



Contrasting Life Traits of Sympatric *Calanus glacialis* and *C. finmarchicus* in a Warming Arctic Revealed by a Year-Round Study in Isfjorden, Svalbard

Maja Hatlebakk^{1,2*†}, Ksenia Kosobokova³, Malin Daase⁴ and Janne E. Søreide¹

¹ Department of Arctic Biology, University Centre in Svalbard, Longyearbyen, Norway, ² Faculty of Biosciences and Aquaculture, Nord University, Bodo, Norway, ³ Shirshov Institute of Oceanology, Department of Marine Ecology, Russian Academy of Sciences, Moscow, Russia, ⁴ Department of Arctic and Marine Biology, Faculty for Bioscience, Fisheries and Economy, UiT The Arctic University of Norway, Tromsø, Norway

OPEN ACCESS

Edited by:

Martin Edwards,
Plymouth Marine Laboratory,
United Kingdom

Reviewed by:

Vladimir G. Dvoretzky,
Murmansk Marine Biological Institute,
Russia
Terry Whitledge,
Retired, Fairbanks, AK, United States

*Correspondence:

Maja Hatlebakk
maja.k.v.hatlebakk@ntnu.no

†Present address:

Maja Hatlebakk,
Institute for Biology, Norwegian
University of Science and Technology,
Trondheim, Norway

Specialty section:

This article was submitted to
Marine Ecosystem Ecology,
a section of the journal
Frontiers in Marine Science

Received: 17 February 2022

Accepted: 11 April 2022

Published: 12 May 2022

Citation:

Hatlebakk M, Kosobokova K, Daase M
and Søreide JE (2022) Contrasting Life
Traits of Sympatric *Calanus glacialis*
and *C. finmarchicus* in a Warming
Arctic Revealed by a Year-Round
Study in Isfjorden, Svalbard.
Front. Mar. Sci. 9:877910.
doi: 10.3389/fmars.2022.877910

The calanoid copepod *Calanus glacialis* dominates the mesozooplankton biomass in the Arctic shelf seas, but its smaller North Atlantic sibling *Calanus finmarchicus* is expanding northwards and may potentially replace it if the climate continues to warm. Here we studied the population structure, overwintering strategies, gonad maturation and egg production of *C. glacialis* and *C. finmarchicus* over a period of 15 consecutive months in a high-Arctic fjord with sub-Arctic ocean climate and no sea ice formation in winter. The relative proportions of *C. glacialis* and *C. finmarchicus* varied throughout the study period, but with an overall dominance of *C. glacialis*. The overwintering population of *C. glacialis* was dominated by copepodite stage CIV (74%) while *C. finmarchicus* overwintered mainly as CV (65%), reflecting a primarily two- and one-year life cycle, respectively. Adult males and females of *C. glacialis* appeared as early as October with a peak during December-January, two months earlier than in *C. finmarchicus*, with a corresponding one-month earlier peak in recruitment for *C. glacialis*. While *C. glacialis* reproduced prior to the bloom with egg production peaking during the bloom, *C. finmarchicus* started egg laying during the bloom and continued to reproduce throughout the summer. Seasonal changes in the population structure suggest that *C. finmarchicus* born early in spring are able to develop to CV during summer and overwinter successfully, while offspring born later in the season do most likely not reach the CV overwintering stage. The ability to reproduce early and the flexibility to alter between 1- and 2-year life cycles give *C. glacialis* an advantage over *C. finmarchicus* in high-Arctic unpredictable environments with short-pulsed primary production regimes. Our data indicate that *C. glacialis* and *C. finmarchicus* occupy similar environmental niches, but different timing in reproduction reduces the competition. If sea temperatures remain within their temperature-tolerance ranges, both *C. glacialis* and *C. finmarchicus* seem to benefit from warming due to accelerating growth and higher survival of the recruits as long as *C. glacialis* has access to a colder refuge by descending to deeper depths.

Keywords: calanoid copepods, Svalbard fjords, reproduction, gonad maturation, population structure, climate

1 INTRODUCTION

Calanoid copepods of the genus *Calanus* dominate (>60%) the mesozooplankton biomass in Arctic and sub-Arctic seas (Jaschnov, 1970; Kosobokova et al., 1998; Blachowiak-Samolyk et al., 2008; Kosobokova and Hirche, 2009; Kosobokova et al., 2011; Kosobokova and Pertsova, 2018) and constitute the key link between primary producers and higher trophic levels (Falk-Petersen et al., 2007). *Calanus* are filter feeders, primarily feeding on microscopic algae, but do also consume alternative prey such as eggs, fungi and heterotrophic microorganisms outside the peak productive spring and summer season (Cleary et al., 2017; Frank-Gopolos et al., 2017). At high latitudes, the spring phytoplankton bloom lasts from two to eight weeks (reviewed by Leu et al., 2015). During this short period, these relatively large copepods convert their food to energy-rich lipids which may comprise up to 70% of their dry weight (Sargent and Falk-Petersen, 1988; Lee et al., 2006). Thus, *Calanus* is a major contributor to the rapid and efficient transfer of energy and essential fatty acids from primary producers to higher trophic levels in the lipid driven arctic marine food web (Falk-Petersen et al., 1990; Dahl et al., 2003).

Three species of the genus *Calanus* co-occur in the European Arctic: the two arctic species *Calanus hyperboreus* and *C. glacialis*, and the boreal *C. finmarchicus* (Conover, 1988; Choquet et al., 2017). These three species are all morphologically similar but differ in body sizes (Kwasniewski et al., 2003; Choquet et al., 2018). All three perform seasonal migrations, descending to deeper depths towards the end of the summer to spend the unproductive winter in a state of dormancy (diapause) (Falk-Petersen et al., 2009). The three species have different core distribution areas and have evolved different life strategies in response to the physical and biological environment they are exposed to. The smallest of the three species, the boreal *C. finmarchicus*, has a 1-year life cycle in the northernmost part of its distribution range and is considered to be primarily an income breeder, i.e. fueling egg production by ingested food (Plourde and Runge, 1993; Madsen et al., 2001; Kjellerup et al., 2012). The mid-sized species, the arctic *C. glacialis*, inhabits the Arctic Ocean with highest abundance confined at present to the outer shelf and slope regions (Ershova et al., 2021). *Calanus glacialis* has a 1–2-year life cycle and performs both income breeding and capital breeding, i.e. it fuels egg production using both ingested food and internal lipid resources (Hirche and Kattner, 1993; Kosobokova, 1999; Madsen et al., 2001). The largest arctic oceanic species *C. hyperboreus* has adapted to the extreme conditions of the oligotrophic Arctic Ocean with a life strategy where reproduction is not as tightly coupled with the spring bloom as in the two smaller ones. *Calanus hyperboreus* starts reproduction at depth in winter purely fueled by internal resources (Hirche, 1997), and the life cycle can be as long as 4 years depending on the extremeness of the environment (Hirche and Niehoff, 1996; Ashjian et al., 2003; Varpe et al., 2009; Ejsmond et al., 2018). All the three species develop through six naupliar (NI–NVI) stages, followed by six copepodite stages (CI–CVI), of which stage CV develops into either adult male (CVI,

AM) or adult female (CVI, AF). Adult males of *Calanus* have a short life span compared to females (Kosobokova, 1999; Hatlebakk et al., 2019), thus the timing of male presence, and consequent mating, is an important and sensitive aspect in the *Calanus* life cycle (Kosobokova, 1998; Kosobokova, 1999; Daase et al., 2018). Females on the other hand are long-lived and females of *C. hyperboreus* and *C. glacialis* may even survive one more winter and reproduce again (Hirche and Niehoff, 1996; Kosobokova, 1999). To develop female gonads is energy demanding. Jónasdóttir (1999) estimated that *C. finmarchicus* required 50% of its stored lipids (wax ester and triacylglycerol) to ripen the gonads. To be ready for descent and overwintering, *Calanus* need to reach a copepodite stage capable of storing a sufficient amount of lipids that allows them to successfully overwinter and fuel molting and/or maturation at the end of winter (Falk-Petersen et al., 2009; Bailey, 2010). *Calanus hyperboreus* can overwinter already as CIII, *C. glacialis* primarily as CIV, and *C. finmarchicus* primarily as CV (Hirche, 1997; Kosobokova, 1999; Falk-Petersen et al., 2009; Daase et al., 2013; Kosobokova and Pertsova, 2018).

Calanus finmarchicus and *C. glacialis* are regarded as important climate beacons in the Svalbard-Barents Sea region (Wassmann et al., 2015). In regions of sympatry, a high proportion of *C. finmarchicus* over *C. glacialis* indicates a strong influence of Atlantic water and a relatively warm climate, often with sea temperatures above zero year-round (Conover, 1988). The predominance of *C. glacialis*, on the other hand, is usually found in regions characterized by a colder arctic regime encompassing a seasonal ice cover and sub-zero water temperatures (Arnkjær et al., 2005). In regions where *C. glacialis* and *C. finmarchicus* co-exist, it has been suggested that extensive hybridization occurs (Parent et al., 2012). However, recent studies show that this is very unlikely (Choquet et al., 2017), even when adult males and females of both species are present at the same time (Choquet et al., 2021). *Calanus finmarchicus* is considered to be a boreal expatriate in the Arctic (Hirche and Kosobokova, 2007; Kosobokova, 2012; Wassmann et al., 2015). It is regularly transported in high numbers into the Arctic with the Atlantic currents, but the late onset of the phytoplankton spring bloom is assumed to limit its ability to mature and reproduce in the Arctic Ocean proper, which prevents it from establishing its own local arctic population (Hirche and Kosobokova, 2007).

Typically, the onset of the productive season is delayed with increasing latitude due to the more extreme seasonality of sunlight and more persistent ice and snow cover preventing light from reaching the water column (Sakshaug, 2004; Falk-Petersen et al., 2007; Leu et al., 2011; Leu et al., 2015). In the seasonally ice-covered waters, the productive season starts with a bloom of ice algae which are adapted to utilize low light levels early in the season (Hancke et al., 2018; Kvernvik et al., 2020). As the ice melts, stratification and increasing light availability in the water column triggers the main pelagic bloom. Warming of the Arctic and the consequential decrease in ice cover is changing the arctic bloom phenology (Carmack and Wassmann, 2006; Leu et al., 2015; Tremblay et al., 2015). This has potentially cascading effects on the distribution of

Calanus copepods, as their reproduction and life cycles are closely linked to the timing of the algal bloom and the length of the productive season (Søreide et al., 2010; Wold et al., 2011; Daase et al., 2013; Dezutter et al., 2019).

Recently, a substantial borealization of the arctic zooplankton community has been predicted with global warming (Hays et al., 2005; Polyakov et al., 2020). Higher sea water temperatures, reduction in sea ice and a prolonged algal growth season will make the environment more favorable for *C. finmarchicus* in the high Arctic (Freer et al., 2021). While there is currently no conclusive evidence that *C. finmarchicus* successfully recruit new generations locally in the high Arctic (Hirche and Kosobokova, 2007; Dvoretzky, 2011; Wassmann et al., 2015; Choquet et al., 2017), there are indications of accelerated development at the northern edge of its current distributional range in the Fram Strait (Tarling et al., 2021) and north of Svalbard (Hop et al., 2021), potentially leading to the production of a second generation in warmer years (Weydmann et al., 2018). In some Arctic regions, such as the areas and fjords surrounding the path of the North Atlantic Current into the Fram Strait and the Barents Sea, an increase in abundances of *C. finmarchicus* has recently been observed (Wassmann et al., 2006; Chust et al., 2014; Weydmann et al., 2014; Aarflot et al., 2018; Hop et al., 2019; Møller and Nielsen, 2020). The latter indicates not only increased advection but also suggests better survival and successful recruitment of *C. finmarchicus* in areas where *C. glacialis* and/or *C. hyperboreus* normally prevail. Subsequently, one may expect that *C. finmarchicus* could become the more dominant species if warming continues. A change from a dominance of larger arctic zooplankton species to smaller boreal ones may have cascading effects on the higher trophic levels, especially those species (e.g. little auks) preying on one item at the time (Kitaysky and Golubova, 2000; Hirche and Kosobokova, 2007; Falk-Petersen et al., 2007; Vihtakari et al., 2018).

For most parts of the Arctic, seasonal zooplankton studies are still rare due to logistical challenges of accessing remote areas regularly over an entire annual cycle, and previous studies describing the seasonal cycle in the *Calanus* community in Svalbard fjords largely lack data from the polar night (Arnkjær et al., 2005; Søreide et al., 2010; Lischka and Hagen, 2016). Here, we investigated the population development of two sympatric *Calanus* species, *C. glacialis* and *C. finmarchicus*, over a period of 15 consecutive months, including the polar night, to study similarities and dissimilarities in their life histories in a high-Arctic fjord (78°N) characterized by sub-Arctic water temperatures (~1-6°C) with no sea ice formation in winter. To gain a better understanding of these two species life histories, we also studied the gonad maturation in *C. glacialis* and *C. finmarchicus*. Specifically, we compared the following between the two species (1) population size and structure, (2) timing of the seasonal vertical migration and (3) timing of the reproductive events in terms of sexual maturation and egg production.

2 MATERIALS AND METHODS

2.1 Sampling Area and Sample Processing

Calanus glacialis and *C. finmarchicus* were collected once a month from June 2015 to August 2016 at Karlskronadjupet

(78°19'N; 015°10'E) (IsK, **Figure 1**), a 274 m deep basin in the central part of the Isfjorden system, Svalbard. The mouth of Isfjorden is open towards the shelf and slope area facing west Spitsbergen, with no sill limiting the inflow of Atlantic and Arctic water reaching this area *via* the West Spitsbergen Current (WSC) and the East Spitsbergen Current (ESC), respectively. Both these currents are flowing from south to north along the shelf break and on the shelf, respectively (Nilsen et al., 2008).

Sampling was conducted from either larger vessels (R/V Helmer Hanssen, K/V Svalbard, R/V Dalmie Zelentsy) or smaller boats (R/V Viking Explorer and UNIS Polaris). Data on the properties of the water column were collected using a SAIV SD204 CTD or a SBE Seabird Electronics CTD. The water mass definition by Skogseth et al. (2020) was used to identify the different water masses throughout the study period. Isfjorden is influenced by both Arctic and Atlantic water coming into the fjord, as well as local hydro-physical processes. In summer, the water column is typically stratified, with fresher surface water overlaying a layer of Atlantic-influenced water, and often a layer of colder local or winter cooled water at the bottom. In the fall and winter, vertical mixing takes place, leading to a homogenous water column gradually cooling off throughout the winter and spring (Nilsen et al., 2008; Skogseth et al., 2020). Fluorescence data from fluorometers attached to the CTDs were used to estimate the average Chlorophyll *a* (Chl *a*) concentration in the depth intervals where zooplankton was sampled (see below). Fluorescence data from the sensors were verified with Chl *a* concentrations measured fluorometrically. Water was collected for Chl *a* at standard depths (1 m, 5 m, 15 m, 50 m, bottom) and the depth of Chl *a* max. The water was filtered on Whatman grade GF/F glass fiber filters and extracted in methanol for 24 hours at 4°C before the Chl *a* concentration was measured with an AU10 Turner Fluorometer (Turner Design, Inc.).

Stratified zooplankton samples for *Calanus* community composition were collected with a MultiNet “Midi” (0.25 m² mouth opening, mesh size 200 µm, Hydro-Bios, Kiel) or a WP2 closing net (0.25 m² mouth opening, mesh size 200 µm, Hydro-Bios, Kiel) and fixed in 4% buffered formaldehyde-seawater solution. Samples were collected at the following depth intervals bottom-200-100-50-20-0 m when using the MultiNet, and bottom-100-50-20-0 m when using the WP2 closing net (**Supplementary, Table S1**). In June 2015, the deepest stratum was not collected due to technical problems. Females for egg production incubations were collected from 50-0 m using a WP2 or WP3 net (1 m² mouth opening, mesh size 1000 µm, Hydro-Bios, Kiel).

2.2 Morphological Identification of *Calanus* spp.

Due to the close morphological similarity of the *Calanus* species, they are commonly identified to species using size classes (for prosome length) derived from length frequency analyses. Recent studies using molecular tools have shown, however, a high but regionally variable overlap in prosome length between *C. finmarchicus* and *C. glacialis* (e.g., Gabrielsen et al., 2012; Choquet et al., 2018). In the present study, species of *Calanus*

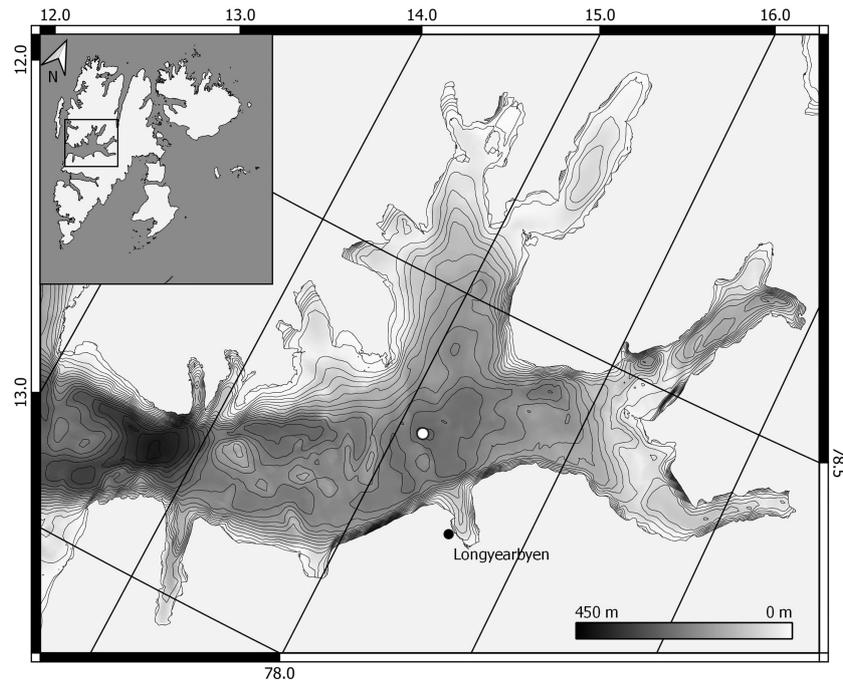


FIGURE 1 | Map of the study area. Sampling station at Karlskronadjupet Isfjorden, Svalbard marked with white marker. (Map data source: NPI, GEBCO).

were distinguished based on size classes established earlier by Daase and Eiane (2007) for the study area with adjustments for CV and adult females after Choquet et al. (2018) and Daase et al. (2018) (Table 1). For live specimens, pigmentation can also be used as an additional species indicator, with *C. glacialis* having more red pigmentation on the antennules and genital segment (females only) compared to *C. finmarchicus* (Nielsen et al., 2014; Choquet et al., 2018). The latter characteristic was additionally used to identify adult females for egg production incubations (see below).

It is difficult to distinguish nauplii to species level morphologically (e.g., Daase et al., 2011), therefore they were not included in our analysis.

2.3 *Calanus* Population Structure

Seasonal changes in the *Calanus* spp. abundance and stage structure were estimated from the formalin preserved samples. The samples were drained, rinsed and then soaked in filtered sea water to wash out the formalin. Large plankters such as

chaetognaths, amphipods and gelatinous taxa were removed from the entire sample using forceps to not interfere with the subsequent subsampling. Subsamples of 2-5 ml were taken from a known total volume of the remaining sample using a micropipette with enlarged opening and analyzed under a stereo microscope. All *Calanus* spp. copepodites in the subsample were enumerated and identified morphologically to species and development stage. Subsamples were taken until a minimum of 100 *Calanus* individuals had been counted.

Abundance was estimated from the subsamples following equation 1:

$$a_i = \frac{s_i}{V_{si}} \times \frac{V_t}{0.25 \text{ m}^2 \times d_i} \tag{1}$$

Where a_i is the number of individuals per m^3 of species a , s_i is the total number of individuals in the subsamples, V_{si} is the subsample volume, V_t is total volume of the sample, and d_i is the sampled distance in depth stratum i in meters. Because

TABLE 1 | Size ranges (prosoma length, mm) used to differentiate between copepodite stages CI-CV and adult females and males (AF/AM) of *C. finmarchicus* and *C. glacialis* based on Daase and Eiane (2007) with adjustments for CV and adults after Choquet et al. (2018) and Daase et al. (2018).

	<i>C. finmarchicus</i>	<i>C. glacialis</i>	Reference
CI	<0.81	0.81-0.9	Daase and Eiane, 2007
CII	<1.17	1.17-1.350	Daase and Eiane, 2007
CIII	1.12-1.47	1.47-2.07	Daase et al., 2018
CIV	1.6-2.01	2.01-3.63	Daase et al., 2018
CV	1.92-2.9	2.9-3.99	Daase et al., 2018
AF/AM	2.4-2.95	2.95-4.63	Daase et al., 2018

abundance in m^3 is influenced by the depth at a given station, the integrated abundance (A_i) was calculated for better comparison to other locations, following equation 2:

$$A_i = \sum_{i=1}^n (a_i \times d_i) \quad (2)$$

Where n is the number of depth strata.

Weighted mean depth (WMD) was calculated for the total population of *C. glacialis* and *C. finmarchicus* as well as copepodite stages within the species according to equation 3:

$$WMD = \frac{\sum_{i=1}^n (a_i d_i) D_i}{\sum_{i=1}^n a_i d_i} \quad (3)$$

Where D_i is average depth in depth stratum i . Further the standard deviation (SD) of WMD was calculated following equation 4:

$$SD = \sqrt{\frac{\sum_{i=1}^n ((a_i d_i) D_i) D_i}{\sum_{i=1}^n a_i d_i} - WMD^2} \quad (4)$$

Results are reported as mean \pm SD.

2.4 Gonad Maturation

The gonad maturation of *Calanus* CVs and adults (CVIs) was examined using formalin-preserved zooplankton samples. Up to thirty specimens of adult females, males and CVs were randomly picked from samples for each date of collection between September 2015 and July 2016. They were stained with 2% borax carmine solution (Tande and Hopkins, 1981), dehydrated and stored in glycerine for further gonad examination. The gonadal stages (GS) of females were assessed under a stereomicroscope (Olympus SZX-10) according to the classification scheme suggested by Kosobokova (1999). Six stages of gonad maturation (GS1 – GS6, **Table 2**) were distinguished. The gonads of CVs were also examined to discriminate between sexually undifferentiated specimens and potential females/males, according to Kosobokova (1998; 1999). In total, gonad maturation was examined in ca. 3000 specimens of *Calanus* spp. The prosome length (PL) of each examined individual was measured to nearest 0.1 mm.

2.5 Egg Production

Monthly from February to August, up to 30 adult females of *C. glacialis* and 30 *C. finmarchicus* were sorted from WP2 and/or WP3 net samples collected from the upper 50 m. Females were incubated individually in 125 ml incubation chambers equipped

with a false bottom of mesh size 300 to 500 μm that allowed eggs to sink through, separating them from the female to avoid predation (Basedow and Tande, 2006). Incubations started within four hours of sampling and lasted for 24 hours in darkness at *in situ* temperatures specified in **Table 3**. After 24 hours of the female incubation, the eggs were removed, transferred to a petri dish and counted under a stereo microscope in a cold lab (4-6°C). The eggs were cultivated in petri dishes in darkness at *in situ* temperatures for eight more days. After eight days, the number of nauplii and unhatched eggs were counted to determine the egg hatching success. Eggs which had not hatched after eight days were considered to be non-viable (Daase et al., 2011).

3 RESULTS

3.1 Environmental Conditions

3.1.1 Hydrography

At the sampling site in Isfjorden proper (Station IsK, 78°N, 015°E, **Figure 1**), positive water temperatures were measured year-round, except in June and July 2015 at depths below 160 m. From August 2015, the intermediate layers were increasingly influenced by Transformed Atlantic Water (TAW) throughout the fall as evident by the prevailing positive temperatures and relatively high salinity (**Figures 2 and S1**). A pronounced influx of Atlantic Water was observed in December 2015, detectable as a distinct layer of + 5°C and increased salinity at around 100 m depth (**Figures 2A, B**). The warm (1-3°C) TAW prevailed in the entire water column until the end of the sampling campaign in August 2016. Water temperature did, however, gradually decrease during winter and spring due to atmospheric cooling and winter convection. Highest water temperatures were measured in the upper 10-20 m in summer, with monthly maximum between 5.1 and 10.6°C in June-August 2015 and between 4.5 and 6.3°C in June-August 2016 (**Figure 2A**). This is typical for surface water in summer, together with low salinity during the same period with minimum of 29.7 to 33.91 in June-August 2015 and 31.6 to 33.9 in June-August 2016 (**Figure 2B, Figure S1**).

3.1.2 Chlorophyll *a*

In Isfjorden, the spring bloom had subsided at the start of the sampling campaign in June 2015 with Chl *a* concentration of 1.5 μg Chl *a* L^{-1} . Relatively high Chl *a* concentrations persisted

TABLE 2 | Gonad maturation stages (GS) of *Calanus* adult females.

Stage	Morphological description
GS1	Immature (young); ovary compact, no oocytes in diverticulae and oviducts
GS2	Anterior diverticulae with single row of small oocytes; single row of small oocytes in part of oviducts; ends of anterior diverticulae widely separated
GS3	Anterior diverticulae with several rows of small oocytes; more than one row of small oocytes in oviducts
GS4	Mature; anterior diverticulae close together, filled with several rows of small and large oocytes; pouches of large oocytes in oviducts
GS5	Semi-spent; few large oocytes in the ovary, diverticulae and oviducts with single irregularly spread oocytes
GS6	Spent; diverticulae and oviducts thin bands; no oocytes in the ovary, posterior of ovary extends to the third thoracic segment

GS, states of gonadal maturity.

TABLE 3 | Egg production and hatching success for *C. glacialis* (*C. gla*) and *C. finmarchicus* (*C. fin*) in Isfjorden from February to August 2016.

Date	Chl a ($\mu\text{g L}^{-1}$)	Temp. ($^{\circ}\text{C}$)	Number of AF		% egg laying AF		EP (eggs fem ⁻¹ day ⁻¹)		max clutch size (eggs)		Hatching success (%)		Population EP (eggs day ⁻¹ m ⁻²)	
			<i>C. fin</i>	<i>C. gla</i>	<i>C. fin</i>	<i>C. gla</i>	<i>C. fin</i>	<i>C. gla</i>	<i>C. fin</i>	<i>C. gla</i>	<i>C. fin</i>	<i>C. gla</i>	<i>C. fin</i>	<i>C. gla</i>
17.02.16	<0.1	3.2	30	30	0	0	–	–	–	–	–	–	0	0
21.03.16	<0.1	3.0	30	30	0	16.7	0	1.4(4.4)	–	20	–	–	0	53.6
04.04.16	0.70	3.3	31	30	12.9	23.3	0.3(1.1)	1.4(3.9)	6	18	30.0	73.2	52.8	538.0
02.05.16	0.13	3.3	29	27	37.9	24	8.3(14.6)	8.9(17.6)	50	55	79.1	93.3	411.6	370.4
09.05.16	2.55	2.0	30	30	70	53.3	21.4(28.1)	18.7(31.7)	96	128	60.3	36.1	–	–
15.05.16	11.18	2.0	30	29	70	82.7	19.8(25.9)	58.9(42.4)	89	129	67.3	87.7	1092.8	4853.2
05.06.16	0.16	3.4	34	10	52.9	70	17.8(27.4)	5.2(7.1)	90	22	89.3	74.0	8845.2	424.4
05.07.16	1.75	3.5	5	1	60	100	18.8(26.9)	38	65	38	50.0	44.7	75.2	142.0
18.08.16	1.18	2.0	16	5	50	100	7.5(13.5)	5.8(9.6)	46	23	14.6	8.7	–	–
31.08.16	<0.1	2.0	6	0	0	0	–	–	–	–	–	–	0	0

Egg production rate (eggs fem⁻¹ day⁻¹) is given as mean (SD).

throughout July and August with 2.2 and 2.4 $\mu\text{g Chl } a \text{ L}^{-1}$, respectively (Figure 2C). From October 2015 to April 2016 typically low winter Chl a concentrations of < 0.01 $\mu\text{g Chl } a \text{ L}^{-1}$ prevailed with an increase first recorded in early May to 2.1 $\mu\text{g Chl } a \text{ L}^{-1}$, and a peak between mid-May and early June when Chl a concentrations were >7.0 $\mu\text{g Chl } a \text{ L}^{-1}$. In July, values of 2.1 $\mu\text{g Chl } a \text{ L}^{-1}$ were similar to observations from the previous summer, dropping to 0.73 $\mu\text{g Chl } a \text{ L}^{-1}$ in late August (Figure 2C).

3.2 Calanus Population Dynamics

We observed large seasonal variability in *Calanus* abundances. For both species, abundance was particularly low during the winter-spring transition from March to May, followed by peaks in summer and autumn (Figure 3). The relative proportions of *C. glacialis* and *C. finmarchicus* varied throughout the study period, but with an overall dominance of *C. glacialis*, which was 0.8 to 9.0 times the abundance of *C. finmarchicus* (Figure 3). The strong increase in abundance of both species in September likely resulted from sampling bias, as strong winds and currents caused the nets to go oblique rather than vertical.

Both species performed pronounced seasonal vertical migration with comparable monthly weighted mean depth (WMD) for most months except August 2016 (Figure 3), when *C. glacialis* was found deeper in the water column than *C. finmarchicus*. From August to January, both species remained deep (WMD > 175 m) until a gradual ascent was observed from January to March (WMD ~125 m). By the onset of the spring bloom in May, both populations were concentrated in the upper 50 m (Figure 3).

From August to April, the *C. glacialis* population was dominated by CIVs (74%), followed by CVs (17%). Adult females were always present but became more abundant from December. Adult males were observed in low numbers (12 ind. m⁻²) from October and increased to 812 ind. m⁻² in December (Figure 4 and Table 4).

The overwintering population of *C. finmarchicus* was dominated by CV (65%), followed by CIV (29%). For *C. finmarchicus*, numbers of adult females and males started to

increase in February, two months later than for *C. glacialis* (Table 4). Females peaked in abundance in May. The *C. finmarchicus* population was dominated by young copepodite stages CI-CIII in May to July, and from August overwintering stages CIV (29%) and CV (68%) prevailed (Figure 5B).

The sex ratio (males:females) in the adult *Calanus* population varied strongly throughout the year. For *C. glacialis*, the maximum sex ratio of 0.12-0.65 was observed between December and February, for *C. finmarchicus* it was at maximum of 0.11-0.25 between February and May (Table 4). For the rest of the year the proportion of males was low or males were completely absent.

Ontogenetic differences in WMD of the different developmental stages were observed. In January, females and males of *C. glacialis* were primarily found in the upper 100 m (WMD = 51 ± 48 m and 107 ± 65 m, respectively) while CIVs were concentrated below 100 m (WMD = 148 ± 51 m) (Supplementary Figure S1C). The abundance of young copepodite stages CI-CIII of *C. glacialis* was highest in June and July and they were concentrated in the upper 50 m (Supplementary Figure S2). By August the population was composed mainly by the overwintering stages CIV and CV concentrated at depth (WMD = 217 ± 40 m) (Figure 4A).

3.3 Egg Production

Females of *C. glacialis* commenced egg production in March at a rate of 1.4 ± 4.4 eggs female⁻¹ day⁻¹ and reached peak egg production during the spring bloom in mid-May with individual rate of 58.9 ± 42.4 eggs female⁻¹ day⁻¹, and total egg production of the surface (50-0 m) population of 4853.6 eggs day⁻¹ m⁻² (Table 3). By June, the egg production had declined to 5.8 ± 9.6 eggs female⁻¹ day⁻¹, along with a distinct decrease of the number of females in the population (Table 3).

Calanus finmarchicus commenced egg production in early April at a rate of 0.3 ± 1.1 eggs female⁻¹ day⁻¹, with a clear increase in early May to 8.3 ± 14.6 eggs female⁻¹ day⁻¹. From May to July, the egg production rate was stable at around 20 eggs female⁻¹ day⁻¹, then decreased to 7.5 ± 13.5 eggs female⁻¹ day⁻¹ in mid-August and ceased by the end of August. Because of the high

female abundance in June, the total egg production of the *C. finmarchicus* female population peaked in June at 8845.2 eggs $\text{day}^{-1} \text{m}^{-2}$ (Table 3).

3.4 Gonad Maturation

3.4.1 Gonad Development in *Calanus* CVs

The *Calanus* CV specimens with sexually undifferentiated gonads were present in Isfjorden all year round, while CVs with sexually differentiated gonads, i.e. potential females (PF) or males (PM) (Kosobokova, 1998), occurred only during particular parts of the year (Figure 5). A bimodal distribution of the CV size frequency was observed and revealed that individuals ≥ 2.6 mm developed to PF between November and

January, while those < 2.6 mm developed to PF first in February–March when CVs > 2.6 mm had disappeared (Figure 5). Only few CVs developing into PM were observed, with the largest ones ≥ 2.9 mm appearing first (between November and January), and the smaller ones < 2.9 mm appearing later, from February to May (Figure 5).

The pattern above suggests that the small-sized CVs most likely represent *C. finmarchicus* while the largest CVs represent *C. glacialis*, but the size delimitation for PF and PM is different, 2.6 and 2.9 mm, respectively. If we apply this revised size delimitation to discriminate between *C. finmarchicus* and *C. glacialis*, one can see that *C. glacialis* CVs with sexually undifferentiated gonads were present in relatively high numbers from May to December

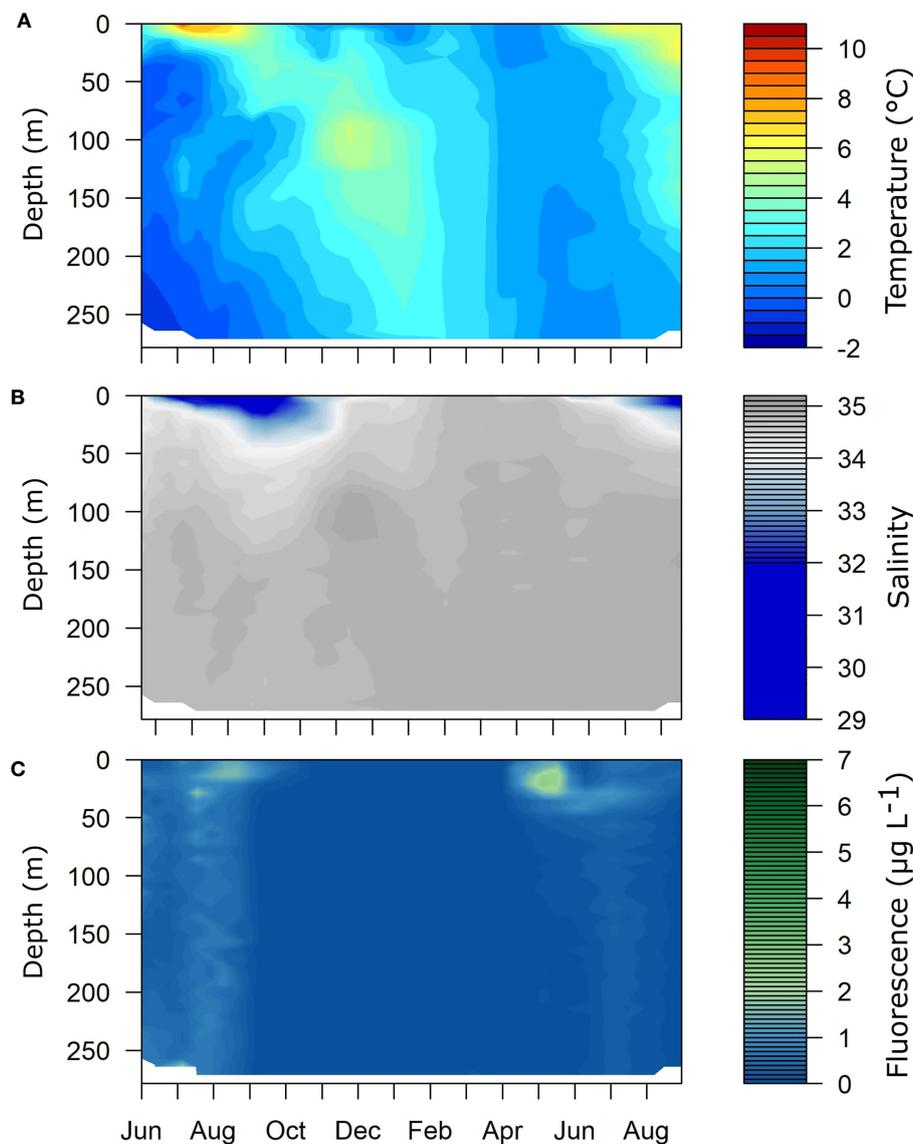


FIGURE 2 | Seasonal changes in (A) water temperature ($^{\circ}\text{C}$), (B) salinity and (C) fluorescence ($\mu\text{g L}^{-1}$) in Isfjorden, station IsK, from June 2015 to August 2016.

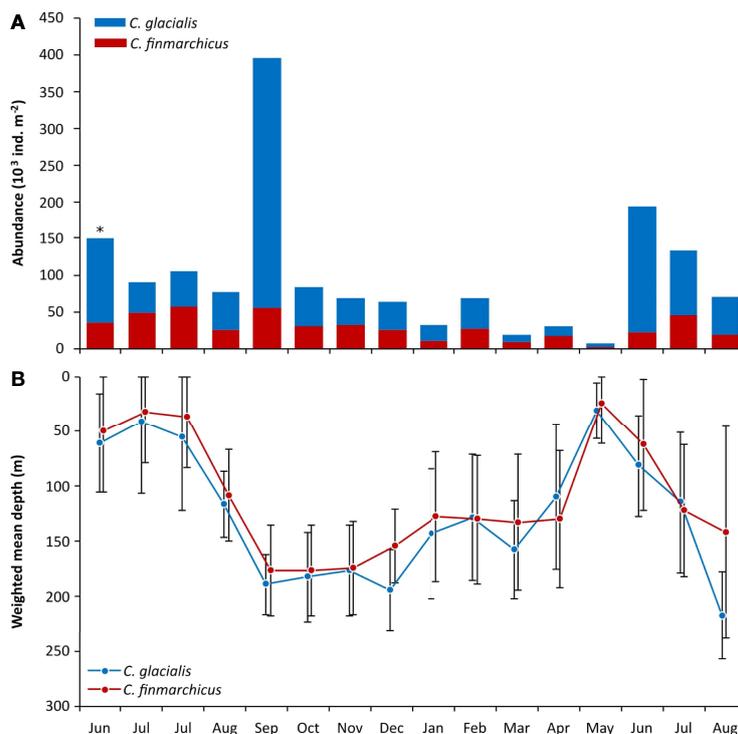


FIGURE 3 | Monthly changes in the (A) total abundance (ind. m⁻²) and (B) weighted mean depth of *C. finmarchicus* (red) and *C. glacialis* (blue) at Karlskronadjupet, Isfjorden from June 2015 to August 2016. * In June 2015 sampling below 180 meters was not possible due to technical issues.

(Figure 5), and in very low numbers from February to April. The gonad transition to PF and PM in CVs started in September. *C. glacialis* CVs with PF gonads peaked between November and February, at the same time as *C. glacialis* CVs with PM gonads (PL 2.9-3.3 mm) appeared (Figure 5).

The *C. finmarchicus* CVs with undifferentiated gonads were present in Isfjorden from August to May, but, in contrast to *C. glacialis*, they were almost absent during June and July 2015 (Figure 5). A few CVs with PF gonads were observed in September-October 2015 and reappeared in February-April 2016. PM of *C. finmarchicus* CV (PL <2.9 mm) were observed after PM of *C. glacialis* CV from February to May 2016. The overall abundance of *Calanus* CV males was, unfortunately, too low to reliably establish size range of potential CV males in any of the two species.

3.4.2 Gonad Development in *Calanus* Adults

With the new size categories applied above to differentiate between two *Calanus* species, we analyzed the gonad maturation data for adult females (AF). The female specimens with PL ≥ 2.6 mm (assumed to be *C. glacialis*) were present in Isfjorden year-round (Figure 6). From June to February, their gonads were in an immature state (GS1). The development of oocytes in the ovaries (GS2) began in February, and by April, almost all AFs were in advanced maturation state ready to

spawn (GS3). From June to August, gradual gonad degradation took place in *C. glacialis* AF indicating termination of spawning. The GS4 females were followed by completely spent GS5 females present between June and January (Figure 6).

The GS1 adult females in the size range of *C. finmarchicus* (<2.6 mm) first appeared in March, in a good agreement with dynamics of the gonad development in *C. finmarchicus* CVs (see above). In April, the gonads of approximately half of *C. finmarchicus* AFs passed to the next stage (GS2), and through May, June and July most AFs had mature gonads of GS3. This period corresponds well to the main reproductive season of *C. finmarchicus* revealed from the egg production experiments. Between August and October abundance of AFs gradually decreased, and all *C. finmarchicus* AFs had spent gonads (GS5). Only very few *C. finmarchicus* adult females were observed in the population between October and March.

Calanus adult males were present already from October (Figure 4) which was also confirmed by the observation of females with spermatophores (Figure 6). Largest adult males (PL 2.9-3.85 mm) peaked in January and February in continuation of the presence of the largest CV males (Figure 5). Later, in April and June, the smaller adult males were observed (PL 2.65-3.3 mm, presumably, *C. finmarchicus*) following the cohort of the smaller CV males.

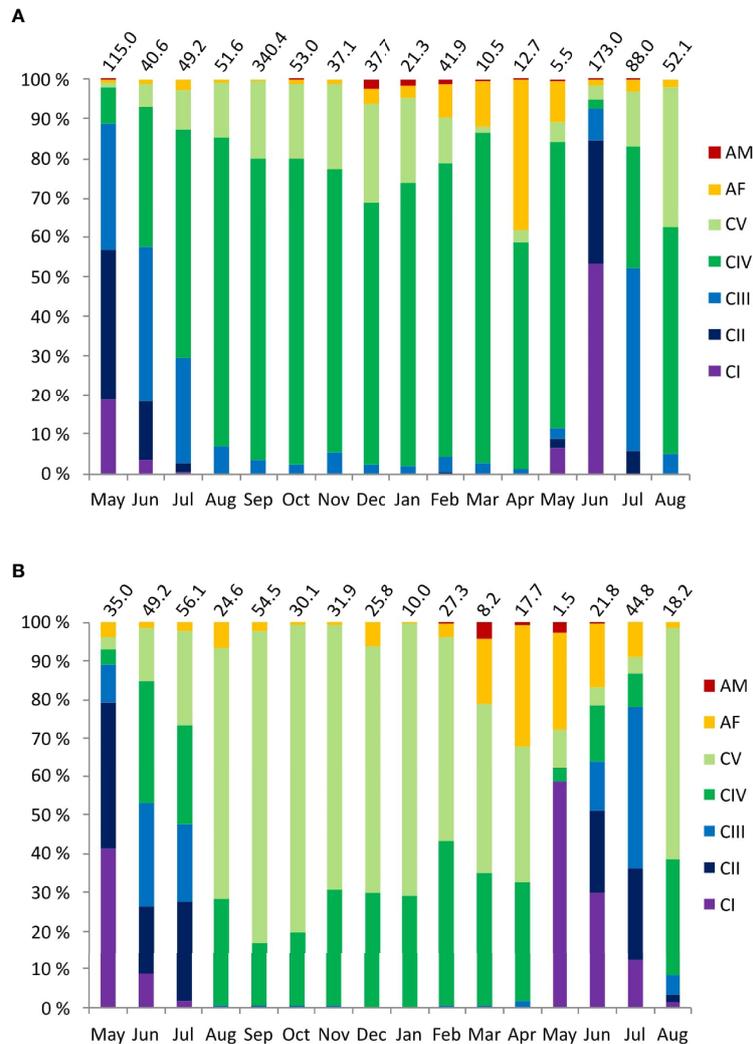


FIGURE 4 | Monthly changes in the relative copepodite stage composition of **(A)** *C. glacialis* and **(B)** *C. finmarchicus* at Karlskronadjupet, Isfjorden from June 2015 to August 2016. Total abundance (ind. m²) each month is noted on top of each bar.

4 DISCUSSION

4.1 Seasonal Migration and Overwintering

The stage composition of the overwintering *Calanus* populations, mainly CV for *C. finmarchicus* and CIV for *C. glacialis*, suggests 1 and 2-year life cycles in these species, respectively, which is in agreement with observations from other Svalbard fjords and elsewhere in the Arctic (e.g., Conover, 1988; Kosobokova, 1999; Madsen et al., 2001; Ashjian et al., 2003; Arnkværn et al., 2005; Hirche and Kosobokova, 2007; Pertsova and Kosobokova, 2010; Kosobokova, 2012; Kosobokova and Pertsova, 2018). A sharp decrease in *Calanus* abundance in late winter/early spring indicates high winter mortality, likely due to depletion of lipid reserves at the end of winter when energy storages are used up for metabolism, molting and maturation while food is not yet

available (Daase et al., 2014; Berge et al., 2020; Daase and Søreide, 2021). In *C. glacialis*, the proportion of CVs diminishes over winter, as they develop to adults, which is in accordance with the observed changes in the gonad development of CVs (Figure 5) and the increase in the proportion of AFs and AMs in the population in December and January (Figure 6). *Calanus glacialis* adult males were only present in high numbers for a short period. They appeared in low numbers in October, peaked in abundance in December to February (Table 4), but disappeared soon, presumably, after mating (Daase et al., 2018; Hatlebakk et al., 2019). In contrast, adult *C. glacialis* females were present in the population throughout the entire year (Figure 4); their overall abundance was highest between February and July. They were less abundant between July to January suggesting senescence of some spent females after termination of spawning (Kosobokova, 1999).

TABLE 4 | Seasonal variations in abundance of adult males (AM) and adult females (AF) and sex ratio (males:females) of *C. finmarchicus* and *C. glacialis* adults.

Date	<i>C. finmarchicus</i>			<i>C. glacialis</i>		
	Abundance (ind m ⁻²)		ratio	Abundance (ind m ⁻²)		ratio
	AM	AF	AM : AF	AM	AF	AM : AF
29/06/2015	0.0	1358.7	0.00	8.0	801.3	0.01
14/07/2015	8.0	724.0	0.01	0.0	492.0	0.00
24/07/2015	0.0	1244.0	0.00	0.0	1346.7	0.00
24/08/2015	0.0	1624.0	0.00	0.0	510.0	0.00
15/09/2015	0.0	1846.4	0.00	0.0	2548.3	0.00
20/10/2015	0.0	198.7	0.00	12.0	645.2	0.02
02/11/2015	0.0	212.9	0.00	4.0	147.1	0.03
01/12/2015	0.0	1628.0	0.00	812.0	1482.7	0.55
11/01/2016	0.0	55.0	0.00	433.4	665.1	0.65
17/02/2016	144.7	931.3	0.16	421.1	3529.9	0.12
21/03/2016	346.0	1400.0	0.25	48.0	1206.0	0.04
04/04/2016	121.0	5538.9	0.02	15.0	4870.3	0.00
15/05/2016	40.0	368.0	0.11	20.0	564.0	0.04
05/06/2016	61.3	3563.2	0.02	53.3	2776.0	0.02
05/07/2016	70.6	4000.3	0.02	70.6	2816.7	0.03
31/08/2016	0.0	256.0	0.00	0.0	1076.0	0.00

While the overwintering population of *C. finmarchicus* was dominated by CVs, almost 30% were comprised by CIVs. The presence of the overwintering CIVs has also been observed in the *C. finmarchicus* populations in the NE Norwegian Sea (e.g., Arashkevich et al., 2004) where CIVs were suggested to be either late-born Generation 1 (G1) of *C. finmarchicus*, or potentially Generation 2 (G2). Arashkevich et al. (2004) reported that in the Norwegian Sea the overwintering population (G0) can reproduce in March (G1), complete development and reproduce by the end of summer (G2). The offspring of G2 only manage to develop to CIV before overwintering (Arashkevich et al., 2004). While it is relatively easy to identify the G0 and G1 generations from the population structure data, it is challenging to identify a possible G2 generation (Aksnes and Blindheim, 1996). Advection in particular complicates the identification of the new generations. *Calanus finmarchicus* CIVs could potentially have been transported to Isfjorden with the influx of Transformed Atlantic Water in December 2015. If these CIVs remained in the upper 600 m in the Norwegian Sea in autumn, as observed by Basedow et al. (2018) in 2014, they were exposed to the Atlantic currents continuously moving northwards (Basedow et al., 2018). However, no significant increase in *C. finmarchicus* population numbers appeared in conjunction with the advective event in December. Recent molecular studies have highlighted the difficulties to distinguish between *C. finmarchicus* and *C. glacialis* which challenge our traditional view of how these two species are distributed geographically (Choquet et al., 2017; Choquet et al., 2018). It is therefore likely that some of the CIVs in our study were misidentified *C. glacialis* CIVs (e.g., Gabrielsen et al., 2012; Choquet et al., 2017) masking the species-specific differences in the population structure and the life cycle duration of these two species in Isfjorden.

The seasonal vertical migration patterns were remarkably similar for the two species. For the *Calanus* population as a

whole, the deepest WMD was registered from September through November. At this time of the year also the lowest metabolic enzyme activity has been observed (Freese et al., 2017; Hatlebakk et al., this issue), indicating this to be the period when diapause is reaching its deepest phase. By January, CVs and adult specimens of the overwintering stock seem to become more active, migrating further up in the water column (**Supplementary Figure S3**). Such a seasonal ascent of adult females and males in January (**Supplementary Figure S4**) was likely related to mating at this time of the year which is in accordance with earlier observation in Svalbard fjords (Freese et al., 2015; Daase et al., 2018). In early May, during the spring bloom both *Calanus* populations were concentrated in the upper 50 m where the algal food was plentiful (**Figures 3 and S2–S4**).

In August 2016, at the end of our study period, the WMD of *C. glacialis* was deeper than that of *C. finmarchicus*, indicating that the former descends earlier to the overwintering depth compared to the latter. *C. glacialis* reduces its metabolism in the absence of food (Morata and Søreide, 2015; Freese et al., 2017), and older copepodite stages CIV–CVI leave the surface layer if temperatures become too high seeking refuge in the colder, deeper waters (Niehoff and Hirche, 2005; Pertsova and Kosobokova, 2010). The earlier descent of *C. glacialis* observed during the present study is most likely also a response to reduced food availability and/or high temperature (**Figure 2**). Our temporal sampling resolution was too coarse to pinpoint the exact difference in the timing of the two species seasonal descent. In future studies, higher sampling frequency around the time of seasonal migration, particularly the descent, which seems to be more synchronized than the seasonal ascent (Kosobokova and Pertsova, 2005; Bailey, 2010), are recommended. Changes in the population structures can happen rapidly (< 1 month) during times with high biological activities and thus species-specific differences could easily have been missed in our study with monthly sampling resolution.

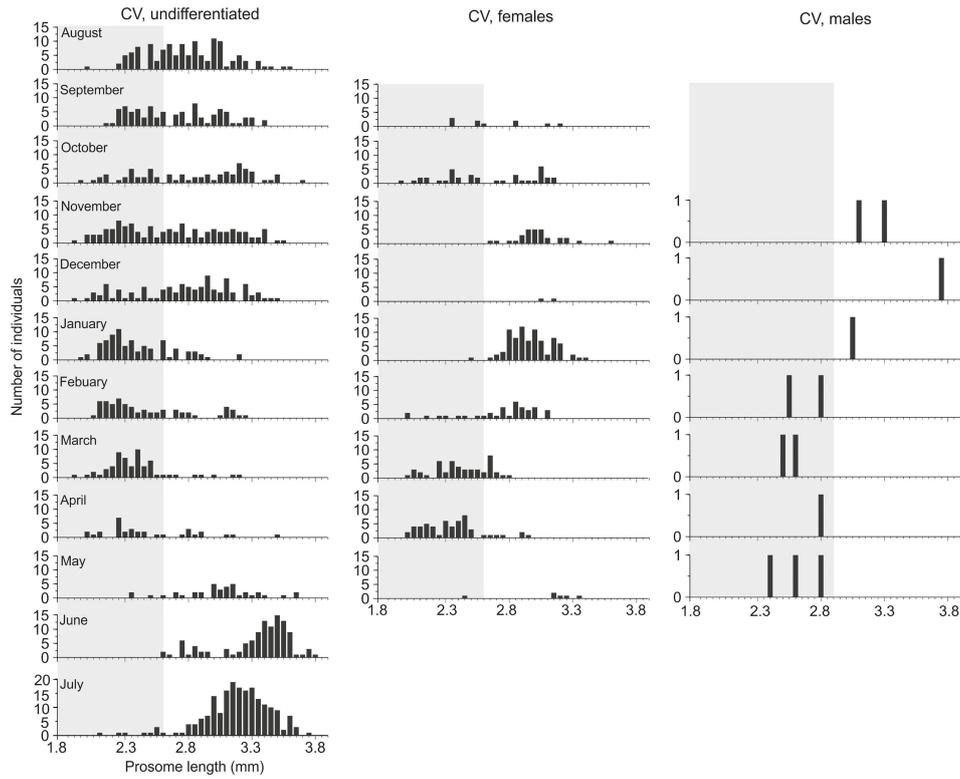


FIGURE 5 | Size structure (prososome length, mm) and maturity stages of *Calanus* copepodite stage V in Isfjorden from August 2015 to August 2016. The size range of *C. finmarchicus* CV is highlighted in gray.

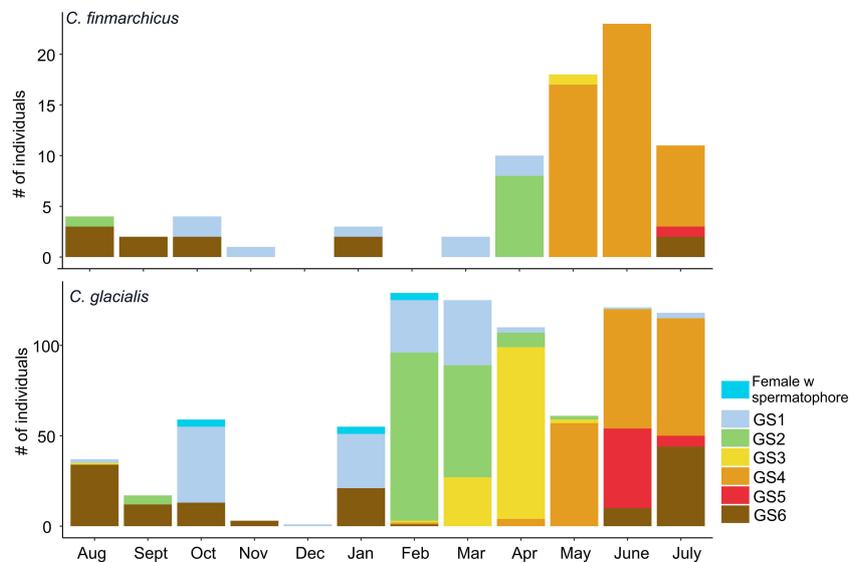


FIGURE 6 | Seasonal changes in gonad maturation of adult females of *Calanus* in Isfjorden from August 2015 to August 2016. For description of gonadal stages (GS1-GS6) see **Table 2**.

4.2 Gonad Maturation, Reproduction, and Recruitment

The simultaneous presence of late copepodites CIV-V of both *Calanus* species during winter and the presence of different generations of *C. glacialis* during summer months (Kosobokova, 1999) makes it difficult to reliably distinguish the two species and their new and overwintered generations based on seasonal changes of the population age structure alone. The experimental evidence that females of at least *C. glacialis* are long living and can lay eggs for up to 10 months when fed (Hirche, 1989; Kosobokova, 1999) further complicates our ability to determine life cycle length without additional tools. The examination of the gonad maturation state in copepods is a tool that provides better insights into copepods life history and reproductive biology as well as an assessment of the life spans in the late phases of their life cycles (Tande and Hopkins, 1981; Tande et al., 1985; Norrbin, 1991; Kosobokova, 1998; Kosobokova, 1999).

Our observations of gonad maturation patterns in *C. glacialis* and *C. finmarchicus* indicate that these two species utilize different reproductive strategies, differing in timing of: 1) sexual gonad differentiation in pre- adult stage CV, 2) molting of the overwintering CVs to adults, 3) gonad maturation in adults, and 4) mating and spawning. Sex differentiation in *C. glacialis* CVs, revealed from the gonad morphology, took place predominantly during fall and winter and terminated by the onset of the primary production period. Most *C. glacialis* CVs developed to potential females during winter, between November and February (Figure 5), as indicated by the almost complete disappearance of CVs with sexually undifferentiated gonads in January-February and simultaneous appearance of potential CV females (Figure 5). A very rare occurrence of potential CV females during later period, from March onward (Figure 5), confirmed that the majority of the overwintering *C. glacialis* CVs have molted to adult females (CVI) by that time. These observations are in a good agreement with the dynamics revealed by the seasonal variation of the stage composition of *C. glacialis* (Figure 4A).

The re-appearance of *C. glacialis* CVs with undifferentiated gonads in May and their presence throughout June and July (Figure 5) reflects the transition of the overwintering *C. glacialis* CIVs (one-year old generation) into the CVs during the primary production season. All these “young” CVs have undifferentiated gonads; they prioritize to accumulate lipids during the summer season and delay development and sexual differentiation of their gonads to the coming winter (January-February).

The seasonal pattern of gonad maturation in *C. glacialis* adult females (Figure 6) corresponds well to variation in reproductive activity of this species revealed from the egg production incubations, suggesting the onset of the reproductive season in March, with May being the month of peak production, fueled by the spring bloom. Similar seasonal variations in gonad maturity of *C. glacialis* have been observed in the White Sea (Kosobokova, 1999) and Disko Bay (Niehoff et al., 2002).

Sex differentiation in *C. finmarchicus* takes place later in the season compared to *C. glacialis*, from March onwards (Figure 5).

Relatively high proportions of *C. finmarchicus* PF CVs were found in March and April, and all CVs completed development and molted to adults between March and May. During the same months, adult females with maturing gonads of stages GS1-GS2 appeared (Figure 6). Females in egg-laying condition (GS3-GS4) within the *C. finmarchicus* size range become most numerous from May to July in a good accordance with results of the egg production incubations, and in August their gonads turn to GS6 stage indicating termination of spawning. Niehoff et al. (2002) followed the gonad maturation of both *C. finmarchicus* and *C. glacialis* females in Disko Bay, and though they used a slightly different gonad classification system, they also found an earlier presence of egg laying *C. glacialis* compared to *C. finmarchicus*. Differences in the timing of appearance of adults between *C. glacialis* and *C. finmarchicus* similar to that observed in our study have been documented previously in other cold-water regions (Kjellerup et al., 2012). The early January appearance of *C. glacialis* males and females in Isfjorden is consistent with Daase et al. (2018), and appearance of *C. finmarchicus* adults in February-March corresponds well with observations further south (Arashkevich et al., 2004; Choquet et al., 2021).

Seasonal changes in sex ratio based on the community data confirm the later appearance of *C. finmarchicus* compared to *C. glacialis*. However, size measurements of *Calanus* males are still rare (Daase et al., 2018). Confirmation of size ranges and verification of males' identification by genetic methods is urgently needed in order to prove the actual differences in the timing of appearance of males of these two species in the study area.

Previous studies have indicated the potential of *C. glacialis* and *C. finmarchicus* to interbreed and produce fertile offspring in the North Atlantic and Canadian Arctic (Parent et al., 2012). However, newer studies using nuclear InDel markers, which are regarded as more reliable tools for detecting potential hybrids (Nielsen et al., 2014; Smolina et al., 2014), show that hybridization is very unlikely (Choquet et al., 2017). One additional reason for absence of hybridization could be the difference in timing of appearance of adults as observed in this study which would provide an efficient temporal barrier for inter-breeding. However, hybridization has also not been detected in nauplii or older copepodite stages in fjords located further south (66°N) where adult males and females of *C. glacialis* and *C. finmarchicus* co-occur, suggesting that hybridization is not occurring between these two *Calanus* species (Choquet et al., 2021).

4.3 Reproductive Strategies and Timing of Reproduction

Both *C. glacialis* and *C. finmarchicus* reproduced over an extended period in Isfjorden, but with different timing in relation to the spring bloom. *Calanus glacialis* produced eggs in low numbers already in March, six weeks prior to the spring bloom, indicating a capital breeding strategy early in the season which has been observed across the Arctic and is regarded as one of the reasons why *C. glacialis* is successful in the Arctic shelf regions (Kosobokova and Hirche, 2001; Swailethorp et al., 2011;

Daase et al., 2013; Kwasniewski et al., 2013). However, peak spawning in *C. glacialis* often coincides with the phytoplankton bloom (Kosobokova and Hirche, 2001; Hirche and Kosobokova, 2003; Niehoff and Hirche, 2005; Daase et al., 2013). A six-fold increase in egg production rates from pre-bloom to peak-bloom conditions in our study indicates that while *C. glacialis* is capable of capital breeding, the switch to income breeding when food is available yields a higher reproductive output that is in a good agreement with earlier studies (Hirche and Kattner, 1993; Kosobokova and Hirche, 2001; Madsen et al., 2001; Hirche and Kosobokova, 2003; Madsen et al., 2008; Søreide et al., 2010; Swalethorp et al., 2011). In Disko Bay, Swalethorp et al. (2011) observed an increase from an average egg production of 0.6 eggs $\text{fem}^{-1} \text{day}^{-1}$ pre-bloom to 26.4 during the peak of the bloom. Another study from Disko Bay by Madsen et al. (2008) also showed an increase of egg production as the spring bloom peaked. Although Chl *a* had already started to build up in the water column at the start of their study, a doubling in egg production (to 48.3 eggs $\text{fem}^{-1} \text{day}^{-1}$) was observed from the start of the study to the peak of the bloom.

Another factor determining the overall population recruitment is the female stock abundance. *Calanus glacialis* had highest numbers of females in April suggesting that an earlier onset of the bloom will be advantageous in ice free fjords to secure early and high egg production. Ice algae was absent at the study location, but fresh algal food is available in low concentrations in ice free parts of Isfjorden/Svalbard fjords from late winter-early spring (Kubiszyn et al., 2017; Kvernvik et al., 2018).

Calanus finmarchicus does not have the same potential for capital breeding as *C. glacialis* and is considered to be a pure income breeder. It needs the algae bloom to fuel the final maturation of gonads. Subsequently, it can first start egg production when food has become available (Hirche, 1996; Niehoff and Hirche, 1996; Niehoff, 2004). In accordance with observed patterns of gonad maturation, with later molting of CVs to adult females and later gonad ripening (Figure 6), *C. finmarchicus* started egg production at the onset of the spring bloom approximately one month later than *C. glacialis*. A later onset of egg production was also observed in Disko Bay by Madsen et al. (2008), where *C. finmarchicus* increased from 20% spawning females pre-bloom in April to >90% at the peak of the spring bloom in early May, while *C. glacialis* was already at 80% spawning females in April. Egg production rates of *C. finmarchicus* peaked first in June after the peak spring bloom, thus later than in *C. glacialis*. These differences in timing of reproduction suggest a mismatch between the offspring of *C. finmarchicus* and the peak spring bloom which provides the optimal feeding conditions. However, *C. finmarchicus* was able to maintain high egg production rates for a longer period compared to *C. glacialis*, which also has been observed in Disko Bay (Swalethorp et al., 2011). In Disko Bay, an average of 46% of the *C. finmarchicus* females were spawning in the post-boom period with an egg production rate of 7 eggs $\text{fem}^{-1} \text{day}^{-1}$, which is somewhat lower than we observed in our study with 50-60% spawning females and 8-19 eggs $\text{fem}^{-1} \text{day}^{-1}$. The longer

spawning season may be explained by *C. finmarchicus* feeding more efficiently on smaller sized algae than *C. glacialis* (Hansen et al., 1994; Levinsen et al., 2000). Such a late summer reproduction increases the predation pressure on eggs and nauplii (Varpe et al., 2009), and may thus have a negative effect on the population growth of *C. finmarchicus* compared to *C. glacialis* which this study suggests with the lower population increase in *C. finmarchicus* compared to *C. glacialis* over the summer.

The differences in the timing of reproduction between the two species were also well reflected in the population composition and gonad maturation patterns. The short period of egg production in *C. glacialis* was followed by a relatively short period when CIs of a new generation were present in the fjord (mainly in June). This suggests that reproduction mainly took place during the spring bloom, leaving time for the offspring to grow and develop to the overwintering stages over summer. For *C. finmarchicus*, reproduction seems to continue throughout the entire summer, as suggested not only by the high egg production rates in June but also the continuous presence of CIs from May to August. The later presence of young stages in *C. finmarchicus* compared to *C. glacialis* was also observed in Disko Bay (Madsen et al., 2001). It is, however, unlikely that the young stages found in late summer will make it to overwintering stage and accumulate enough reserves to survive the winter, but this needs to be addressed in more details in future studies. Furthermore, it should be noted that morphological identification of *C. finmarchicus* vs. *C. glacialis* is particularly difficult for the younger stages where the sizes significantly overlap, so we cannot exclude misidentification of the species that might bias our conclusions. Molecular identification of young life stages in particular is needed to gain more insights into differences in the population development and reproductive strategies between these two *Calanus* species.

4.4 Fate of *C. finmarchicus* and *C. glacialis* in a Warming Arctic

The winter of 2015-2016 has been described as the warmest winter on record in the Arctic with the largest positive temperature anomalies observed over the region of the Barents and Kara Seas (Cullather et al., 2016; Overland and Wang, 2016). Locally in Isfjorden, the winter 2015-2016 was characterized by relatively strong inflow of Atlantic water and little sea ice formation, which is anyway restricted to side-fjords in the inner part of the Isfjorden system (Muckenhuber et al., 2016). Such conditions have been defined as a 'winter open situation' (Tverberg et al., 2019; Skogseth et al., 2020). The spring and summer following a 'winter open situation' are typically relatively warm (Tverberg et al., 2019), which was the case in 2016 in Isfjorden (Skogseth et al., 2020; this study).

Advection of the North Atlantic populations with Atlantic water is considered the main contributor to the *C. finmarchicus* population in the Arctic (Speirs et al., 2006; Hirche and Kosobokova, 2007; Kosobokova and Hirche, 2009; Wassmann et al., 2015; Choquet et al., 2017). Kwasniewski et al. (2003) argued for two populations of *C. finmarchicus* in Kongsfjorden,

Svalbard: a local population in the inner basin and an advected population in the outer basin. Our study site is comparable to the outer basin of Kongsfjorden, with no sill mitigating the influx of water masses from outside the fjord. Thus, advection likely is contributing to the *C. finmarchicus* population in Isfjorden, particularly during periods of high Atlantic inflow. Nevertheless, despite the high influx of Transformed Atlantic Water and relatively warm conditions we found a pronounced dominance of the arctic *C. glacialis* over the boreal *C. finmarchicus* during most part of our 15 months study period. Particularly in summer, the population was strongly skewed towards *C. glacialis*, which contributed up to 90% in June 2016. Throughout summer, young copepodite stages with a succession from CI to CIII dominated in the *C. glacialis* population, indicating successful reproduction and development of a new generation. The abundance of *C. glacialis* was not only higher compared to *C. finmarchicus*, but also compared to maximum abundances reported from other fjords in Svalbard of more Arctic character with a seasonal ice cover providing access to early growing ice algae (Arnkvaern et al., 2005; Leu et al., 2011; Lischka and Hagen, 2016; Hop et al., 2019). Early access to ice algae provides favorable feeding conditions for *C. glacialis* at the beginning of the spawning season, speeding up gonad maturation and support early egg production which allows early offspring to be ready to feed when the spring bloom starts (Niehoff et al., 2002; Søreide et al., 2010; Daase et al., 2013). This likely would improve the reproductive output and increase survival, and we would therefore expect higher population size in seasonally ice-covered locations (i.e. Arnkvaern et al., 2005, and Lischka and Hagen, 2016) compared to our study site. However, the abundance of both *C. glacialis* and *C. finmarchicus* observed in our study was consistently higher year-round compared to other, seasonally ice-covered, study sites (Arnkvaern et al., 2005; Leu et al., 2011; Lischka and Hagen, 2016). The high abundance, successful reproduction and dominance of *C. glacialis* in Isfjorden indicate that this species is thriving also under warmer, more Atlantic-influenced conditions and likely even benefits from these warmer conditions, presumably, due to increased growth rates and a better match between the spring bloom and presence of females. Increased growth and developmental rates at higher temperatures allow a higher portion of offspring to reach the overwintering stage and accumulate sufficient lipids for successful overwintering (Coyle and Gibson, 2017) as long as these temperatures remain within the species temperature tolerance range (Pertsova and Kosobokova, 2010).

While Carstensen et al. (2012) identified a threshold of $\sim 6^{\circ}\text{C}$ as the temperature range above which *C. glacialis* abundance and biomass decreases in the Fram Strait, observations of isolated local populations of *C. glacialis* in the Sub-Arctic White Sea indicate that different life stages of this species are adapted to survive different temperature ranges, and for some of them upper temperature limits are significantly higher than prevailing in situ temperature in the high Arctic (Kosobokova, 1999; Pertsova and Kosobokova, 2010; Kosobokova and Pertsova, 2018). Thus, its older stenothermal stages (CV – CVI) do prefer water

temperatures close to and below 0°C and stay in surface waters only as long as temperatures correspond to their preferences ($< +6^{\circ}\text{C}$). When annual surface temperatures reaches the limits of the comfortable temperature regime and passes over $+6^{\circ}\text{C}$, CV-CVI copepodites descend into deeper colder layers. In contrast, the younger copepodite stages I-III of the new generation are resistant to a wider temperature range; they develop successfully near the surface even after the temperature has passed to positive and reach up to 15°C (Pertsova and Kosobokova, 2010).

Freer et al. (2021) recently demonstrated that habitat suitability for *C. finmarchicus* has increased in areas that experienced warming and a reduction in sea ice. Furthermore, an increase in abundances of the boreal *C. finmarchicus* has recently been observed in some Arctic regions that experience distinct warming and sea ice loss (Chust et al., 2014; Weydmann et al., 2014; Aarflot et al., 2018; Hop et al., 2019; Møller and Nielsen, 2020), indicating not only increased advection but also more successful recruitment. Moreover, recent studies have shown that autumn blooms will become more common in the Arctic (Ardyna et al., 2014). At temperate latitudes, autumn blooms are triggered by wind driven mixing breaking down stratification that result in an upward supply of nutrients (Chiswell et al., 2013). Loss of sea ice and increased frequency and intensity of fall storms have led to an increase in the average number of stormy days over open waters in the Arctic during September and October (Ardyna et al., 2014). The occurrence of a second peak of algal biomass in autumn and an earlier onset of the spring bloom, in addition to the ability of *C. finmarchicus* to feed more efficiently than *C. glacialis* on small algae typically dominating the summer production (Hansen et al., 1994), may benefit *C. finmarchicus* in the Arctic. Combined with increased developmental rates, this could provide the necessary time and resources for late *C. finmarchicus* recruits to reach overwintering stage CV and accumulate enough lipids for overwintering, and thus allowing *C. finmarchicus* to fulfill its life cycle further north than today (Tarling et al., 2021).

So far, there is little evidence that an increase in habitat suitability for *C. finmarchicus* comes to the detriment of *C. glacialis*, as time series data show that an increase in *C. finmarchicus* is not accompanied by a decrease in *C. glacialis* (Hop et al., 2019; Møller and Nielsen, 2020). The high flexibility in the life history strategies of *C. glacialis* is regarded as key to explain its success across Arctic shelf seas and the Arctic Ocean (Ershova et al., 2021). The existence of relict populations in Sub-Arctic waters in more southern latitudes demonstrates that this species is adapted to a relatively wide range of environmental conditions (Kosobokova, 1999; Niehoff and Hirche, 2005; Choquet et al., 2017; Kosobokova and Pertsova, 2018). A northward extension of its distribution range into the central Arctic Ocean with retreating sea ice has recently been demonstrated (Ershova et al., 2021), suggesting that *C. glacialis* needs a certain period of open water to complete its life cycle in the ice-covered regions. Based on our study and earlier data from the White Sea, we conclude that *C. glacialis* may be more resistant to predicted climate warming than believed (Hirche and Kosobokova, 2007; Pertsova and Kosobokova, 2010; Carstensen et al., 2012). We observed here

that *C. glacialis* is able to thrive in relatively warm waters in the absence of sea ice, but there is likely an upper limit of warming that it will be able to withstand. Apparently, it is able to cope with warming in different parts of its range, as long as cold waters lying under the warmed surface waters will serve as a refuge (Pertsova and Kosobokova, 2010). However, if temperature continues to increase over the entire water column, a tipping point could be reached, and the negative effects may outweigh the positive. In particular, higher winter temperatures at depth can potentially lead to increased metabolic costs during overwintering, risking premature depletion of stored lipids (Coyle and Gibson, 2017) and increased winter mortality (Daase and Søreide, 2021).

Within the *Calanus* complex, a size shift towards smaller individuals may not necessarily be caused by a shift in species composition, but a change in growth rates of the arctic species under warmer conditions may also lead to overall smaller body sizes of these (Ejzmond et al., 2018; Renaud et al., 2018). Using a life history model, Renaud et al. (2018) suggest that a shift to smaller body size in *Calanus* populations may be accompanied by shorter life span and higher population turnover rate which actually will lead to a higher total lipid production rate by *Calanus* spp. However, a shift to smaller-sized *Calanus* spp. can impact predators who select for larger-sized prey (Martens et al., 2015), such as the little auk (*Alle alle*). This may result in change of the species composition and impact timing when the lipids in form of *Calanus* spp. are available for higher trophic levels (Hedeholm et al., 2010; Martens et al., 2015; Blanchard et al., 2017; Møller and Nielsen, 2020).

4.5 Conclusions

Arctic warming and loss of sea ice may facilitate a northward expansion and successful recruitment of new generations of *C. finmarchicus* locally in Arctic waters. However, due to the extreme seasonality in the light regime, there is a limit in the potential prolongation of the productive season, and the bloom phenology will likely remain short-pulsed and unpredictable due to high inter-annual variability in sea ice coverage. Overall, arctic *Calanus* species are still better adapted to these conditions than *C. finmarchicus* (Falk-Petersen et al., 2009; Daase et al., 2013; Ershova et al., 2021). Although the co-existence of different *Calanus* species is still not completely understood, our data indicate that even though both *C. glacialis* and *C. finmarchicus* occupy very similar niches, they don't necessarily compete for the same resources during recruitment. *Calanus glacialis* utilizes the early spring bloom, while *C. finmarchicus* can utilize the post-bloom and autumn bloom to accumulate lipids at a time when the majority of the *C. glacialis* specimens have migrated to deeper waters for overwintering. As long as sea temperatures remain within their respective temperature-tolerance ranges, both *C. glacialis* and *C. finmarchicus* seem to benefit from warming due to accelerating growth and higher survival of the recruits.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MH has contributed to sampling, sample and data analysis, compiling first draft and edited the manuscript based on feedback from co-authors. KK has contributed to sample and data analysis, provided extensive feedback in the editing process. MD has contributed to sampling, sample and data analysis, provided extensive feedback in the editing process. JS has contributed to sampling, data analysis, compiling first draft and extensive feedback in the editing process. All authors contributed to the article and approved the submitted version.

FUNDING

Funding was provided by the Norwegian Research Council (NRC) through the project COPPY (227139) and the Fram Centre Flagship Arctic Ocean (project FADE, 2019–2021). KK conducted research within the framework of the state assignment of IO RAS (theme No. FMWE–2021–0007) and was partially supported by the Russian Science Foundation (grant No. 19-17-00058). MD received additional funding through the NRC project Deep Impact (300333).

ACKNOWLEDGMENTS

We thank the captains and crew of RV *Helmer Hanssen*, RV *Dalnie Zelentsy*, RV *Viking Explorer* and UNIS logistics for making it possible to conduct the year-round sampling for this study. We are very grateful to Kasia Dmoch, Helene Eide and Runa Solvang for their contribution to analysis of sample material. This study is a contribution to the ARCTOS research network (arctos.uit.no).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.877910/full#supplementary-material>

Supplementary Figure S1 | TS-diagram of water masses recorded each month at Karlskronadjupet in Isfjorden, split into panels according to season: (a) summer 2015, (b) autumn 2015, (c) winter 2015–2016, (d) spring 2016 and (e) summer 2016. External water masses (Grey shade): AtW = Atlantic water, ArW = Arctic water; Local water masses (135° lines): SW = surface water, LW = Local water, WCW = winter cooled water; mixed water masses (45° lines) TAW = Transformed Atlantic water, IW = intermediate water. Dashed grey line indicates freezing point. Solid grey lines show isopycnals at intervals of 1. Water mass definitions based on Skogseth et al. (2020).

Supplementary Figure S2 | Seasonal changes in vertical distribution of copepodite stages and adults of *C. finmarchicus* in Isfjorden between June 2015 and August 2016. Note differences in scale of x-axis.

Supplementary Figure S3 | Weighted mean depth for (a) Adult females, (b) CV and (c) CIV of *C. finmarchicus* (red) and *C. glacialis* (blue) at Karlskronadjupet, Isfjorden from June 2015 to August 2016.

Supplementary Figure S4 | Seasonal changes in vertical distribution of copepodite stages and adults of *C. glacialis* in Isfjorden between June 2015 and August 2016. Note differences in scale of x-axis.

REFERENCES

- Aarflot, J. M., Skjoldal, H. R., Dalpadado, P., and Skern-Mauritzen, M. (2018). Contribution of *Calanus* Species to the Mesozooplankton Biomass in the Barents Sea. *ICES. Mar. Sci.* 75 (7), 2342–2354. doi: 10.1093/icesjms/fsx221
- Aksnes, D., and Blindheim, J. (1996). Circulation Patterns in the North Atlantic and Possible Impact on Population Dynamics of *Calanus Finmarchicus*. *Ophelia* 44, 7–28. doi: 10.1080/00785326.1995.10429836
- Arashkevich, E., Tande, K., Pasternak, A., and Ellertsen, B. (2004). Seasonal Moulting Patterns and the Generation Cycle of *Calanus Finmarchicus* in the NE Norwegian Sea, as Inferred From Gnathobase Structures, and the Size of Gonads and Oil Sacs. *Mar. Biol.* 146, 119–132. doi: 10.1007/s00227-004-1416-5
- Ardyna, M., Babin, M., Gosselin, M., Devred, E., Rainville, L., and Tremblay, J.É. (2014). Recent Arctic Ocean Sea Ice Loss Triggers Novel Fall Phytoplankton Blooms. *Geophys. Res. Lett.* 41 (17), 6207–6212. doi: 10.1002/2014GL061047
- Arnkvaern, G., Daase, M., and Eiane, K. (2005). Dynamics of Coexisting *Calanus Finmarchicus*, *Calanus Glacialis* and *Calanus Hyperboreus* Populations in a High-Arctic Fjord. *Pol. Biol.* 28, 528–538. doi: 10.1007/s00300-005-0715-8
- Ashjian, C. J., Campbell, R. G., Welch, H. E., Butler, M., and Van Keuren, D. (2003). Annual Cycle in Abundance, Distribution, and Size in Relation to Hydrography of Important Copepod Species in the Western Arctic Ocean. *Deep-Sea. Res. Part I-Oceanogr. Res. Pap.* 50 (10-11), 1235–1261. doi: 10.1016/S0967-0637(03)00129-8
- Bailey, A. (2010). Lipids and Diapause in *Calanus* Spp. In a High-Arctic Fjord: State-Dependent Strategies? Tracking Lipids Through the Polar Night. [Master's thesis] (Tromsø, Norway: University of Tromsø and University Centre in Svalbard).
- Basedow, S. L., Sundfjord, A., von Appen, W. J., Halvorsen, E., Kwasniewski, S., and Reigstad, M. (2018). Seasonal Variation in Transport of Zooplankton Into the Arctic Basin Through the Atlantic Gateway, Fram Strait. *Front. Mar. Sci.* 5, 194. doi: 10.3389/fmars.2018.00194
- Basedow, S. L., and Tande, K. S. (2006). Cannibalism by Female *Calanus Finmarchicus* on Naupliar Stages. *Mar. Ecol. Prog. Ser.* 327, 247–255. doi: 10.3354/meps327247
- Berge, J., Daase, M., Hobbs, L., Falk-Petersen, S., Darnis, G., and Søreide, J. E. (2020). “Zooplankton in the Polar Night,” in *Polar Night Marine Ecology*. Eds. J. Berge, G. Johnsen and J. H. Cohen (Cham: Springer), 113–159.
- Blachowiak-Samolyk, K., Søreide, J. E., Kwasniewski, S., Sundfjord, A., Hop, H., Falk-Petersen, S., et al. (2008). Hydrodynamic Control of Mesozooplankton Abundance and Biomass in Northern Svalbard Waters (79–81 N). *Deep. Sea. Res. II.* 55, 2210–2224. doi: 10.1016/j.dsr2.2008.05.018
- Blanchard, J. L., Heneghan, R. F., Everett, J. D., Trebilco, R., and Richardson, A. J. (2017). From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems. *Trends Ecol. Evol.* 32, 174–186. doi: 10.1016/j.tree.2016.12.003
- Carmack, E., and Wassmann, P. (2006). Food Webs and Physical–Biological Coupling on Pan-Arctic Shelves: Unifying Concepts and Comprehensive Perspectives. *Prog. Oceanogr.* 71, 446–477. doi: 10.1016/j.pocean.2006.10.004
- Carstensen, J., Weydmann, A., Olszewska, A., and Kwasniewski, S. (2012). Effects of Environmental Conditions on the Biomass of *Calanus* Spp. In the Nordic Seas. *J. Plankt. Res.* 34, 951–966. doi: 10.1093/plankt/fbs059
- Chiswell, S. M., Bradford-Grieve, J., Hadfield, M. G., and Kennan, S. C. (2013). Climatology of Surface Chlorophyll *a*, Autumn–Winter and Spring Blooms in the Southwest Pacific Ocean. *J. Geophys. Res.-Ocean.* 118 (2), 1003–1018. doi: 10.1002/jgrc.20088
- Choquet, M., Burckard, G., Skreslet, S., Hoarau, G., and Søreide, J. E. (2021). No Evidence for Hybridization Between *Calanus Finmarchicus* and *Calanus Glacialis* in a Subarctic Area of Sympatry. *Limnol. Oceanogr.* 66, S314–S325. doi: 10.1002/lno.11583
- Choquet, M., Hatlebakk, M., Dhanasiri, A. K. S., Kosobokova, K., Smolina, I., Søreide, J. E., et al. (2017). Genetics Redraws Pelagic Biogeography of *Calanus*. *Biol. Lett.* 13 (12), 20170588. doi: 10.1098/rsbl.2017.0588
- Choquet, M., Kosobokova, K., Kwasniewski, S., Hatlebakk, M., Dhanasiri, A. K., Melle, W., et al. (2018). Can Morphology Reliably Distinguish Between the Copepods *Calanus Finmarchicus* and *C. Glacialis*, or is DNA the Only Way? *Limnol. Oceanogr.-Meth.* 16, 237–252. doi: 10.1002/lom3.10240
- Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y., and Irigoien, X. (2014). Are *Calanus* Spp. Shifting Poleward in the North Atlantic? A Habitat Modelling Approach. *ICES. J. Mar. Sci.* 71 (2), 241–253. doi: 10.1093/icesjms/fst147
- Cleary, A. C., Søreide, J. E., Freese, D., Niehoff, B., Gabrielsen, T. M., and Fields, H. E. D. (2017). Feeding by *Calanus Glacialis* in a High Arctic Fjord: Potential Seasonal Importance of Alternative Prey. *ICES. J. Mar. Sci.* 74, 1937–1946. doi: 10.1093/icesjms/fsx106
- Conover, R. J. (1988). Comparative Life Histories in the Genera *Calanus* and *Neocalanus* in High Latitudes of the Northern Hemisphere. *Hydrobiologia* 167, 127–142. doi: 10.1007/BF00026299
- Coyle, K. O., and Gibson, G. A. (2017). *Calanus* on the Bering Sea Shelf: Probable Cause for Population Declines During Warm Years. *J. Plankt. Res.* 39 (2), 257–270. doi: 10.1093/plankt/fbx005
- Cullather, R. I., Lim, Y. K., Boisvert, L. N., Brucker, L., Lee, J. N., and Nowicki, S. M. (2016). Analysis of the Warmest Arctic Winter 2015–2016. *Geophys. Res. Lett.* 43 (20), 10–808. doi: 10.1002/2016GL071228
- Daase, M., and Eiane, K. (2007). Mesozooplankton Distribution in Northern Svalbard Waters in Relation to Hydrography. *Pol. Biol.* 30, 969–981. doi: 10.1007/s00300-007-0255-5
- Daase, M., Falk-Petersen, S., Varpe, Ø., Darnis, G., Søreide, J. E., Wold, A., et al. (2013). Timing of Reproductive Events in the Marine Copepod *Calanus Glacialis*: A Pan-Arctic Perspective. *Can. J. Fish. Aquat. Sci.* 70 (6), 871–884. doi: 10.1139/cjfas-2012-0401
- Daase, M., Kosobokova, K., Last, K. S., Cohen, J. H., Choquet, M., Hatlebakk, M., et al. (2018). New Insights Into the Biology of *Calanus* Spp. (Copepoda) Males in the Arctic. *Mar. Ecol. Prog. Ser.* 607, 53–69. doi: 10.3354/meps12788
- Daase, M., and Søreide, J. E. (2021). Seasonal Variability in non-Consumptive Mortality of Arctic Zooplankton. *J. Plankt. Res.* 43, 565–585. doi: 10.1093/plankt/fbab042
- Daase, M., Søreide, J. E., and Martynova, D. (2011). Effects of Food Quality on Naupliar Development in *Calanus Glacialis* at Subzero Temperatures. *Mar. Ecol. Prog. Ser.* 429, 111–124. doi: 10.3354/meps09075
- Daase, M., Varpe, Ø., and Falk-Petersen, S. (2014). Non-Consumptive Mortality in Copepods: Occurrence of *Calanus* Spp. Carcasses in the Arctic Ocean During Winter. *J. Plankt. Res.* 36 (1), 129–144. doi: 10.1093/plankt/fbt079
- Dahl, T. M., Falk-Petersen, S., Gabrielsen, G. W., Sargent, J. R., Hop, H., and Millar, R.-M. (2003). Lipids and Stable Isotopes in Common Eider, Black-Legged Kittiwake and Northern Fulmar: A Trophic Study From an Arctic Fjord. *Mar. Ecol. Prog. Ser.* 256, 257–269. doi: 10.3354/meps256257
- Dezutter, T., Lalande, C., Dufresne, C., Darnis, G., and Fortier, L. (2019). Mismatch Between Microalgae and Herbivorous Copepods Due to the Record Sea Ice Minimum Extent of 2012 and the Late Sea Ice Break-Up of 2013 in the Beaufort Sea. *Prog. Oceanogr.* 173, 66–77. doi: 10.1016/j.pocean.2019.02.008
- Dvoretzky, V. G. (2011). Distribution of *Calanus* Species Off Franz Josef Land (Arctic Barents Sea). *Pol. Sci.* 5, 361–373. doi: 10.1016/j.polar.2011.06.004
- Ejmond, M. J., McNamara, J. M., Søreide, J., and Varpe, Ø. (2018). Gradients of Season Length and Mortality Risk Cause Shifts in Body Size, Reserves and Reproductive Strategies of Determinate Growers. *Funct. Ecol.* 32, 2395–2406. doi: 10.1111/1365-2435.13191
- Ershova, E. A., Kosobokova, K. N., Banas, N. S., Ellingsen, I., Niehoff, B., Hildebrandt, N., et al. (2021). Sea Ice Decline Drives Biogeographical Shifts of Key *Calanus* Species in the Central Arctic Ocean. *Glob. Change Biol.* 27 (10), 2128–2143. doi: 10.1111/gcb.15562
- Falk-Petersen, S., Hopkins, C. C. E., and Sargent, J. R. (1990). “Trophic Relationships in the Pelagic, Arctic Food Web,” in *Trophic Relationships in the Marine Environment*. Eds. M. Barnes and R. N. Gibson (Aberdeen: Aberdeen University Press), 315–333.
- Falk-Petersen, S., Mayzaud, P., Kattner, G., and Sargent, J. R. (2009). Lipids and Life Strategy of Arctic *Calanus*. *Mar. Biol. Res.* 5, 18–39. doi: 10.1080/1745100802512267
- Falk-Petersen, S., Pavlov, V., Timofeev, S., and Sargent, J. R. (2007). “Climate Variability and Possible Effects on Arctic Food Chains: The Role of *Calanus*,” in *Arctic Alpine Ecosystems and People in a Changing Environment* (Heidelberg: Springer).
- Frank-Gopolos, T., Friis Møller, E., and Gissel Nielsen, T. (2017). The Role of Egg Cannibalism for the *Calanus* Succession in the Disko Bay, Western Greenland. *Limnol. Oceanogr.* 62, 865–883. doi: 10.1002/lno.10472

- Freer, J. J., Daase, M., and Tarling, G. A. (2021). Modelling the Biogeographic Boundary Shift of *Calanus Finmarchicus* Reveals Drivers of Arctic Atlantification by Subarctic Zooplankton. *Glob. Change Biol.* 28, 429–440. doi: 10.1111/gcb.15937
- Freese, D., Niehoff, B., Søreide, J. E., and Sartoris, F. J. (2015). Seasonal Patterns in Extracellular Ion Concentrations and pH of the Arctic Copepod *Calanus Glacialis*. *Limnol. Oceanogr.* 60 (6), 2121–2129. doi: 10.1002/lno.10158
- Freese, D., Søreide, J. E., Graeve, M., and Niehoff, B. (2017). A Year-Round Study on Metabolic Enzymes and Body Composition of the Arctic Copepod *Calanus glacialis*: Implications for the Timing and Intensity of Diapause. *Mar. Biol.* 164, 3. doi: 10.1007/s00227-016-3036-2
- Gabrielsen, T. M., Merkel, B., Søreide, J., Johansson-Karlsson, E., Bailey, A., Vogedes, D., et al. (2012). Potential Misidentifications of Two Climate Indicator Species of the Marine Arctic Ecosystem: *Calanus Glacialis* and *C. Finmarchicus*. *Pol. Biol.* 35, 1621–1628. doi: 10.1007/s00300-012-1202-7
- GEBCO Compilation Group. (2020). GEBCO 2020 Grid. doi: 10.5285/a29c5465-b138-234d-e053-6c86abc040b9
- Hancke, K., Lund-Hansen, L. C., Lamare, M. L., Højlund Pedersen, S., King, M. D., Andersen, P., et al. (2018). Extreme Low Light Requirement for Algae Growth Underneath Sea Ice: A Case Study From Station Nord, NE Greenland. *J. Geophys. Res.-Ocean.* 123, 985–1000. doi: 10.1002/2017JC013263
- Hansen, B., Verity, P., Falkenhaus, T., Tande, K. S., and Norrbin, F. (1994). On the Trophic Fate of *Phaeocystis Pouchetti* (Harriot). 5. Trophic Relationships Between *Phaeocystis* and Zooplankton—An Assessment of Methods and Size Dependence. *J. Plankt. Res.* 16 (5), 487–511. doi: 10.1093/plankt/16.5.487
- Hatlebakk, M., Graeve, M., Boissonnot, L., and Søreide, J. E. (2019). Lipid Storage Consumption and Feeding Ability of *Calanus Glacialis* Jaschnov 1955 Males. *J. Exp. Mar. Biol. Ecol.* 521, 151226. doi: 10.1016/j.jembe.2019.151226
- Hatlebakk, M., Niehoff, B., Choquet, M., Hop, H., Wold, A., Hoarau, G., et al. (this issue). Seasonal Enzyme Activities of Sympatric *Calanus Glacialis* and *C. Finmarchicus* in the High-Arctic. *Fron. Mar. Sci.* doi: 10.3389/fmars.2022.877904
- Hays, G. C., Richardson, A. J., and Robinson, C. (2005). Climate Change and Marine Plankton. *Trends Ecol. Evol.* 20, 337–344. doi: 10.1016/j.tree.2005.03.004
- Hedeholm, R., Grønkjær, P., Rosing-Asvid, A., and Rysgaard, S. (2010). Variation in Size and Growth of West Greenland Capelin (*Mallotus Villosus*) Along Latitudinal Gradients. *ICES. J. Mar. Sci.* 67, 1128–1137. doi: 10.1093/icesjms/fsq024
- Hirche, H. J. (1989). Egg Production of the Arctic Copepod *Calanus Glacialis*—Laboratory Experiments. *Mar. Biol.* 103, 311–318. doi: 10.1007/BF00397264
- Hirche, H. J. (1996). The Reproductive Biology of the Marine Copepod, *Calanus Finmarchicus* — A Review. *Ophelia* 44 (1–3), 111–128. doi: 10.1080/00785326.1995.10429842
- Hirche, H. J. (1997). Life Cycle of the Copepod *Calanus Hyperboreus* in the Greenland Sea. *Mar. Biol.* 128, 607–618. doi: 10.1007/s002270050127
- Hirche, H. J., and Kattner, G. (1993). Egg Production and Lipid Content of *Calanus Glacialis* in Spring: Indication of a Food-Dependent and Food-Independent Reproductive Mode. *Mar. Biol.* 117, 615–622. doi: 10.1007/BF00349773
- Hirche, H. J., and Kosobokova, K. N. (2003). Early Reproduction and Development of Dominant Calanoid Copepods in the Ice Zone of the Barents Sea – Need for a Change of Paradigms? *Mar. Biol.* 143, 769–781. doi: 10.1007/s00227-003-1122-8
- Hirche, H. J., and Kosobokova, K. (2007). Distribution of *Calanus Finmarchicus* in the Northern North Atlantic and Arctic Ocean—expatriation and Potential Colonization. *Deep-Sea. Res. II* 54, 2729–2747. doi: 10.1016/j.dsr2.2007.08.006
- Hirche, H. J., and Niehoff, B. (1996). Reproduction of the Arctic Copepod *Calanus Hyperboreus* in the Greenland Sea-Field and Laboratory Observations. *Pol. Biol.* 16, 209–219. doi: 10.1007/BF02329209
- Hop, H., Wold, A., Meyer, A., Bailey, A., Hatlebakk, M., Kwasniewski, S., et al. (2021). Winter-Spring Development of the Zooplankton Community Below Sea Ice in the Arctic Ocean. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.609480
- Hop, H., Wold, A., Vihtakari, M., Daase, M., Kwasniewski, S., Gluchowska, M., et al. (2019). “Zooplankton in Kongsfjorden, (1996–2016) in Relation to Climate Change,” in *The Ecosystem of Kongsfjorden*. Eds. H. Hop and C. Weincke (Svalbard: Springer), P.229–P.300.
- Jaschnov, W. (1970). Distribution of *Calanus* Species in the Seas of the Northern Hemisphere. *International. Rev. Der. Gesamten. Hydrobiol. Und. Hydrograph.* 55, 197–212. doi: 10.1002/iroh.19700550203
- Jónasdóttir, S. H. (1999). Lipid Content of *Calanus Finmarchicus* During Overwintering in the Faroe–Shetland Channel. *Fish. Oceanogr.* 8, 61–72. doi: 10.1046/j.1365-2419.1999.00003.x
- Kitaysky, A. S., and Golubova, E. G. (2000). Climate Change Causes Contrasting Trends in Reproductive Performance of Planktivorous and Piscivorous Alcids. *J. Anim. Ecol.* 69 (2), 248–262. doi: 10.1046/j.1365-2656.2000.00392.x
- Kjellerup, S., Dunweber, M., Swailethorp, R., Nielsen, T. G., Møller, E. F., Markager, S., et al. (2012). Effects of a Future Warmer Ocean on the Coexisting Copepods *Calanus Finmarchicus* and *C. Glacialis* in Disko Bay, Western Greenland. *Mar. Ecol. Prog. Ser.* 447, 87–108. doi: 10.3354/meps09551
- Kosobokova, K. N. (1998). New Data on the Life Cycle of *Calanus Glacialis* in the White Sea (Based on Seasonal Observations of its Genital System Development). *Oceanology* 38 (3), 347–355.
- Kosobokova, K. N. (1999). The Reproductive Cycle and Life History of the Arctic Copepod *Calanus Glacialis* in the White Sea. *Pol. Biol.* 22, 254–263. doi: 10.1007/s0030000050418
- Kosobokova, K. N. (2012). “Zooplankton of the Arctic Ocean,” in *Community Structure, Ecology, Spatial Distribution* (Moscow, Russia: GEOS), 272.
- Kosobokova, K. N., Hanssen, N., Hirche, H. J., and Knickmeier, K. (1998). Composition and Distribution of Zooplankton in the Laptev Sea and Adjacent Nansen Basin in the Summer 1993. *Pol. Biol.* 19, 63–76. doi: 10.1007/s0030000050216
- Kosobokova, K. N., and Hirche, H. J. (2001). Reproduction of *Calanus Glacialis* in the Laptev Sea, Arctic Ocean. *Pol. Biol.* 24, 33–43. doi: 10.1007/s0030000000171
- Kosobokova, K. N., and Hirche, H. J. (2009). Biomass of Zooplankton in the Eastern Arctic Ocean – a Base Line Study. *Prog. Oceanogr.* 82, 265–280. doi: 10.1016/j.pocean.2009.07.006
- Kosobokova, K. N., Hopcroft, R. R., and Hirche, H. J. (2011). Patterns of Zooplankton Diversity Through the Depths of the Arctic’s Central Basins. *Mar. Biodiver.* 41, 29–50. doi: 10.1007/s12526-010-0057-9
- Kosobokova, K. N., and Pertsova, N. M. (2005). Zooplankton of the Deep Basin of the White Sea at the End of Hydrological Winter. *Oceanology* 45 (6), 866–878.
- Kosobokova, K. N., and Pertsova, N. M. (2018). “Zooplankton of the White Sea: Communities’ Structure, Seasonal Dynamics, Spatial Distribution, and Ecology,” in *Biogeochemistry of Atmosphere, Ice and Water of the White Sea: The White Sea Environment. Part I, Hdb Env. Chem.* Eds. A. P. Lisitzin and V. Gordeev (Cham, Switzerland: Springer), 223–266. doi: 10.1007/978-2018-347
- Kubiszyn, A. M., Wiktor, J. M., Wiktor, J. M., Jr., Griffiths, C., Kristiansen, S., and Gabrielsen, T. M. (2017). The Annual Planktonic Protist Community Structure in an Ice-Free High Arctic Fjord (Adventfjorden, West Spitsbergen). *J. Mar. Syst.* 169, 61–72. doi: 10.1016/j.jmarsys.2017.01.013
- Kvernvik, A. C., Hoppe, C. J. M., Lawrenz, E., Prášil, O., Greenacre, M., Wiktor, J. M., et al. (2018). Fast Reactivation of Photosynthesis in Arctic Phytoplankton During the Polar Night. *J. Phycol.* 54, 461–470. doi: 10.1111/jpy.12750
- Kvernvik, A. C., Rokitta, S. D., Leu, E., Harms, L., Gabrielsen, T. M., Rost, B., et al. (2020). Higher Sensitivity Towards Light Stress and Ocean Acidification in an Arctic Sea-Ice-Associated Diatom Compared to a Pelagic Diatom. *New Phytol.* 226 (6), 1708–1724. doi: 10.1111/nph.16501
- Kwasniewski, S., Hop, H., Falk-Petersen, S., and Pedersen, G. (2003). Distribution of *Calanus* Species in Kongsfjorden, a Glacial Fjord in Svalbard. *J. Plankt. Res.* 25, 1–20. doi: 10.1093/plankt/25.1.1
- Kwasniewski, S., Walkusz, W., Cottier, F. R., and Leu, E. (2013). Mesozooplankton Dynamics in Relation to Food Availability During Spring and Early Summer in a High Latitude Glaciated Fjord (Kongsfjorden), With Focus on *Calanus*. *J. Mar. Syst.* 111–112, 83–96. doi: 10.1016/j.jmarsys.2012.09.012
- Lee, R. F., Hagen, W., and Kattner, G. (2006). Lipid Storage in Marine Zooplankton. *Mar. Ecol. Prog. Ser.* 307, 273–306. doi: 10.3354/meps307273
- Leu, E., Mundy, C., Assmy, P., Campbell, K., Gabrielsen, T., Gosselein, M., et al. (2015). Arctic Spring Awakening—Steering Principles Behind the Phenology of Vernal Ice Algal Blooms. *Prog. Oceanogr.* 139, 151–170. doi: 10.1016/j.pocean.2015.07.012
- Leu, E., Søreide, J., Hessen, D., Falk-Petersen, S., and Berge, J. (2011). Consequences of Changing Sea-Ice Cover for Primary and Secondary Producers in the European Arctic Shelf Seas: Timing, Quantity, and Quality. *Prog. Oceanogr.* 90, 18–32. doi: 10.1016/j.pocean.2011.02.004
- Leu, E., Søreide, J., Hessen, D., Falk-Petersen, S., and Berge, J. (2011). Consequences of Changing Sea-Ice Cover for Primary and Secondary

- Producers in the European Arctic Shelf Seas: Timing, Quantity, and Quality. *Prog. Oceanogr.* 90, 18–32. doi: 10.1016/j.pocean.2011.02.004
- Levinsen, H., Turner, J. T., Nielsen, T. G., and Hansen, B. W. (2000). On the Trophic Coupling Between Protists and Copepods in Arctic Marine Ecosystems. *Mar. Ecol. Prog. Ser.* 204, 65–77. doi: 10.3354/meps204065
- Lischka, S., and Hagen, W. (2016). Seasonal Dynamics of Mesozooplankton in the Arctic Kongsfjord (Svalbard) During Year-Round Observations From August 1998 to July 1999. *Pol. Biol.* 39, 1859–78. doi: 10.1007/s00300-016-2005-z
- Møller, E. F., and Nielsen, T. G. (2020). Borealization of Arctic Zooplankton—Smaller and Less Fat Zooplankton Species in Disko Bay, Western Greenland. *Limnol. Oceanogr.* 65, 1175–1188. doi: 10.1002/lno.11380
- Madsen, S. D., Nielsen, T. G., and Hansen, B. W. (2001). Annual Population Development and Production by *Calanus Finmarchicus*, *C. Glacialis* and *C. Hyperboreus* in Disko Bay, Western Greenland. *Mar. Biol.* 139, 75–93. doi: 10.1007/s002270100552
- Madsen, S. J., Nielsen, T. G., Tervo, O. M., and Söderkvist, J. (2008). Importance of Feeding for Egg Production in *Calanus Finmarchicus* and *C. Glacialis* During the Arctic Spring. *Mar. Ecol. Prog. Ser.* 353, 177–190. doi: 10.3354/meps07129
- Martens, E. A., Wadhwa, N., Jacobsen, N. S., Lindemann, C., Andersen, K. H., and Visser, A. (2015). Size Structures Sensory Hierarchy in Ocean Life. *P. R. Soc B-Biol. Sci.* 282 (1815), 20151346. doi: 10.1098/rspb.2015.1346
- Morata, N., and Søreide, J. E. (2015). Effect of Light and Food on the Metabolism of the Arctic Copepod *Calanus Glacialis*. *Pol. Biol.* 38, 67–73. doi: 10.1007/s00300-013-1417-2
- Muckenhuber, S., Nilsen, F., Korosov, A., and Sandven, S. (2016). Sea Ice Cover in Isfjorden and Hornsund, Svalbard, (2000–2014) From Remote Sensing Data. *Cryosphere.* 10, 149–158. doi: 10.5194/tc-10-149-2016
- Niehoff, B. (2004). The Effect of Food Limitation on Gonad Development and Egg Production of the Planktonic Copepod *Calanus Finmarchicus*. *J. Exp. Mar. Biol. Ecol.* 307, 237–259. doi: 10.1016/j.jembe.2004.02.006
- Niehoff, B., and Hirche, H. J. (1996). Oogenesis and Gonad Maturation in the Copepod *Calanus Finmarchicus* and the Prediction of Egg Production From Preserved Samples. *Pol. Biol.* 16 (8), 601–612. doi: 10.1007/BF02329058
- Niehoff, B., and Hirche, H. J. (2005). Reproduction of *Calanus Glacialis* in the Lurefjord (Western Norway): Indication for Temperature-Induced Female Dormancy. *Mar. Ecol. Prog. Ser.* 285, 107–115. doi: 10.3354/meps285107
- Niehoff, B., Madsen, S. D., Hansen, B., and Nielsen, T. (2002). Reproductive Cycles of Three Dominant *Calanus* Species in Disko Bay, West Greenland. *Mar. Biol.* 140, 567–576. doi: 10.1007/s00227-001-0731-3
- Nielsen, T. G., Kjellerup, S., Smolina, I., Hoarau, G., and Lindeque, P. (2014). Live Discrimination of *Calanus Glacialis* and *C. Finmarchicus* Females: Can We Trust Phenological Differences? *Mar. Biol.* 161, 1299–1306. doi: 10.1007/s00227-014-2419-5
- Nilsen, F., Cottier, F., Skogseth, R., and Mattsson, S. (2008). Fjord–shelf Exchanges Controlled by Ice and Brine Production: The Interannual Variation of Atlantic Water in Isfjorden, Svalbard. *Cont. Shelf. Res.* 28, 1838–1853. doi: 10.1016/j.csr.2008.04.015
- Norrbín, M. F. (1991). Gonad Maturation as an Indication of Seasonal Cycles for Several Species of Small Copepods in the Barents Sea. *Pol. Res.* 10, 421–432. doi: 10.1111/j.1751-8369.1991.tb00663.x
- NPI. (2015). Map data © Norwegian Polar Institute, version: January 2015.
- Overland, J. E., and Wang, M. (2016). Recent Extreme Arctic Temperatures are Due to a Split Polar Vortex. *J. Climate* 29 (15), 5609–5616. doi: 10.1175/JCLI-D-16-0320.1
- Parent, G. J., Plourde, S., and Turgeon, J. (2012). Natural Hybridization between *Calanus finmarchicus* and *C. glacialis* (Copepoda) in the Arctic and Northwest Atlantic. *Limnol. Oceanogr.* 57, 1057–1066. doi: 10.4319/lno.2012.57.4.1057
- Pertsova, N. M., and Kosobokova, K. N. (2010). Interannual and Seasonal Variation of the Population Structure, Abundance, and Biomass of the Arctic Copepod *Calanus Glacialis* in the White Sea. *Oceanology* 50, 531–541. doi: 10.1134/S0001437010040090
- Plourde, S., and Runge, J. A. (1993). Reproduction of the Planktonic Copepod *Calanus Finmarchicus* in the Lower St. Lawrence Estuary: Relation to the Cycle of Phytoplankton Production and Evidence for a *Calanus* Pump. *Mar. Ecol. Prog. Ser.* 102, 217–227. doi: 10.3354/meps102217
- Polyakov, I. V., Alkire, M. B., Bluhm, B. A., Brown, K. A., Carmack, E. C., Chierici, M., et al. (2020). Borealization of the Arctic Ocean in Response to Anomalous Advection From Sub-Arctic Seas. *Front. Mar. Sci.* 7, 491. doi: 10.3389/fmars.2020.00491
- Renaud, P. E., Daase, M., Banas, N. S., Gabrielsen, T. M., Søreide, J. E., Varpe, Ø., et al. (2018). Pelagic Food-Webs in a Changing Arctic: A Trait-Based Perspective Suggests a Mode of Resilience. *ICES. J. Mar. Sci.* 75, 1871–1881. doi: 10.1093/icesjms/fsy063
- Søreide, J. E., Leu, E. V., Berge, J., Graeve, M., and Falk-Petersen, S. (2010). Timing of Blooms, Algal Food Quality and *Calanus Glacialis* Reproduction and Growth in a Changing Arctic. *Glob. Change Biol.* 16 (11), 3154–3163. doi: 10.1111/j.1365-2486.2010.02175.x
- Sakshaug, E. (2004). “Primary and Secondary Production in the Arctic Seas,” in *The Organic Carbon Cycle in the Arctic Ocean*. Eds. R. Stein and R. W. Macdonald (Berlin, Heidelberg: Springer), 57–81.
- Sargent, J., and Falk-Petersen, S. (1988). “The Lipid Biochemistry of Calanoid Copepods,” in *Biology of Copepods* (Dordrecht, Netherlands: Springer).
- Skogseth, R., Olivier, L. L. A., Nilsen, F., Falck, E., Fraser, N., Tverberg, V., et al. (2020). Variability and Decadal Trends in the Isfjorden (Svalbard) Ocean Climate and Circulation - a Thermometer for Climate Change in the Arctic Ocean. *Prog. Oceanogr.* 187, 102394. doi: 10.1016/j.pocean.2020.102394
- Smolina, I., Kollias, S., Poortvliet, M., Nielsen, T., Lindeque, P., Castellani, C., et al. (2014). Genome-and Transcriptome-assisted Development of Nuclear Insertion/deletion Markers for *Calanus* species (Copepoda: Calanoida) Identification. *Molec. Ecol. Res.* 14, 1072–1079. doi: 10.1111/1755-0998.12241
- Speirs, D. C., Gurney, W. S., Heath, M. R., Horbelt, W., Wood, S. N., and De Cuevas, B. A. (2006). Ocean-Scale Modelling of the Distribution, Abundance, and Seasonal Dynamics of the Copepod *Calanus Finmarchicus*. *Mar. Ecol. Prog. Ser.* 313, 173–192. doi: 10.3354/meps313173
- Swalathorp, R., Kjellerup, S., Dünweber, M., Nielsen, T. G., Møller, E. F., Rysgaard, S., et al. (2011). Grazing, Egg Production, and Biochemical Evidence of Differences in the Life Strategies of *Calanus Finmarchicus*, *C. Glacialis* and *C. Hyperboreus* in Disko Bay, Western Greenland. *Mar. Ecol. Prog. Ser.* 429, 125–144. doi: 10.3354/meps09065
- Tande, K. S., Hassel, A., and Slagstad, D. (1985). “Gonad Maturation and Possible Life Cycle Strategies in *Calanus Finmarchicus* and *Calanus Glacialis* in the Northwestern Part of the Barents Sea,” in *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*. Eds. J. S. Gray and M. E. Christiansen (New York: Chichester: Wiley and Sons), P. 141–P. 155.
- Tande, K. S., and Hopkins, C. C. E. (1981). Ecological Investigations of the Zooplankton Community of Balsfjorden, Northern Norway: Genital System in *Calanus Finmarchicus* and the Role of Gonad Development in the Overwintering Strategy. *Mar. Biol.* 63, 159–164. doi: 10.1007/BF00406824
- Tarling, G. A., Freer, J. J., Banas, N. S., Belcher, A., Blackwell, M., Castellani, C., et al. (2021). Can a Key Boreal *Calanus* Copepod Species Now Complete its Life-Cycle in the Arctic? Evidence and Implications for Arctic Food-Webs. *Ambio*, 51, 333–344. doi: 10.1007/s13280-021-01667-y
- Tremblay, J.É., Anderson, L. G., Matrai, P., Couple, P., Bélanger, S., Michel, C., et al. (2015). Global and Regional Drivers of Nutrient Supply, Primary Production and CO₂ Drawdown in the Changing Arctic Ocean. *Prog. Oceanogr.* 139, 171–196. doi: 10.1016/j.pocean.2015.08.009
- Tverberg, V., Skogseth, R., Cottier, F., Sundsfjord, A., Walczowski, W., Inall, M. E., et al. (2019). “The Kongsfjorden Transect: Seasonal and Inter-Annual Variability in Hydrography,” in *The Ecosystem of Kongsfjorden*. Eds. H. Hop and C. Weincke (Svalbard: Springer), P. 49–P.104.
- Varpe, Ø., Jørgensen, C., Tarling, G. A., and Fiksen, Ø. (2009). The Adaptive Value of Energy Storage and Capital Breeding in Seasonal Environments. *Oikos* 118, 363–370. doi: 10.1111/j.1600-0706.2008.17036.x
- Vihtakari, M., Welcker, J., Moe, B., Chastel, O., Tartu, S., Hop, H., et al. (2018). Black-Legged Kittiwakes as Messengers of Atlantification in the Arctic. *Sci. Rep.* 8 (1), 1–11. doi: 10.1038/s41598-017-19118-8
- Wassmann, P., Kosobokova, K. N., Slagstad, D., Drinkwater, K. F., Hopcroft, R. R., Moore, S. E., et al. (2015). The Contiguous Domains of Arctic Ocean Advection: Trails of Life and Death. *Prog. Oceanogr.* 139, 42–65. doi: 10.1016/j.pocean.2015.06.011
- Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., et al. (2006). Food Webs and Carbon Flux in the Barents Sea. *Prog. Oceanogr.* 71, 232–287. doi: 10.1016/j.pocean.2006.10.003
- Weydmann, A., Carstensen, J., Goszczko, I., Dmoch, K., Olszewska, A., and Kwasiński, S. (2014). Shift Towards the Dominance of Boreal Species in the Arctic: Inter-Annual and Spatial Zooplankton Variability in the West Spitsbergen Current. *Mar. Ecol. Prog. Ser.* 501, 41–52. doi: 10.3354/meps10694

- Weydmann, A., Walczowski, W., Carstensen, J., and Kwaśniewski, S. (2018). Warming of Subarctic Waters Accelerates Development of a Key Marine Zooplankton *Calanus Finmarchicus*. *Glob. Change Biol.* 24 (1), 172–183. doi: 10.1111/gcb.13864
- Wold, A., Darnis, G., Søreide, J. E., Leu, E., Philippe, B., Fortier, L., et al. (2011). Life Strategy and Diet of *Calanus Glacialis* During the Winter–Spring Transition in Amundsen Gulf, South-Eastern Beaufort Sea. *Pol. Biol.* 34, 1929–1946. doi: 10.1007/s00300-011-1062-6

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s Note: All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Copyright © 2022 Hatlebakk, Kosobokova, Daase and Søreide. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.