

MASTER THESIS

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Phenology and dynamics of 4 co-existent
Calanus species assessed with molecular
tools in a North Atlantic fjord

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Abstract

The major aim of this study was to investigate the timing of four *Calanus* species main phenological events and to establish their ecological niche in an area where they co-occur. The recently unveiled area of co-occurrence of *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus* and *C. helgolandicus* located in a Norwegian fjord, the Skjerstadvjord (northern Norway), represents an ideal opportunity to study the limits of each species' ecological niche. For this purpose, I investigated the *Calanus* species composition and vertical distribution over approximately one year, from April 2017 to March 2018, using multinet sampling. As *Calanus* spp. are morphologically very similar, species composition was determined by the use of molecular markers to identify individual to species level. In average over a year, *C. glacialis* was the most abundant species (60%), followed by *C. hyperboreus* (21%) and *C. finmarchicus* (19%), while *C. helgolandicus* accounted for less than 1 % of the total *Calanus* abundance. My data suggest that *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* reproduced in the fjord at approximately the same time between January/February. A seasonal descent at great depths taking place around July indicated the start of the diapause phase for *C. finmarchicus* and *C. hyperboreus*. For these two, the diapause lasted until January, month of ascent. *Calanus glacialis* started its diapause earlier, in June, and some individuals ascended in January too. A Spring ascent was observed starting from March for *C. glacialis* and *C. hyperboreus*, while a seasonal ascent was seen in May for *C. finmarchicus*. The data suggested *C. glacialis* and *C. hyperboreus* to be mainly capital breeders, most likely spawning early in the season independently of the April phytoplankton bloom, while *C. finmarchicus* seemed to rely on the energy input from this spring bloom to complete spawning. I suggested that *C. finmarchicus* and *C. glacialis* are more likely to complete their life-cycle within 1 year in the Skjerstadvjord, according to the interpretation of my data. It was unclear in the case of *C. hyperboreus* though. Species ecological niches' overlap or distinctiveness were related to the environmental factors temperature, salinity, water depth and Chl a concentration. My data also suggest and confirm the view of *C. finmarchicus* as being a drifting species of the fjord, with the same view for *C. hyperboreus*, whereas *C. glacialis* vertical migration patterns suggested that species to be a resident of the fjord.

Abstrakt

Hovedformålet med denne studien var å undersøke timingen av fire *Calanus* arters viktigste fenologiske hendelser og å etablere deres økologiske nisje i et område hvor de sameksisterer. Det nylige avdukete området av co-forekomst av *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus* og *C. helgolandicus* i den norske fjorden, Skjerstadvjord (Nord-Norge), representerer en ideell mulighet til å studere grensene for hver art's økologiske nisje. For dette formålet, undersøkte jeg *Calanus* arters komposisjon og vertikal fordeling over omtrent ett år, fra april 2017 til mars 2018, med MultiNet prøvetaking. Ettersom *Calanus* artene er morfologisk svært like, ble artenes komposisjon bestemt ved bruk av molekylære markører for å identifisere individene til arts nivå. I gjennomsnitt over et år, var *C. glacialis* den mest tallrike arten (60%), etterfulgt av *C. hyperboreus* (21%) og *C. finmarchicus* (19%), mens *C. helgolandicus* utgjorde mindre enn 1% av den totale *Calanus* rikeligheten. Mine data tydet på at *C. finmarchicus*, *C. glacialis* og *C. hyperboreus* forplanter seg i fjorden på omtrent samme tid mellom januar/februar. En sesongmessig nedstigning på stort dyp som fant sted rundt juli indikerte starten av diapause fasen for *C. finmarchicus* og *C. hyperboreus*. For disse to, varte diapausen til januar, måneden av oppstigningen. *Calanus glacialis* startet sin diapause tidligere, i juni, og noen individer steg også i januar. Vårens oppstigning ble observert fra mars for *C. glacialis* og *C. hyperboreus*, mens den sesongmessige oppstigningen ble sett i mai for *C. finmarchicus*. Dataene foreslo at *C. glacialis* og *C. hyperboreus* hovedsakelig forplantet seg ved hjelp av indre lagrede energi-reserver, og mest sannsynlig med gyting tidlig i sesongen uavhengig av oppblomstringen av planteplankton i april, mens *C. finmarchicus* syntes å stole på energi innspillet fra denne våroppblomstringen for å fullføre gyting. Jeg foreslo at *C. finmarchicus* og *C. glacialis* mest sannsynlig fullfører sin livssyklus innen 1 år i Skjerstadvjorden, i henhold til tolkningen av mine data. Dette var uklart når det gjelder *C. hyperboreus*. Artenes økologiske nisjer i forhold til om de overlappet eller var særpreget var knyttet til miljøfaktorene temperatur, saltholdighet, vann dybde og klorofyll konsentrasjon. Dataene mine foreslår også og bekrefter oppfatningen av *C. finmarchicus* som en drivende art i fjorden, med samme oppfatning for *C. hyperboreus*, mens *C. glacialis* sitt vertikale migrasjon mønster foreslo at denne arten var fastboende i fjorden.

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1. Introduction

1.1 *Calanus* in the North Atlantic and Arctic

Planktonic copepods of the genus *Calanus* (Crustacea; Copepoda; Calanoida) are dominating the zooplankton biomass in North Atlantic and Arctic marine ecosystems (Jaschnov, 1970; Fleminger & Hulseman, 1977; Conover, 1988, Mauchline, 1998; Søreide et al., 2008; Broms et al., 2009). *Calanus* species represent a group of fundamental importance in the marine food webs in the northern hemisphere (Falk-Petersen et al., 2009), as consumers of primary producers and as prey for a number of ecologically and commercially important species such as Atlantic and polar cods (Sundby, 2000; Lønne & Gulliksen, 1989), marine birds (e.g. little auk) (Weslawski et al., 1999; Steen et al., 2007), marine mammals (Bluhm & Gradinger, 2008) and for large pelagic fish stocks such as the Norwegian spring-spawning herring (Gislason & Astthorson, 2002; Varpe et al., 2005). Additionally, they are main elements of the biological pump as contributors to the vertical flux of carbon in the ocean, both by transporting carbon produced in the upper part of the water column downward as dense, quickly sinking fecal pellets and as vertical migrants feeding in the shallower ocean layers at night and returning to their daytime environment at depth where they metabolize carbon or are consumed by other organisms (Wilson et al., 2008; Hernández-LeÓN et al., 2010).

Four *Calanus* species are present throughout the North Atlantic and Arctic Oceans (Fig.1): *Calanus helgolandicus* (Claus, 1863), *C. finmarchicus* (Gunnerus, 1770), *C. glacialis* (Jaschnov, 1955) and *C. hyperboreus* (Krøyer, 1838).

C. helgolandicus is associated to more temperate environments, such as coastal and continental shelf habitats, and is distributed from the Mediterranean Sea to the North Sea and southern coast of Norway (Conover, 1988), along with being recorded as far north as 70° N in the Norwegian Sea (Choquet et al., 2017) (Fig.1).

C. finmarchicus is an oceanic species that has its spatial distribution closely associated with North Atlantic water masses (Jaschnov, 1970; Conover, 1988; Choquet et al., 2017 - Fig.1). Its core distribution area is located in the Norwegian Sea and the Labrador Sea, yet the northward transport of Atlantic water brings high numbers of *C. finmarchicus* expatriates into sub-Arctic and Arctic seas, as far north as 87°N and as far east in the Arctic as the eastern boarder of the Laptev Sea (Hirche & Kosobokova, 2007; Falk-Petersen et al., 2009; Fig.1).

C. glacialis is considered as a shelf species associated with Arctic water masses, dominantly distributed north of the Polar front along the Arctic shelf seas and the Barents Sea shelf, and in the White Sea (Jaschnov, 1970; Conover, 1988, Fig.1). *C. glacialis* is also distributed in many Norwegian fjords, as far south as 60°N (Choquet et al., 2017) (Fig.1).

C. hyperboreus is described as a native species in sub-Arctic and Arctic oceanic water masses with its centre of distribution located in the Greenland Sea (Hirche, 1991), the Labrador Sea and the Arctic Ocean (Conover, 1988; Mumm, 1993), and is assumed to be advected into areas as the shelf seas and also further south in the Norwegian Sea (Broms et al., 2009). *C. hyperboreus* is also identified as a species widely distributed along the Norwegian coast, all places north of 58°N (Choquet et al., 2017) (Fig.1).

The preferred habitat of each species is usually associated with their distinct temperature niche, bathymetry and the area's productivity. *C. helgolandicus* is regarded as a pseudo-oceanic temperate species, generally found distributed in 9-20°C waters, in regions influenced by bathymetry with a distribution mainly centred over areas in the 0-500 m depth range (Bonnet et al., 2005; Helaouët & Beaugrand, 2007). The oceanic species *C. finmarchicus* is found in colder water between 4 and 12°C and is usually distributed in deeper areas compared to *C. helgolandicus* (Jaschnov, 1961; Helaouët & Beaugrand, 2007). The ecological niche of these two species is suggested well separated, and a broader ecological niche is reported for *C. finmarchicus* in terms of tolerated thermal interval, nutrient supply and oxygen level, making it more suited to cope with greater environmental variability (Helaouët & Beaugrand, 2007). *C. glacialis*, a typical shelf species, has a critical threshold between 5 and 6°C (Carstensen et al., 2012). Although we did not find any specific study reporting on the temperature preference of the Arctic species *C. hyperboreus*, we can assume that the species is adapted to the colder environments, and flexible enough to also cope with more boreal environments such as the Norwegian fjords (Choquet et al., 2017).

The distinction in their temperature and habitat preference make the species of the genus *Calanus* useful indicators of specific water masses. Therefore, they are often used to track the effects of climate change on ecosystems. Indeed, they are among the first organisms to respond to climate variability by shifting the distribution of their populations (Poloczanska et al., 2013).

Impacts of global warming have already been observed, they consist in poleward movements in species distribution, shifts in phenology and changes in abundance and community structure (Richardson, 2008; Villarino et al., 2015; Beaugrand et al., 2002). In response to Arctic

warming and sea ice withdrawal, relevant indicator species are of interest for tracing a potential Atlantification of the Arctic water masses (Wassmann et al., 2011).

From another perspective, the overall high abundance of *Calanus* spp. in northern areas has sparked a growing interest for commercial utilization of these copepods. Examples of this type of exploitation is the harvest of *Calanus* oil for human use in type of pills containing a healthy form of omega-3 that is reported to act against insulin resistance and other obesity-induced metabolic disorders (<https://www.calanus.no/>), and the exploitation of *Calanus* as source of oil in commercial aquaculture (Olsen et al., 2004).

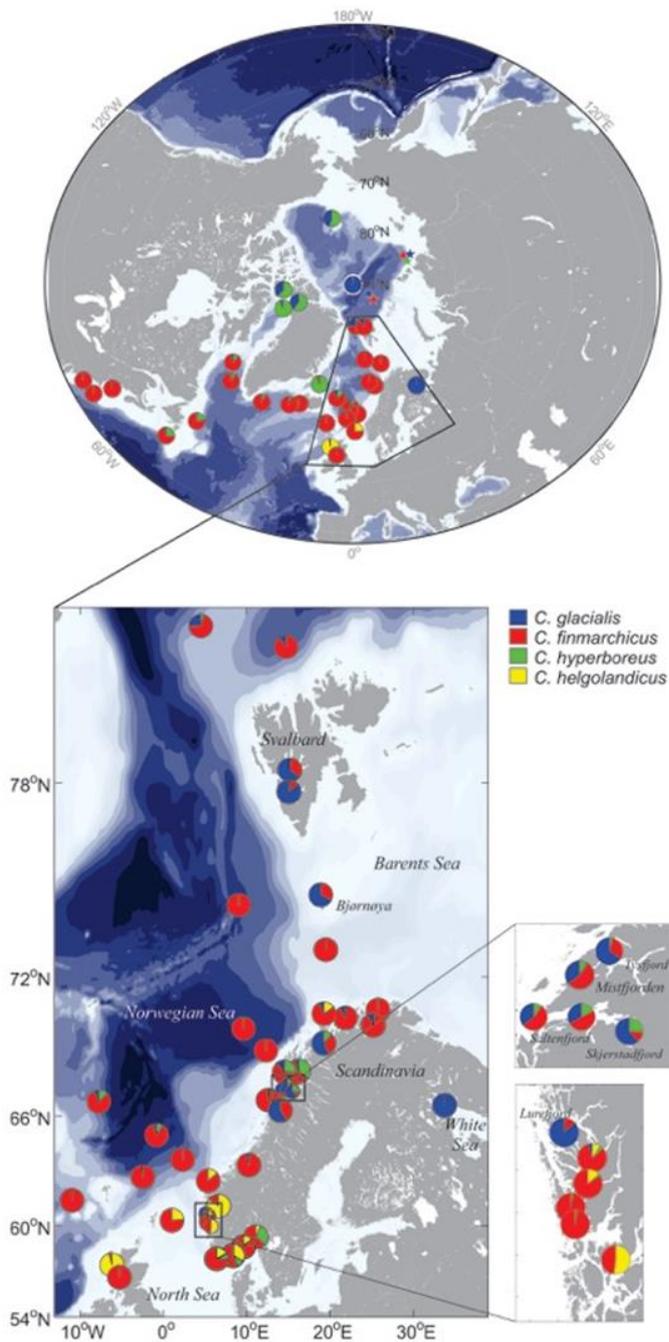


Figure 1: Spatial distribution ranges of the four *Calanus* species in the North Atlantic and Arctic Oceans based on molecular species identification. Pie charts represent relative frequencies of *C. glacialis* (blue), *C. finmarchicus* (red), *C. hyperboreus* (green) and *C. helgolandicus* (yellow) in each sample (source: Choquet et al., 2017).

1.2 *Calanus* life cycle

Calanus species display high similarity in morphology and life cycle, which includes eggs hatching into nauplius larvae followed by six naupliar stages (NI-NVI), the NVI moults to the first of six copepodite stages (CI-CVI), where CVI represents the final molt into adults and separation of the sexes (female or male, AF or AM, respectively) (Fig.2).

Calanus are mainly herbivorous, but they are known to occasionally switch to predation on microzooplankton or even turn to cannibalism when phytoplankton resources are in short supply (Ohman & Runge, 1994; Levinsen et al., 2000; Ohman & Hirche, 2001).

The capacity of high-energy lipid storage in the form of large oil sacs filled with wax esters is an important adaptive life history trait for the *Calanus* species since they all have diapause as a part of their life cycle (Lee et al., 2006). Lipid content of *Calanus* is linked to body size thus both larger Arctic species, *C. hyperboreus* and *C. glacialis*, have higher energy reserves at high latitudes, whereas the smaller and smallest in size, *C. finmarchicus* and *C. helgolandicus* respectively, have a lower lipid content (Lee et al., 2006; Falk-Petersen et al., 2009). Their body mass with extreme lipid-richness is what makes *Calanus* spp. a major source of energy and attractive preys for higher trophic levels such as fish, birds and marine mammals (Falk-Petersen et al., 1990).

The hibernation phase, or diapause, leads to an arrest in the development during copepodite stages CIII, CIV or CV (Fig.2), and diapausing *Calanus* rely on the large energy reserves accumulated during spring for survival when they descend to overwinter in deeper water layers in late summer/winter and do not feed anymore for 3 to 8 months (region and species dependent) (Hirche, 1997; Hirche, 1983; Conover & Siferd, 1993; Scott et al., 2000).

A one-year life cycle is typical for *C. finmarchicus* and *C. helgolandicus* throughout much of their distribution range (Broms et al., 2009; Bonnet et al., 2005; Fig.2), with the potential for producing two generations per year in the more productive areas. For the more extensively studied *C. finmarchicus*, such areas are the southern and eastern part of the Norwegian Sea and the Irminger Sea (Broms & Melle, 2007; Heath et al., 2008).

Both *C. finmarchicus* and *C. helgolandicus* are considered to be mostly income breeders (Varpe et al., 2009) – which means that they rely on an external food source (the spring phytoplankton bloom) to promote gonad maturation and subsequent reproduction and spawning of females near the surface (Bonnet et al., 2005; Niehoff et al., 1999). However, in some cases, *C. helgolandicus* has also been shown to breed from stored lipid reserves independent of food supply (capital breeder strategy) (Planque & Fromentin, 1996), but then with a decreased efficiency in egg production (Rey-Rassat et al., 2002). Early ascent and spawning prior to the spring bloom is recorded for *C. finmarchicus* in the Norwegian Sea and the Barents Sea (Skjoldal et al., 1987; Niehoff et al., 1999).

For *C. glacialis*, both one- and two-year life cycles are usually expected (Fig.2), and the species is known to switch its reproductive strategy depending on the environmental conditions in its area of distribution. When *C. glacialis* inhabits the seasonally ice-covered shelf-seas in the Arctic, two primary production events are observed: the early ice algae bloom and the later phytoplankton bloom (Ji et al., 2013). Feeding on the ice algae bloom to fuel spawning prior to the onset of the spring phytoplankton bloom (income breeding) enables the new generation to exploit the vernal primary production event for growth and development (Hagen, 1999). When its habitat is ice-free water, *C. glacialis* may alter its reproductive strategy; relying on its internal lipid storage for gonad maturation and egg production (capital breeding) in spring so that the offspring may take advantage of the spring bloom (Daase et al., 2013).

C. hyperboreus separates from the three other species by having the most flexible life cycle and by mainly breeding during the polar night. Its life cycle duration is known to vary depending on food availability and on the geographical location: if distributed in colder regions it may take two, three or possibly more years to reach maturity (Fig.1), while a shorter generation time of one year is reported for the warmer regions of distribution such as fjords in western Norway (Matthews et al., 1978; Dawson, 1978; Hirche, 1997; Broms et al., 2009; Gislason, 2018). The main spawning period of *C. hyperboreus* mostly takes place in winter while still present in deep water, where they spawn in response to internally stored lipids (Conover & Siferd, 1993; Hirche & Niehoff, 1996).

The overall strategy shared by all four species is to time reproduction in such a way that the new generation is able to feed on large quantities of maximum primary production in the water column to increase the potential for growth, development and successful recruitment (Cushing, 1990).

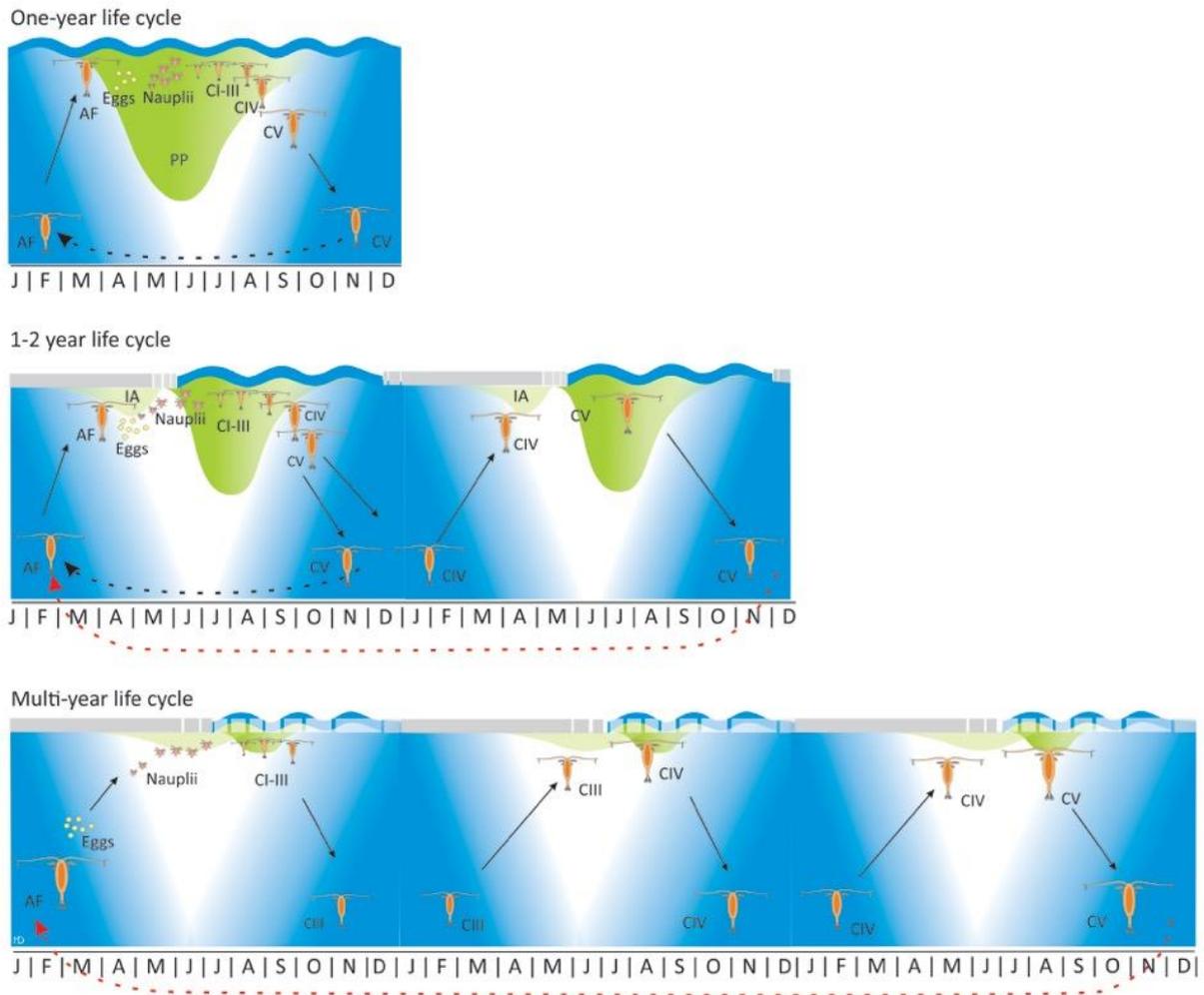


Figure 2: One-year life cycle (upper) is most frequent for *C. finmarchicus* and *C. helgolandicus*. 1- / 2-year life cycle (middle) is common for *C. glacialis*. Multi-year life cycle (bottom) is widespread for *C. hyperboreus*. CI-CV: copepodite stages CI to CV. AF: adult female. IA: ice algae; PP: phytoplankton. Solid black arrows: seasonal migration; hatched red and black arrows connect the cycle (source: Choquet et al., 2017).

1.3 The importance of correct identification of *Calanus* and related problems

In the light of *Calanus* species key role in the marine food webs and as climate indicators, correct separation to species level is crucial. Furthermore, accurate identification is essential to address questions about their phenology, population dynamics, abundance and distribution.

For long, morphological discrimination of *Calanus* species has mostly relied on subtle morphological characteristics in late copepodite stages (Frost, 1974; Fleminger & Hulsemann, 1977, 1987). *C. hyperboreus* can be distinguished from the others by a characteristic acute spine

on the 5th metasome segment in copepodite stages CIV, CV and CVI. It has been suggested that adults of *C. finmarchicus* and *C. glacialis* could be separated by specific traits, such as the structure of the fifth pair of swimming legs or urosome pores (Jaschnov, 1970; Fleminger & Hulsemann, 1977). However, due to the fastidious examination required by these methods, the traditional way to separate all *Calanus* spp. developmental stages is by prosome length measurements (Unstad & Tande, 1991; Hirche et al., 1994; Kwasniewski et al., 2003; Arnkværn et al., 2005; Forest et al., 2011). A more recently developed approach is to separate them based on presence or absence of red pigmentation on the antennules and genital somite of live females (Nielsen et al., 2014).

Overlap among *Calanus* species prosome lengths, especially in regions of sympatry, has been repeatedly reported by molecular-based studies (Choquet et al., 2017; Choquet et al., 2018; Lindeque et al., 2006; Parent et al., 2011; Gabrielsen et al., 2012). It is believed that temperature affect physiological development time and growth in most organisms and in zooplankton (McLaren et al., 1988) so that individuals distributed at higher water temperatures grow faster and complete their life cycle with shorter duration and smaller adult body size than those distributed at lower temperatures. However, variability in structural size between and within populations may not be so straightforward, other factors such as variations of the start and duration of primary production blooms and predation pressure by visual predators may also have a significant impact in shaping these characteristics (Fiksen & Carlotti, 1998).

In a recent study where *Calanus* species were identified both morphologically and genetically, none of the morphological traits in use proved to reliably discriminate between *C. glacialis* and *C. finmarchicus* (Choquet et al., 2018), resulting in a persistent problem in the identification of individuals to species level (Gabrielsen et al., 2012; Smolina et al., 2014).

Furthermore, it has also been suggested that *Calanus finmarchicus* and *C. glacialis* may be able to hybridize (Parent et al., 2012), which is adding to the need of using nuclear molecular markers in order to achieve reliable identification of potential hybrid individuals from parental species. Therefore, a set of molecular markers of the type InDel was developed a few years ago with the purpose of distinguishing among species and also to detect the presence of hybrids. The use of these InDel markers for species ID in a few hundred of individuals in the Skjerstadvjord found no evidence of hybrids between these two species though (Choquet et al., 2017).

The large-scale use of these InDel markers for species identification has led to the discovery of several areas where the two species co-occur in high proportions (many Norwegian fjords) (Choquet et al., 2017). In particular for some Norwegian fjords, like the Skjerstadvjord, not only *C. finmarchicus* and *C. glacialis* co-occur, but also *C. hyperboreus* and *C. helgolandicus* have been reported (Choquet et al., 2017).

This co-occurrence of the four species in a single fjord raises questions about the population dynamics enabling coexistence and the potential overlap of their ecological niches. To gain an understanding of this it is important to study how each species vary in their life strategy and respond to physical and biological environmental conditions, which requires a description of their temporal and spatial pattern in terms of vertical distribution, temperature preference and stage composition, since these are known to differ.

1.4 Objectives

This study combines field investigations with molecular species identification to examine the dynamics that enables the co-existence of *C. finmarchicus*, *C. glacialis*, *C. hyperboreus* and *C. helgolandicus* populations in a North Atlantic fjord. To address this aim, the study places emphasis on three objectives:

1. Investigate the timing of the four *Calanus* species' phenological events
2. Examine the vertical distribution of *Calanus* spp. in the water column during the phenological events
3. Establish the ecological niche for the co-occurring *Calanus* species

2. Materials and methods

2.1 Study area

In this study, one fjord located in Bodø, on the coast of northern Norway, was investigated. The Skjerstadvfjord is a sill fjord that is a part of the Saltfjord – Skjerstadvfjord system. This fjord system has deep basins on either side, yet the glacially carved Skjerstadvfjord basin represent the inner and deepest part of this fjord system (maximum depth ~ 544 m) and is connected to the outer Saltfjord's basin (maximum depth ~ 375 m) and the coast outside through a shallow sill (depth 26 m) in the narrow entrance channel called Saltstraumen.



Figure 3: Map of the study area Skjerstadvfjord (source: norgeskart.no)

At the head of the fjord a few rivers supply the highest amount of melt water in summer, leaving the surface layer in the Skjerstadvfjord strongly stratified in this period, although the water masses experience being stratified throughout the year (Eliassen et al., 2001).

Measurements of water mass properties in the Skjerstadvfjord by Eliassen et al. (2001) show a thermocline at ~ 125 m depth with small seasonal variations in temperature (4.2 - 4.4°C) and salinity (33.5) of the deep water below.

Saltstraumen is the main area of water exchange between the Saltfjord and the Skjerstadvfjord, and due to the very shallow nature of the sill in Saltstraumen one could expect a very poor

deepwater renewal in the Skjerstadvjord (Inall & Gillibrand, 2010). Exchange of deep water is an important mechanism for the fjord's capacity to get rid of organic material and other pollutants along with the need for replenishment of oxygen, and this water renewal occurs when the water above sill level outside the fjord is denser than the resident deep water (Eliassen et al., 2001; Gade & Edwards, 1980; Arneborg et al., 2004). For this fjord system, that means that deep water exchange occurs when the water in the Saltfjord that is dense enough (located at ~ 100 m, salinity of ~34.1) is lifted above sill level and led downward along the bottom of the Skjerstadvjord basin (salinity 33.5). The Skjerstadvjord is reported to have sufficient deep water renewal and an oxygen saturation of above 80 % in the deep water throughout the year (Skreslet, 2002).

2.2 Sampling strategy and method

Sampling took place from April 2017 to March 2018 (Table 1) and was carried out during daylight at time intervals varying from 3 weeks to a month from April 2017 to July 2017. Due to logistic constraints between September 2017 and March 2018, sampling was conducted only once every other month.

Zooplankton was collected on board the Nord University research vessel «Tanteyen» from the same single station located at the deepest part of the Skjerstadvjord basin (67°14.166'N, 14°44.432'E). A MultiNet of the type mini with 0.125 m² opening and 200 µm mesh size (Hydro-Bios, Germany) was vertically towed from close to the bottom to surface in the five depth ranges 500-300, 300-200, 200-100, 100-50, and 50-0 m. Application of the MultiNet generation of the Multiple Plankton Sampler as sampling instrument for collection of zooplankton in successive water layers by use of net bags pre-programmed to trigger in different target depths represent one of the great advances in the development of quantitative zooplankton collecting systems (Wiebe & Benfield, 2003).

Salinity, temperature, oxygen level and fluorescence were measured monthly in the whole water column from April 2017 to March 2018, with the exception of February 2018, by a CTD (SAIV-SD204, Norway).

Directly after sampling, the contents of the nets cod-ends were quickly transferred into individual buckets with seawater. Back in the laboratory, samples from different depth ranges were combined, resulting in three final «samples» corresponding to: 500-200, 200-50 and 50-0 m.

Table 1: Overview of sampling dates and number of individuals genetically analyzed (“Nb of ind.”) in the Skjerstadvjord (67°14.166’N, 14°44.432’E) in the depth ranges 500-200, 200-50 and 50-0 m (monthly summed for the three depth ranges)

Date	Nb of ind.
06.04.2017	68
11.05.2017	96
08.06.2017	91
26.06.2017	35
14.09.2017	39
20.11.2017	67
26.01.2018	46
16.03.2018	76

2.2.1 Morphological identification

Directly after sampling, a total of up to 96 live individuals of copepodite stages CIV, CV and CVI (females and males) of *Calanus* spp. were randomly subsampled each sampling date, a total of up to 32 individuals per sample (518 specimens in total) (Table 1). Each sample containing a recorded volume of seawater were kept in ice-filled trays and split into 2 ml subsamples of the total sample. In these subsamples, the copepodite stage was identified. On the subsampled individuals kept alive in seawater, *Calanus* developmental stages were separated by the number of legs, urosome segments, prosome segments and genital somite of females under a stereomicroscope (Leica). Following that, each specimen was individually stored in 70 % undenatured ethanol at 5°C for subsequent molecular species identification.

2.2.2 Molecular species identification

Twelve nuclear molecular markers, type Insertion/Deletion (InDel), were developed for the purpose of molecular identification of all the species of *Calanus* present in the North Atlantic and Arctic Oceans (Smolina et al., 2014). Nuclear Insertion/Deletion (InDel) polymorphism is based on the insertion or deletion of nucleotides, where InDel amplification by the Polymerase

Chain Reaction (PCR) and genotyping allows for *Calanus* species discrimination based on species-specific allele size differences (Smolina et al., 2014). The co-dominant nature of these nuclear markers makes them appropriate tools for identification of hybrids (Smolina et al., 2014). Each *Calanus* individual (a total of 518 individuals) were genotyped using a subset of only six Insertion/Deletion (InDel) nuclear markers: T_4700, T_1338, T_1966, T_3133, T_461 and G_150 (Smolina et al., 2014). The power of these 6-markers combination for reliable species identification has been demonstrated in previous studies (Choquet et al., 2017).

Prior to DNA extraction, isolated individuals were rinsed in nuclease-free water to remove the residual ethanol. DNA was extracted individually from two antennules using a HotSHOT DNA extraction protocol (Montero-Pau et al., 2008) following (Choquet et al., 2017).

PCR reactions were done in multiplex, with 6 markers together at once in a single reaction. PCR mix contained 1.25 μL of DNA, reverse and fluorescently labelled forward primers with a final concentration of 0.25 μM each, 2.5 μL of the enzymatic solution AccuStart II PCR ToughMix (Quantabio) (enzymatic solution) and 0.02 μL of MgCl_2 . A Veriti 96-Well Fast Thermal Cycler (Applied Biosystems, USA) was used for PCR amplification. The cycling parameters included an initial denaturation step at 94°C for 2 min followed by 35 cycles of primer annealing of 94°C for 10 s, 55°C for 10 s, 72°C for 10 s, and a final extension phase at 72°C for 5 min.

Prior to genotyping, PCR products were diluted as follow: 45 μL of pure water were added to each PCR product. Then, for each individual, 2 μL of this dilution were transferred to a new PCR plate where 38 μL of pure water was added to each well. Finally, 9 μL of a mixture of Formamide (8.9 μL per individual) and Liz Standard 500 (0.1 μL per individual) were transplanted to each well of a reaction plate, followed by the transfer of 1 μL of the diluted PCR product of each individual. The plate was then placed in a thermocycler (Techne TC – 412, Keison Products, United Kingdom) to denature the DNA at 95°C for 5 min.

Fragment analysis of the single-stranded PCR products was run on a 3500 xL Genetic Analyzer (Applied Biosystems, USA). Alleles were subsequently scored using GENEIOUS version 9.1.8 (<http://www.geneious.com>) and double-checked manually.

2.3 Data analyses

The CTD profile data were analyzed using RStudio version 3.5.1 (R Core Team, 2018) for temperature, salinity and fluorescence. Due to technical error of equipment for oxygen level measurements, the oxygen profile was not further analyzed.

Estimates of copepodite abundances (ind. m⁻³) were calculated by assuming 100 % filtration efficiency of the Multinet. Relative abundances refer to the total number of a species as a percentage of all individuals in a sample, and the total numbers of a species in all samples. Illustrative plot showing relative abundances in percentage of *Calanus* species throughout the study period was created in Microsoft Excel (version 1809, 2018).

The explanatory plot showing the seasonal *Calanus* spp. abundances of copepodite stages CIV, CV and CVI (CVIF: females, CVIM: males) were also created with Microsoft Excel (version 1809, 2018).

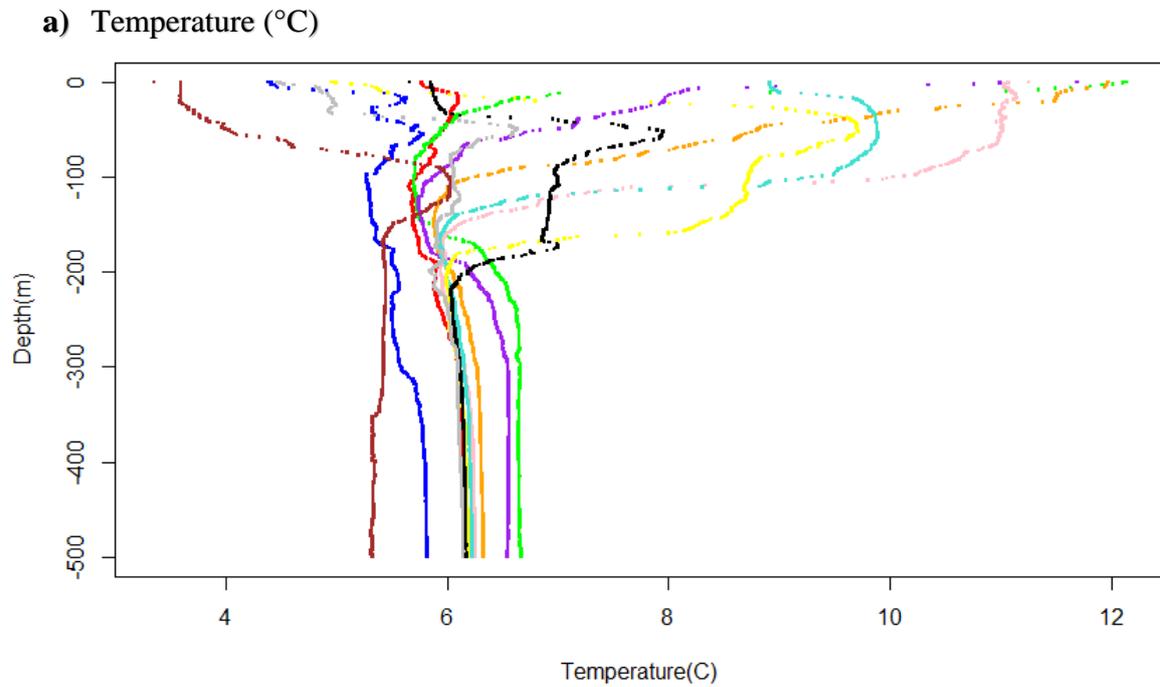
The illustrative figures showing the seasonal vertical distribution of *Calanus* species in the water column were created using RStudio version 3.5.1 (R Core Team, 2018) based on R-script.

3. Results

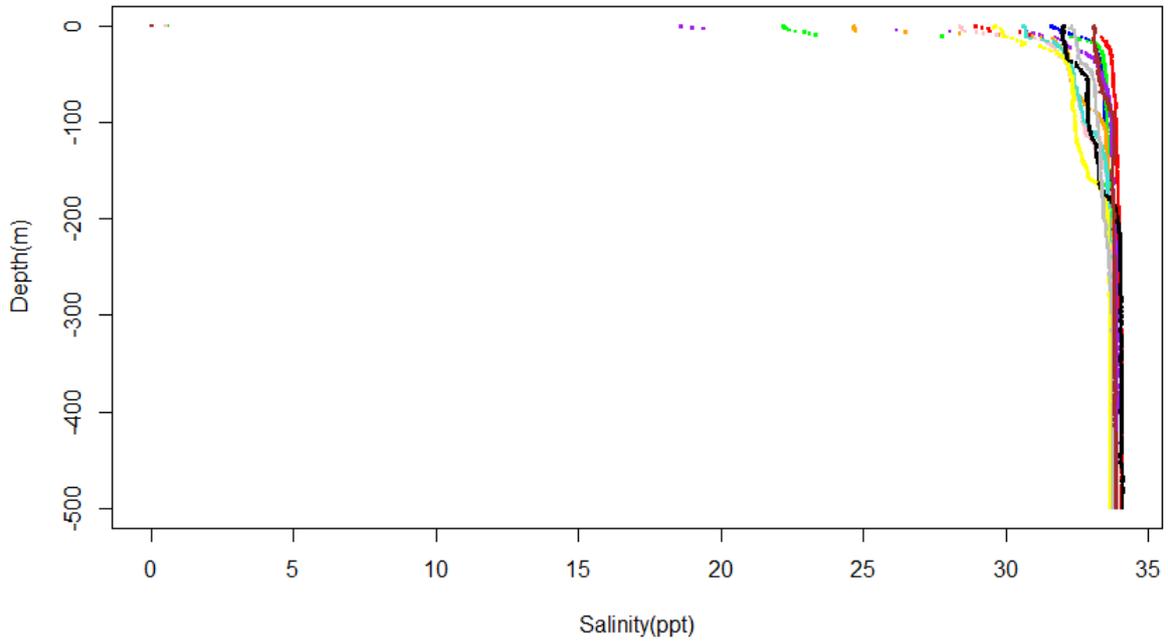
3.1 Environmental and biological parameters

The seasonal temperature changes in the depth ranges 0-50, 50-200 and 200-500 m were within approximately 3.3-12.1, 4.0-11 and 5.3-6.6°C, respectively (Fig. 4a). Water temperatures at the surface increased from May (5.8° C), reached their maximum values in June (12.1° C) and stayed relatively high until September (11.3° C - 12.0° C) before decreasing from October (8.9° C) to March (3.3° C) (Fig. 4a). The seasonal salinity changes in the depth ranges 0-50, 50-200 and 200-500 m were within approximately 18.6-33.8, 32.2-34.0 and 33.5-34.1, respectively (Fig. 4b). Salinity decreased in surface waters to < 30 from May to September (Fig. 4b) and salinity increased with depth. Below ~ 200 m, both temperature and salinity were very homogenous, the temperatures stayed between 5.3° C – 6.7° C and salinity varied between 33.5-34.1. (Fig. 4a, 4b). Water column Chl a (Chlorophyll a concentration (as estimated by fluorescence measurements) began to increase in March, peaked in April (7.49 µg/L at 0 m depth), stayed relatively high until July (2.49 µg/L at 0 m depth) and indicated a second peak

in September to October ($2.49 \mu\text{g/L}$ at 0 m depth) (Fig. 4c). Fluorescence measurements showed typical low chlorophyll a concentration with depth and in winter (November – January) (Fig.4c).



b) Salinity (ppt)



c) Fluorescence (ug/L)

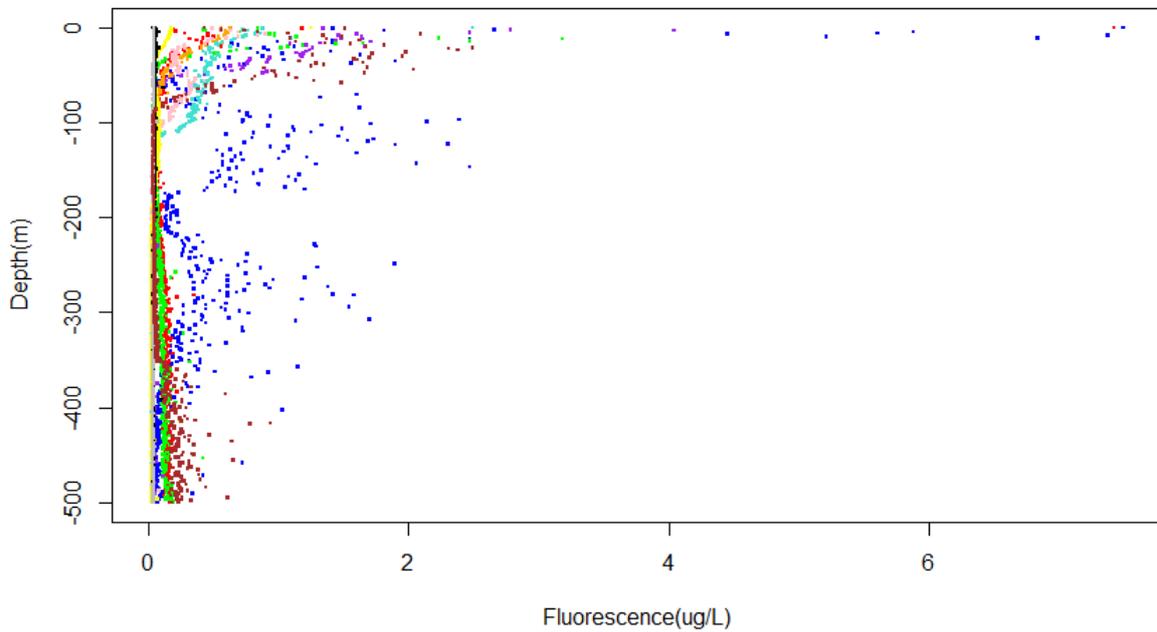


Figure 4: Profiles of a) temperature, b) salinity and c) fluorescence of the water column in the Skjerstadfjord throughout the study period from April 2017 to March 2018. Months of sampling are displayed by colour-coding: April (blue); May (red); June (green); July (purple); August

(orange); September (pink); October (turquoise); November (yellow); December (black); January (grey); March (brown).

3.2 Species composition

Copepodites of all four species were identified in the fjord during the study period, although the occurrence of *C. helgolandicus* was very low. Over the whole studied period, *C. glacialis* dominated in terms of abundance (60 %), *C. hyperboreus* was the second most abundant (21 %), followed by *C. finmarchicus* (19 %), while *C. helgolandicus* accounted for less than 1 % of the total numbers of *Calanus* spp. from all samples (Fig.5). *C. glacialis* peaked in abundance in May (44 ind. m⁻³), while abundance of *C. finmarchicus* and *C. hyperboreus* reached a maximum in November with 11 ind. m⁻³ and 10 ind. m⁻³, respectively (Fig.6). *C. finmarchicus* and *C. hyperboreus* numbers had declined by January, and by March the *C. finmarchicus* population was absent while numbers of *C. hyperboreus* continued to decline (Fig.6). Abundance was low for all species in July (Fig.6), while a subsequent increase in numbers was seen in *C. glacialis* from September to January before declining in March.

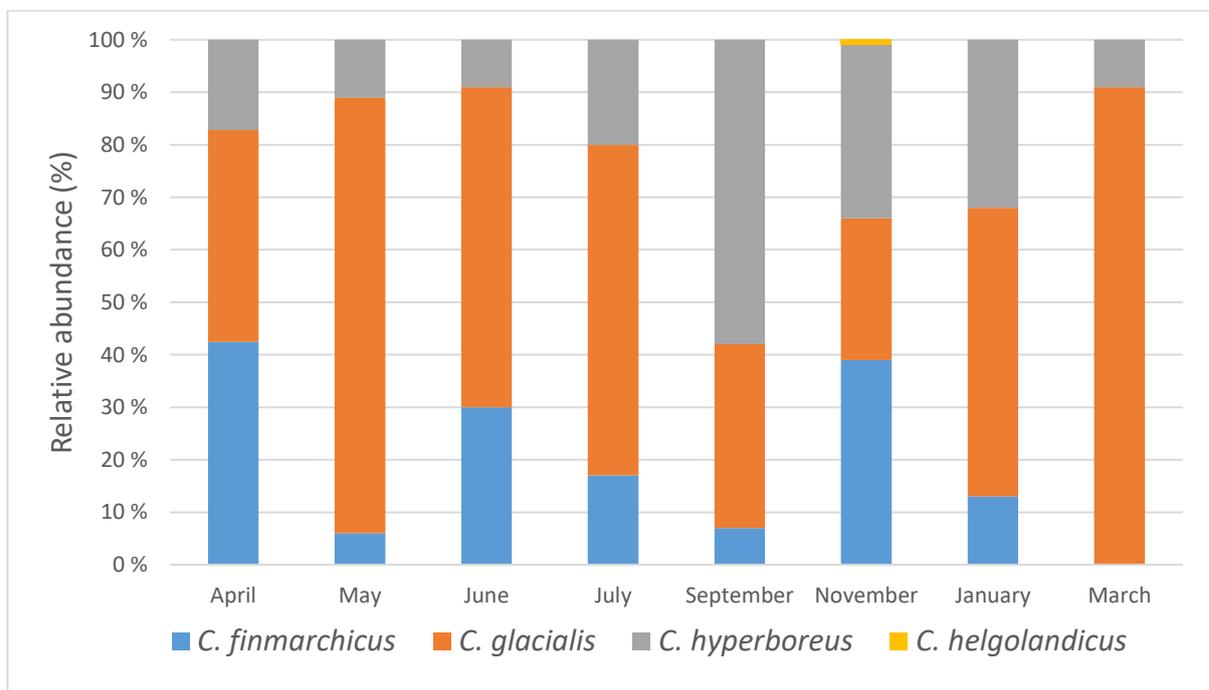


Figure 5: Relative abundance in percentage of *Calanus* spp. throughout the study period from April 2017 to March 2018 in the Skjerstadvjord.

3.3 Stage composition and vertical distribution

Too few individuals of *C. helgolandicus* were detected throughout the study period to evaluate its stage composition and vertical distribution in the water column ((Fig.6;7d).

Developmental stages CIV and adult females (CVIF) dominated the *C. finmarchicus* population in April, and were still present in May and June (Fig.6). Females were not encountered in July-September (Fig.6), but were present in small numbers in November and January. Copepodite stage CV dominated the population from June onward, peaked in abundance in November and were still present in January (Fig.6). Adult males (CVIM) appeared in May and June and peaked in abundance in January (Fig.6). In May and June, all developmental stages (CIV- CVIF/CVIM) of the *C. finmarchicus* population were present (Fig.6). Most of the *C. finmarchicus* population was distributed in the 500-200 m layer in April (Fig.7a) and had surfaced to the upper 50 m from May to June. I did not detect any individuals in the 200-50 m layer in July (Fig.7a), nor in the upper 50 m in September and November. The majority of the population had descended to depths below 200 m from July to January (Fig.7a).

The developmental stages CIV and CV both peaked for the *C. glacialis* population in May (Fig.6). The CIV individuals of the population were nearly absent by June, and nearly not encountered again until January, while the CV's continued to be the dominant copepodite stage until January (Fig.6). The adult females dominated the population in March and April and remained in the population until June (Fig.6). Females were absent between July-September (Fig.6) before appearing in small numbers in November. Males appeared in very small numbers in January (Fig.6). The majority of the *C. glacialis* population was concentrated in the 500-200 m depth range in April (Fig.7b) and had ascended to the upper 50 m in May. The population was mainly distributed in the 500-200 m layer from June to January (Fig.7b), whereas in March no individuals were detected in this depth range and the main population had ascended to the upper 50 m. In July, no individuals were detected in the 200-0 m layer, and none in the 50-0 m layer in September- November (Fig.7b).

Copepodite stage CIV peaked for the *C. hyperboreus* population in May, but individuals of this stage were present from April-June and their numbers increased from September to November (Fig.6). The dominant developmental stage from May to January was CV (Fig.6), which peaked in November. Females dominated the population in March and April, peaked in May, and appeared in increasing numbers in September and November (Fig.6). Males were present in January (Fig.6). The *C. hyperboreus* population was mainly concentrated in the 500-

200 m layer from April to May (Fig.7c) and part of the population had ascended to the upper 50 m in June. The whole population was at depths below 200 m from July to November, and the majority of the population was distributed at this depth range in January (Fig.7c). The population was concentrated in the upper 50 m layer in March (Fig.7c).

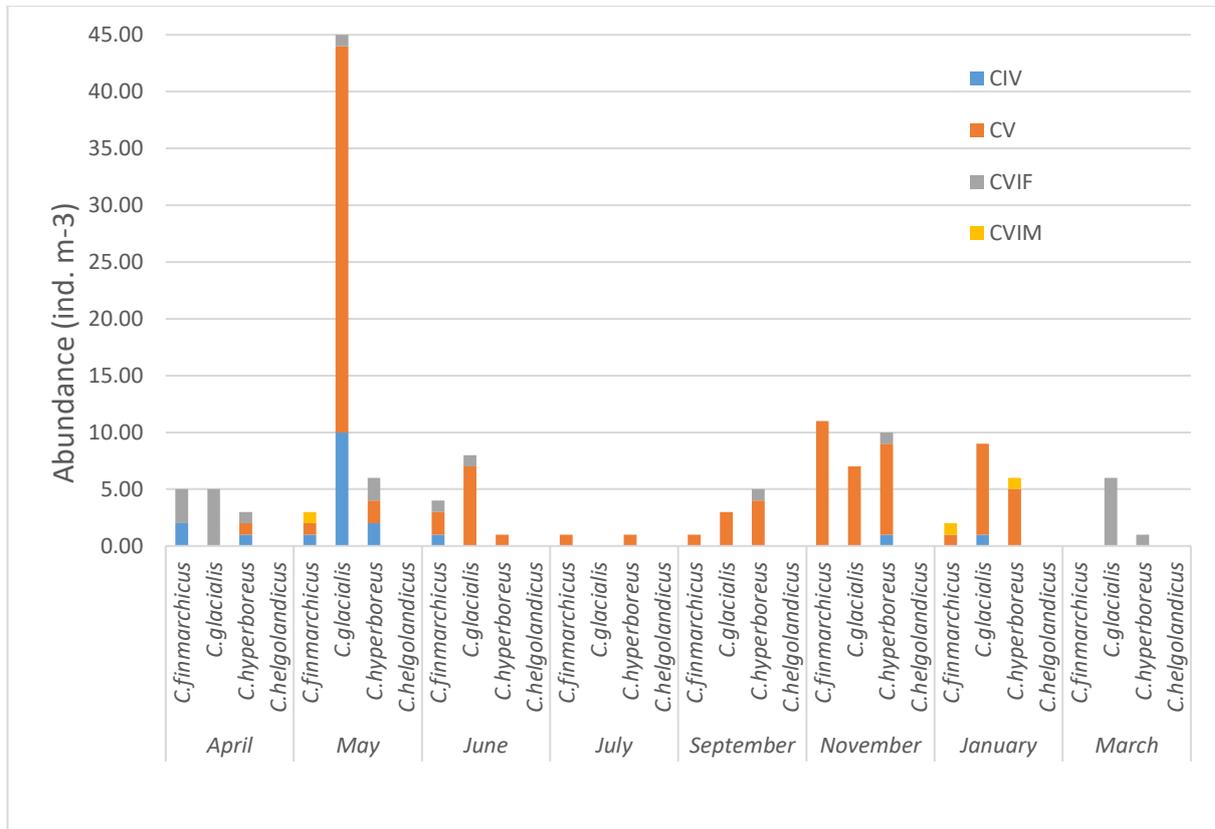
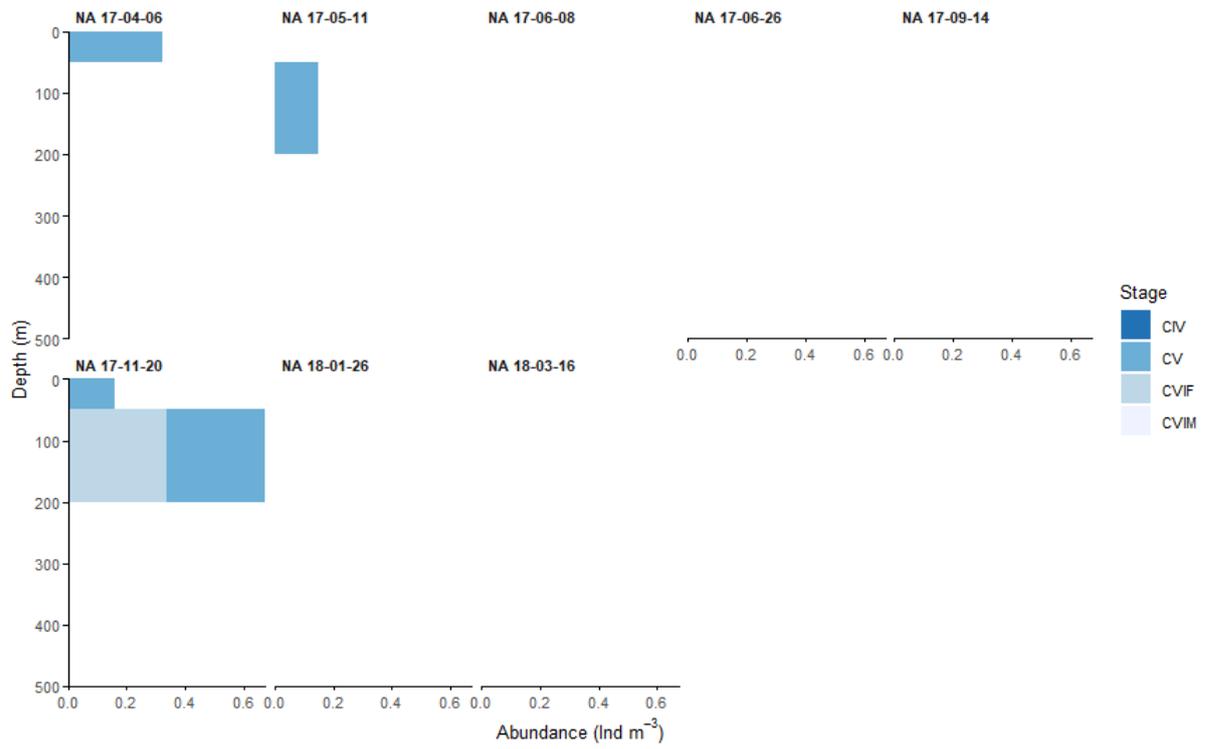
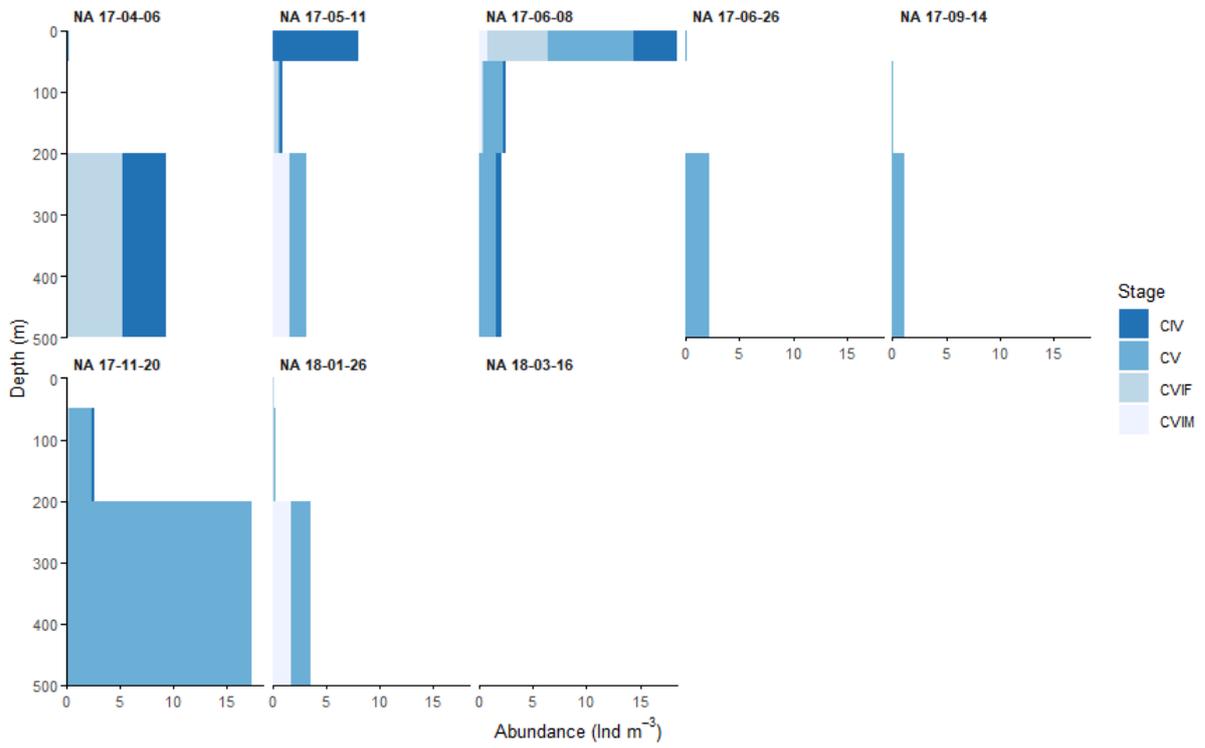


Figure 6: *Calanus* spp. abundances of copepodite stages CIV, CV and CVI (CVIF: females, CVIM: males) in the Skjerstadvjord from April 2017 to March 2018, represented monthly from April - July 2017 and bimonthly from September 2017 - March 2018.

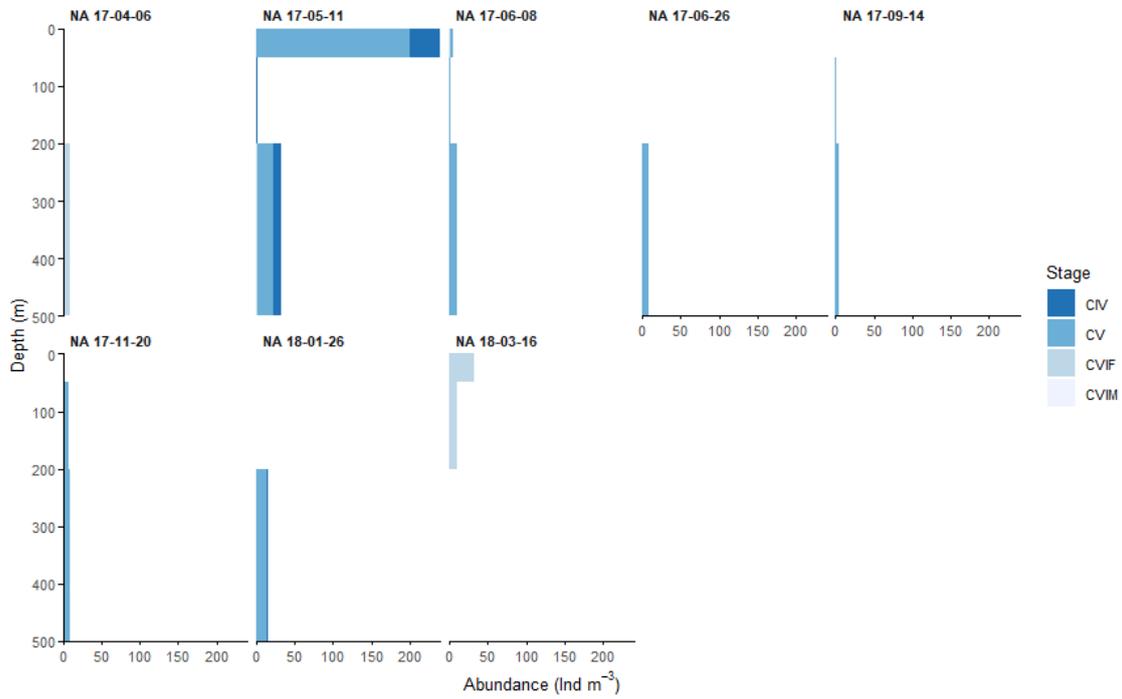
a) *Calanus helgolandicus*



b) *Calanus finmarchicus*



c) *Calanus glacialis*



d) *Calanus hyperboreus*

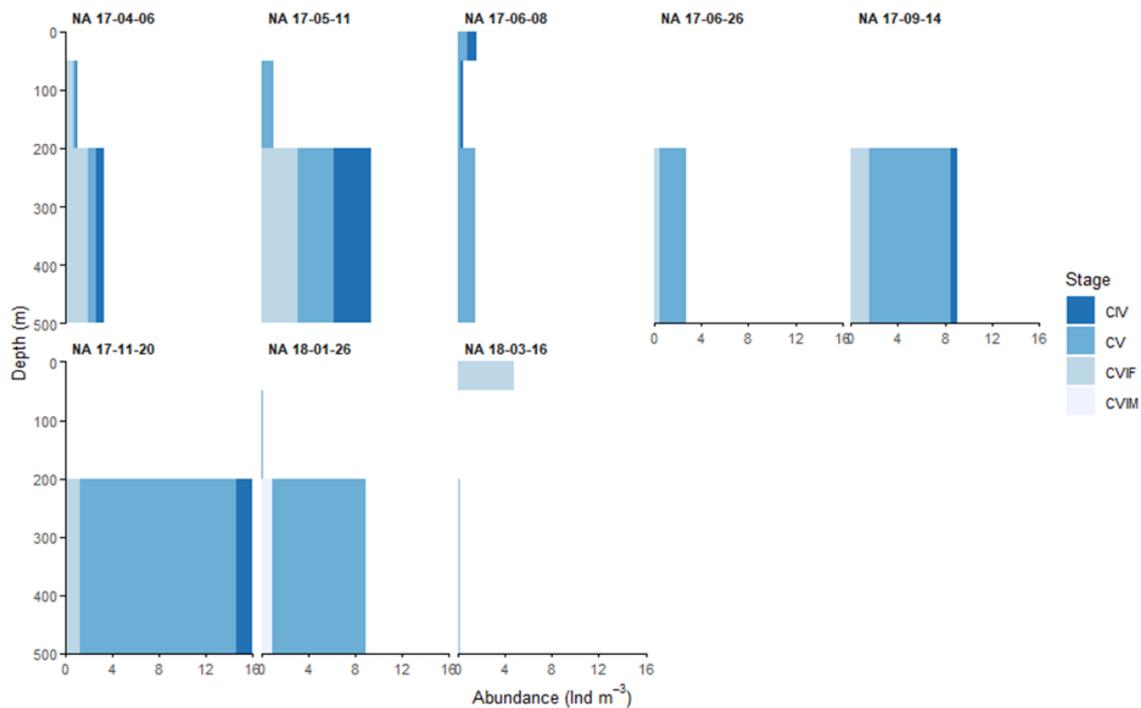


Figure 7: Seasonal vertical distribution of a) *C. helgolandicus*, b) *C. finmarchicus*, c) *C. glacialis*, d) *C. hyperboreus* in the water column in the Skjerstadvjord during the study period from April 2017 to March 2018.

4. Discussion

4.1 Species composition in the Skjerstadvjord

The *Calanus* species composition in the Skjerstadvjord was averaged over a year of monthly sampling with the use of molecular tools to distinguish among species. This revealed that *C. glacialis* is the dominant species (60 %), followed by *C. hyperboreus* (21 %), *C. finmarchicus* (19 %) and finally *C. helgolandicus* (< 1 %). These findings resemble the *Calanus* species composition reported by Choquet et al. (2017). All four *Calanus* species genetically identified here were also reported in the neighboring Saltfjord by Lindeque et al. (2004), as the only location representing co-occurrence of all four *Calanus* spp. in a wide geographical area investigated in the North Atlantic, with sites extending from Tromsø, northern Norway (69°N) to the English Channel (50°N). The co-occurrence of these four species is also documented in the Osterfjord, southern Norway (60°N) (Choquet et al., 2017).

The identification of a few specimens of *C. helgolandicus* in the Skjerstadvjord is in accordance with what was previously reported for surrounding northern Norwegian fjords

(Choquet et al., 2017). This species distribution range was recently stretched as far north as 70°N in the Norwegian Sea, where its contribution in a *C. finmarchicus* dominated community was of a more substantial degree (~ 15 %) (Choquet et al., 2017). *C. helgolandicus* is known to be more abundant in its southern range within the North Atlantic, characterized by warmer water temperatures, where it often co-occurs with *C. finmarchicus* and sometimes with *C. glacialis* in fjords along western Norway, and with *C. finmarchicus* and *C. hyperboreus* at more southern Norwegian locations (Fleminger & Hulsemann, 1977; Planque & Fromentin, 1996; Helaouët & Beaugrand, 2007). Dominance of *C. helgolandicus* over co-occurring *C. finmarchicus* was recorded in the Sognefjord, western Norway (61°N) (Lindeque et al., 2004; Choquet et al., 2017), as well as in the Oslofjord located south-east in Norway with coexisting *C. finmarchicus* and *C. hyperboreus* (Bucklin et al., 1999), and also recently reported for the North Sea as a response to *C. finmarchicus* moving northward due to rising ocean temperatures (Wilson et al., 2016).

So far, *C. finmarchicus* is reported as the dominant contributor to the *Calanus* species composition in Norwegian coastal waters and fjords (Wiborg, 1954; Skreslet & Rød, 1986; Skreslet et al., 2000), in the Norwegian Sea (Broms et al., 2009), south of the polar front in the Barents Sea (Tande, 1991), and also often found as the most prevalent species in fjords in Svalbard (Koszteyn & Kwasniewski, 1989; Kwasniewski et al., 2003). Here, surprisingly, the species was only the third most abundant in the Skjerstadfjord. This is particularly striking when we consider that morphological-based distribution suggested that *C. finmarchicus* were dominating the *Calanus* community in boreal fjords (Conover, 1988). Therefore, this finding emphasizes the importance of using molecular tools for species identification.

Calanus glacialis is traditionally considered to be associated with Arctic water masses north of the polar front, being the dominant species of the *Calanus* spp. community on the northeast Greenland shelf and also in the polar front region of the Barents Sea. The species also prevails in the Billefjord, a sill fjord located in the high-Arctic Svalbard area, where it co-exists with *C. hyperboreus* and *C. finmarchicus* (Hirche & Kwasniewski, 1997; Hansen et al., 1990; Arnkværn et al., 2005). Recent results based on the use of molecular tools for species identification revealed *C. glacialis* as dominant species in several Norwegian fjords such as the Tysfjord and Ranfjord (Choquet et al., 2017), where it was believed to be *C. finmarchicus* dominated populations. And so was the case for the Lurefjord, another sill fjord located in southern Norway, when molecular tools were applied for species identification (Lindeque et al., 2004; Choquet et al., 2017). There, *C. glacialis* (69 %) co-occurs with *C. finmarchicus* and

C. helgolandicus (Bucklin et al., 2000) while in northern Norwegian fjords *C. glacialis* mostly co-occurs with *C. finmarchicus* and *C. hyperboreus* (Choquet et al., 2017, Fig.2). The challenge of distinguishing between the morphologically similar *C. finmarchicus* and *C. glacialis* is likely to have led to biased descriptions of the species distribution ranges. In particular, *C. glacialis* may have been often misidentified as *C. finmarchicus* when using prosome length to identify species (Choquet et al., 2017; 2018). Here, our results indicate that *C. glacialis* was dominating the *Calanus* community every month sampled over a year, except in September and November.

Calanus hyperboreus was found to be the second most abundant *Calanus* species in the Skjerstadvjord, and dominated the *Calanus* community only in September. In other regions where the species is present, *C. hyperboreus* is often outnumbered numerically by coexisting *C. finmarchicus* and *C. glacialis* e.g. in the Arctic Ocean and most of the Nordic Seas, in the Kongsfjord (Svalbard) (Thibault et al., 1999; Hirche, 1997; Falk-Petersen et al., 1999; Broms et al., 2009), as well as when distributed along the Norwegian coast (Choquet et al., 2017). *C. hyperboreus* represents the *Calanus* species of largest size, contains the highest amount of lipids (Falk-Petersen et al., 2009), and is therefore a richer source of food compared to its congeners for the ecosystem it inhabits. The high abundances of *C. hyperboreus* measured throughout this study may indicate that the predation pressure on large copepods from visual predators such as fish is low (Eiane et al., 2002) in the Skjerstadvjord, and may serve as one of the explanations to why this species populates this fjord.

4.2 *Calanus* life cycles in the Skjerstadvjord

4.2.1 Life cycle of *Calanus finmarchicus*

The major part of the population present as stage CV in the months that indicate migration to overwintering depths from July to January along with the high proportion of stage CIV in April, suggests that developmental stages CIV and CV are the main overwintering stages in the fjord. Concordant with what was reported in the Balsfjord (69°N), northern Norway (Tande, 1982), stages CV and a smaller portion of CIV dominated the overwintering *C. finmarchicus* population, with a molt into adults and separation of the sexes with subsequent gonad maturation beginning from copepodite stage CV in January, when recorded Chl a measurements were at its lowest.

The spring ascent to the surface for the majority of the population was recorded in May and June. Considering that *C. finmarchicus* mainly is regarded as an income breeder (Varpe et al.,

2009) with subsequent maturation and spawning after the start of the spring bloom (Niehoff et al., 1999), and taking into consideration that the spring phytoplankton bloom was recorded to take place in April, it seems like *C. finmarchicus* relies on internal energy reserves as a capital breeder to develop into adults and for gonad maturation, while needing the energy input from the spring bloom to complete spawning. This would be in accordance with the development strategy reported by Tande & Hopkins (1981) for the *C. finmarchicus* population in the Balsfjord. The higher abundance of CIV in May than June indicates further development to CV by June.

Males of *C. finmarchicus* peaking in abundance in January together with the small number of females present in January (Appendix A) gives the potential for reproduction taking place between January/February, which would be in accordance with previously reported reproductive period for this species in the Skjerstadvjord (Choquet, 2017). The males peaking in abundance in January, a head of time of the females, is in agreement with the observations from Conover (1988) as the lives of males are usually very brief compared to females, they are the first ones to molt to be ready to fertilize newly mature females. In this study however, an unusual second encounter of males were present in May and June, with the potential of a second generation being produced at this time.

Based on the above, I suggest that *C. finmarchicus* has an annual life cycle in the Skjerstadvjord, with copepodite stages CIV and CV overwintering in the fjord, and with the potential of two generations produced per year within the annual cycle. A multigeneration life cycle is common for *C. finmarchicus* in its more southern distribution ranges along the Norwegian coast and in the Norwegian Sea (Wiborg, 1954; Conover, 1988; Matthews et al., 1978). A 1-year life cycle, or less, is frequently reported in higher latitudes for *C. finmarchicus*, from Norwegian fjords (Tande, 1982; Matthews et al., 1978), from the Norwegian Sea (Broms & Melle, 2007; Broms et al, 2009), the Iceland Sea (Gislason, 2018), the Barents Sea (Melle & Skjoldal, 1998), as well as from fjords on western Greenland (Madsen et al., 2001) and the high-Arctic Billefjord (Arnkvaern et al., 2005).

4.2.2 Life cycle of *Calanus glacialis*

Choquet (2017) reported on the potential reproduction of the *C. glacialis* population in the Skjerstadvjord in January/February, and the results of my study support that view to some degree by the small window of males present in January (Appendix B), although the lack of co-

occurring females at this time leaves room for interpretation. The relatively low number of individuals analysed may explain the lack of females in our data.

This view could further be supported by the peak in abundance of females distributed in the upper 50 m in March, which may represent the spring ascent of mature females that have begun spawning after successful reproduction. For the *C. glacialis* population investigated in the Lurefjord, southern Norway (Niehoff & Hirche, 2005), spawning was reported as starting in the beginning of March with a peak in egg production at the end of March. I assume that the egg production was fueled by internal fat reserves as this species is known to be a capital breeder, in some cases, which means it can achieve some parts of its development / life-cycle independently of the spring phytoplankton bloom. In this study, the females may have fed on the start of the bloom in March as income breeders before spawning. Start of spawning in March is similar to what is observed in the Disko Bay, west Greenland (Niehoff et al., 2002), and earlier than the time reported for *C. glacialis* in the Barents Sea (March/April) (Hirche & Kosobokova, 2003), in southeastern Hudson Bay, Canada (April) (Tourangeau & Runge, 1991), in the White Sea (May/June) (Kosobokova, 1999), and in the east Greenland shelf (May) (Hirche & Kwasniewski, 1997). Further experiments to study gonad maturity stage, egg production rate of females and inclusion of the stage distribution of following developmental stages of nauplii to copepodite stage CIII would be a necessary next step to provide more than assumptions regarding the exact timing of these events. Spawning in March would give the feeding stages from NIII the opportunity to feed on the spring bloom. Therefore, it seems reasonable to assume that the individuals CIV and CV mainly distributed in the surface in May are part of the new generation, recruited in February/March, and that they are feeding on the phytoplankton bloom to prepare for diapause.

The dominant abundance of CV along with the small record of CIVs in the overwintering population from June to January may suggest a mixed 1- and 2-year life cycle in the Skjerstadvjord, where the main *C. glacialis* population experiences a 1-year life cycle with CV as overwintering stage, while some individuals seem to use 2 years to complete their life cycle with CIV as diapausing developmental stage the first year. This is similar to what is reported for *C. glacialis* in the high-Arctic Rijpfjord and the ice-free Arctic Kongsfjord on Svalbard (Daase et al., 2013), and in the Barents Sea (Melle & Skjoldal, 1998), although the portion of the population in need of a second year for completion of the life cycle was substantially higher at these Arctic locations than it was the case in the more southernly distributed Skjerstadvjord. A two-year life cycle was also reported for *C. glacialis* in the White Sea, with CIV as diapausing

stage the first year and CIV as overwintering stage with subsequent spawning the second year (Kosobokova, 1999).

However, the presence of CIVs in the overwintering population may also have resulted from late spawning females. When a second year for completion of the life cycle with CIV as diapausing stage the first year is reported for Arctic locations (Daase, 2013), it is in an environment where water temperatures are substantially lower year-round and the food supply in form of ice algae and phytoplankton bloom is more pronounced and briefly distributed (Ji et al., 2013). When distributed in the more southernly Skjerstadvjord, where water temperatures year-round are considerably higher (own data) and the spring phytoplankton bloom is more widely distributed over the productive season (Vidal, 1980) it is likely that development from CIV to adult may be completed within the annual cycle (McLaren et al., 1988). This is further supported by the report of Kosobokova (1999), which describes a development from egg to diapausing stage CIV in the time frame of 2-3 months for *C. glacialis* in the White Sea, characterized by lower water temperatures.

Based on the above, I suggest a 1-year life cycle for *C. glacialis* in the Skjerstadvjord with developmental stages CIV and CV as overwintering stages.

4.2.3 Life cycle of *Calanus hyperboreus*

The short time frame of occurrence of *C. hyperboreus* males in January (Appendix C) suggests that reproduction is taking place in January/February. This would be in accordance with what was previously reported as the reproductive period for *C. hyperboreus* in the Skjerstadvjord (Choquet, 2017). An early breeding period in February (or January/February) is consistent with what was found when investigating the *C. hyperboreus* population in one of the northern Norwegian fjords in Malangen, south of Tromsø (69°N) (Pasternak et al., 2001), while the breeding period was reported as starting already in November in the Greenland Sea (Hirche & Niehoff, 1996). Matthews et al. (1978) found a peak in adult male abundance in January for the *C. hyperboreus* population in the Korsfjord, western Norway, with a follow-up of fertilized adult females peaking in numbers shortly after. In all cases, *C. hyperboreus* matured, reproduced and shed eggs in response to internally stored lipids independent of a phytoplankton food source (Varpe et al., 2009).

The current study showed similarities with the fjord population of *C. hyperboreus* investigated in Malangen (Pasternak et al., 2001) with respect to other life cycle events and

their timing. In particular, same overwintering stages CIV, CV and CVI females were observed, with a spring ascent and feeding period of females beginning at the start of the bloom in March and only lasting until April. Differences however, would be the lack of feeding stages CIV and CV present in this study when the bloom starts in March along with a shorter feeding period of three months (from April to June) in stages CIV and CV compared to Malangen (from March-July) (Pasternak et al., 2001). The very small part of the feeding stages CIV and CV distributed in the surface layers during spring ascent until June questions the feeding success of *C. hyperboreus* in the Skjerstadvjord. Pasternak (2001) on the other hand, found that the lipid accumulation of *C. hyperboreus* CVs was very high already in April after a month of feeding, and observed the start of diapause for this stage as a result shortly after, while the CIVs and CVs still in need of requiring higher lipid reserves before descent stayed in the surface to feed, which also could serve as an explanation for the observed vertical distribution found in this study from April to June. A relatively small amount of time spent in the surface layers during summer has been reported in other distribution areas too (Hirche & Niehoff, 1996; Gislason, 2018).

There was a very marked descent to deeper water layers for most of the *C. hyperboreus* population from July to January in the Skjerstadvjord. [In comparison](#), Hirche (1997) presents a later spring ascent (April) but same descent (July) for *C. hyperboreus* in the Greenland Sea.

Matthews et al., 1978 proposes an annual life cycle for *C. hyperboreus* in the Korsfjord, with a relatively fast development of naupliar stages, low occurrence of copepodite stages CI-CIII followed by an early increase in abundance of stage CIV in March and April. Hirche (1997) questions the larger copepod *C. hyperboreus*' ability for an annual generation cycle even in southern distribution areas like the Korsfjord due to this species short growth period in spring/summer, and proposes the possibility of the CIIIs being present as overwintering stages instead of being part of the new generation, which would indicate a two-year life cycle.

An annual life cycle is reported for *C. hyperboreus* in Norwegian fjords and both 1- and 2-year life cycles are reported from the Norwegian Sea (Matthews et al., 1978; Wiborg, 1954; Sømme, 1934; Broms et al., 2009). In the Vestfjord, a Norwegian sea area between the Lofoten islands and Salten in Nordland county, Sømme (1934) observed that $\sim 1/4$ of the *C. hyperboreus* stock did not reach maturity in spring, with continuation in stages CIV and CV for approximately ten months, which would indicate a two-year cycle for that part of the

population. At higher latitudes, in the Greenland Sea and the Arctic Ocean, *C. hyperboreus* have a generation cycle of at least 4 years (Hirche, 1997; Dawson, 1978).

The results of this study do not allow to make clear conclusions about the exact duration of *C. hyperboreus* life cycle in the Skjerstadvjord. This is evident from previous studies that reflects the flexibility of this species life cycle duration (Matthews et al., 1978; Hirche, 1997; Wiborg, 1954; Sømme, 1934; Broms et al., 2009; Dawson, 1978). Further experiments with analysis of earlier developmental stages from nauplii to copepodite stage CIII, along with higher sampling numbers and resolution in time would be a necessary next step to make clear conclusions about the exact life cycle length of this species in the Skjerstadvjord.

4.2.4 Ecological niches: overlap and distinctness

The timing of reproduction was the same for all three species (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*) in the Skjerstadvjord, between January/February although a higher temporal resolution may be needed to detect potential variation among species. Also, the collection of more individuals and identification of younger stages would allow to address this question with more precision. However, from the temporal resolution we had, the ecological niches of the species seemed distinct in regard to the patterns of vertical migration, with *C. hyperboreus* most likely reproducing at deeper water layers compared to *C. finmarchicus* and *C. glacialis* which seemed to reproduce at surface layers.

Over its distribution area, *Calanus hyperboreus* is unique in that it has the deepest winter distribution (~800–1000 m), reproduces at depth in February–March in the absence of phytoplankton food, and spends relatively short time in the surface layers during summer (Gislason, 2018). The earlier ascent of *C. glacialis* and *C. hyperboreus* that I reported in March, prior to the spring bloom, is a strategy for timing the spawning in a way that allows the new generation to exploit the phytoplankton bloom in April (Cushing, 1990). This ability may explain the fact that these two species were numerically more “successful” compared to *C. finmarchicus*, which has to rely on the onset of the bloom to initiate spawning.

C. glacialis was mostly found in the surface, most likely feeding (albeit we did not collect data to demonstrate the feeding) in the month of May, when temperatures in the surface layer were between 5.8–6.0°C, and within the recorded threshold of its well-being (between 5–6°C) (Carstensen et al., 2012). In comparison, *C. finmarchicus* continued to feed in the surface layer

in June when temperature varied from 6°C to above 11°C in the uppermost layers, within its broader ecological niche in terms of tolerated thermal interval (Helaouët & Beaugrand, 2007). *C. hyperboreus* that is also assumed to be adapted to colder environments, as for *C. glacialis*, was found feeding in the surface layers in June at the same time than the boreal *C. finmarchicus*, suggesting that the ecological niche of *C. hyperboreus* in terms of tolerated temperature interval is larger in boreal waters compared to *C. glacialis*.

In June, *C. glacialis* had mostly descended to deeper water layers even though Chl a concentration was still reported to be relatively high in the surface layer. The water temperatures at the surface reached its maximum values in June (ranging from 6-12°C in the uppermost layers), while in the deeper water layers (200-500 m) temperature ranged from 6.4-6.6°C. This may be seen as a response to that temperature is an important factor for initiation of diapause in this species. Increased temperature as a key factor for termination of females found spawning in the surface layers and as prominent cue for initiation of diapause is reported for this species both in the Lurefjord and in the White Sea (Kosobokova, 1998; Niehoff & Hirche, 2005).

The observed decrease in surface salinity in the 0-50 m depth range in the Skjerstadvjord beginning in May and reaching its lowest values in June and July was probably a result of the high amount of meltwater discharge (Eliassen et al., 2001). This probably caused an estuarine circulation to develop, which is characterized by a strong stratification often dominated by salinity instead of temperature (Dyer, 1997). The vertical salinity profiles observed in this study support that view by displaying a clear stratification with an increase of salinity with depth, while vertical temperature profiles showed a less pronounced temperature stratification throughout the study period, although a decrease in temperature with depth could be observed most months. The river runoff brings freshwater with low salinity into the Skjerstadvjord, the lesser density of this fresh water compared to the seawater in the fjord makes this water buoyant and a strong halocline forms with high vertical stability that can inhibit vertical mixing with water below the halocline (Talley et al., 2011). The resulting density difference occurring between the brackish surface layer in the Skjerstadvjord and the coastal water outside creates a horizontal pressure gradient (Aure et al., 2007) forcing the fresh water from inside the fjord out towards the Saltfjord, with biological impacts for zooplankton feeding in the euphotic zone at this time. In June when surface salinity was at its lowest, the majority of the *C. finmarchicus* population (stages CIV- CVI; males and females) and part of the *C. hyperboreus* population (stages CIV and CV) were distributed in the surface water layers, with the possible consequence

that the brackish surface outflow flushed them out of the fjord and into the Saltfjord. A similar event was reported for the investigated *C. finmarchicus* and *C. helgolandicus* populations in the Saltfjord, where development of an estuarine circulation most likely was responsible for creating a brackish outflow that flushed nauplii produced in June onto shelf waters (Skreslet et al., 2000). *C. glacialis* on the other hand, reported to descend to deep water layers in June, would to a much lesser degree be affected by this process due to its vertical position and would still mainly populate the Skjerstadvjord. These observations are also in line with the molecular results reported in Choquet et al. (2017). Indeed, using a set of microsatellite markers, the authors reported higher levels of genetic differentiation among *C. glacialis* individuals from Norwegian fjords compared to *C. finmarchicus* from the same fjords (including the Skjerstadvjord). This suggests that there is less inter-fjords exchange of individuals of *C. glacialis* than there is for *C. finmarchicus*. What I observed in the present study seems to confirm the status of *C. finmarchicus* and *C. hyperboreus* as being drifting species (Bucklin 2000), while *C. glacialis* higher level of genetic isolation may be explained by its descent at depth in early summer, avoiding the flushing out of the fjord. Therefore, we can assume that *C. glacialis* is a species resident of the fjord (Kaartvedt, 1993) in contrast to *C. finmarchicus* and *C. hyperboreus*.

In September, the temperature was high in the upper 50 m of the water column. This could possibly be caused by the yearly surface advection of shelf water inflow to the Saltfjord at this time being further advected into the Skjerstadvjord, an event also known to import plankton as well as heat (Haakstad, 1979). This event, along with wind-driven surface advection and a compensating inflow of seawater from the Saltfjord flowing in underneath the outflowing surface brackish water creating nutrient and zooplankton transport upward, could be responsible for the sudden increase in abundance of *C. finmarchicus* CIVs and CVs observed in the 50-200 m depth range from September to November, likely imported from the Saltfjord then. Similar physical processes between the shelf water outside and the Saltfjord were reported to create import of *C. finmarchicus* CVs to the Saltfjord between August and November (Skreslet et al., 2000). There is however no support for in this study that *C. hyperboreus* was imported back into the Skjerstadvjord from September to November, as was the case for *C. finmarchicus*. Again, the analysis of more samples and more individuals with more temporal resolution may help to draw the right conclusions.

Conclusion

This study revealed a surprising dominance of *C. glacialis* over co-occurring *C. hyperboreus*, *C. finmarchicus* and *C. helgolandicus* in the Skjerstadvjord. This emphasizes the need for use of molecular tools for species identification in plankton ecology studies. All three species, comprising *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* reproduced in the fjord at approximately the same time between January/February. Results suggest that *C. glacialis* is a resident species in the fjord (Kaartvedt, 1993), in contrast to *C. finmarchicus* and *C. hyperboreus* being drifting species (Bucklin, 2000). Further experiments with analysis of earlier developmental stages from nauplii to copepodite stage CIII, along with higher sampling numbers and resolution in time would be a necessary next step to make clearer conclusions. The low sampling numbers in this study limits the use of significant statistical testing and the results should therefore be interpreted with caution. Awareness concerning the potential bias related to the phenomena of zooplankton patchiness and zooplankton diel vertical migrations should also be made in plankton ecology studies. Since zooplankton perform diel vertical migration where feeding in the shallower ocean layers take place at night and with a return to their daytime environment at depth (Lampert, 1989), it would be good to sample always the same time of the day, or to include daytime and night-time sampling. But due to logistical constraints, this is rarely done. Zooplankton patchiness (Kaartvedt, 1993) is always a potential bias when estimating species composition, due to the possibility that sampling may take place outside the patch and lead to underestimation of abundance or species present.

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Appendix A

Seasonal abundance data of *C. finmarchicus*

Table 1: Abundance data of copepodite stages CIV to CVI (males: CVIM and females: CVIF) of *C. finmarchicus* in the three depth ranges (0-50, 50-200, 200-500 m) throughout the sampling period from April 2017 to March 2018 in the Skjerstadvjord

Trip	Date	Species	Depth	CIV	CV	CVIF	CVIM
1	06.04.2017	<i>C.finmarchicus</i>	500-200	4.00	0.00	5.33	0.00
1	06.04.2017	<i>C.finmarchicus</i>	200-50	0.05	0.05	0.00	0.00
1	06.04.2017	<i>C.finmarchicus</i>	50-0	0.00	0.32	0.00	0.00
2	11.05.2017	<i>C.finmarchicus</i>	500-200	0.00	1.55	0.00	1.55
2	11.05.2017	<i>C.finmarchicus</i>	200-50	0.15	0.15	0.45	0.15
2	11.05.2017	<i>C.finmarchicus</i>	50-0	8.00	0.00	0.00	0.00
3	08.06.2017	<i>C.finmarchicus</i>	500-200	0.51	1.54	0.00	0.00
3	08.06.2017	<i>C.finmarchicus</i>	200-50	0.21	1.87	0.21	0.21
3	08.06.2017	<i>C.finmarchicus</i>	50-0	4.00	8.00	5.60	0.80
4	26.06.2017	<i>C.finmarchicus</i>	500-200	0.00	2.23	0.00	0.00
4	26.06.2017	<i>C.finmarchicus</i>	200-50	0.00	0.00	0.00	0.00
4	26.06.2017	<i>C.finmarchicus</i>	50-0	0.00	0.16	0.00	0.00
5	14.09.2017	<i>C.finmarchicus</i>	500-200	0.00	1.07	0.00	0.00
5	14.09.2017	<i>C.finmarchicus</i>	200-50	0.05	0.05	0.00	0.00
5	14.09.2017	<i>C.finmarchicus</i>	50-0	0.00	0.00	0.00	0.00
6	20.11.2017	<i>C.finmarchicus</i>	500-200	0.00	17.33	0.00	0.00
6	20.11.2017	<i>C.finmarchicus</i>	200-50	0.34	2.02	0.34	0.00
6	20.11.2017	<i>C.finmarchicus</i>	50-0	0.00	0.00	0.00	0.00
7	26.01.2018	<i>C.finmarchicus</i>	500-200	0.00	1.78	0.00	1.78
7	26.01.2018	<i>C.finmarchicus</i>	200-50	0.00	0.21	0.05	0.05
7	26.01.2018	<i>C.finmarchicus</i>	50-0	0.00	0.00	0.16	0.00
8	16.03.2018	<i>C.finmarchicus</i>	500-200	0.00	0.00	0.00	0.00
8	16.03.2018	<i>C.finmarchicus</i>	200-50	0.00	0.00	0.00	0.00
8	16.03.2018	<i>C.finmarchicus</i>	50-0	0.00	0.00	0.00	0.00

Appendix B

Seasonal abundance data of *C. glacialis*

Table 1: Abundance data of copepodite stages CIV to CVI (males: CVIM and females: CVIF) of *C. glacialis* in the three depth ranges (0-50, 50-200, 200-500 m) throughout the sampling period from April 2017 to March 2018 in the Skjerstadvjord

Trip	Date	Species	Depth	CIV	CV	CVIF	CVIM
1	06.04.2017	<i>C.glacialis</i>	500-200	0.00	0.00	8.67	0.00
1	06.04.2017	<i>C.glacialis</i>	200-50	0.00	0.11	0.48	0.00
1	06.04.2017	<i>C.glacialis</i>	50-0	0.00	0.00	0.00	0.00
2	11.05.2017	<i>C.glacialis</i>	500-200	9.33	21.77	1.55	0.00
2	11.05.2017	<i>C.glacialis</i>	200-50	1.05	1.34	0.15	0.00
2	11.05.2017	<i>C.glacialis</i>	50-0	40.00	200.00	0.00	0.00
3	08.06.2017	<i>C.glacialis</i>	500-200	0.00	10.24	0.51	0.00
3	08.06.2017	<i>C.glacialis</i>	200-50	0.42	2.08	0.00	0.00
3	08.06.2017	<i>C.glacialis</i>	50-0	0.00	4.00	1.60	0.00
4	26.06.2017	<i>C.glacialis</i>	500-200	0.00	8.46	0.00	0.00
4	26.06.2017	<i>C.glacialis</i>	200-50	0.00	0.11	0.00	0.00
4	26.06.2017	<i>C.glacialis</i>	50-0	0.00	0.00	0.00	0.00
5	14.09.2017	<i>C.glacialis</i>	500-200	0.00	5.33	0.00	0.00
5	14.09.2017	<i>C.glacialis</i>	200-50	0.00	0.27	0.00	0.00
5	14.09.2017	<i>C.glacialis</i>	50-0	0.00	0.00	0.00	0.00
6	20.11.2017	<i>C.glacialis</i>	500-200	0.00	9.33	0.00	0.00
6	20.11.2017	<i>C.glacialis</i>	200-50	0.00	6.05	0.67	0.00
6	20.11.2017	<i>C.glacialis</i>	50-0	0.16	0.16	0.00	0.00
7	26.01.2018	<i>C.glacialis</i>	500-200	1.78	13.32	0.00	0.00
7	26.01.2018	<i>C.glacialis</i>	200-50	0.00	0.11	0.00	0.05
7	26.01.2018	<i>C.glacialis</i>	50-0	0.16	0.00	0.00	0.00
8	16.03.2018	<i>C.glacialis</i>	500-200	0.00	0.00	0.08	0.00
8	16.03.2018	<i>C.glacialis</i>	200-50	0.00	0.00	10.24	0.00
8	16.03.2018	<i>C.glacialis</i>	50-0	0.00	0.00	32.40	0.00

Appendix C

Seasonal abundance data of *C. hyperboreus*

Table 1: Abundance data of copepodite stages CIV to CVI (males: CVIM and females: CVIF) of *C. hyperboreus* in the three depth ranges (0-50, 50-200, 200-500 m) throughout the sampling period from April 2017 to March 2018 in the Skjerstadfjord

Trip	Date	Species	Depth	CIV	CV	CVIF	CVIM
1	06.04.2017	<i>C.hyperboreus</i>	500-200	0.67	0.67	2.00	0.00
1	06.04.2017	<i>C.hyperboreus</i>	200-50	0.16	0.16	0.75	0.00
1	06.04.2017	<i>C.hyperboreus</i>	50-0	0.00	0.00	0.00	0.00
2	11.05.2017	<i>C.hyperboreus</i>	500-200	3.11	3.11	3.11	0.00
2	11.05.2017	<i>C.hyperboreus</i>	200-50	0.00	1.05	0.00	0.00
2	11.05.2017	<i>C.hyperboreus</i>	50-0	0.00	0.00	0.00	0.00
3	08.06.2017	<i>C.hyperboreus</i>	500-200	0.00	1.54	0.00	0.00
3	08.06.2017	<i>C.hyperboreus</i>	200-50	0.21	0.21	0.00	0.00
3	08.06.2017	<i>C.hyperboreus</i>	50-0	0.80	0.80	0.00	0.00
4	26.06.2017	<i>C.hyperboreus</i>	500-200	0.00	2.23	0.45	0.00
4	26.06.2017	<i>C.hyperboreus</i>	200-50	0.00	0.00	0.00	0.00
4	26.06.2017	<i>C.hyperboreus</i>	50-0	0.00	0.00	0.00	0.00
5	14.09.2017	<i>C.hyperboreus</i>	500-200	0.53	6.93	1.60	0.00
5	14.09.2017	<i>C.hyperboreus</i>	200-50	0.00	0.00	0.00	0.00
5	14.09.2017	<i>C.hyperboreus</i>	50-0	0.00	0.00	0.00	0.00
6	20.11.2017	<i>C.hyperboreus</i>	500-200	1.33	13.33	1.33	0.00
6	20.11.2017	<i>C.hyperboreus</i>	200-50	0.00	0.00	0.00	0.00
6	20.11.2017	<i>C.hyperboreus</i>	50-0	0.00	0.00	0.00	0.00
7	26.01.2018	<i>C.hyperboreus</i>	500-200	0.00	7.99	0.00	0.89
7	26.01.2018	<i>C.hyperboreus</i>	200-50	0.00	0.11	0.00	0.00
7	26.01.2018	<i>C.hyperboreus</i>	50-0	0.00	0.00	0.00	0.00
8	16.03.2018	<i>C.hyperboreus</i>	500-200	0.00	0.00	0.24	0.00
8	16.03.2018	<i>C.hyperboreus</i>	200-50	0.00	0.00	0.00	0.00
8	16.03.2018	<i>C.hyperboreus</i>	50-0	0.00	0.00	4.80	0.00

Appendix D

Seasonal abundance data of *C. helgolandicus*

Table 1: Abundance data of copepodite stages CIV to CVI (males: CVIM and females: CVIF) of *C. helgolandicus* in the three depth ranges (0-50, 50-200, 200-500 m) throughout the sampling period from April 2017 to March 2018 in the Skjerstadvjord

Trip	Date	Species	Depth	CIV	CV	CVIF	CVIM
1	06.04.2017	<i>C.helgolandicus</i>	500-200	0.00	0.00	0.00	0.00
1	06.04.2017	<i>C.helgolandicus</i>	200-50	0.00	0.00	0.00	0.00
1	06.04.2017	<i>C.helgolandicus</i>	50-0	0.00	0.32	0.00	0.00
2	11.05.2017	<i>C.helgolandicus</i>	500-200	0.00	0.00	0.00	0.00
2	11.05.2017	<i>C.helgolandicus</i>	200-50	0.00	0.15	0.00	0.00
2	11.05.2017	<i>C.helgolandicus</i>	50-0	0.00	0.00	0.00	0.00
3	08.06.2017	<i>C.helgolandicus</i>	500-200	0.00	0.00	0.00	0.00
3	08.06.2017	<i>C.helgolandicus</i>	200-50	0.00	0.00	0.00	0.00
3	08.06.2017	<i>C.helgolandicus</i>	50-0	0.00	0.00	0.00	0.00
4	26.06.2017	<i>C.helgolandicus</i>	500-200	0.00	0.00	0.00	0.00
4	26.06.2017	<i>C.helgolandicus</i>	200-50	0.00	0.00	0.00	0.00
4	26.06.2017	<i>C.helgolandicus</i>	50-0	0.00	0.00	0.00	0.00
5	14.09.2017	<i>C.helgolandicus</i>	500-200	0.00	0.00	0.00	0.00
5	14.09.2017	<i>C.helgolandicus</i>	200-50	0.00	0.00	0.00	0.00
5	14.09.2017	<i>C.helgolandicus</i>	50-0	0.00	0.00	0.00	0.00
6	20.11.2017	<i>C.helgolandicus</i>	500-200	0.00	0.00	0.00	0.00
6	20.11.2017	<i>C.helgolandicus</i>	200-50	0.00	0.34	0.34	0.00
6	20.11.2017	<i>C.helgolandicus</i>	50-0	0.00	0.16	0.00	0.00
7	26.01.2018	<i>C.helgolandicus</i>	500-200	0.00	0.00	0.00	0.00
7	26.01.2018	<i>C.helgolandicus</i>	200-50	0.00	0.00	0.00	0.00
7	26.01.2018	<i>C.helgolandicus</i>	50-0	0.00	0.00	0.00	0.00
8	16.03.2018	<i>C.helgolandicus</i>	500-200	0.00	0.00	0.00	0.00
8	16.03.2018	<i>C.helgolandicus</i>	200-50	0.00	0.00	0.00	0.00
8	16.03.2018	<i>C.helgolandicus</i>	50-0	0.00	0.00	0.00	0.00

