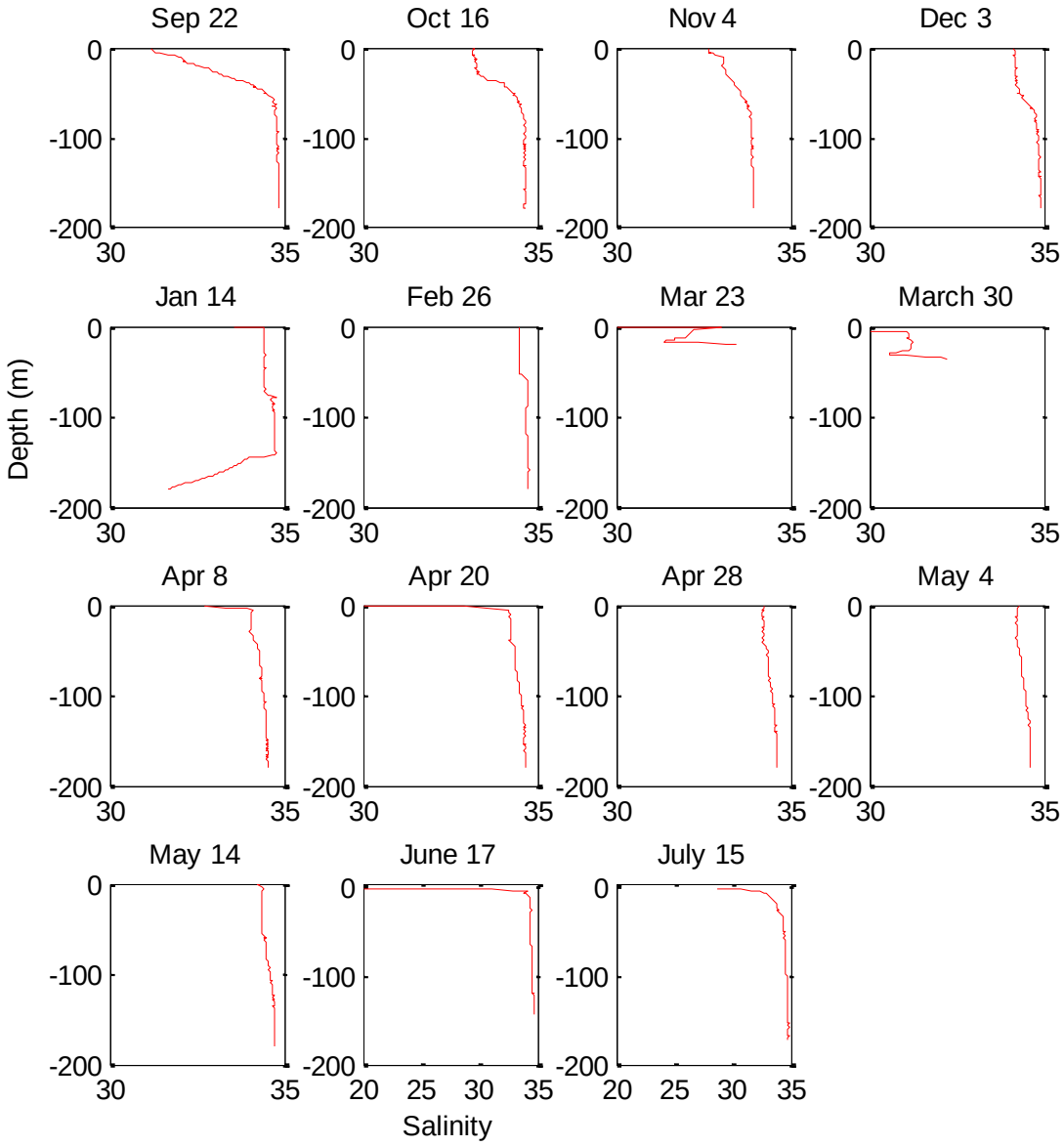
Appendix Figure 4. Distributions of total lipid in deep and surface for *C. finmarchicus* CIV and CV. Asterisks indicate a significant difference in the distribution of total lipid between the surface and deep populations.



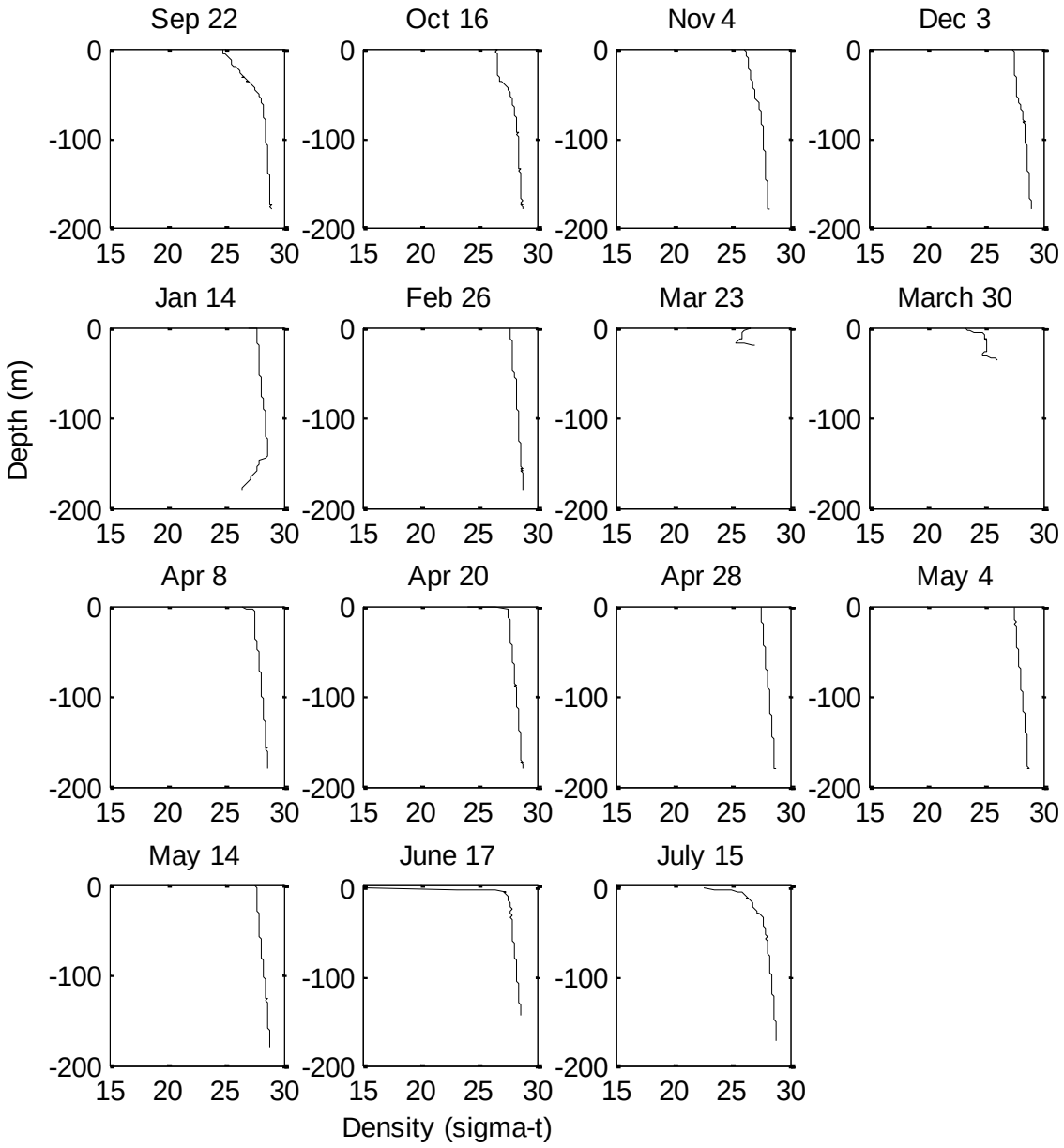
Appendix Figure 5. Relative copepodite stage composition and total *C. hyperboreus* density in Billefjorden 2008-2009. Stage composition is represented by colored bars, with proportion noted on the lefthand y-axis. Density (line, scale on right y-axis) is presented in indiv. m^{-2} and includes all stages of *C. hyperboreus*.



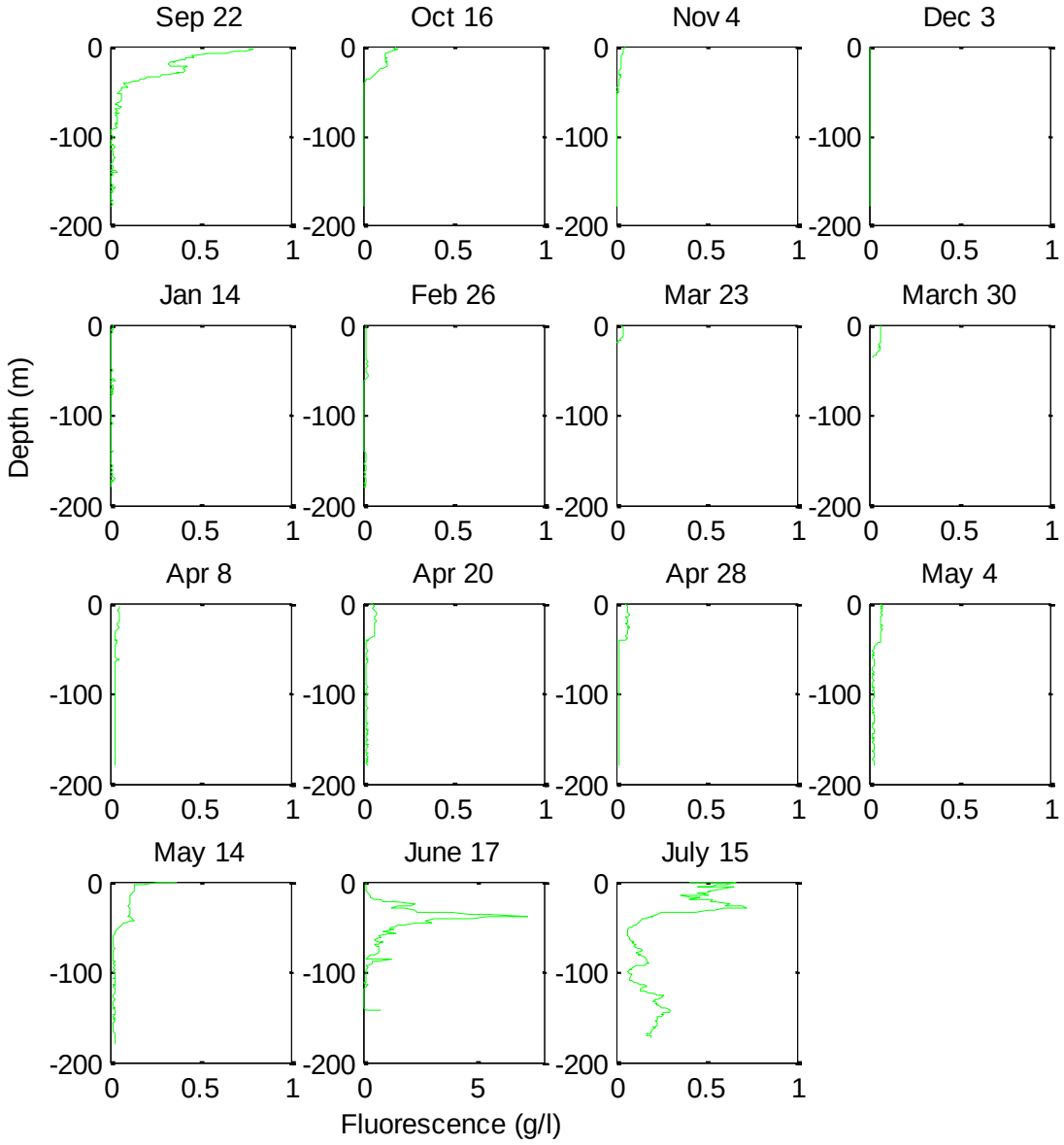
Appendix Figure 6. Water temperature (°C) from CTD casts in Adolfbukta, Billefjorden from fifteen sampling dates between 22.September 2008 and 15.July 2009. On 23.March and 30.March 2009, the CTD casts only measured the surface 20m and 40m, respectively. Sampling dates with sea ice cover were: 14. January 2009- 14.May 2009, the other dates were without sea ice. Note different x-axis scale on first (Sept 22) and last (July 15) plots.



Appendix Figure 7. Salinity from CTD casts in Adolfbukta, Billefjorden from fifteen sampling dates between 22.September 2008 and 15.July 2009. On 23.March and 30.March 2009, the CTD casts only measured the surface 20m and 40m, respectively. Sampling dates with sea ice cover were: 14. January 2009- 14.May 2009, the other dates were without sea ice. Note the different x-axis scale on the last two graphs (June and July).



Appendix Figure 8. Density (sigma-t) from CTD casts in Adolfbukta, Billefjorden from fifteen sampling dates between 22.September 2008 and 15.July 2009. On 23.March and 30.March 2009, the CTD casts only measured the surface 20m and 40m, respectively. Sampling dates with sea ice cover were: 14. January 2009- 14.May 2009, the other dates were without sea ice.



Appendix Figure 9. Fluorescence from CTD casts in Adolfbukta, Billefjorden from fifteen sampling dates between 22.September 2008 and 15.July 2009. On 23.March and 30.March 2009, the CTD casts only measured the surface 20m and 40m, respectively. Sampling dates with sea ice cover were: 14. January 2009- 14.May 2009, the other dates were without sea ice. Notice the different x-axis scale on the June 17 graph.