RESEARCH ARTICLE
The intriguing co-distribution of the copepods *Calanus hyperboreus* and *Calanus glacialis* in the subsurface chlorophyll maximum of Arctic seas
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Studying the distribution of zooplankton in relation to their prey and predators is challenging, especially *in situ*. Recent developments in underwater imaging enable such fine-scale research. We deployed the Lightframe On-sight Keyspecies Investigation (LOKI) image profiler to study the fine-scale (1 m) vertical distribution of the copepods *Calanus hyperboreus* and *C. glacialis* in relation to the subsurface chlorophyll maximum (SCM) at the end of the grazing season in August in the North Water and Nares Strait (Canadian Arctic). The vertical distribution of both species was generally consistent with the predictions of the Predator Avoidance Hypothesis. In the absence of a significant SCM, both copepods remained at depth during the night. In the presence of a significant SCM, copepods remained at depth in daytime and a fraction of the population migrated in the SCM at night. All three profiles where the numerically dominant copepodite stages C4 and C5 of the two species grazed in the SCM at night presented the same intriguing pattern: the abundance of *C. hyperboreus* peaked in the core of the SCM while that of *C. glacialis* peaked just above and below the core SCM. These distributions of the same-stage congeners in the SCMs were significantly different. Lipid fullness of copepod individuals was significantly higher in *C. hyperboreus* in the core SCM than in *C. glacialis* above and below the core SCM. Foraging interference resulting in the exclusion from the core SCM of the smaller *C. glacialis* by the larger *C. hyperboreus* could explain this vertical partitioning of the actively grazing copepodite stages of the two species. Alternatively, specific preferences for microalgal and/or microzooplankton food hypothetically occupying different layers in the SCM could explain the observed partitioning. Investigating the observed fine-scale co-distributions further will enable researchers to better predict potential climate change effects on these important Arctic congeners.

Keywords: Arctic copepods; Underwater imaging; Automated zooplankton identification using machine learning; Fine scale vertical distribution; Resource partitioning; Predator avoidance

Introduction
Herbivorous zooplankton channel the energy from microalgal primary producers to primary carnivores and play many roles in the oceanic carbon cycle (Hobson et al., 2002; Wassmann et al., 2006; Darnis and Fortier, 2012). In Arctic seas, copepods dominate the zooplankton with the primarily herbivorous genus *Calanus* accounting for up to 80% of mesozooplankton biomass (Søreide et al., 2008; Darnis and Fortier, 2012). Among several adaptations to the extreme seasonality of the arctic pelagic ecosystem, *C. hyperboreus* and *C. glacialis* extract and accumulate large lipid reserves from ice microalgae and phytoplankton during a short grazing season in late spring and summer (Falk-Petersen et al., 2007; Søreide et al., 2010; Wassmann, 2011; Daase et al., 2013). By making the energy captured during the short microalgal bloom available to higher trophic levels over the rest of the year, this build-up of lipid reserves by copepods is a pivotal process in arctic ecosystems (e.g., Falk-Petersen et al., 2009). By feeding fish, marine mammals and seabirds, copepod lipids underpin much of the ecosystem services provided to northern communities (Darnis et al., 2012). Like many arctic zooplankton species, *Calanus hyperboreus* and *C. glacialis* complete a seasonal vertical migration (SVM) from their autumn-winter position at depth towards the productive surface layer in spring and summer (Dawson, 1978; Hirche, 1997; Ashjian et al., 2003; Darnis and Fortier, 2014). In ice-covered waters and in open waters during the period of day-night succession in spring and autumn, limited diel vertical migrations (DVM) superimpose on the SVM of the two species (e.g., Fortier et...
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al., 2001; Daase et al., 2015; Darnis et al., 2017). Consistent with the Predator Avoidance Hypothesis (e.g., Lampert, 1989), feeding at night in the food-rich surface layer and migrating to depth in daytime would enable Calanus copepods to avoid visual predators such as seabirds and fish (Runge and Ingram, 1991; Fortier et al., 2001).

The interactions among zooplankton grazers, their microalgal food and their predators, at scales of decimeters to several meters during the short feeding migration to the surface layer in spring–summer, likely dictate the efficiency of lipid transfer in the arctic marine food web (Darnis et al., 2012; Durham and Stocker, 2012; Schmid et al., 2018). Elucidating these interactions may provide crucial insights into how ongoing changes in the sea-ice, turbulence, and temperature regimes of the summer surface layer may disrupt the pelagic ecosystem of Arctic seas (Falk-Petersen et al., 2007; Søreide et al., 2010; Darnis et al., 2012). The vertical resolution of traditional zooplankton sampling systems is generally insufficient to describe zooplankton distribution at these scales. Using ground-breaking technologies at the time, Herman (1983) showed how, in northwestern Baffin Bay in late July and early August, the copepodite stage C5 of Calanus hyperbores distributed in the subsurface chlorophyll maximum (SCM), while C. glacialis C5 and C. finmarchicus C5 on average distributed above the SCM, presumably at the depth of maximum phytoplankton productivity.

The Lightframe Onsight Key-species Investigation (LOKI) optical profiler (Schultz et al., 2010; Schmid et al., 2016) captures the fine-scale vertical distribution of mesozooplankton. The optical resolution of images is sufficient for either visual (Schulz et al., 2010; Hirche et al., 2014) or computer-assisted (Schmid et al., 2016, 2018) taxonomic identification of zooplankton organisms. Computer-assisted identification has the advantage that large quantities of plankton images (tens to hundreds of millions) can be identified efficiently (Luo et al., 2018) when human expert identification is no longer practical. Some imagers, such as LOKI, make it possible to estimate the lipid reserves of Calanus spp. (Schmid et al., 2018).

In the present study, the LOKI profiler was deployed from 10 m above the seafloor to the surface at six stations in northern Baffin Bay to investigate the fine-scale vertical co-distribution (1 m resolution) of Calanus hyperbores, C. glacialis and chlorophyll a at different hours of the day, at the end of the grazing season in August. Zooplankton images were identified automatically by a classifier developed using machine learning (Schmid et al., 2016). The observed distributions of Calanus in relation to its microalgal food at different light intensities were then compared to the predictions of the Predator Avoidance Hypothesis. The Ideal Free Distribution model for phenotypes of unequal competitive abilities was used to interpret the co-distribution of actively grazing C4 and C5 copepodites of the two species in the subsurface chlorophyll maximum (SCM).

Materials and Methods

Study area

The North Water (NOW, Figure 1) is a large, recurrent and biologically productive polynya between Greenland and Ellesmere Island (Muench, 1971; Stirling, 1980; Barber...
et al., 2001). Typically, the polynya forms in late April or early May when the flux of Arctic ice through Nares Strait is blocked by the formation of an ice bridge in Smith Sound, and northerly winds push the remaining ice south (Muench, 1971; see April et al., 2019, for recent climate-driven changes to the polynya). The ice-free region reaches its maximum extent (ca. 70,000 km²) in July. The polynya sensu stricto ceases to exist in August when the tongue of ice that separates it from the rest of Baffin Bay melts and all of Baffin Bay becomes free of ice. Arctic Surface Water enters the North Water through Nares Strait. By comparison to the adjacent Canadian Archipelago, the early removal of the ice in the NOW (April–May versus July–August in the Archipelago) results in an early phytoplankton bloom, the early development of the zooplankton community, and strong recruitment of juvenile polar cod Boreogadus saida (Fortier et al., 2002; Ringuette et al., 2002; LeBlanc et al., 2019).

**LOKI deployment**

Concurrent vertical profiles of temperature, salinity, light, fluorescence, and mesozooplankton abundance were obtained by deploying the Lightframe On-sight Keyspecies Investigation (LOKI) profiler at six stations in the North Water and Nares Strait (Figure 1) between 15 August and 28 August during the 2013 ArcticNet expedition of the research icebreaker CCGS Amundsen. The LOKI profiler (Schultz et al., 2010) captures images of the particles funneled into a photographic chamber by a 0.28-m² aperture, 1.5-m long, 200-μm mesh conical net. At each station (Table 1) the LOKI was deployed to 10 m above the seafloor and then hauled back to the surface at a constant speed of 24 m min⁻¹. During the ascent, images of mesozooplankton were stored automatically on an internal solid-state drive. Ancillary sensors simultaneously recorded temperature and oxygen (Aanderaa Oxygen Optode 4330F), conductivity (Aanderaa Conductivity Sensor 3919), chlorophyll fluorescence (TriOS MicroFlu – chl) and pressure (Aanderaa Pressure Sensor 4017D) every second. Particles passing through the photographic chamber were collected in a 200-μm mesh cod-end and preserved in 4% formaldehyde-seawater solution buffered with sodium borate. For full information on LOKI hardware and software settings see Schmid et al. (2016).

**Automatic identification of copepod taxa using machine learning**

Images of 179,270 zooplankton and particles were identified automatically using a Random Forests machine learning model (Breiman, 2001), which is efficient at correctly identifying the copepodite stages of *C. hyperboreus* and *C. glacialis* (Schmid et al., 2016). Details of the protocol for image preparation, the development of the classifier, and its application to the automatic identification of mesozooplankton are given in Schmid et al. (2015, 2016). From the set of 179,270 images, 41,231 were identified as *Calanus* copepodes (C1 to females and males). Of these, 18,974 were identified as *C. hyperboreus* and 17,637 as *C. glacialis* (Figure 2). Due to their morphological similarities and size overlaps, *C. glacialis* C2 and *C. hyperboreus* C1 as well as *C. glacialis* C3 and *C. hyperboreus* C2 cannot be discriminated by the classifier (Schmid et al., 2016). The classifier identified 2203 images as *C. glacialis* C2/C. hyperboreus C1 and 2417 as *C. glacialis* C3/C. hyperboreus C2.

In addition, the classifier cannot distinguish *C. finmarchicus* from other *Calanus*. Taxonomic analysis of the cod-end collections based on prosome length and morphometric criteria found 213 *C. finmarchicus* m⁻² at station NOW East (0.64% of *Calanus*) and 142 m⁻² at NOW West (0.57% of *Calanus*). Based on the same criteria, *C. finmarchicus* was absent at stations further north. Given the overlap in size of *C. finmarchicus* and *C. glacialis*, especially in the southern reaches of their sympatric distribution, the reliability of discriminating the two species based on size and morphometrics has been questioned (e.g., Parent et al., 2011; Choquet et al., 2018). However, consistent with our identification, Parent et al. (2011) found none and few *C. finmarchicus*, respectively, at two stations in NW Baffin Bay and the Canadian Archipelago using molecular techniques. The classifier would most likely identify the few *C. finmarchicus* present at the southernmost stations as *C. glacialis*.

Counts of each *Calanus* taxon were binned for each 1 m of the water column, prior to correcting counts for the likelihoods of incorrect identifications (Solow et al., 2001). These likelihoods were determined previously based on visual validations of automatic classifier identifications (Schmid et al., 2016). Corrected counts were used to estimate the abundance (number m⁻²) of the copepodite stages (or stage combinations) for the two species.

The lipid fullness (LF) of *Calanus hyperboreus* and *C. glacialis* in the SCM was estimated from LOKI images of copepods in a suitable lateral orientation following Schmid et al. (2018). LF was calculated as the ratio of the lipid sac area to prosome area times 100 (Vogedes et al., 2010) for 44 C4 and 57 C5 *C. glacialis*, and 72 C4 and 43 C5 *C. hyperboreus*.

**Table 1**: Details of the LOKI deployments. DOI: https://doi.org/10.1525/elementa.388.t1

| Station   | Date (m/d/y) | Local time | Latitude N | Longitude W | Depth (m) |
|-----------|--------------|------------|------------|-------------|-----------|
| NOW West  | 8/16/2013    | 2:40       | 76° 17' 37" | 77° 45' 30" | 275       |
| NOW East  | 8/18/2013    | 10:40      | 76° 12' 57" | 71° 07' 31" | 639       |
| Petermann | 8/22/2013    | 15:30      | 80° 32' 39" | 61° 07' 05" | 838       |
| Kane Basin| 8/25/2013    | 3:15       | 79° 10' 38" | 71° 10' 36" | 185       |
| NS East   | 8/27/2013    | 3:40       | 77° 12' 24" | 73° 15' 21" | 329       |
| NS West   | 8/28/2013    | 23:00      | 77° 11' 36" | 77° 01' 27" | 449       |
Fluorescence, chlorophyll a and light

Water samples collected with the main CTD-Rosette profiler of the ship were analyzed to determine chlorophyll a (Chl a) concentrations at a minimum of 6 depths at each station. Phytoplankton pigments were extracted and analyzed with a Thermo Scientific HPLC system as described in Thaler et al. (2017). The fluorescence signals (FS) recorded by the fluorometers of the CTD-Rosette and the LOKI profiler deployed within the same 30-min period at the same station were strongly correlated (FS_{LOKI} = 0.007 + 0.96 FS_{CTD-Rosette}, r^2 = 0.87, n = 2743). Hence, the HPLC-derived Chl a values were used to transform the fluorescence signal of the LOKI into Chl a concentration. Photosynthetically active radiation (E_{PAR}, µmole photons m^{-2} s^{-1}) at the surface and in the water column was recorded with a Biospherical QCP-2300 mounted on the CTD-Rosette.

To provide background information on the seasonal-spatial development of the surface phytoplankton bloom in the study area, surface Chl a concentration was mapped monthly from April to September 2013 using MODerate resolution Imaging Spectroradiometer (MODIS) level 3 data from the Aqua satellite. This chl a concentration was calculated at a resolution of 4 km/pixel using NASA’s standard algorithms (Hu et al., 2012). Sea ice concentrations at a resolution of 25 km/pixel were derived from Nimbus-7 SMMR and DMSP SSM/1-SSMIS passive microwave data (https://nsidc.org/data/NSIDC-0051).

Statistical analyses

Patchiness and spatial autocorrelation of abundance estimates invalidate the use of traditional parametric statistics to compare the vertical distribution of planktonic organisms sampled simultaneously by nets, pumps, or profilers (Venrick, 1986). W’, a modification of the Kolmogorov-Smirnov statistic insensitive to patchiness (Solow et al., 2000), was used to test for differences between the vertical distributions of Calanus hyperboreus and C. glacialis copepodites. The significance of W’ was tested by randomization (1000 iterations).

Results

Ice break-up and the first detection of surface chlorophyll occurred in April on the Greenland side of the North Water (Figure 3). The surface phytoplankton bloom developed in May and June in the center of the polynya and reached maximum extent in July. Northern Baffin Bay cleared of ice in August. At that time significant concentrations of surface chlorophyll were detected primarily in the open waters of the partially ice-covered Nares Strait (Figure 3). The ice cover started to form again by September.

Copepodite stage composition and distribution

Copepodites of Calanus were more abundant and at a more advanced developmental stage in the North Water and Nares Strait than at the northernmost stations of Kane Basin and Petermann Glacier (Table 2). Calanus hyperboreus C3, C4 and C5 and C. glacialis C4 and C5 dominated numerically at the four stations in the North Water and Nares Strait (Table 2). C1, C2 and females (F) were the most abundant taxa in Kane Basin and at the Petermann Glacier.

Fine-scale vertical distributions of Calanus copepodite stages

The vertical distribution of Calanus copepods in relation to the subsurface chlorophyll maximum (SCM) and incident photosynthetic active radiation (E_{PAR}) levels was documented for three different cases.

Figure 2: LOKI images of target species. The copepodites C4, C5 and female (F) of Calanus hyperboreus and C. glacialis. DOI: https://doi.org/10.1525/elementa.388.f2
Case 1: Low Chl a concentration in low light. At station Kane Basin, Chl a concentration was low (≤1 mg m⁻³) with a weak SCM at 40-m depth (Figure 4). Incident Eᵦ was low (18 µE m⁻² s⁻¹) at the time of the LOKI profile. The abundance of Calanus glacialis C1 peaked in the SCM, with the bulk of this stage distributed between the SCM and 80 m (Figure 4). C. hyperboreus C3–C5 and C. glacialis C4–C5 were distributed between 40 and 120 m with peak abundance immediately under the SCM. Females of the two species presented a similar but slightly deeper (60–140 m) distribution than younger copepodite stages. The dicothermal thermocline and the strong halocline had no obvious influence on the vertical distribution of the copepods (Figure 4). The vertical distributions of C. hyperboreus and C. glacialis males are presented in Figure S1.

Case 2: High Chl a concentration in daylight. Station Peterman Glacier with a well-developed SCM (>5 mg Chl a m⁻³ between 10 and 50 m) was profiled in daytime (15h30, 697 µE m⁻² s⁻¹). While some of the younger copepodite stages (C1 to C3) of both Calanus species were found in the SCM, most of them and the larger stages (e.g., C. hyperboreus C3, C. glacialis C4) were distributed at the base of the SCM and below (Figure 5). Similar patterns of
copepod daytime (10h40, 652 µE m⁻² s⁻¹) vertical distribution in relation to a strongly marked SCM (3 mg Chl a m⁻³, at 30 m) were observed at station NOW East (Figure S2).

**Case 3: Intermediate Chl a concentration in low light.** Stations NOW West, NS West and NS East were sampled during polar twilight (23h00 to 03h40, E₉0, 2–18 µE m⁻² s⁻¹), with Chl a ranging from 1.5 mg m⁻³ to 3.4 mg m⁻³ in the well-developed SCM located between 20 and 40 m. At station NS East, for example, the abundance of *Calanus* copepodes C1 to C5 tracked the Chl a profile, peaking in or around the SCM (Figure 6). Females remained below the SCM. Similar patterns of copepod vertical distribution were observed at stations NOW West and NS West (Figures S3 and S4, respectively).

Vertical co-distributions of *Calanus hyperboreus* and *C. glacialis* at Case 3 stations (NOW West, NS West and NS East) showed that the numerically dominant C4 and C5 copepodes (Table 2) were actively grazing at night in the well-developed SCM. The large *C. hyperboreus* occupied the core of the SCM, while the smaller *C. glacialis* distributed preferably above and below maximum Chl a concentration (Figure 7). For instance, at both NOW West and NS West, *C. hyperboreus* C4 abundance peaked in the SCM, while *C. glacialis* C4 abundance was maximum at intermediate Chl a concentration both above and below the SCM (Figure 7). The same patterns were observed for *C. hyperboreus* and *C. glacialis* C5 at Station NS East. These vertical distributions of same-stage *C. hyperboreus* and *C. glacialis* in the SCM differed significantly, in all instances (*W*, p ≤ 0.006; Figure 7 and Table S1).

The lipid fullness (LF) of *Calanus hyperboreus* in the core SCM reached higher values than those of *C. glacialis* above or under the core SCM (Figure 8). For a given station or when pooled among the three stations (Figure S5), the mean LF of *C. hyperboreus* C4 and C5 in the core SCM was significantly higher than that of *C. glacialis* C4 and C5 at the periphery of the SCM (Welch Two Sample t-test: C4: t = −3.70, p < 0.001; C5: t = −4.77, p < 0.0001).

**Discussion**

**A south-north gradient in ecosystem maturity**

The stations sampled in mid- to late August covered the south–north gradient in decreasing ecosystem maturity often seen in arctic seas in midsummer (e.g., Rabindranath et al., 2010; Ardyna et al., 2013; Gosselin and Poulin, 2016). A deep (25–35 m) SCM with relatively low standing stocks of small microalgae (80 mg m⁻² Chl a within the top 100 m, 10% of cells > 20 µm; Gosselin and Poulin, 2016) grazed primarily by the advanced (C4 and C5) copepodite stages of *Calanus* characterized the southern stations in the North Water (Table 2). Female *Calanus* of both species were already distributed below the SCM even at night, indicating the start of the migration to diapause at depth. By contrast, the northern Petermann Glacier station presented an intense phytoplankton bloom (250 mg m⁻² Chl a within the top 100 m) of relatively large cells (46% of cells > 20 µm; Gosselin and Poulin, 2016) grazed primarily by younger *Calanus* C1–C3 copepodites and females (Table 2). Consistent with previous studies (Klein et al., 2002; Ringuette et al., 2002), the northward propagation of the ice break-up from the North Water in April–May to Kane Basin and beyond in August, explains the late-summer gradient from post-bloom conditions at southern stations to early-bloom conditions in Nares Strait.

### Table 2: Abundance (number m⁻³) of *Calanus* copepodite stages over the water column by station based on LOKI profiles. DOI: https://doi.org/10.1525/elementa.388.t2

| Taxa                        | NOW  | NOW  | NS   | NS   | Kane | Petermann  |
|-----------------------------|------|------|------|------|------|------------|
|                             | East | West | East | West | Basin| Glacier   |
| *Calanus hyperboreus* C3    | 1886 | 1680 | 2620 | 2824 | 868  | 626        |
| *C. hyperboreus* C4         | 8802 | 6002 | 3496 | 5778 | 657  | 502        |
| *C. hyperboreus* C5         | 6614 | 3864 | 2542 | 4020 | 637  | 350        |
| *C. hyperboreus* F          | 722  | 982  | 1838 | 1684 | 1534 | 2422       |
| *C. hyperboreus* M          | —    | —    | —    | —    | 234  | 442        |
| *Calanus glacialis* C1      | —    | 550  | 1202 | 428  | 1304 | 2312       |
| *C. glacialis* C4           | 7156 | 5962 | 3358 | 5220 | 692  | 438        |
| *C. glacialis* C5           | 6802 | 3518 | 2978 | 5378 | 911  | 622        |
| *C. glacialis* F            | 888  | 730  | 1682 | 1996 | 1624 | 2632       |
| *C. glacialis* M            | —    | —    | —    | —    | 277  | 482        |
| *C. hyperboreus* C1/C. glacialis C2 | — | 658  | 1242 | 682  | 1765 | 3042       |
| *C. hyperboreus* C2/C. glacialis C3 | 424 | 942  | 1394 | 756  | 1910 | 2680       |
| Total                       | 33294| 24888| 22352| 28766| 12413| 16550      |

* Latitude of stations increases from left to right.

* Not detected/confirmed absence.
Figure 4: Vertical distributions of *Calanus* at station Kane Basin. Vertical distributions (ind. m$^{-3}$) of *C. hyperboreus* and *C. glacialis* stages (black bars), chlorophyll $a$ (green lines), temperature (red lines), and salinity (cyan lines). Sampling time: 3h15; near surface $E_{PAR}$ 18 $\mu$E s$^{-1}$ m$^{-2}$. DOI: https://doi.org/10.1525/elementa.388.f4
Figure 5: Vertical distributions of *Calanus* at station Peterman Glacier. Vertical distributions (ind. m$^{-3}$) of *C. hyperboreus* and *C. glacialis* stages (black bars), chlorophyll *a* (green lines), temperature (red lines), and salinity (cyan lines). Sampling time: 15h30; near surface *E$_{PAR}$* 697 µE s$^{-1}$ m$^{-2}$. DOI: https://doi.org/10.1525/elementa.388.f5
Figure 6: Vertical distributions of *Calanus* at station NS East. Vertical distributions (ind. m⁻³) of *C. hyperboreus* and *C. glacialis* stages (black bars), chlorophyll *a* (green lines), temperature (red lines), and salinity (cyan lines). Sampling time: 3h40; near surface *E*_{PAR} 2 µE s⁻¹ m⁻². DOI: https://doi.org/10.1525/elementa.388.f6
Figure 7: Fine-scale distributions of *Calanus* in the SCM at Case 3 stations. Abundances (ind. m$^{-3}$) of C4 and C5 *C. hyperboreus* (left panels) and *C. glacialis* (right panels) copepods (black bars) in the subsurface chlorophyll maximum (green lines) at NOW West, NS West, and NS East stations. Each panel inset is a LOKI image of the enumerated copepod, with 1-mm scale bar. The vertical range bars indicate the depth range of the subsurface chlorophyll maximum over which W', which tests for differences between the vertical distribution of the two species, and its statistical significance were computed. See Table S1 for the remaining comparisons of *Calanus* C4 and C5 stages with W' statistic and p-value. DOI: https://doi.org/10.1525/elementa.388.f7
Predator Avoidance Hypothesis and the vertical distribution of Calanus

At our sampling latitudes (76–81°N) in mid- to late August, the midnight sun is ending as the sun increasingly descends on the horizon at night, and some twilight develops. The resulting daily variations in irradiance at the depth of the SCM were sufficient to trigger a DVM in actively grazing C4 and C5 stages of Calanus that are completing their lipid reserves before overwintering at depth (e.g., Schmid et al., 2018). At any one time, only part of the populations of Calanus copepodites partake in the grazing diel migration. The non-migrating fraction of the population is interpreted as satiated individuals remaining at depth in low Chl a concentration and where predation pressure is low (e.g., Pearre, 2003; Ringelberg, 2010).

All three types of vertical distributions observed at the different stations were consistent with the Predator Avoidance Hypothesis which predicts that if, and only if, the energy gain from grazing in high microalgal concentrations offsets the cost of vertical migrations, grazers will migrate up into the food-rich surface waters at night and migrate down and out of the euphotic zone in daytime to avoid visual predators (Lampert, 1989; DeMeester et al., 1999; Fortier et al., 2001). At station Kane Basin at night (Case 1) the Chl a gradient between the SCM and the deeper layers was likely insufficient to trigger a feeding...
migration (Gliwicz and Pijanowska, 1988; Lampert, 1989; Hays, 2003). At stations NOW East and Petermann Glacier sampled during the day (Case 2), the large *C. hyperboreus* and *C. glacialis* remained at depth despite higher phytoplankton concentrations in the SCM, likely to avoid visual predators, in particular the abundant planktivorous seabirds nesting and foraging in the area in August (e.g., Karnovsky et al., 2008). In agreement with previous reports (Brooks and Dodson, 1965; Fortier et al., 2001; Hays, 2003; Daase et al., 2015; Schmid et al., 2018), the largest *Calanus* developmental stages, most susceptible to predation, showed the strongest avoidance behavior by moving deeper where illumination is further reduced, while smaller and less conspicuous taxa remained in the SCM.

Conditions of low light and abundant food in the SCM (Case 3) conducive to active nighttime grazing by herbivorous copepods (Daase et al., 2008, 2015; Falk-Petersen et al., 2008; Rabindranath et al., 2010; Baumgartner et al., 2011; Berge et al., 2014) prevailed at stations NS East, NS West and NOW West. At these stations, the distributions of all *Calanus* taxa, except females, generally aligned with the Chl *a* profile, with copepod abundances peaking in the SCMs. The resulting distributions again were consistent with the predictions of the Predator Avoidance Hypothesis (Gliwicz and Pijanowska, 1988; Lampert, 1989; DeMeester et al., 1999; Fortier et al., 2001). At this stage in the maturation of the ecosystem, *Calanus* females, the exception that confirms the rule, had acquired the full lipid load necessary to overwinter and had stopped migrating to the SCM to feed (Schmid et al., 2018).

**Fine scale vertical habitat partitioning in the SCM**

Using an electronic counter based on the Coulter principle and carried by a horizontally-towed, vertically-oscillating vehicle, Herman (1983) showed how *Calanus hyperboreus* C5 distributed in the subsurface chlorophyll maximum (SCM), while *C. glacialis* and *C. finmarchicus* C5 distributed on average above the SCM, presumably at the calculated depth of maximum phytoplankton productivity. Our results confirm the concentration of grazing *C. hyperboreus* C4 and C5 in the core SCM. *C. glacialis* C4 and C5, however, were found both above and below the peak SCM. This pattern suggests some foraging interference, with the large *C. hyperboreus* excluding the smaller *C. glacialis* from peak Chl *a* concentrations in the center of the SCM and relegating its congener to medium food availability above and below the SCM.

The Ideal Free Distribution (IFD) model predicts that under density-dependent competition (or interference) animals of equal competitive abilities foraging on a continuously renewed food resource (continuous input situation) will spread spatially in proportion to the available resource so as to minimize competition and maximize individual gain in energy (Fretwell and Lucas, 1969). However, when phenotypes of unequal competitive abilities exploit such a food source and the payoff of a given competitor is reduced by the addition of other competitors to the patch, the best phenotypes should occupy the best patches of food and therefore gain some fitness advantage (Parker and Sutherland, 1986). In the present study, continuous phytoplankton production at the nitracline replenished the SCM (Martin et al., 2010), thus maintaining the sub-surface maximum in the microalgal food of *Calanus* congeners (a continuous input situation). While the two *Calanus* congeners are morphologically nearly identical (Figure 2), C4 and C5 of *C. hyperboreus* are 4.4 and 3.2 times heavier, respectively, than the corresponding *C. glacialis* (for C4: 457 vs 104 μg C, for C5: 1022 vs 320 μg C; Forest et al., 2011). Assuming that a larger size provides some competitive advantage, the monopolization of the richer core of the SCM by the larger *C. hyperboreus* is consistent with the first prediction of the IFD model for two phenotypes of unequal competitive abilities (Parker and Sutherland, 1986). Because their food is diluted, the larger the copepod, the more food limited it tends to be in situ (Saiz and Calbet, 2007; Kiorboe, 2011). As well, the amplitude of diel vertical migrations of copepods increases with size (Fortier et al., 2001; Eiane and Ohman, 2004). This dependence of feeding and migrations on size led Kiorboe (2011) to conclude that “Large zooplankters may compensate for the declining specific clearance rate by being better able to find and utilize patches of food on a larger scale than smaller zooplankters — hence increasing their feeding rates — or by being better able to avoid predation, e.g. through diurnal vertical migration — hence decreasing their mortality rate”. The observed co-distribution of grazing *C. hyperboreus* and *C. glacialis* in the SCM is consistent with this conclusion.

A second prediction of the IFD model is that the large phenotype *C. hyperboreus* grazing in the core SCM will gain some fitness advantage over the small phenotype *C. glacialis* grazing at the periphery of the SCM (Parker and Sutherland, 1986). *C. hyperboreus* grazing in the SCM attained a higher relative lipid load than *C. glacialis* grazing at the periphery. On average, *C. hyperboreus* starts to migrate to diapause earlier and at lower lipid fullness (~50%) than *C. glacialis* (~60%) of the same developmental stage (Schmid et al., 2018). Grazing in the rich core SCM may enable *C. hyperboreus* to initiate the seasonal migration to depth earlier than *C. glacialis*. An earlier migration to depth would reduce exposure to visual predators such as seabirds and fish in the surface layer. Hence, *C. hyperboreus* could achieve some fitness advantage over *C. glacialis* by monopolizing the core rich SCM, although the smaller size and thus lesser vulnerability of *C. glacialis* to predation would compensate some of this advantage.

Alternatively, the vertical partitioning of grazing *Calanus hyperboreus* and *C. glacialis* in the SCM could reflect some differential distribution of their respective preferred food. *Calanus* copepods exhibit a strong selectivity for larger phytoplankton cells and some selectivity for phytoplankton species (e.g., Mullin, 1963; Frost, 1972). Moreover, *Calanus* will readily feed on microzooplankton (see Campbell et al., 2016, for a review). Recent research has shown that different phytoplankton taxa occupy different vertical niches within the SCM (Monier et al., 2015; Latasa et al., 2016). Thus, grazing *C. hyperboreus* and *C. glacialis* may be
choosing their vertical position in the SCM according to the distribution of a preferred cell size, phytoplankton taxon or microzooplankton prey. Health and nutritional quality, for instance, the lipid content of the different prey, may also influence the distribution of the grazers. Advances in the development of microplankton underwater imaging systems (e.g., Orenstein et al., 2015) should soon allow a taxonomic comparison of the fine-scale vertical distribution of zooplankton grazers and their food across the SCM.

Parametric statistics cannot be used to compare the vertical distribution of patchy variables sampled simultaneously by the same instrument (Venrick, 1986). Non-parametric tests robust to patchiness have been proposed for both the case of un-replicated (Solow et al., 2000) and replicated (Beet et al., 2003) profiles. In the present exploratory study, the three stations representing Case 3 cannot be considered replicates as the SCM differed in vertical position and width (Figure 7). Hence, W‘ for un-replicated profiles (Solow et al., 2000) was used to confirm that the vertical distributions of C. glacialis and C. hyperboreus in the SCM were different. Unfortunately, W‘ does not test for the precise hypothesis of exclusion (negative correlation or contingency) of C. glacialis from the SCM by C. hyperboreus. However, given the general agreement of the co-distribution of Calanus congeners in the SCM reported here and by Herman (1983), and the repetition of the inverse distribution at the three stations where the two species actively grazed in the SCM, we believe that the observed exclusion patterns warrant further investigation to distinguish between competitive grazing, size-dependent fitness advantage, and prey specificity as the underlying explanations for the observed distributions of these key species in the northern Baffin Bay ecosystem. In particular, climate change would likely affect the aforementioned three possible scenarios differently. In a scenario where the observed distribution patterns are due to the prey preference of Calanus, climate change-induced shifts in the phytoplankton cell size spectrum could lead to changes in copepod co-distributions, with unknown consequences. Where the observed co-distributions are driven by competition and size, copepod co-distributions would likely be affected more indirectly through their feeding success and growth. Ultimately, further study of the fine-scale distributions of these key species will improve understanding of climate change impacts on Arctic marine ecosystems.

Data Accessibility Statement

Data on vertical distributions of copepods, copepod lipid fullness, and chl a, as well as R-code can be found at: https://zenodo.org/record/2535745; DOI 10.5281/zenodo.2535745.

Supplemental files

The supplemental files for this article can be found as follows:

- Table S1. Modified Kolmogorov-Smirnov (K-S) tests for detecting the significant difference of two plankton profiles. The remaining three combinations of Calanus pairings at case 3 stations are shown, including the W‘ statistic, p-value, as well as the range of the subsurface chlorophyll maximum (SCM), indicating the vertical range over which the tests were performed. The modified K-S test is insensitive to patchiness. DOI: https://doi.org/10.1525/elementa.388.s1
- Figure S1. Vertical distributions (ind. m–3) of Calanus males at station Kane Basin. Calanus hyperboreus and C. glacialis males (black bars), chlorophyll a (green lines), temperature (red lines), and salinity (cyan lines). Sampling time and near surface Ew were 3h15 and 18 µE s–1 m–2, respectively. DOI: https://doi.org/10.1525/elementa.388.s1
- Figure S2. Vertical distributions (ind. m–3) of Calanus at station NOW East. Calanus hyperboreus and C. glacialis stages (black bars), chlorophyll a (green lines), temperature (red lines), and salinity (cyan lines). Sampling time and near surface Ew were 10h40 and 652 µE s–1 m–2, respectively. DOI: https://doi.org/10.1525/elementa.388.s1
- Figure S3. Vertical distributions (ind. m–3) of Calanus at station NOW West. Calanus hyperboreus and C. glacialis stages (black bars), chlorophyll a (green lines), temperature (red lines), and salinity (cyan lines). Sampling time and near surface Ew were 2h40 and 18 µE s–1 m–2, respectively. DOI: https://doi.org/10.1525/elementa.388.s1
- Figure S4. Vertical distributions (ind. m–3) of Calanus at station NS West. Calanus hyperboreus and C. glacialis stages (black bars), chlorophyll a (green lines), temperature (red lines), and salinity (cyan lines). Sampling time and near surface Ew were 23h00 and 11 µE s–1 m–2, respectively. DOI: https://doi.org/10.1525/elementa.388.s1
- Figure S5. Frequency distributions of Calanus lipid fullness at Case 3 stations. Individual values of lipid fullness (LF) for C4 and C5 Calanus hyperboreus and C. glacialis were pooled for the three stations representing Case 3. Only individuals found in the subsurface chlorophyll maximum are considered (same individuals as in Figure 8). The black and grey solid lines are the Gaussian Kernel smoothed density curves of LF for C. hyperboreus and C. glacialis, respectively. DOI: https://doi.org/10.1525/elementa.388.s1

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Competing interests
The authors have no competing interests to declare.

Author contributions
• Approved the submitted version for submission: MS, LF
• Drafted and/or revised the article: MS, LF
• Contributed to analysis and interpretation of data: MS, LF
• Contributed to acquisition of data: MS, LF
• Contributed to conception and design: MS, LF
• Contributed to acquisition of data: MS, LF

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