From fringe to basin: unravelling the survival strategies of *Calanus hyperboreus* and *C. glacialis* in the Arctic Ocean

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ABSTRACT: The large calanoids *Calanus hyperboreus* and *C. glacialis* dominate the zooplankton biomass in the central Arctic Ocean (CAO), but the absence of early life stages has raised speculation whether they complete their life cycle there, or whether they represent expatriates advected from adjacent regions. Our study, conducted across 2 transects of the CAO during fall 2011, focused on the distribution, stage composition, dry weight, individual lipid content, and egg production of these species. Although reproductive activity and early developmental stages were observed only on the fringes of the deep basins, late-stage copepodite and adult female abundances remained steady across the study area for *C. glacialis* and increased away from the shelves for *C. hyperboreus*. We found no decline in lipid content or dry weight in adult *C. glacialis* away from productive regions and only a minor reduction in adult *C. hyperboreus*. However, the lipid content and dry weight in C5 copepodites significantly decreased away from the shelf break, particularly in *C. hyperboreus*. This suggests that although early life stages struggle to survive in the resource-limited conditions of the deep CAO and even subadults remain vulnerable to starvation, adults have the resilience to survive long enough to be eventually transported by ocean currents to more favourable regions for reproduction. As such, we suggest that both species of *Calanus* are neither 'residents' nor 'expatriates' in the Arctic basins, but rather ontogenetic migrants that take advantage of different habitats within the Arctic Ocean to maximise their survival and reproductive success.

KEY WORDS: *Calanus* · Central Arctic · Zooplankton · Lipids · Dry weight · Biogeography

1. INTRODUCTION

The large copepods *Calanus hyperboreus* and *C. glacialis* dominate the mesozooplankton biomass in the central Arctic Ocean (CAO) (Kosobokova & Hirche 2001, 2009, Hopcroft et al. 2005) and thus play a key role in the Arctic food web. Due to low temperatures and short periods of food availability, both species have adapted multi-year life cycles with several stages able to enter a diapause (Conover 1988, Hirche 1998, 2013). Reaching a developmental stage capable of diapause with sufficient reserves at the end of summer (predominantly stage C3 for *C. hyperboreus* and C4 for *C. glacialis*) is critical to survive the long overwintering period and for subsequent completion of their life cycle. Large lipid reserves are also required in female *C. hyperboreus* to fuel reproduction (Hirche & Niehoff 1996, Hirche 2013), while in *C. glacialis*, only the beginning of the spawning period is fuelled by internal reserves (Smith 1990, Hirche & Kattner 1993, Kosobokova & Hirche 2001). This bet-hedging strategy helps to synchronize the first feed-

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ing naupliar stages with the spring phytoplankton or ice-algal bloom.

Calanus species are broadly distributed across the entire Arctic Ocean (Kosobokova 2012). However, the absence of early developmental stages (Dawson 1978, Rudyakov 1983), low abundances in the basins (Wassmann et al. 2015, Kvile et al. 2018, Ershova et al. 2021), and observations of low ingestion rates (Olli et al. 2007) have led to the conclusion that both *C. hyperboreus* and *C. glacialis* cannot maintain permanent populations in the CAO. Instead, they represent expatriated populations (Ekman 1953, Beklemishev 1976) that require permanent advection from neighbouring shelf regions having better feeding conditions (Ashjian et al. 2003, Kvile et al. 2018). Similar conclusions were drawn from models (Ji et al. 2012, Wassmann et al. 2015, Feng et al. 2016). Other authors distinguished *C. glacialis* as a species associated with the more productive shelf waters of the Arctic seas (Carstensen et al. 2012) from *C. hyperboreus* as primarily a species of the CAO basin (Conover 1988). This paradigm has been recently reconsidered by Ershova et al. (2021), who suggested that *C. glacialis* was a seasonal ice zone associated species, rather than a shelf species, and its distribution range may be changing together with the changing ice conditions of the Arctic. Nonetheless, data coverage on Arctic *Calanus* congeners is still poor and often regionally and seasonally limited (Freer & Tarling 2023), especially within deeper strata where animals typically diapause, as most surveys only sample the upper 200 m (Thibault et al. 1999, Olli et al. 2007, Freer & Tarling 2023). A synoptic assessment of the physiological state of *Calanus* or their dry weight/lipid content in the Arctic Ocean is also missing.

Here we present a broad-scale assessment of the abundance and physiological condition of the Arctic's 2 most important copepod species, *C. hyperboreus* and *C. glacialis*, based on 2 transects from the Eurasian shelves to the deep basins of the CAO, using samples of the entire water column from the 2011 expedition of RV 'Polarstern' (ARK XXVI/3) collected during August/September at the end of the growth season. We used stage composition and egg production as an index for population development, while measurements of dry weight (DW) and lipid content of older copepodite stages and adult females were used to estimate the precondition for overwintering and subsequent reproduction. Our goal was to document the distribution of these 2 species during a period of extreme changes in climate and ice cover, and to shed light on their survival strategy within the harsh environment of the central Arctic. We discuss our findings in the context of other recent published works on *Calanus* distribution in the Arctic and speculate whether these species are basin 'residents' that are able to complete their life cycle and sustain stable populations within the deep Arctic Ocean, or whether they represent expatriated individuals from the Arctic's marginal seas.

2. MATERIALS AND METHODS

2.1. Environmental conditions

The hydrography and water mass properties (temperature, salinity, and oxygen concentration) of the sampled transects are described elsewhere (Schauer 2012). Chlorophyll *a* (chl *a*) values for the sampled stations were obtained from the data set published on PANGAEA (Nöthig et al. 2015). These were collected at depths of 0, 10, 25, 50, 75, 100, 150, and 200 m, and were subsequently averaged across the upper 50 m. Sea ice concentrations at each station were obtained from cruise observation data (Schauer 2012).

2.2. Zooplankton sampling

Zooplankton were collected during the ARK-XXVI/3 (TransArc) cruise onboard RV 'Polarstern' in August—September 2011. In total, 29 stations were sampled from the shelf north of Franz Josef Land across the Eurasian basins, the North Pole, and the Makarov Basin to the Canada Basin (Fig. 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m745p041_supp.pdf). For establishing species composition and distribution, zooplankton were collected by a multiple closing net (Multinet MAXI, 0.5 m² mouth opening; Hydrobios). The Multinet was equipped with 9 nets (150 μm mesh) that collected stratified samples of the entire water column from the surface to ca. 10 m above the seafloor. Nine standard depth intervals were sampled: 0—25, 25—50, 50—100, 100—200, 200—500, 500—1000, 1000—2000, 2000—3000 m, and 3000 m—bottom. Samples were preserved in 4% borax-buffered formalin. Animals used for experiments and DW and lipid measurements were collected with a Bongo net (mesh 330 μm) that was deployed to 200 or 300 m at Stations (Stns) 188 to 245 (Fig. 1; Table S1). Thereafter, to reduce wire-time, we fashioned a frame of 0.5 m² which was mounted beside the mouth of the Multinet and fitted it with a 150 μm net and a non-filtering cod-end to
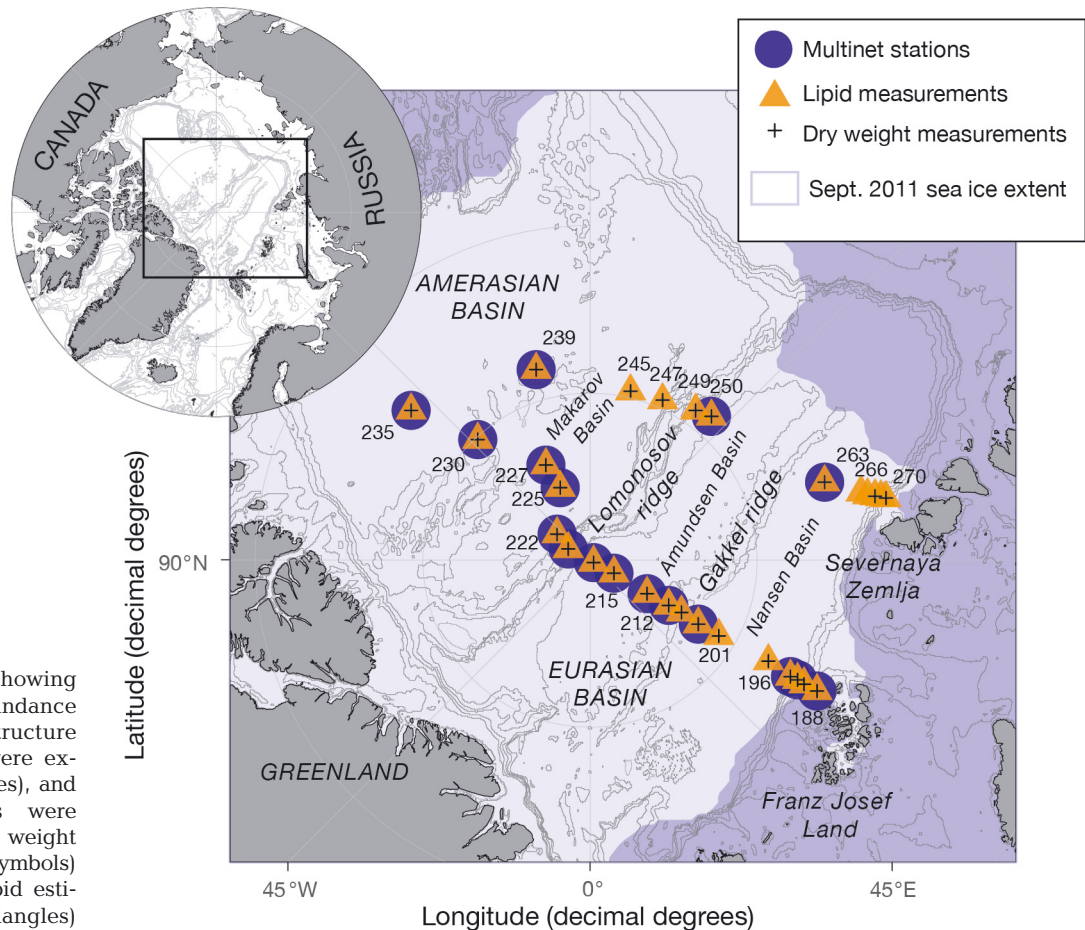
Fig. 1. Study area, showing stations where abundance and population structure of *Calanus* spp. were examined (blue circles), and where individuals were collected for dry weight measurements (+ symbols) and imaged for lipid estimation (orange triangles)

yield live material. All samples were diluted with filtered seawater and kept in a cold room at 0°C until sorting.

2.3. Species identification and length measurements

Formalin-preserved samples were analysed under a stereomicroscope to species level, typically with the whole sample being counted. In a few cases, the sample was split quantitatively in such a way that a minimum of 100 individuals of the most common species were present in the lowest split with increasingly larger fractions examined for less abundant taxa. The prosome length of *Calanus* copepodite stages and adults was measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment and was used to distinguish *Calanus* species, according to Hirche (2013). Body pigmentation (antennule and genital somite 'redness') was also used as an additional criterion, since most samples were pro-

cessed on board the vessel soon after collection, and copepods still retained their initial colour. The combination of these 2 criteria works perfectly for distinguishing *C. finmarchicus* and *C. glacialis* in the central Arctic Basin, as differences in size and 'redness' are pronounced. The correctness of our earlier identifications has been confirmed by molecular tools in several locations in the CAO (see Choquet et al. 2017, their Fig. 2).

2.4. Dry weight

For lipid and DW measurements, typically 50 individuals each of copepodite stage 5 (C5) and adult females (AF) of both *C. hyperboreus* and *C. glacialis* were randomly selected under a stereomicroscope from the live samples at each station. The animals were positioned laterally in shallow water within glass embryo dishes and imaged with a 4 MPx colour mosaic camera (Spot Insight, Diagnostic Instruments). The sorted specimens were then rinsed briefly with

distilled water, placed on pre-weighed tin cups, and frozen at −25°C. Two replicates of 25 individuals of each species/stage were typically preserved in this way. These samples were dried at 60°C for 48 h, and their DW was measured on a Sartorius microbalance to the nearest 0.01 mg.

2.5. Length and lipid volume

Lipid volume and body length were measured in all individuals that were used for DW measurements. Linear measurements from all individuals in each image (~200 animals per station) were completed with the camera's software, whereas area measurements were undertaken using the 'Quick-selection' tool in Adobe Photoshop. To calculate lipid sac volume, we applied the method described by Coleman (2022). We assumed that the lipid sac is best represented as a cylinder, and then divided the measured lipid sac area by the measured lipid sac length to find the average height (i.e. diameter) of the cylinder. This was done in order to account for the varying height and shape of the lipid sac. We then used this average diameter to estimate the volume of the lipid sac:

$$V = \Pi \times (\text{average diameter of lipid sac}/2)^2 \times \text{length of lipid sac} \tag{1}$$

Lipid volume was converted into mass using a lipid density of 0.9 mg mm^{-3} determined for *C. finmarchicus* (Miller et al. 1998).

2.6. Egg production experiments

Egg production experiments were set up for *C. glacialis* during the first 9 stations; thereafter, the ovaries of all individuals were visibly immature, hence no experiments were conducted. Typically, 48 single females were incubated for at least 48 h in 15 ml cell wells that were inspected for eggs every 12 h, with any eggs removed to avoid cannibalism. In female *C. hyperboreus*, the ovaries were immature at all stations, therefore no egg production experiments were conducted.

2.7. Statistical analysis

All data analyses were conducted in R version 4.1.2 (R Core Team 2017). The distribution in individual lipid content was visualised as density plots for each species/stage. Deviations from normality were quan-

tified as distribution skewness, with values of 0 indicating normality, negative values indicating a left-skewed distribution, and positive values indicating a right-skewed distribution. Mean individual DW was compared to mean individual lipid weight at each station using simple linear regression, both as a way of validating each measurement method, and to examine inter-stage and inter-species differences in this relationship. The mean individual DW was also compared to published literature values for each species and stage.

The relationships between lipid weight and station depth, ice cover, and chl *a* were explored using generalised linear mixed models (GLMMs) using the R package 'glmmTMB' (Brooks et al. 2017), with station included as a random term. These were fitted with the Tweedie distribution (log-link), which is a flexible distribution type suitable for non-negative, highly right-skewed data (Dunn & Smyth 2008). All 3 explanatory variables were included in the original model, and the best model was selected via Akaike's information criterion (AIC) (Akaike 1974). The resulting models were validated by plotting the Pearson residuals against fitted values, sampling stations, and all covariates. Absence of remaining spatial and temporal trends was validated by plotting the residuals against sampling date and latitude. The generalised R^2 was defined as the difference between the null deviance and the residual deviance, divided by the null deviance. Since there were only 2 DW measurements per station for each species/stage, the relationship of DW to physical variables was fitted as a generalised linear model (GLM) with a Gamma distribution.

3. RESULTS

3.1. Environmental conditions

Sea ice concentrations during the expedition ranged from completely open water at Stns 269–270 north of Severnaya Zemlja to 100% ice cover over the Lomonosov Ridge and in the Makarov Basin, but typically were between 70 and 90% at most stations (Fig. 2a). Ice thickness varied from <1 m at some stations in the Eurasian Basin to 2.8 m in the Makarov Basin. Overall, the ice concentration and thickness were highest over the Amerasian Basin stations relative to the Eurasian Basin, although the 3 stations over the Gakkel Ridge also had very thick ice (>2 m) compared to surrounding stations. Sea ice concentration was moderately correlated with increasing depth
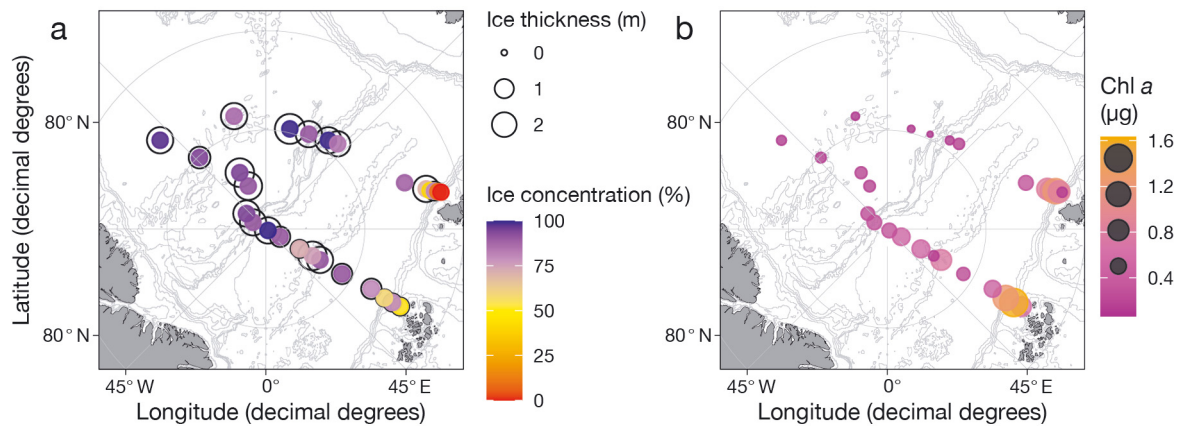
Fig. 2. (a) Sea ice conditions (concentration and thickness) and (b) chlorophyll *a* concentration (integrated across upper 50 m) at the examined stations

(r = 0.53) and increasing distance to the shelf break (r = 0.69).

Chl *a* concentrations were low during the expedition, with values ranging from 0.1 to 1.64 µg l^{-1} (Fig. 2b). The highest concentrations were observed at the stations near the continental slope and the lowest in the Amerasian Basin. Chl *a* values were inversely correlated to ice thickness (r = −0.52) and distance to shelf break (r = −0.71).

3.2. Abundance and population structure of *Calanus glacialis* and *C. hyperboreus*

Total *C. glacialis* abundance typically varied from 500 to 2000 ind. m^{-2}, with Stn 188 on the shelf having an exceptionally high abundance of >100 000 ind. m^{-2} (Fig. 3; Table S2). The lowest abundances were in the Amundsen Basin. Early developmental stages (C1−C3) were found in extremely high numbers on the shelf at Stn 188 and were nearly absent elsewhere (Fig. 3a). Abundances of stages C4−C5 were also highest on the shelf and the basins' perimeters and declined sharply in deeper waters, again with a minimum observed in the Amundsen Basin (<100 ind. m^{-2}). In contrast, AF maintained relatively steady numbers (300−1500 ind. m^{-2}) across the entire study area. AF dominated the *C. glacialis* population at all stations, with the exception of those in the shelf and slope region (Fig. 3a). Adult males were nearly absent at all stations (Table S2).

Overall, *C. hyperboreus* abundance varied between 900 and 5000 ind. m^{-2} and was typically higher than that of *C. glacialis*, with the exception of Stn 188 on the shelf (Fig. 3b; Table S2, Fig. S1). High numbers of early life stages (C1−C2) were only observed at 1 station in the Amundsen Basin (4200 ind. m^{-2}) and were

absent or only observed as single individuals elsewhere (Fig. 3b). The C3 stage was only found in high numbers (500−2000 ind. m^{-2}) at the 3 stations close to the shelf break, with abundances of this stage in the basins never exceeding 100−150 ind. m^{-2}. C4−C5 copepodites were the dominant stages at most stations and were evenly distributed across the study area, with abundances ranging from 500 to 3000 ind. m^{-2}. Abundances of AF ranged from 150 to 700 ind. m^{-2} and were highest within the deep basin stations and lowest on the shelf (Fig. 3b). Similar to *C. glacialis*, adult males were also nearly absent from the samples (Table S2).

3.3. Vertical distribution

In general, the *C. glacialis* population was much shallower in the water column than *C. hyperboreus* (Fig. 4; Table S3), with 49.5% of all *C. glacialis* stages between 0 and 50 m and only a very small portion (ca. 3%) below 200 m. In contrast, 30.4% of the *C. hyperboreus* population were found below 200 m, with some individuals found even in the deepest layer sampled (i.e. 3000−4000 m). Nonetheless, some variability in the vertical distribution of *C. glacialis* was observed, with the population at stations near the shelf concentrated in the surface 10 m, while further in the basins, they were typically concentrated at 25−50 m depth.

C. hyperboreus exhibited a variety of vertical distribution patterns across the study area. While at most stations, the largest part of the population was concentrated in the upper 50 m (Fig. 4; Table S3), the density in the deeper layers was highly variable. For example, at stations in the Amundsen Basin (Stns 212− 222) the population often split, with maxima observed both in the uppermost layer and between 500 and
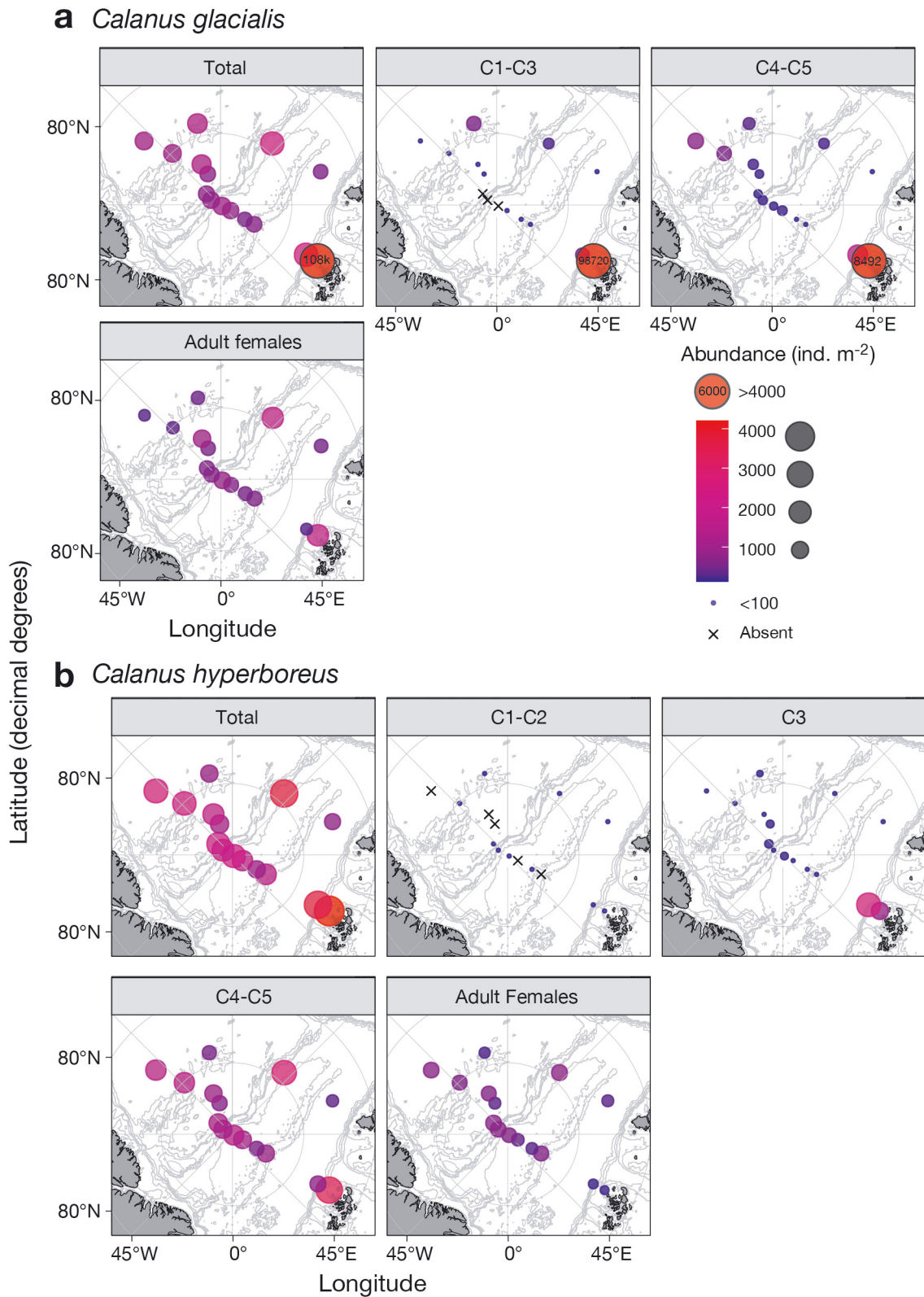
Fig. 3. Total and developmental stage depth-integrated abundance of (a) *Calanus glacialis* and (b) *C. hyperboreus* in the study area. Note that bubble colour and size both indicate abundance values for better clarity
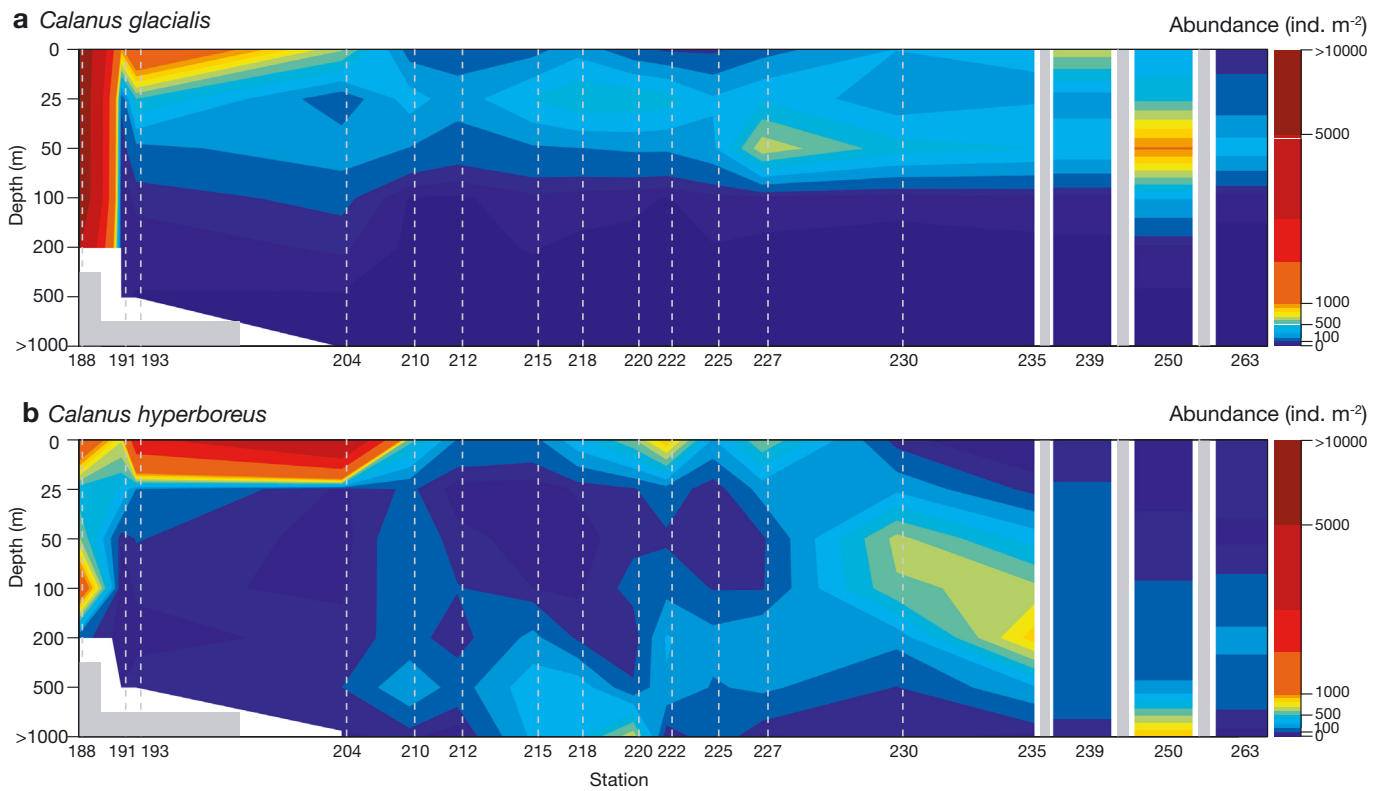
Fig. 4. Vertical distribution of (a) *Calanus glacialis* and (b) *C. hyperboreus* across the study area. Dashed lines indicate station locations; solid lines between stations indicate stations outside of the main transect (for station locations, see Fig. 1). Note the non-linear scales of both depth and abundance ranges

2000 m. Maxima at intermediate depths were observed in the Canada Basin (Stns 230−239), while at Stns 220 and 250, the population was concentrated in the deepest sampled layers, below 2000 and 3000 m, respectively.

3.4. Physiological condition

For the C5 stage, mean individual DW varied between 0.4 and 1.2 mg in *C. glacialis* and between 1.0 and 4.1 in *C. hyperboreus*, while mean lipid weight was estimated as 0.13−1.2 mg in *C. glacialis* and 0.2−1.6 in *C. hyperboreus* (Fig. 5). For AF, mean individual DW varied between 0.8 and 1.5 mg in *C. glacialis* and between 2.9 and 6.5 in *C. hyperboreus*, while mean lipid weight was estimated as 0.4−1.0 mg in *C. glacialis* and 1.0−4.6 in *C. hyperboreus*. There was a strong and significant (p < 0.001) correlation between mean DW and mean estimated lipid weight, with the relationship slightly stronger in C5 (R^2 = 0.95) than in AF (R^2 = 0.84) for both species (Fig. 5a). In *C. glacialis*, the slope of the regression line between lipids and DW was similar for C5 and AF, but the intercept was higher in AF, indicating that females had a consistently higher DW at the same lipid content. In *C. hyperboreus*, both the slope and intercept were different between the stages, with the slope being much steeper for AF. Unlike *C. glacialis*, there was almost no overlap in weight or lipid content between the 2 stages for this species.

At the individual level, a large spread in lipid fullness was observed for both species and stages (Fig. 5b). The C5 stage of *C. glacialis* had a bimodal distribution of individual lipid weight (Fig. 5b), with 2 distinct groups of very lipid-rich vs. very lipid-poor animals. The lipid weight in the more numerous lipid-rich C5 group overlapped completely with AF. The C5 copepodites of *C. glacialis* also had the highest total proportion of lipids, averaging about 65−75% of DW (Fig. 6). In contrast, AF of *C. glacialis* had a relatively small range of lipid fullness across individuals that followed a normal distribution (Fig. 5b; Fig. S1). Lipids in this group typically composed 60−65% of DW.

The C5 copepodites of *C. hyperboreus* had a wide range in individual lipid values (0.1−3.8 mg), but
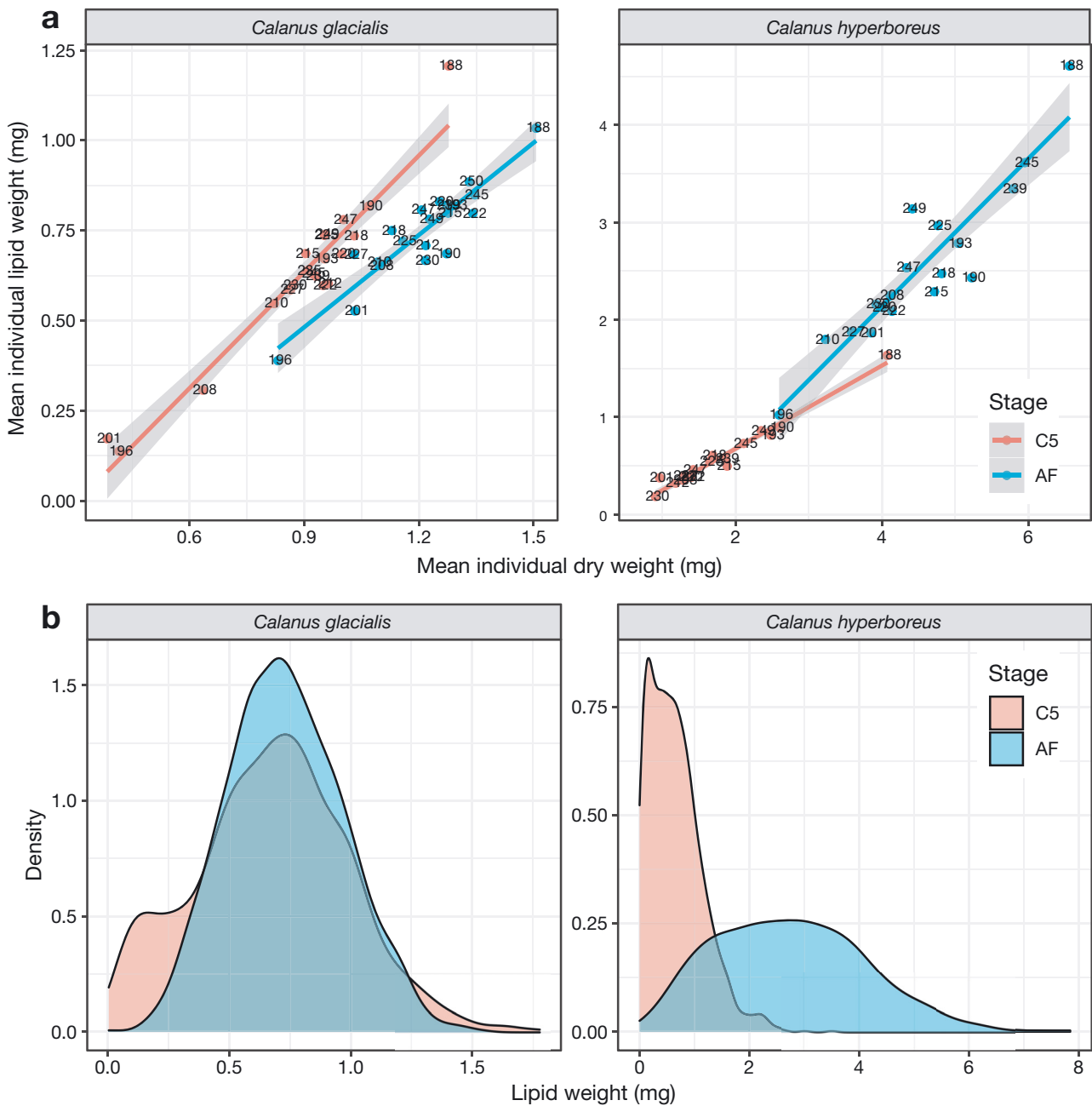
Fig. 5. (a) Mean individual dry weight (DW) vs. mean individual lipid weight at each station for C5 copepodites and adult females (AF) of *Calanus glacialis* and *C. hyperboreus*. Solid lines indicate the linear regression between the 2 parameters and the gray bar is the 95% confidence interval of the regression line. (b) Distribution of individual lipid weight in C5 copepodites and adult females (AF) of all individuals of *Calanus glacialis* and *C. hyperboreus* across the study area

their distribution was sharply skewed, with lipid-poor animals far outnumbering the lipid-rich ones across the study area (Fig. 5b; Fig. S2). This skewness was most pronounced at the deep basin stations, and least pronounced or absent at the stations close to the shelf and slope (Fig. S3). On average, lipids composed only 30% of the DW in this group (Fig. 6). AF

of *C. hyperboreus* also showed a slight skewness of individual lipid weight toward lipid-poor, but it was much less pronounced than for the C5 stage (Fig. 5b; Fig. S2). Overall, there was a large range in individual lipid values within this group (0.1–7.8 mg), and on average, lipids made up 50–60% of their DW (Fig. 6).
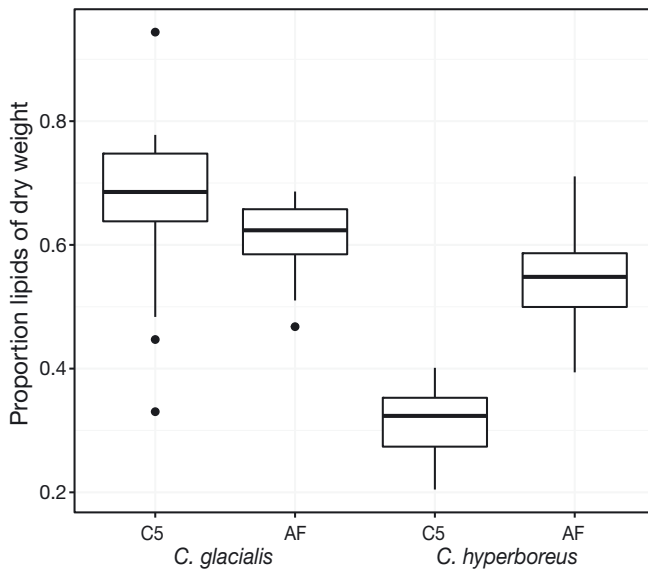
Fig. 6. Proportion of lipids to total dry weight in C5 copepodites and adult females (AF) of *Calanus glacialis* and *C. hyperboreus* for all individuals across the study area. Bar: median; box: interquartile range (IQR); whiskers: max./min. values ≤1.5 × IQR above/below box; dots: outliers

3.5. Environmental drivers of lipid concentration and DWs

In *C. glacialis* C5 copepodites, both lipid content and DW declined significantly with bottom depth (Fig. 7; Fig. S4, see model summary in Table S4), although no relationship was detected with distance to shelf break, sea ice cover, or chl *a*. AF demonstrated no changes in lipid content or DW across any of the examined variables. AF of *C. hyperboreus* showed a decline in both lipid content and DW with bottom depth and increasing sea ice concentration, although the best GLMM via AIC included only depth (Fig. 7; Fig. S4, Table S4). The trend was even more pronounced in the *C. hyperboreus* C5 stage than in adults; the best model predicting lipid content in this stage included depth and chl *a* distribution (Fig. 7; Figs. S3 & S5, Table S4). In all models, the conditional R^2 was much higher than marginal R^2, highlighting the high station-to-station variability.

3.6. Egg production experiments with *C. glacialis*

C. glacialis produced eggs only at the first 4 stations (Table 1, only data from stations where eggs were produced) situated along the transect from the Franz Josef Land shelf to the Nansen-Gakkel Ridge (Stns 188−210). These experiments were undertaken dur-

ing the first half of August. Egg production ranged from 0.6 to 9.6 eggs female^{-1} d^{-1}, with highest values occurring at Stns 190 and 191.

4. DISCUSSION

By definition, resident species are those that are able to maintain an independent population without external supply (Ekman 1953), and there has been ongoing speculation whether both Arctic *Calanus* species, *C. glacialis* and *C. hyperboreus*, are residents in the CAO or if they represent expatriated populations that are advected from neighbouring regions (Olli et al. 2007, Ji et al. 2012, Feng et al. 2016, Kvile et al. 2018). While this may seem entirely semantic, such distinctions are critical for predicting future trajectories for these species within a changing Arctic Ocean, as well as for setting appropriate parameters and boundaries within modelling studies. In the following sections, we discuss the interplay between the distribution of these 2 species, their physiological conditions, and the broader ecological implications of their survival and reproduction strategies. We argue that while reproduction and growth of both species in the CAO are limited, they nonetheless do not represent a dead-end expatriated population. On the contrary, the deep basins may provide refugia for mature adults which allow them to avoid predation and serve as a resupply source for the productive marginal seas.

4.1. Population structure and distribution

Both *Calanus* species were unevenly distributed throughout the study domain. The total abundance of both species peaked at the stations on the outer shelf and continental slope, then dropped dramatically away from the slope. Consistent with the notion that both species originate on the shelf/slope area (Wassmann et al. 2015, Feng et al. 2016, Kvile et al. 2018), we observed very few individuals of developmental stages earlier than C4 in *C. glacialis* or C3 in *C. hyperboreus* anywhere in the basins. Similar to prior studies (Kosobokova & Hirche 2001, Kosobokova 2012, Ershova et al. 2021), we found the highest abundances of C1 and C2 of both species at the shelf break and slope stations of the Barents Sea, Kara Sea, off Franz Josef Land, and Laptev Sea, whereas in the inner basins, young stages were only found at the Alpha and Lomonosov Ridges at very low concentrations. However, the trend of decreasing abundance away from the continental slope did not hold for AF of
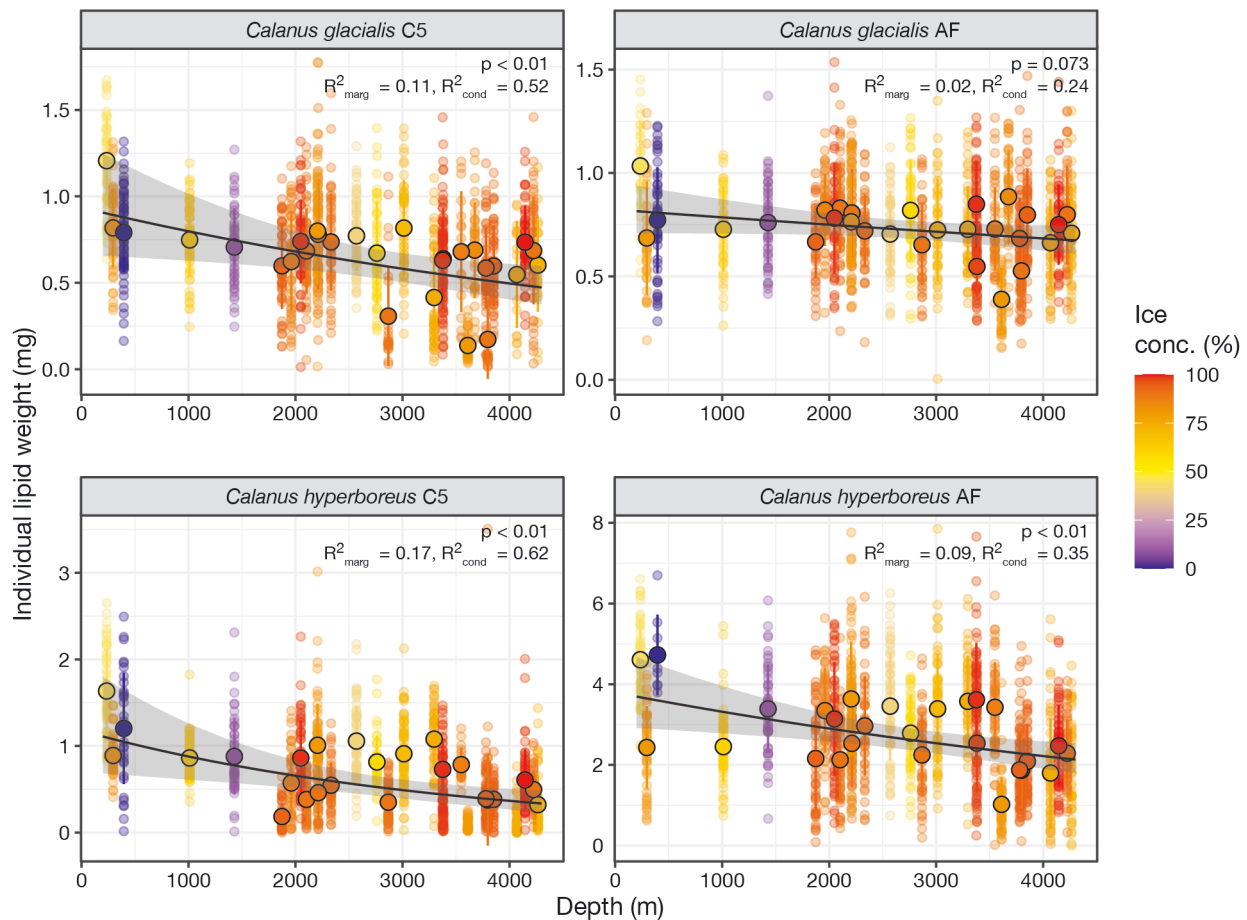
Fig. 7. Generalised linear mixed model (GLMM) results of individual lipid weight vs. bottom depth for C5 copepodites and adult females (AF) of *Calanus glacialis* and *C. hyperboreus.* Black solid line indicates model fit; gray band shows 95% confidence interval. Circles with black outline indicate mean value for that station; error bars (coloured solid lines) show standard deviation. Transparent circles show individual lipid values. R^2_{marg} indicates fit by fixed term only; R^2_{cond} indicates fit with random factors included. For summary statistics, see Table S4 in the Supplement

C. glacialis or stages C4–AF of *C. hyperboreus.* Instead, the number of AF of *C. hyperboreus* actually increased in the basin relative to the slope region and remained stable for *C. glacialis.*

The differences in stage composition and distribution highlight the interspecies differences in life cycle strategies between *C. hyperboreus* and *C. glacialis.* The latter typically begins reproduction around April and can continue producing eggs as long as October in various regions of the Arctic (Hirche & Kattner 1993, Søreide et al. 2010, Hatlebakk et al. 2022). In contrast, *C. hyperboreus* reproduces at depth between November and May, with the exact period varying with region (Hirche & Niehoff 1996, Ashjian et al. 2003, Swalethorp et al. 2011). While the immature gonads and the low number of early copepodites of *C. hyperboreus* in August 2011 is therefore unsurprising, in regions with successful recruitment, we would expect to see an abundance of the C3 stage, which is

the first overwintering stage of this species. A somewhat surprising result, on the other hand, was the very high abundance of C1–C2 stages of *C. hyperboreus* in the 0–25 m layer at Stn 204 on the Gakkel Ridge. One explanation for this outlier could be lateral advection by a recirculating branch of the Atlantic boundary current (Rudels et al. 1994) from a more productive

Table 1. Egg production rates (EPR, eggs female^{-1} d^{-1}) and spawning frequency (SF, % females d^{-1}) of *Calanus glacialis* during research cruise ARK 26 (August 2011)

Stn	Date	No. of females	Duration (h)	EPR	SF d^{-1} (%)
188	9 Aug	40	48	0.58	1.25
190	9 Aug	40	59	8.63	23.8
191	10 Aug	47	25.5	9.59	24.03
193	10 Aug	44	55	3.18	11.9
196	11 Aug	45	48	0	0

shelf area. This station was also near the ice edge, which has been shown to have a strong association with higher abundances of *C. glacialis* and *C. hyperboreus* juveniles (Ershova et al. 2021), but overall, the presence of early copepodites of *C. hyperboreus* this late in the season was unexpected, as this species typically reproduces much earlier in the year.

The ongoing egg production of *C. glacialis* that we observed during August 2011 and the much higher proportion of young copepodites, particularly around the basin margins, confirm the notion that *C. glacialis* in the Arctic Ocean spawns later in the season and over a longer period than *C. hyperboreus*. However, the low egg production rates (<10 eggs female^{-1} d^{-1}) despite relatively high chl *a* concentrations, as compared to maxima of up to 100 eggs female^{-1} d^{-1} observed on the East Greenland shelf (Hirche & Kwasniewski 1997), suggests that we captured the end of the spawning period for this species.

4.2. Physiological condition and implications for *Calanus* survival in the Arctic Ocean

The multi-year life cycles of Arctic *Calanus*, reaching as long as 2 yr for *C. glacialis* and 4−6 yr for *C. hyperboreus* (Dawson 1978, Hirche 1997, 1998) require copepodite stages to store energy in the form of lipids in order to overwinter, and for females to build up gonads that can allow them to spawn prior to the spring bloom (Hirche & Kattner 1993, Hirche & Niehoff 1996). Additionally, in contrast to most other copepods, the females of both species are believed to be iteroparous, which allows them to reproduce more than once during their life span in subsequent years (Hirche 1989, Kosobokova 1999, Swalethorp et al. 2011). Therefore, it is not only the abundance, but also the physiological condition of the *Calanus* populations that is relevant to their chances of successful overwintering and subsequent reproduction. Our measurements of DW and lipid content provide unique insight on the physiological state of both *Calanus* species in the CAO and highlight the interspecies differences in their patterns of accumulating lipids, and, consequently, their life history strategies.

In contrast to overall abundance trends, the stable abundance and lipid composition in *C. glacialis* females (Figs. 3 & 7) challenge the notion that this species is a true expatriate in the CAO. If this were the case, one would expect to see a decline in both their numbers (due to mortality) and physiological condition (due to lipid utilization) as they move away from their presumed preferential habitat, i.e. the outer
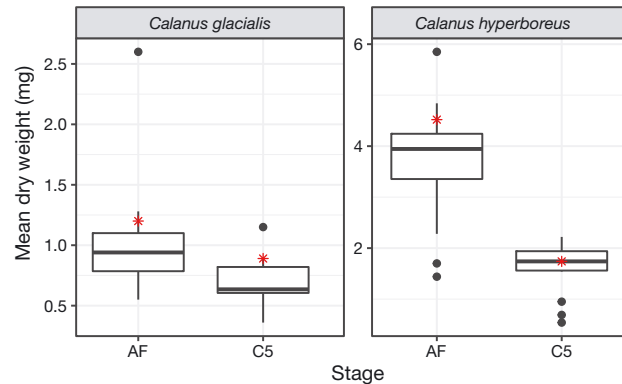

Fig. 8. Mean individual dry weights of C5 copepodites and adult females (AF) of *Calanus glacialis* and *C. hyperboreus* from compiled literature data (see Table 2). Boxplot details as in Fig. 6. Red asterisks indicate mean values for this study

shelf and slope area. Yet both their abundance and individual lipid content remained consistently high across the study area, and their mean DW in our study of the CAO was higher than literature values in more productive regions such as the Barents Sea, Svalbard fjords, and the Canadian Archipelago (Fig. 8, Table 2), although we cannot exclude that part of this discrepancy may be caused by methodological differences. Despite high lipid reserves, they seem to be incapable of successful reproduction in the CAO, as has been observed in several previous works (Kosobokova & Hirche 2001, Kosobokova 2012), and also supported by the absence of early life stages away from the shelf break (Ershova et al. 2021). However, the high lipid content suggests that they may be able to survive until the next year and continue their life cycle, if they became advected to a more favourable environment.

C. glacialis have a mixed capital/income strategy when it comes to reproducing. They can start egg production in the absence of food (Hirche & Kattner 1993, Kosobokova & Hirche 2001, Daase et al. 2013), but will cease quickly if food does not become available (Hirche 1989). If provided with sufficient nourishment, they can continue reproduction for many consecutive months, often until late fall (Hatlebakk et al. 2022). In the food-poor environment of the deep Arctic Basin, they cease reproduction, and the very low metabolic demand at cold temperatures together with low predation pressure seemingly ensures their long-term survival. This result is at odds with modelling studies predicting that food limitation within the Arctic basins will prohibit successful overwintering of this species there (Feng et al. 2016, 2018). Notably, these models ignore omnivory, which may be important when phytoplankton is scarce (Campbell et al. 2009). Predation on other metazoans (Cleary et al.

Table 2. Compilation of literature values of dry weight (DW) ranges (mg) of C5 and adult female (AF) *Calanus glacialis* and *C. hyperboreus*. AO: Arctic Ocean; NWT: Northwest Territory; GS: Greenland Sea; NEW: Northeast Water Polynya; gC: grams carbon

Reference	Month	Location	C5			AF		
			Min.	Max.	Mean	Min.	Max.	Mean
C. glacialis								
Ikeda & Skjoldal (1989)	–	Barents Sea	–	–	–	0.42	0.65	0.55
Scott et al. (2000)	–	Kongsfjord	–	–	0.62	–	–	2.60
Diel & Tande (1992)	–	Malangen Fjord	0.95	1.30	1.15	1.10	1.29	1.12
Kjellerup et al. (2012)	–	Disko Bay	–	–	–	0.60	0.82	0.71
Båmstedt & Tande (1985)	–	Barents Sea	0.49	0.76	0.62	0.75	1.20	0.95
Hirche & Kattner (1993)	–	Barents Sea	–	–	–	–	–	0.75
Hirche et al. (1994)	–	NEW, GS	–	–	–	0.81	0.86	0.84
Hirche & Kwasniewski (1997)	–	NEW	–	–	–	–	–	0.80
Hirche & Kosobokova (2003)	–	Barents Sea	–	–	0.60	–	–	0.80
Tourangeau & Runge (1991)	–	Hudson Bay	–	–	–	0.50	1.00	
Conover & Huntley (1991)	Jul	NWT	–	–	0.36	–	–	0.77
Conover & Huntley (1991)	Aug	NWT	–	–	0.57	–	–	0.94
Conover & Huntley (1991)	Sept	NWT	–	–	0.73	–	–	0.95
Conover & Huntley (1991)	Apr	NWT	–	–	0.65	–	–	1.08
Ashjian et al. (2003)[a]	–	Western AO	0.65	1.27	0.85	1.12	1.65	1.28
This study	–	Central AO	0.39	1.28	0.89	0.83	1.51	1.20
C. hyperboreus								
Conover & Huntley (1991)	Jul	NWT	–	–	1.54	–	–	3.96
Conover & Huntley (1991)	Aug	NWT	–	–	1.89	–	–	4.05
Conover & Huntley (1991)	Sept	NWT	–	–	1.98	–	–	3.94
Conover & Huntley (1991)	Apr	NWT	–	–	0.95	–	–	2.28
Hirche et al. (1994)	–	NEW	1.11	1.65	1.70	3.98	4.32	4.15
Hirche et al. (1994)	–	GS	0.49	0.59	0.54	1.68	1.72	1.70
Hirche (1997)	Feb/Mar	GS	–	–	–	2.12	5.33	3.54
Hirche (1997)	Apr	GS	0.57	0.89	0.69	1.20	1.94	1.44
Hirche (1997)	Jun/Jul	GS	0.81	3.21	1.90	1.82	5.74	3.89
Hirche (1997)	Aug	GS	0.92	2.84	1.80	2.43	7.83	4.84
Hirche (1997)	Nov/Dec	GS	1.33	3.31	2.22	3.20	6.44	4.80
Plourde et al. (2003)	–	Lower St. Lawrence	0.68	3.66	2.00	1.04	5.52	3.50
Scott et al. (2000)	–	Kongsfjord	–	–	1.58	–	–	2.92
Auel et al. (2003)	–	Fram Strait	1.95	2.16	2.06	3.54	4.35	3.95
Ashjian et al. (2003)[a]	–	Western AO	0.66	3.23	1.58	4.18	6.94	5.85
This study	–	Central AO	0.70	4.07	1.74	2.36	7.31	4.52

[a]DW = gC × 2.22

2017), including cannibalism on eggs and nauplii (Hirche 2013), could provide sufficient carbon to sustain metabolic costs to ensure their survival. If food availability increases in the Arctic Basin under climate change scenarios, they can presumably resume reproduction, as has already been observed for ice-reduced conditions during fall of 2016 (Ershova et al. 2021). This high adaptability of AF may be less pronounced in the C5 stage, as both abundance and DW/lipid content of individuals declined with bottom depth and distance to the shelf break. The apparent bimodal distribution in their lipid content, with the high-lipid group fully overlapping that of AF, suggests the simultaneous occurrence of individuals from different generations: a new generation that has recently moulted from C4 (and has not had time to build up lipid reserves), and the previous year's generation that has survived at least one winter and will soon moult into adults. Despite low lipid reserves, the new-generation *C. glacialis* females may still spawn in the next year after several weeks of feeding (Hirche 1989), but not as early as those that spawn from overwintering lipid reserves without accompanying food intake.

Although the mean DW of *C. hyperboreus* was higher than (or well within) the range of literature values (Table 2, Fig. 8), the individual lipid content across the study area showed a more complicated picture, highlighting the limitations of characterising communities using bulk measurements such as mean DW. The abundance of *C. hyperboreus* C5 copepodites was high across the study area; in fact, outside of

the shelf area, it was the most numerous *Calanus* species/stage present. However, the log-normal distribution of individual lipid stores shows that most of these observed *C. hyperboreus* C5 individuals were in poor condition towards the end of the productive season, with an average of less than 30 % lipid to body weight, and many individuals with nearly empty lipid stores. Lipid-rich individuals were also present, but at most stations, they represented a minority of the population. This, together with the pronounced decline in lipid content and DW away from the shelf break, suggests that a strong selection process occurs at the C5 stage for this species. The lipid-poor individuals may not survive the winter season, or they will have to postpone their development by another year, while the lipid-rich ones will likely successfully moult into adults. In contrast, the abundance of AF increased in the deep basins relative to the shallower areas near the shelf break, likely due to reduced predation pressure within these refugia and their ability to survive with very little food. Their reproduction is known to be decoupled from the spring bloom (Hirche 2013), which could explain why there was a slight decline in lipid stores as we moved away from food-rich areas, unlike what we observed for *C. glacialis* females.

4.3. Shelf−basin interactions as a key component in Arctic *Calanus* life cycles

Based on our findings, we suggest that the success of *C. glacialis* and *C. hyperboreus* in the CAO is dependent upon both advection from the outer shelf/slope region, as well as their ability to survive at late developmental stages without losing the ability to reproduce in the deep basin. While the Arctic Basin is characterised by severe food limitation, it also serves as a refugium for the large, slow-developing adults against predation, allowing them to accumulate there and thus maintain their numbers.

The Arctic Ocean is often referred to as the Arctic Mediterranean Sea (Aagaard et al. 1985, Eldevik et al. 2020, Wassmann et al. 2020), as it is almost entirely surrounded by land masses and about half of its area is occupied by continental shelf (Bluhm et al. 2015). Plankton in the Arctic Ocean are subject to strong currents such as the Arctic Circumpolar Boundary Current (Carmack et al. 1995, Woodgate et al. 2001, Rudels 2008, Aksenov et al. 2011), the Transpolar Drift as a countercurrent system (Armitage et al. 2017, Charette et al. 2020, Timmermans & Marshall 2020), and various mechanisms for on- and off-shelf ex-

change (Williams & Carmack 2015). We propose that Arctic *Calanus* utilize both more productive outer shelf/slope waters of the Arctic Ocean and the deep basins during different parts of their life cycle. Rather than being 'expatriates' in the basins, the adult stages of each species are able to maintain both their numbers and physiological condition, which may allow them to eventually be carried to more favourable breeding grounds. Overwintering at low temperatures in the deep basins guarantees slow consumption of reserves and reduced predation pressure, while development on the basins' margins in warmer and more productive ice-free waters supports faster growth rates to reach the next diapausing stage sooner. It is plausible that in some areas, *C. hyperboreus* eggs spawned in deep waters by overwintering females within the Arctic Ocean Boundary Current float to the surface and may be carried towards the shelf by eddies or downwelling currents (Llinás et al. 2009, Nishino et al. 2011, Walkusz et al. 2012) before reaching a stage that requires feeding. Our current state of knowledge about Arctic circulation systems suggests that well-defined shelfward advective events of surface waters are a relatively rare and unpredictable occurrence on a pan-Arctic scale (Carmack & Wassmann 2006, Bluhm et al. 2015, Williams & Carmack 2015) and thus unlikely to be a successful spawning strategy. In contrast, the deep (Atlantic) water circulation in the Arctic basins consists of several cyclonic cells (Rudels & Carmack 2022) that should result in a tendency for deeper animals within these cells to be moved toward their edges. This is complicated by the general tendency of surface water to either converge in the Beaufort Gyre or move toward the central basins and then follow the transpolar drift to exit through the Fram (or Davis) Strait. The exact nature of the interactions between these layers and how they may be changing are at present poorly understood (Timmermans & Marshall 2020).

This pattern of spatial decoupling of overwintering/spawning vs. growth/development is likely particularly pronounced in *C. hyperboreus*, which require deep waters for overwintering, compared to *C. glacialis* that can also successfully overwinter in shallower regions when deeper waters are not easily accessible (Hirche & Kosobokova 2011, Kosobokova & Pertsova 2018, Hatlebakk et al. 2022). *C. hyperboreus* females may be reproducing in the central Arctic basins, since their reproduction is decoupled from food intake (Hirche 1997), but their offspring would have low likelihood to survive there. This is evidenced by the near absence of early life stages, and especially the first overwintering C3 stage (Dawson

1978, Kvile et al. 2018, Ershova et al. 2021). In contrast, if *C. hyperboreus* could delay reproduction until reaching a favourable habitat, the offspring that are produced within the more productive waters of the outer shelves, or the marginal ice zone, have a good chance of reaching the C3 stage and surviving until the next summer. Once a copepod reaches the C4–C5 stages, its ability to survive long periods of starvation increases dramatically, as is evidenced by the high abundance of these stages within the deep basin.

We hypothesize that this survival strategy comes at the cost of very slow development, with each stage taking a year (or possibly longer), and the skewed distribution in lipid content suggests that the majority of them may still fail to accumulate sufficient lipids in the short summer season to reach the next developmental stage, with potentially fatal consequences. By the time they reach the C5/adult stage, the shallower depths and increased risk of predation from fishes in marginal seas and slope waters (Benoit et al. 2014, Aune et al. 2021) outweigh the benefit of better feeding conditions. The late developmental stages and adults that are advected by currents away from the slope into the ice-covered basin have a much higher chance of survival, as has also been recently demonstrated by Langbehn et al. (2023). Although the natural life span of adult copepods is not known, the absence of a decline (and even an increase) in abundance and lipid richness away from their presumed 'source of origin' (the productive basin margins) suggests that they could self-sustain for many consecutive years. Despite low probability of producing viable offspring while residing in the Arctic's central basins, it seems that the AF are able to replenish their lipid stores by the end of the growing season, leaving them prepared for capitalizing on advection that could place them in more productive habitats in a subsequent year.

Spatial separation of spawning and resting grounds is a widely implemented strategy in terrestrial and marine environments, and the use of offshore refugia for overwintering populations is well documented for other calanoid species (Coyle et al. 2013, 2019, Melle et al. 2014). In upwelling regions, different depth distributions of copepodite stages provide a mechanism to utilize counter currents for maintenance of the populations of copepods (Peterson 1998) and fish larvae (Rodriguez et al. 2015) within the same current system. In the North Sea, the population of *C. finmarchicus* is replenished each spring by advection from an overwintering stock located beyond the shelf edge in the Norwegian Sea (Backhaus et al. 1994, Heath et al. 1999, Gao et al. 2021). Similarly, in the Labrador/Irminger Seas, *C. finmarchicus* growth and reproduction mainly occur in the shallow margins, whereas the deep basins serve as collection areas and refugia for overwintering individuals (Melle et al. 2014). It is likely that Arctic *Calanus* similarly use the different habitats of the Arctic Ocean during the span of their life cycles, even if this represents a passive strategy associated with their exceptional ability to store lipids and withstand starvation rather than an active behavioural migration.

5. SUMMARY AND OUTLOOK

Calanus glacialis and *C. hyperboreus* are key Arctic zooplankton species that have developed unique adaptations that allow them to maintain populations both on the fringes and the deep basins of the CAO. These include long life cycles with the ability to overwinter as juveniles as early as the C3 stage, long spawning periods, iteroparity in females, partial (*C. glacialis*) or complete (*C. hyperboreus*) capital breeding, effective energy storage (and overwintering physiology), and possible utilization of the Arctic Ocean circulation system to transport individuals to different regions of the Arctic Ocean during different stages of their life cycle. The large spatial scales and strong circulation patterns found in the Arctic Ocean ensure that the multi-annual life cycles of *C. hyperboreus* and *C. glacialis* proceed across multiple locations and are thus influenced in sequence by the local temporal and spatial variability at each. Although the outer shelf/slope region of the Arctic Ocean is the most favourable for the development of both species, the less productive deep waters of the Arctic Basin likely provide a benefit to adult stages due to reduced predation pressure refugia and low metabolic demands for overwintering. As such, the adults of both species in the deep basin represent ontogenetic migrants, rather than true expatriates. Differences between species such as depth distribution, body size, resource allocation between AF and C5, and reproductive timing and mode allow the co-existence of both species within the Arctic Ocean. Future research should focus on resolving the interactions among these factors and emphasize sampling earlier in the season during peak spawning times of both species. Applying particle tracking models can further highlight the importance of offshore refugia in the life histories of these species and allow us to predict future ecosystem responses to a warming environment.

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