

# Surface aggregations of *Calanus finmarchicus* during the polar night

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While marine ecosystems in polar areas were thought to be mostly inactive during the polar night, recent observations in the Arctic highlight that dynamic biological interactions occur across all trophic levels. One particularly interesting observation made repeatedly is the occurrence of *Calanus finmarchicus*, a key species at the base of the food web, in the upper part of the water column in early January. This contrasts with the confirmed life cycle of this copepod, which predicts descent to overwintering depths in autumn and ascent at the end of the winter. Here, we compiled 6 years of data from the polar night to explore this unusual behaviour and to investigate the underlying mechanisms that may cause these surface aggregations. Highest abundance of *C. finmarchicus* in surface waters was closely related to Polar Surface Water in the vicinity of the sea ice edge. A total of six hypotheses are assessed to explain this distribution pattern, which includes passive transport and active behaviour as a way to improve survival chances or food access. In the context of climate change and sea ice decrease, the presence of lipid-rich copepods in cold surface waters could be a key parameter in driving the spatial distributions of top predators in the Arctic.

**Keywords:** Arctic Ocean, ice edge, overwintering, vertical distribution, vertical migration.

## Introduction

Copepods of the genus *Calanus* are lipid-rich organisms that accumulate large energy stores in form of wax esters during the productive season. These lipids sustain the organisms during the low productive season, and fuel maturation and reproduction at the end of the overwintering period (Falk-Petersen *et al.*, 2009). Due to their high energy content, *Calanus* spp. are an important, high quality food source for planktivorous predators, and are a key resource in polar and subpolar regions (Pershing and Stamieszkin, 2020). The life history strategies of *Calanus* species in the North Atlantic and Arctic have been described extensively (e.g. Conover, 1988; Bonnet *et al.*, 2005; Daase *et al.*, 2013; Melle *et al.*, 2014). There are species-specific differences in for example generation time, energy requirements for reproduction and growth, and timing of reproductive events, reflecting adaptations to environmental conditions in their main area of distribution (Falk-Petersen *et al.*, 2009). However, the general life cycle is similar for all *Calanus* species and includes an ontogenetic vertical migration at the end of the summer, when the copepods migrate to greater depth where they spend the winter in a state of diapause. This migration to deeper and colder waters is regarded as an adaptation to avoid predation in surface layers, to reduce metabolic costs, and it may help to retain the population in an area by limiting the exposure to advective processes in upper water layers (Hirche, 1996; Brierley, 2014; Chen *et al.*, 2021). The ascent towards surface waters usually takes place in late winter with variations in the timing depending on environmental

conditions (primary productivity and sea temperature; Melle *et al.*, 2014).

*Calanus finmarchicus* is an Atlantic species with its core habitat in the basins of the North Atlantic. The copepod is transported in large numbers northward from the Norwegian Sea into the Arctic basin *via* the Fram Strait (Basedow *et al.*, 2018; Wassmann *et al.*, 2019) and is commonly observed west and north of Svalbard, an area heavily influenced by the inflow of relatively warm Atlantic Water (AW). During the polar night and throughout winter, when primary production is low and other food sources are scarce, the supply of lipid-rich organisms might be crucial for the survival of permanent resident planktivorous species of seabirds, fish, and marine mammals. But by residing at overwintering depths, a large part of the *Calanus* population is inaccessible for most of these predators. However, recent observations have revealed the unexpected presence of *C. finmarchicus* in the surface layer off north Svalbard coast in early January (Daase *et al.*, 2014; Berge *et al.*, 2015a, 2020, Daase and Søreide 2021). An individual based life-history model also indicates that an early ascent from overwintering depth does not necessarily reduce fitness (Hobbs *et al.*, 2020). Concurrently, high levels of activity have been observed at different trophic levels during the polar night, previously thought to be a period of rest for the marine ecosystem (Berge *et al.*, 2015b). Furthermore, population strategies that are emerging from recent individual-based models (Maps *et al.* 2012, Bandara *et al.* 2021) indicate a flexible overwintering strategy with copepods descending to over-

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wintering and ascending almost continuously over the year (bet-hedging strategy).

The increasing observations and model-based support, indicate that lower trophic level dynamics in the Arctic during winter are not yet well-understood. With changes in sea ice extent and concomitant bloom phenology, species are able to extend their spatial distribution range into areas previously not suitable (Strand *et al.*, 2017; Ershova *et al.*, 2021, Freer *et al.*, 2022). However, the lack of a full comprehension of life history strategies and adaptation in key species hampers our understanding of how the poleward flux of boreal species will affect food webs and ecosystem functioning (Haug *et al.*, 2017; Kaartvedt and Titelman, 2018).

The presence of *C. finmarchicus* in surface waters during winter needs to be described and explained more systematically, to be able to assess the evolution of this newly documented behaviour and its impact on higher trophic levels. In this study, we gathered published and unpublished data collected west and north of the Svalbard Archipelago during the polar night. We aim to determine whether the presence of *C. finmarchicus* close to the surface during the polar night is a reoccurring feature or only an occasional phenomenon, and to assess potential mechanisms that might explain this unexpected distribution pattern.

## Methods

Data on mesozooplankton composition and abundance were collected in concert with data on the physical environment in the study area between ca. 80°N, 12°E and 82°N, 20°E, with the addition of one transect located upstream along the west coast of Svalbard (Figure 1, map produced with the Matlab package M\_Map (Pawlowicz, 2020)). Samples were collected during five cruises with R/V *Helmer Hanssen* in January 2012, 2014, 2015, 2016, and 2017 as part of different projects dealing with the ecological impacts of the AW inflow into the Arctic Ocean and polar night ecology (Table 1). We present here both published (4: A1–3, E1; Daase *et al.*, 2014; Baseow *et al.*, 2018, Daase and Søreide 2021) and unpublished (10) datasets for a total of 14 stations.

## Zooplankton sampling and data analysis

The mesozooplankton community was sampled by depth stratified vertical hauls with a multiple opening/closing net (Multinet, Hydrobios, Kiel, mouth opening 0.25 m<sup>2</sup>, 180 µm mesh size) hauled from close to the seafloor (or ca 1000 m depth) to the surface with a towing speed of 0.5 m s<sup>-1</sup>. Samples were preserved in a 4% formaldehyde-in-seawater solution until analysis ashore. Between 3 and 6 sampling depth layers were used across the cruises. To compare differences in abundance and population structure in different depth layers between stations, we fitted the data into five predefined layers: 1000–600 m, 600–200 m, 200–100 m, 100–50 m, and 50–0 m depth.

Multinet samples were examined under a Leica stereomicroscope for enumeration and taxonomic analyses of zooplankton. From the preserved samples, sub-samples were obtained with a 5-ml automatic pipette, with the pipette tip cut at 5 mm diameter to allow free collection of mesozooplankton. Large (total length > 5 mm) organisms were removed and counted before taking sub-samples. The number of sub-samples analyzed was chosen so that at least 150 *Calanus* spp.

were counted from each sample. Samples with low abundance were examined in their entirety. A few copepodite stage III were found but were not included in this study where we focused on older overwintering stages. Hereafter, the denomination *C. finmarchicus* CIV to adult refers to the sum of CIV, CV, and adults (both male and female) stages. Copepodite stages of the morphologically similar *Calanus glacialis* and *C. finmarchicus* were distinguished based on prosome length using previously established size classes (Daase *et al.*, 2018). Genetic identification conducted on 44 randomly selected *Calanus* individuals sampled at station C1 (Choquet *et al.*, 2017) showed very similar species composition to the length-based identification, with the contribution to the *Calanus* pool estimated as *C. finmarchicus* 89.9%, *C. glacialis* 9.5%, and *C. hyperboreus* 0.5% using length-based identification, and *C. finmarchicus* 91%, *C. glacialis* 9%, and *C. hyperboreus* 0% using the genetic method.

The weighted mean depth (WMD) of *C. finmarchicus* was calculated for each station following the equation (Roe *et al.*, 1984):

$$WMD = \frac{\sum_{i=1}^n ab_i z_i dz_i}{\sum_{i=1}^n ab_i dz_i},$$

where  $n$  is the number of layers, and for a layer  $i$ ,  $ab_i$  is the abundance of *C. finmarchicus* per cubic meter in the layer,  $z_i$  the mean depth of the layer, and  $dz$  the thickness of the layer.

For three of the cruises (2015–2017), the prosome length of *C. finmarchicus* CV were recorded. This allowed us to describe the size distribution of individuals of the same developmental stage at different locations and depths. When the size distributions showed a strong bimodal pattern, we fitted a Gaussian mixture model to the data to define the mean length of the two different size groups. This analysis was performed using Matlab (version R2014a) and the function fitgmdist.

## Hydrography and physical parameters

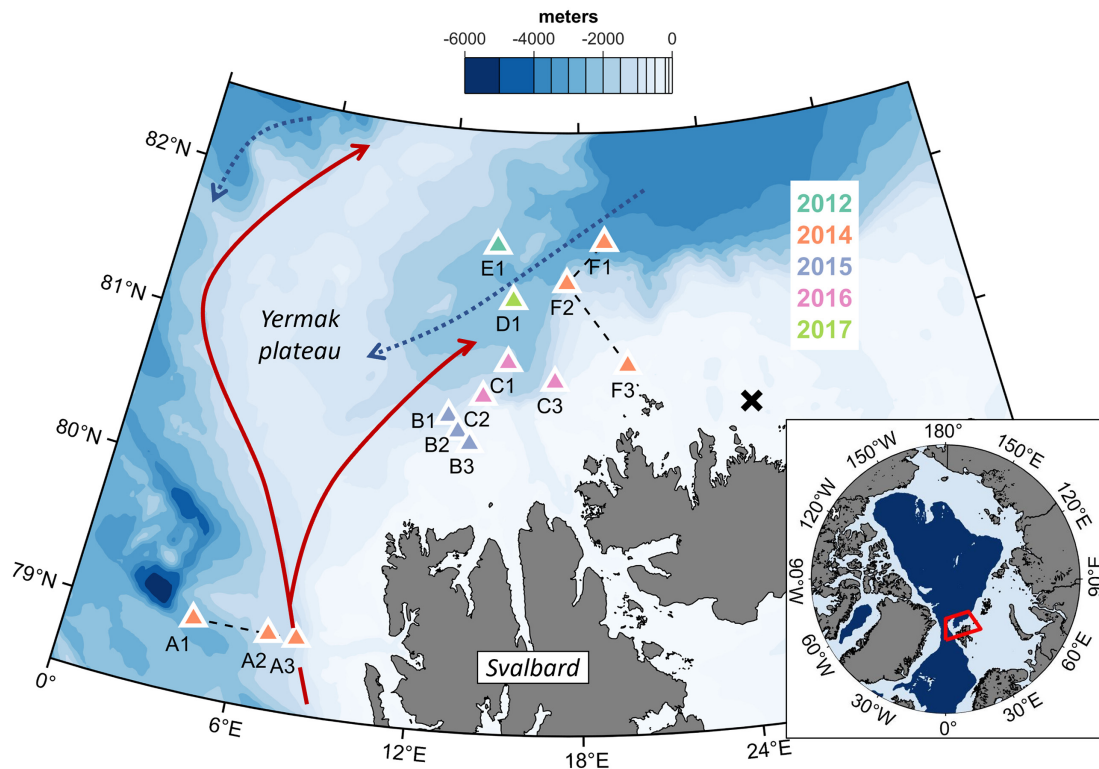
At each station, measurements of temperature and salinity were obtained by a ship-board conductivity, temperature, and depth (CTD) profiler (SBE911plus, SeaBird Electronics). In addition, a certain number of CTD casts were performed in between the stations to better resolved water mass distribution. CTD data were quality-checked to identify and remove out-of-range values.

To investigate the relationship between surface aggregations of *C. finmarchicus* and water masses, we identified different water masses using T–S diagrams (Supplementary Figure S1). For this, potential temperature  $\Theta$  and density were computed using the seawater package (version 3.3.4) in python (version 2.7.11).

To investigate if surface aggregation may be caused by upwelling along the shelf slope, we computed the offshore Ekman transport from 6-h frequency wind data measured at the geographical point 80.65°N, 25.00°E (source: eKlima.met.no). It represents the flow in m<sup>3</sup> s<sup>-1</sup> integrated over the surface Ekman layer for a cell of 1-m width, and was calculated following the equation:

$$Q_y = (\rho_{air} CD U_y) / (\rho_{wat} f),$$

with the density of air,  $\rho_{air} = 1.25$  kg m<sup>-3</sup>, the density of water,  $\rho_{wat} = 1027$  kg m<sup>-3</sup>, the drag coefficient,  $CD = 1.6 \cdot 10^{-3}$ ,  $f$  being the Coriolis parameter, and  $U$  the wind speed. The system axis was set parallel to the coast so that the  $Q_y$  component showed offshore/inshore Ekman transport. Then, to test



**Figure 1.** Location of the sampling stations around Svalbard Islands. The years of sampling are shown. The main inflow of AW into the Arctic Basin (red line), and approximate location and movement of Polar Surface Water are shown (blue dashed line). The black cross represents the wind station.

**Table 1.** Sampling details including sea ice coverage (from 0 to 1; 1 = fast ice), distance to the open ocean ice edge (defined as sea ice coverage > 0.3), and sea temperature range in the top 50 m.

Station	Date	Latitude (°N)	Longitude (°E)	Bottom depth (m)	Sea ice coverage	Distance to ice edge (km)	Temperature range (°C)
A1	January 12th, 2014	79.00	4.36	2 564	–	43	–0.8–1.2
A2	January 13th, 2014	79.00	7.01	1 197	–	97	4.9–5.9
A3	January 13th, 2014	79.00	8.00	1 087	–	117	5.0–5.0
B1	January 8th, 2015	80.59	12.62	1 000	0.01	37	–1.8–0.80
B2	January 8th, 2015	80.49	13.05	609	0.00	47	2.0–3.2
B3	January 8th, 2015	80.41	13.55	229	–	58	2.9–3.0
C1	January 15th, 2016	80.96	14.96	1 628	0.00	39	–1.5–2.5
C2	January 16th, 2016	80.73	13.98	591	–	57	3.2–3.5
C3	January 15th, 2016	80.84	16.94	608	–	60	3.5–3.5
D1	January 12th, 2017	81.38	15.07	2 289	0.31	41	2.6–3.1*
E1	January 13th, 2012	81.74	14.25	2 276	0.94	0	–1.85–1.00
F1	January 10th, 2014	81.77	19.16	3 168	0.87	0	–1.8
F2	January 9th, 2014	81.5	17.43	1 767	0.29	19	–1.1–0.9
F3	January 8th, 2014	80.95	20	125	0.01	86	0.2–0.3

\*Top 10 m missing.

for relative differences in wind conditions between years, an estimation of the Ekman transport was calculated by averaging  $Q_y$  values over a 10-d period prior to the first sampling station (the maximum interval between first and last station was 2 d). We restricted this analysis to 2014, 2015, and 2016 when *C. finmarchicus* abundance data and CTD measurements are available along shelf-offshore transects that provide a more detailed insight into water mass distribution and aggregation patterns to aid the interpretation of eventual upwelling events.

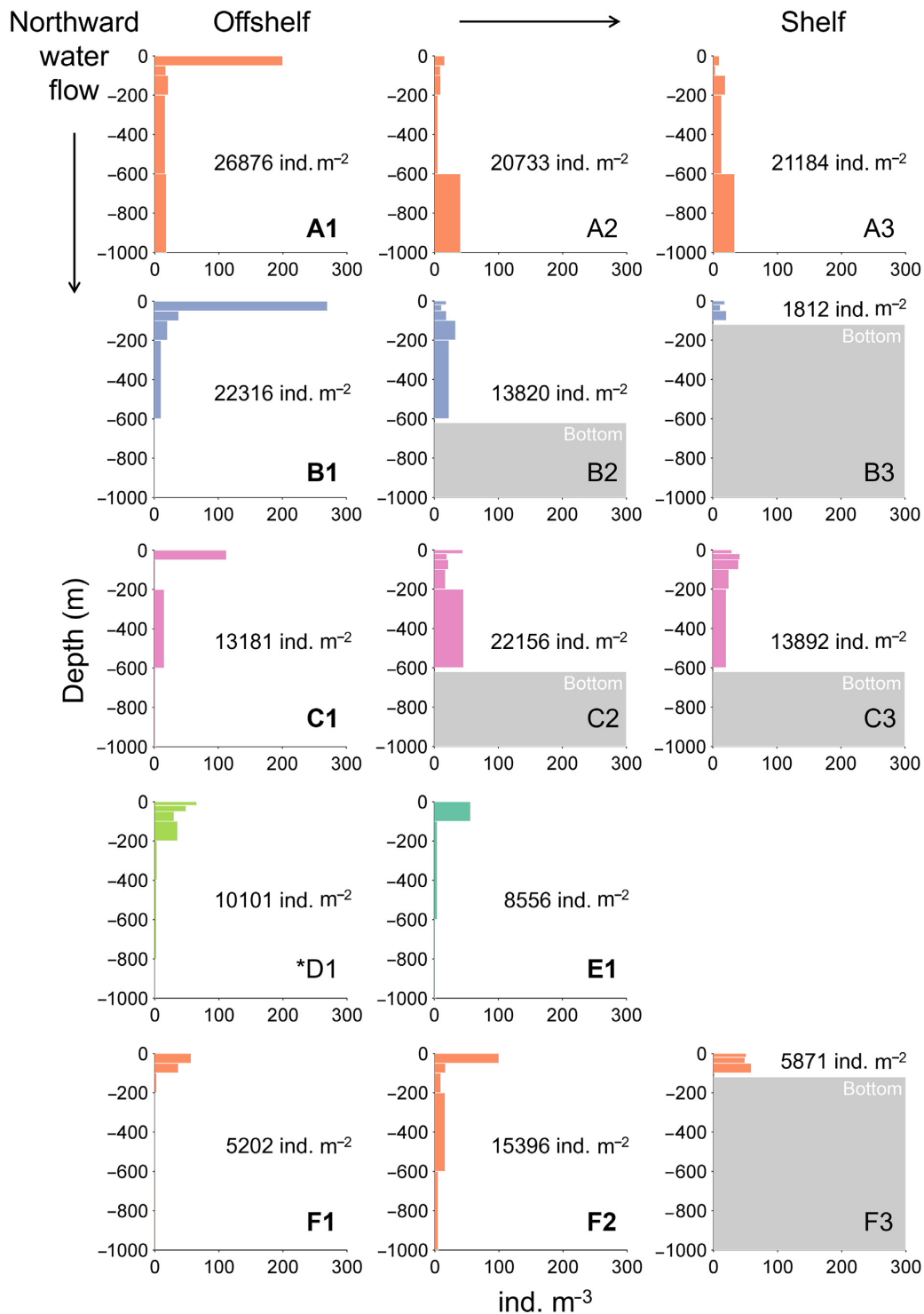
To analyze if surface aggregations were related to the presence of sea ice, sea ice concentrations at the sampling locations were computed as a 3-d average prior to the sampling

date, based on the product 'PHY\_001\_030' available on the Copernicus platform.

## Results

### *Calanus finmarchicus* horizontal and vertical distribution

A general decrease of *C. finmarchicus* (CIV to adult) integrated abundance was observed from southwest to northeast, with highest abundance found at the offshore station on the west coast of Svalbard ( $\sim 26\,800$  ind.  $m^{-2}$ ; transect A; Figure 2). Within each transect, maximum abundances were usually found off the shelf above the continental slope. Along the



**Figure 2.** Vertical distribution of *C. finmarchicus* CIV to adults in the water column during January 2012 and 2014–2017 (see Figure 1 for colour code). Polar Surface Waters occurred at stations in bold (undefined at D1). The abundance integrated over the water column (ind. m<sup>-2</sup>) are also shown. Station locations go from southwest to northeast (a)–(f) and from offshore to shelf (1)–(3).

northern coast, the stations located farthest offshore showed relatively low abundances (C1, D1, E1, and F1).

Higher densities of *C. finmarchicus* were found within the upper layers of some of the stations offshore, with maximum values in the surface layer (0–50 m, up to 270 ind. m<sup>-3</sup>) while densities decreased sharply downward. Other stations showed a relatively uniform depth distribution of

*C. finmarchicus*, with slightly higher abundances occurring sporadically in deep layers (Figure 2). These differences in *C. finmarchicus* vertical distribution are supported by the WMD of the copepods being located closer to surface for the stations close to the ice edge (standardized WMD of 0.07–0.34), compared to other stations (0.45–0.68, Table 2).



**Table 2.** WMD of *C. finmarchicus* (CIV to adult). The last column shows where the WMD is located relatively to the height of the whole sampling profile (standardized WMD). For example, if the WMD is 50 m and the water column height is 100 m, the standardized WMD is equal to 0.5, but if the water column height is 1000 m then the standardized WMD is equal to 0.05. Polar Surface Waters (PSW) occurred at stations in underlined italic.

Stations	Water column height (m)	WMD (m)	Standardized WMD
<u>A1</u>	1 000	339	0.34
A2	1 000	681	0.68
A3	1 000	619	0.62
<u>B1</u>	1 000	128	0.13
<u>B2</u>	600	300	0.50
B3	100	53	0.53
<u>C1</u>	1 000	256	0.26
<u>C2</u>	600	339	0.57
C3	600	266	0.45
*D1	1 000	173	0.17
<u>E1</u>	1 000	182	0.18
<u>F1</u>	1 000	66	0.07
<u>F2</u>	1 000	300	0.30
F3	100	52	0.52

\*Occurrence of PSW undefined.

### Hydrography and Ekman transport

In all years the predominating water mass was AW (potential temperature  $\Theta > 1^\circ\text{C}$ ; Rudels *et al.*, 2005; Pérez-Hernández *et al.*, 2017), which occupied roughly the upper 600 m (Figures 3 and 4). The AW layer was thickest along the shelf break. Below the layer of AW, the water column was thermally stratified and occupied by gradually colder AW and by Modified AW ( $0^\circ\text{C} < \Theta < 2^\circ\text{C}$ ,  $\sigma_T > 27.7$ ; Rudels *et al.*, 2000). Polar Surface Water (PSW), characterized by low salinity ( $< 34.9$ ) and temperature ( $\Theta < 0^\circ\text{C}$ ) was observed above AW at most of the offshore stations, except for the stations A2 and A3 located on the west coast of Svalbard. The layer of PSW reached down to ca. 100 m farthest northeast (transect F), but occupied only the upper ca. 20 m further southwest, at stations B1 and C1.

Southeasterly winds were dominating during the research cruises conducted in 2014–2016 resulting in a positive offshore Ekman transport. The averaged Ekman transport was the highest in 2015 reaching  $43.4 \text{ m}^3 \text{ s}^{-1}$  (Figure 5).

### Calanus distribution in relation to hydrography

Highest *C. finmarchicus* abundances ( $> 100 \text{ ind. m}^{-3}$ ) were found in water masses with characteristics corresponding to PSW ( $\Theta < 0^\circ\text{C}$ , and  $S < 34.9$ ; Figure 6). The large increase in the contribution of *C. finmarchicus* to the total copepod pool in these surface layers compared to the deeper layers demonstrates that this surface aggregation process was specific to *C. finmarchicus* and not found in the rest of the copepod community (Table 3).

### Calanus stage and size composition

In all years and at all stations the *C. finmarchicus* population was dominated by copepodite stage V (CV), except for offshore station E1 (Supplementary Table S1). Copepodite stage IV was the second most abundant stage, while only few or no adults were observed (usually  $< 5\%$  of the *C. finmarchicus* pool; data not shown). Abundance of *C. finmarchicus* CV was lower in deep layers at offshore stations such as D1, E1,

F1, and F2 but that was generally associated with low total *Calanus* abundances.

For a number of stations and depth layers, *C. finmarchicus* CV showed a bimodal length frequency distribution (Supplementary Table S2), with the two size classes differing significantly in prosome length (mean difference of ca. 0.4 mm, Supplementary Figure S2). This was particularly obvious at offshore stations B1, C1, and D1, where two size groups were observed in most layers. However, no patterns emerged between size patterns and distance to the coast or depth layer.

### Discussion

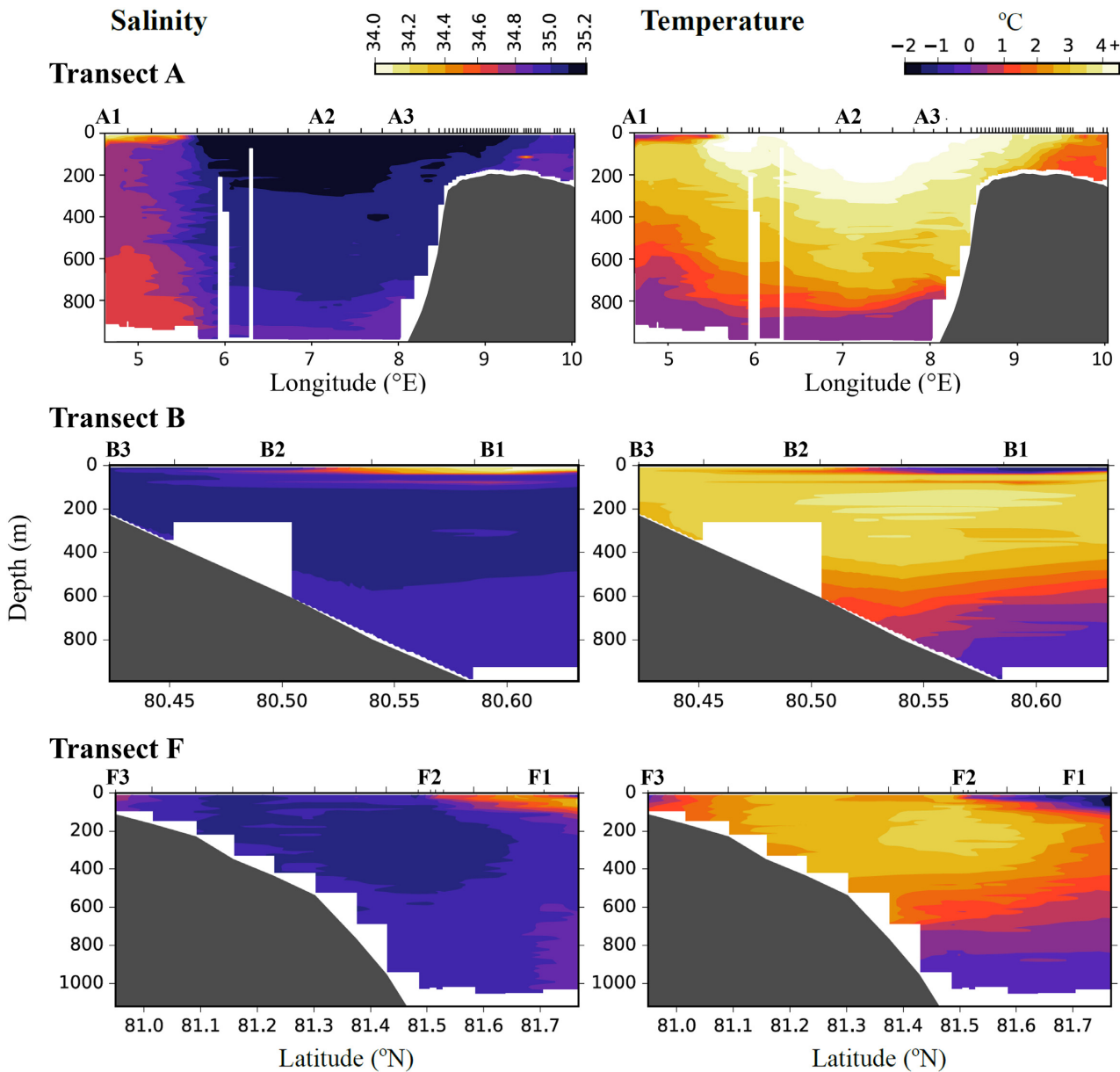
Our data collected during six polar night campaigns show that *C. finmarchicus* aggregated in PSW during the polar night and that this is a recurring feature. The presence of part of the population in the surface layer during winter has been reported previously from Svalbard fjords (Daase *et al.*, 2018; Berge *et al.*, 2020), in the western Barents Sea (Pedersen *et al.*, 1995), and in the Greenland Sea Gyre (Hirche, 1991; Fort *et al.*, 2010). However, in this study we highlight the occurrence of high concentration aggregations (usually  $> 100 \text{ ind. m}^{-3}$ ), representing sometimes more than half of the total *C. finmarchicus* population, constrained in a thin layer near the surface (depth of 0–50 m). We observed these surface aggregations in different years and over a large geographical area, particularly off shelf and in proximity to the ice edge.

One important piece of information currently missing is whether the individuals observed in the surface layer in January had descended to overwintering depth at all or if they remained in surface waters since summer. Previous observations of *C. finmarchicus* attested that part of the population was present in the surface layer during the period from October to January in the North Atlantic (Hirche, 1991; Pedersen *et al.*, 1995). However, these studies recorded only small abundances and the process behind these observations remains unclear. In our study area, *Calanus* spp. have been observed in surface as late as end of September (Walkusz *et al.*, 2009), but no data are available on *Calanus* abundances and distributions for the period October–December. We can, therefore, not assess whether the high concentrations observed in January were due to recent aggregations or had persisted since late autumn.

To explain these unusual surface aggregations in mid-winter, we discuss six hypotheses independently. However, the hypotheses are not mutually exclusive, and the behaviour of *C. finmarchicus* outside its core habitat is probably best explained by a combination of two or more of these. Our study is based on samples collected during cruises with various scientific objectives, implying that some type of contextual data were not systematically sampled conjointly, limiting us in testing thoroughly some of the hypotheses. Therefore, the following discussion is rather meant to set a framework for future explorations.

#### Hypothesis #1—advection by upwelling

Perhaps the most intuitive way to explain the aggregation of *C. finmarchicus* in surface layers is upwelling, forcing the population from their overwintering depth in deeper AW layers to the surface. North of Svalbard in winter, the winds blow mostly from two directions, northwest and southeast (Cohen *et al.*, 2017). Southeasterly winds produce offshore Ekman transport by pushing coastal surface water offshore, which

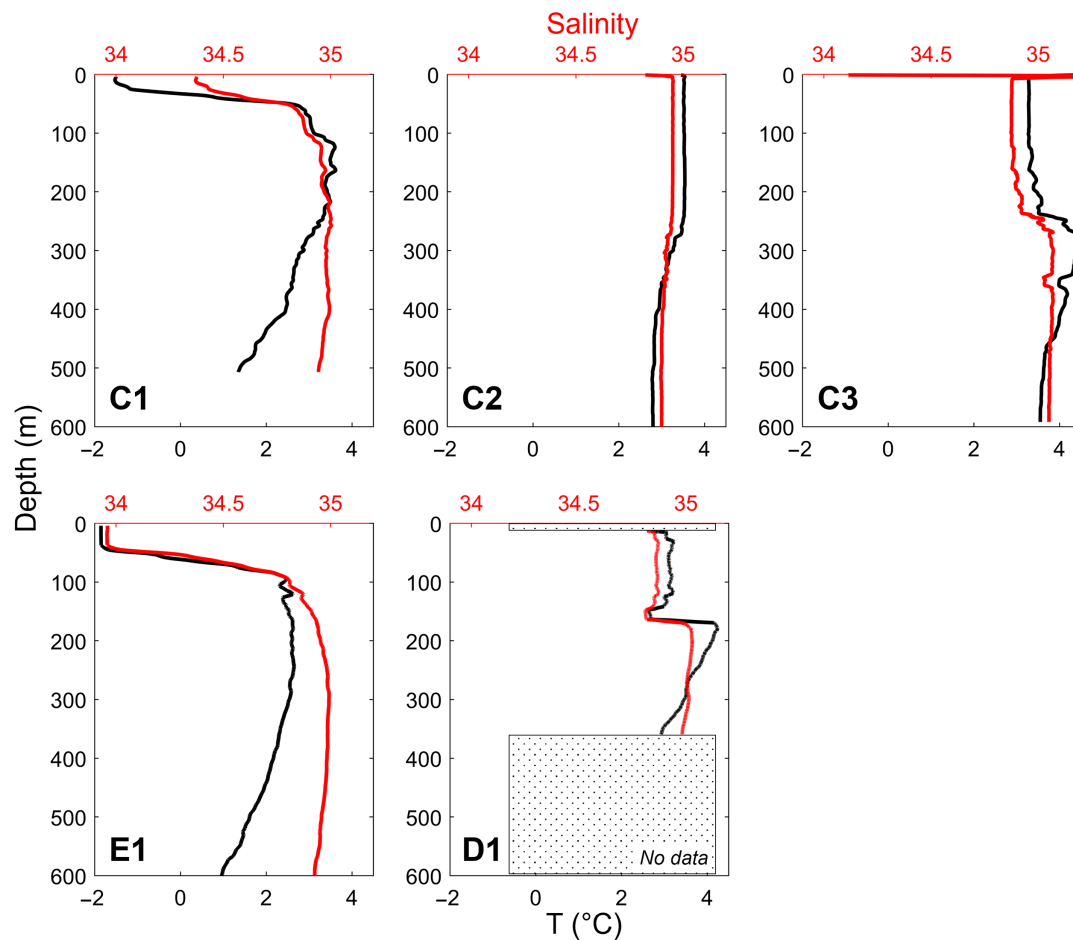


**Figure 3.** Salinity (left) and temperature (right) along one longitudinal transect and two latitudinal transects crossing the Atlantic inflow into the Arctic Ocean, sampled in January 2015 (b) and 2014 (a) and (f). Ticks on the top axis indicate locations of CTD profiles. Stations where Multinet samples were taken are labelled. See Figure 1 for positions of stations.

eventually leads to coastal upwelling (Lind and Ingvaldsen, 2012). When the winds are steady over a time period long enough to initiate this physical process, it can concentrate the organisms in the surface layer and then transport them offshore. Prevailing southeasterly winds caused a positive offshore Ekman transport in the 3 years for which we have shelf-offshore data. The year 2015 in particular, was characterized by strong southeasterly winds over 10 d preceding the cruise, resulting in the highest volume of surface water moved offshore compared to the other years (Figure 4). However, the vertical distribution of *Calanus* at the shelf station (B3) and on the slope (B2) do not show any sign of surface aggregation. Therefore, even though the physical processes make this hypothesis plausible, our observations do not support the notion that *C. finmarchicus* is being aggregated in PSW due to physical forcing.

### Hypothesis #2—evolutionary pressure to be transported back to the Norwegian Sea

Life history strategies of *C. finmarchicus* have evolved as adaptations to the environmental conditions in its core habitat (North Atlantic). These conditions change dramatically the further north the population is advected, particular in terms of the seasonality in incoming solar radiation and of temperature, and associated changes in phytoplankton bloom phenology. The ability of *C. finmarchicus* to survive in the polar basin is hampered by the short phytoplankton growing seasons and low temperatures (Ji *et al.*, 2012), and it largely fails to reproduce in the Arctic Ocean (Hirche and Kosobokova, 2007). The continuous advection into the Arctic is, therefore, regarded as a “death trail” (Wassmann *et al.*, 2015). The only way to exit this conveyor belt into the Arctic Ocean is to reach PSW. In our study area, PSW is decoupled from the main cur-



**Figure 4.** Salinity and temperature profiles at five stations sampled in January 2012 (E1), 2016 (C1-3), and 2017 (D1). See Figure 1 for positions of stations.

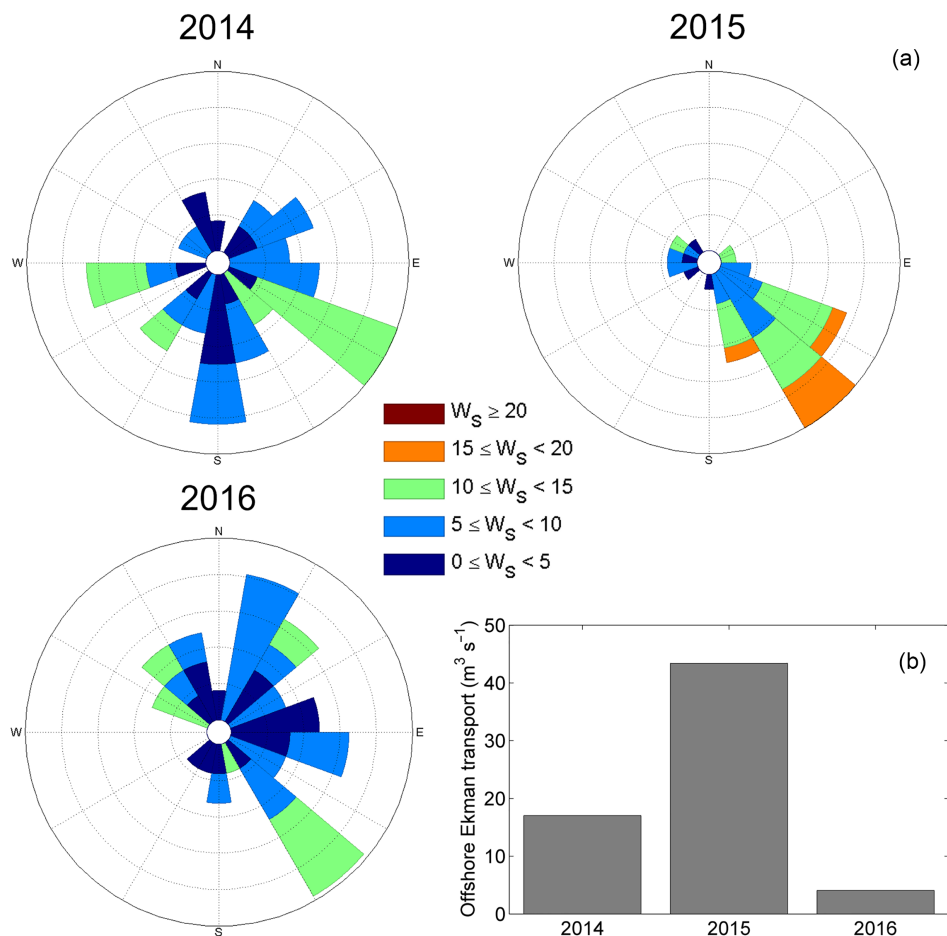
rent below and mainly flows toward the southwest, i.e. out of the Arctic Ocean and into the Fram Strait (Lundesgaard *et al.*, 2021). However, the mainly wind-driven PSW movement is rather unpredictable on shorter time scales (Proshutinsky and Johnson, 1997). Under favourable conditions, the copepods would be transported southwestward across the Yermak plateau and could then reach a branch of recirculating AW further southward (Hattermann *et al.*, 2016). This hypothesis might seem counter-intuitive at first. Indeed, copepods would need to use energy to actively ascend from deeper water, which provide adequate conditions for overwintering, to less favourable surface waters with temperatures close to freezing, just to reach an uncertain path back to its core habitat. Currently, it is also unclear which proximate cues the copepods would use to reach PSW. However, the outlined transport out of the Arctic Ocean is likely the only option for copepods to reach waters where they could reproduce successfully, so even if only a small part of the population would succeed to do so, over time it might create a selection pressure favouring aggregation in PSW.

### Hypothesis #3—avoidance of mesopelagic predators

Stages CIV to adult of *C. finmarchicus* are fed upon by a large variety of species, including and micronekton such as lantern fish (Pepin, 2013) or polar cod (Lønne and Gulliksen, 1989;

Cusa *et al.*, 2019). Planktivorous fish can impact the vertical distribution of *Calanus* (Dale *et al.*, 1999), and it has been shown that they can actively predate at high latitude during the polar night (Berge *et al.*, 2015a). The presence of predators may, thus cause *Calanus* to abandon overwintering depth. High predation pressure within a given water layer results in a decrease in the prey population, either because the prey actively migrates away to avoid being predated on, or because the prey gets consumed by the predators in that water layer. While both options impact the vertical distribution of the prey, the first option does not affect prey abundance integrated over the entire water column. Among the three transects that contain slope and offshore stations with similar depths (Figure 5; transect A, B, and C), *C. finmarchicus* abundances were slightly higher offshore along the transects A and B (transect A1 > A2 and B1 > B2) suggesting that predation pressure on *C. finmarchicus* distributed in AW was not higher at the offshore stations. Fish surveys conducted during the 2016 cruise in the same study area (Geoffroy *et al.*, 2019) found that the dominant fish species, *Sebastes mentella*, was mainly feeding on euphausiids and biomass of other planktivorous fish was low. Furthermore, most fish were located in AW above the shelf and in surface water further offshore, making it unlikely that the avoidance of fish predation leads *Calanus* to aggregate in the upper water column.

Other potential predators include carnivorous copepods (e.g. *Paraeuchaeta* spp.; Yen, 1985; Tønnesson *et al.*, 2006)



**Figure 5.** (a) Wind rose graphs produced from observational data measured at  $80.65^\circ\text{N}$ ;  $25.00^\circ\text{E}$  for a period of 10 d prior to the sampling date for 2014–2016. It indicates the direction from which the wind was blowing. The colours refer to the wind speed and the length of the bar to the percentage compared to all wind measurements. (b) Averaged offshore Ekman transport over the same time period.

and macrozooplankton such as chaetognaths (Petursdottir *et al.*, 2012; Espinasse *et al.*, 2018) or amphipods (Kraft *et al.*, 2012). Chaetognath species, such as *Eukrohnia hamata*, in particular can be found in very high abundances (Błachowiak-Samołyk *et al.*, 2015), but during winter these populations mainly consist of small specimens. Data on macrozooplankton distribution along two transects A and F (data not shown) show that the largest chaetognaths, which have the ability to prey on *Calanus* CIV to adult, were distributed evenly over the entire water column. They are, therefore, unlikely to push *Calanus* to migrate upwards. Overall, even though our dataset does not allow us to refute the predator avoidance hypothesis, we also did not find any evidence to support it.

#### Hypothesis #4—anticipating the phytoplankton spring bloom

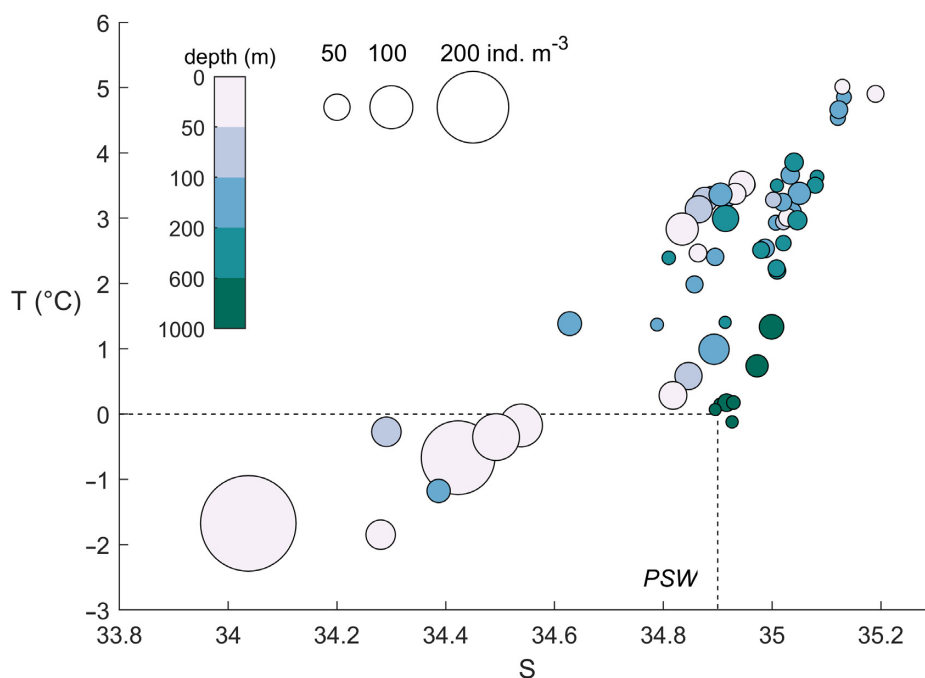
Berge *et al.* (2015a) speculated that it may be advantageous for herbivorous grazers to become active long before the onset of the spring bloom. This would enable the copepods to take advantage of primary production as soon as the light returns and phytoplankton development starts. When light is returning, some phytoplankton species can start to reproduce within a day even at low irradiance levels as early as February (Morin *et al.*, 2020; Randelhoff *et al.*, 2020). The advantage for *Calanus* of being distributed in surface layers where

the primary production will start first could thus balance the metabolic cost associated with activity during the polar night. However, our available data are not sufficient to evaluate this hypothesis. For example, we do not know to which extent the copepods were active and, therefore, even less how much energy would be required to maintain this level of activity. Moreover, although *C. finmarchicus* aggregated in PSW, they did not aggregate in the nearby stations above the slope (Figure 5; A2, B2, and C2). We do not have data describing when primary production commences in the different parts of the study area and, therefore, cannot conclude on how this could spatially trigger *Calanus* ascent. To evaluate the validity of the hypothesis, one would need comparative time-series data, rather than spatial snapshots.

#### Hypothesis #5—feeding on organic matter associated to sea ice

The aggregation of *C. finmarchicus* in surface waters was particularly pronounced at stations close to the ice edge, suggesting that the proximity to the sea ice might provide advantages. Many species are sustained directly or indirectly by particulate organic matter (POM), algae, and microzooplankton communities associated to sea ice (Seuthe *et al.*, 2011; Stoecker and Lavrentyev, 2018; Olsen *et al.*, 2019). While predominantly herbivorous during the spring bloom, *Calanus* spp. ex-





**Figure 6.** Scatter plot of *C. finmarchicus* CIV to adult abundances (ind. m<sup>-3</sup>) west and north of Svalbard in January as a function of mean sea potential temperature and salinity in the water layer where the samples were collected. The size of the circle corresponds to the abundance and the colour to the mean depth of the water layer. Based on data from all stations and layers.

**Table 3.** Relative contribution (%) of *C. finmarchicus* to the total copepod abundance for each sample. PSW occurred at stations in underlined italic.

Stations	Depth (m)					
	0–50	50–100	100–200	200–600	600–1 000	0–1 000/bottom
<i>A1</i>	50.5	41.8	42.4	46.4	22.1	45.2
<i>A2</i>	14.8	21.1	56.6	65.4	59.5	32.8
<i>A3</i>	15.1	17.6	34.8	46.5	58.5	35.2
<i>B1</i>	64.4	51.3	58.8	33.9	2.37	56.5
<i>B2</i>	14.5	27.4	48.9	26.6	–	23.9
<i>B3</i>	13.5	17.9	–	–	–	14.9
<i>C1</i>	45.0	x	27.0	33.6	5.0	37.3
<i>C2</i>	22.0	19.5	25.8	28.9	–	23.2
<i>C3</i>	55.1	68.2	49.4	51.0	–	56.5
<i>F1</i>	62.7	11.9	2.20	2.03	0.64	16.0
<i>F2</i>	42.6	27.7	14.7	37.8	4.93	29.0
<i>F3</i>	8.91	12.3	11.6	17.8	8.91	12.3

hibits a more omnivorous diet outside bloom scenarios and can feed on POM related to sea ice (Søreide *et al.*, 2013; Kohlbach *et al.*, 2016). Both *C. glacialis* and *C. hyperboreus* have been found to aggregate closely under the ice during ice algae blooms. The sea ice around Svalbard in January consists mainly of young ice from the previous one or two seasons drifting from the eastern part of the Arctic Ocean. While the absence of light inhibits any local primary production in January, the ice can transport dead or resting biological material produced earlier in the season (Olsen *et al.*, 2017). During winter storms, generally associated with a sharp increase in temperature due to their southern provenance (Cohen *et al.*, 2017), the ice cover undergoes strong pressure resulting in deformation and weakening of the ice (Itkin *et al.*, 2017), and even melting (Duarte *et al.*, 2020). This can result in POM and microorganisms being released into the water column where it presents a substantial food source during winter that could attract *C. finmarchicus* to the surface layer. While it may seem

risky for *Calanus* to exit diapause and search for food in surface waters, it has been modelled that if food is available even in low concentrations there is no difference in fitness between *Calanus* spp. emerging early from overwintering and those remaining at depth for longer (Hobbs *et al.*, 2020). Stable isotopes analysis could be an easy way to highlight any interactions between *C. finmarchicus* and sea ice biota during the polar night, as the latter often show high nitrogen isotopic values (Fripiat *et al.*, 2014; Espinasse *et al.*, 2019). Lipid composition has also been shown to be a useful marker of sea ice origin (Amiraux *et al.*, 2021).

#### Hypothesis #6—second generation

The bimodal size distribution observed for CV in some of the water layers suggests the presence of two generations from the same year. The occurrence of a second generation is not uncommon in warmer water further south (Head *et al.*, 2013),

but has so far not been documented in Arctic waters. *Calanus finmarchicus* is thought to descend to overwintering depths as soon as it has accumulated sufficient lipids (Fiksen and Carlotti, 1998). If a second generation (G2) was spawned late the previous summer, it is possible that these late recruits would not have stored enough lipids to trigger the downward migration, and therefore, would need to remain in surface waters. However, we did not observe a smaller mean size of copepods in the surface layer compared to deeper layers, rather the opposite. Although our data might indicate the presence of a second generation, they do not support the hypothesis that it is the second generation that aggregates in surface waters. Further investigation in lipid content of the individuals distributed in the different depth layers might be a complementary way to approach this question.

### Implications and conclusions

Based on our dataset, we conclude that mechanisms described in the hypotheses 2, 4, and 5, and to a lesser extent 3, may contribute to the observed high abundances in surface waters close to the ice edge and deserve further attention. All of these hypotheses imply that *C. finmarchicus* is not in dormancy but remains at least partly active during winter. This is in line with observations from the Arctic demonstrating that copepods conduct diel vertical migration (Berge *et al.*, 2009, 2015a, b; Darnis *et al.*, 2017) and are actively mating (Daase *et al.* 2018) during the polar night.

The *C. finmarchicus* concentrations in the PSW were relatively high (between 100 and 300 ind. m<sup>-3</sup>) compared to abundance estimates from late summer north of Svalbard (6–85 ind. m<sup>-3</sup>; Daase and Eiane, 2007; Hop *et al.*, 2019). Such high concentrations could be beneficial for predators such as fish or large mammals. Only few whale species reside year round in the Arctic, most notable the Bowhead whale, which is planktivorous and distributed close to the ice edge (Vacquié-Garcia *et al.*, 2017). These whales might, thus find a substantial food source in the surface aggregations of *Calanus* during mid-winter. Bowhead whales were brought close to extinction in the 18th century but recent observations indicate that the population size in our study area is increasing (Vacquié-Garcia *et al.*, 2017). This could indicate that the whales find favourable conditions associated with the rapid environmental changes currently observed in the Arctic (Falk-Petersen *et al.*, 2015). *Calanus* is also an important food source for juvenile polar cod (*Boreogadus saida*; Lønne and Gulliksen, 1989; Cusa *et al.*, 2019). When other food sources such as ice-associated amphipods become scarce due to the loss of sea ice, the importance of *C. finmarchicus* in their diet might further increase and large aggregations in proximity to the ice could be a valuable asset.

To conclude, we suggest that the implications of *C. finmarchicus* being distributed in cold surface waters during mid-winter should be considered in Arctic predator ecology studies. We suggest monitoring the spatial extent of this phenomenon closely as it is likely to evolve with seawater temperature increase, potentially having a strong impact on the rest of the Arctic marine ecosystem during winter. Indeed, warming temperatures could provide a more suitable environment for *Calanus* to reproduce successfully in the future and eventually colonize the Arctic (Tarling *et al.*, 2021), although the lack of light could be the ultimate limiting factor (Ljungström *et al.*, 2021). Monthly or bi-monthly sampling from October to January is required to describe the temporal dynamic of sur-

face aggregations, and especially (1) to define if the *Calanus* observed in surface in January ascended from overwintering depth or never descended, and (2) to delineate interactions between the surface aggregations and the rest of the population. We reviewed the most plausible hypotheses behind this behaviour and provide the basis for further studies that could address these specifically.

### Supplementary material

Supplementary material is available at the ICESJMS online version of the manuscript.

### Data availability

Abundance data shown in Figures 4 and 5 are available as supplementary material.

### Conflicts of interest

The authors have no conflict of interest to declare.

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