



Contrasting copepod community composition in two Greenland fjords with different glacier types

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ABSTRACT

Greenland's fjord ecosystems are strongly influenced by meltwater discharge from glaciers. Marine-terminating glaciers can significantly enhance primary production during the melt season (compared to land-terminating glaciers), but their impact on secondary producers is not well understood. Here, we study seasonal changes in the zooplankton community ($> 50 \mu\text{m}$) and grazing rates along two fjord transects in southwest Greenland influenced by different glacier types. Zooplankton biomass was comparable between the fjords, but community composition differed during summer. Nuup Kangerlua, a predominantly marine-terminating system, was characterized by large, herbivorous copepods and a longer summer grazing period in connection with the summer bloom. Ameralik, influenced by a land-terminating glacier, was characterized by small, omnivorous copepods, particularly *Microsetella norvegica* and *Oncaea* spp., and indicated a faster post-bloom transition towards regenerated production. Local hydrographic conditions also impact copepod biomass. A station with high biomass was found in Ameralik, potentially linked to a frontal zone where fjord water masses meet, providing favorable grazing conditions. We hypothesize that a future transformation from marine- to land-terminating glaciers could result in an increased abundance of smaller copepods, as observed in Ameralik. Such a community would constitute a less lipid-rich food source for higher trophic levels.

KEYWORDS: copepod; zooplankton; glacier; Greenland; fjord

INTRODUCTION

As the Greenland Ice Sheet melts, increases in the release of glacial meltwater and icebergs are transforming the receiving fjords (Sejr *et al.*, 2017; Torsvik *et al.*, 2019) with consequences for their ecosystems. Recent evidence has shown that implications will be partly dependent on whether the delivery is primarily via marine-terminating glaciers, or only via land-terminating glaciers, due to the different hydrographical patterns involved. Surface runoff from glaciers results in strong stratification with a turbid, low salinity surface layer which can warm up strongly during summer in fjords with land-terminating glaciers (Boone *et al.*, 2017; Monteban *et al.*, 2020). At the fronts of marine-terminating glaciers, meltwater is also released at depth. Since it has relatively low density, it rises to the surface entraining nutrient-rich deep water (Meire *et al.*, 2023). Fjords with marine-terminating glaciers have been shown to support high primary productivity in summer due to this subglacial discharge and upwelling of nutrients (Calleja *et al.*, 2017; Meire *et al.*, 2017; Kanna *et al.*, 2018), a mechanism that is absent in systems with land-terminating glaciers.

How glacier type impacts the biomass and composition of zooplankton, the main secondary producers in Arctic pelagic systems, remains an open question. The widespread distribution

and environmental sensitivity of zooplankton make them key marine environmental indicators, which may therefore signal shifts in coastal food webs that can help predict the future direction of fjord ecosystems (Falk-Petersen *et al.*, 2007). Copepods dominate the zooplankton in Arctic pelagic environments (Hopkins, 1969). Studies in glacial fjords reveal gradients in their distribution, linked to glacial inputs (Arendt *et al.*, 2010; Middelbo *et al.*, 2017; Trudnowska *et al.*, 2020). The *Calanus* complex, including *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus*, is a primary focus in Arctic research. These large copepods constitute a significant portion of the biomass in glacial fjords during spring, emerging from winter diapause to feed on the spring phytoplankton bloom (Falk-Petersen *et al.*, 2009). However, smaller copepod species are often under-sampled due to the prevalent use of 200 μm mesh nets and the focus on spring and early summer sampling (Hopcroft *et al.*, 2001). These smaller copepods are increasingly recognized as major components of high-latitude zooplankton communities (Hopcroft *et al.*, 2005; Middelbo *et al.*, 2018), dominating in terms of abundance and biomass towards the end of summer as larger *Calanus* copepods hibernate (Møller *et al.*, 2006; Svendsen *et al.*, 2011). Due to their lower lipid content (Kattner and Hagen, 2009), which makes them a poorer food source for higher

trophic levels, shifts in community composition favoring smaller copepods will impact the entire food web, including commercial fisheries.

Nuup Kangerlua is a large and productive fjord system on the southwest coast of Greenland fed by both marine- and land-terminating glaciers. It has been a site of long-term zooplankton monitoring since 2005, revealing distinct zooplankton assemblages in different parts of the fjord with varied environmental conditions. Along-fjord transects have shown *Calanus* species dominating in the offshore and outer fjord region and an increasing contribution of other species including *Metridia longa*, *Pseudocalanus* spp. and *Microsetella norvegica* in the inner fjord in the post-spring bloom and summer period (Arendt *et al.*, 2010; Tang *et al.*, 2011; Swalethorp *et al.*, 2015). Seasonal data from Nuup Kangerlua outside of the spring and early summer period, however, are limited, and multi-season studies are only available at lower spatial resolution. The available data suggest that small copepods, together with protozooplankton, are major components of the zooplankton community in Nuup Kangerlua after the initial peak of *Calanus* copepods (Arendt *et al.*, 2013; Riisgaard *et al.*, 2014; Grønkjær *et al.*, 2019). The neighboring fjord Ameralik shares the mouth region with Nuup Kangerlua but is only influenced by a land-terminating glacier. The lack of any extensive zooplankton observations from Ameralik to date and the different glacial influences present an interesting opportunity to compare the pelagic copepod communities between these fjords. Here we present the first seasonal copepod survey of Nuup Kangerlua and Ameralik covering a full transect of the main fjord branch. By comparing the results from these fjord systems, we aim to better understand the seasonal zooplankton dynamics and influence of glacier type on the copepod community.

METHODS

Study site and stations

This study was conducted in the neighboring sill fjords Nuup Kangerlua (also known as Godthåbsfjord) and Ameralik, which share a mouth region in southwest Greenland close to Nuuk (64°N, 52°W, Fig. 1). The West Greenland Current flows northwards in the coastal region outside the fjords. The upper layer of this current is composed of relatively cool and fresh southwest Greenland Coastal Water, and the underlying water is the warmer and more saline Subpolar Mode Water (Rysgaard *et al.*, 2020).

The bathymetry and circulation patterns for Nuup Kangerlua are described by Mortensen *et al.* (2011, 2013, 2014, 2020) and for Ameralik by Stuart-Lee *et al.* (2021). Nuup Kangerlua is ~190 km long, has an area of ~2000 km² and a maximum depth of ~625 m (Mortensen *et al.*, 2011). Meltwater from the Greenland Ice Sheet enters Nuup Kangerlua via three land-terminating glaciers and three marine-terminating glaciers, the largest of which (Kangiata Nunaata Sermia) has a grounding depth of ~250 m (Mortensen *et al.*, 2013). Sea ice typically covers the inner fjord during the winter from around station GF13, breaking up during the spring, and icebergs are abundant year-round. Ameralik is a smaller fjord to the south of GF and has a length of ~75 km, an area of ~400 km² and a maximum depth of ~700 m. Glacial meltwater enters Ameralik primarily from the glacial river Naajat Kuuat. No glaciers terminate directly in Ameralik, and the fjord remains mostly ice-free throughout the year.

Along-fjord transects were made in spring (May), summer (July), and autumn (September) 2019, covering 15 stations during each campaign (Fig. 1). Sampling took place aboard the Greenland vessels RV Sanna, Polar Dive and Tulu. Complementary datasets from these campaigns, including measurements of potential temperature, salinity, turbidity, SPM and Chl-a, are described by Stuart-Lee *et al.* (2021, 2023).

Hydrography and Chl-a fluorescence

At every station a SeaBird SBE19plus CTD was used to collect depth profiles for temperature, conductivity, turbidity, fluorescence and photosynthetically active radiation, which were subsequently averaged over 1 m vertical intervals. Sensors were calibrated annually by the manufacturer and salinity precision was typically within the range of 0.005–0.010.

Water samples for Chl-a analysis were collected by Niskin bottles at 1, 5, 10, 15, 20, 30, 40 and 50 m water depths. From each sample, 500 mL was filtered through 25 mm Whatman GF/F filters, which were then frozen at –80°C (May) or –20°C (July and September) for later analysis. Following extraction in 10 mL 96% ethanol for 24 hours, a TD-700 Turner Designs fluorometer was used to measure fluorescence before and after the addition of 200 µL 1 M HCl solution. Results were used in turn to calibrate the CTD fluorescence profiles as per Lyngsgaard *et al.* (2014).

Zooplankton

Zooplankton samples were collected with a Hydro-Bios Multinet Mini equipped with 5 nets of 50 µm mesh and an opening size of 0.125 m². A total of 203 samples were collected at a subset of between 11 and 16 stations, depending on the season (see Table S1). Sampling was mostly conducted during daylight hours, as constrained by operation of the vessel, but the full sampling times span from 02:30 to 21:05 local time. Depth intervals were programmed before deployment. The topmost net sampled the upper 50 m and the remaining net intervals varied according to the water column depth (Table S1). Where possible, sampling intervals were kept consistent between campaigns for each station. The multinet was hauled vertically at ~0.4 ms⁻¹. After deployment, nets were thoroughly back-rinsed with seawater and the contents of the cod-ends were rinsed into tubs and preserved immediately with 4% final concentration borax-buffered formaldehyde. The volume of water sampled was calculated as the depth of the sampled water layer multiplied by the surface area of the net.

Preserved samples were sent to the Arctic Agency (Poland) for identification, counting, and measuring at species or genera, stage and sex level. *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* were identified as stage CV, male or female. The remaining stages are grouped together as *Calanus* spp. Note that the *Oncaea* spp. will most likely also include the genus *Triconia*. For every species and stage combination represented in each sample, the prosome length (or total length for nauplii) was measured for up to 10 individuals. As per Hop *et al.* (2019), copepods were categorized as small when the mean adult female length was < 2.5 mm, and otherwise as large (Table S3). Feeding preferences (Table 1) are generalizations based on observed behavior, which is known to be flexible, and have been assigned as per Blachowiak-Samolyk *et al.* (2007) and sources within.

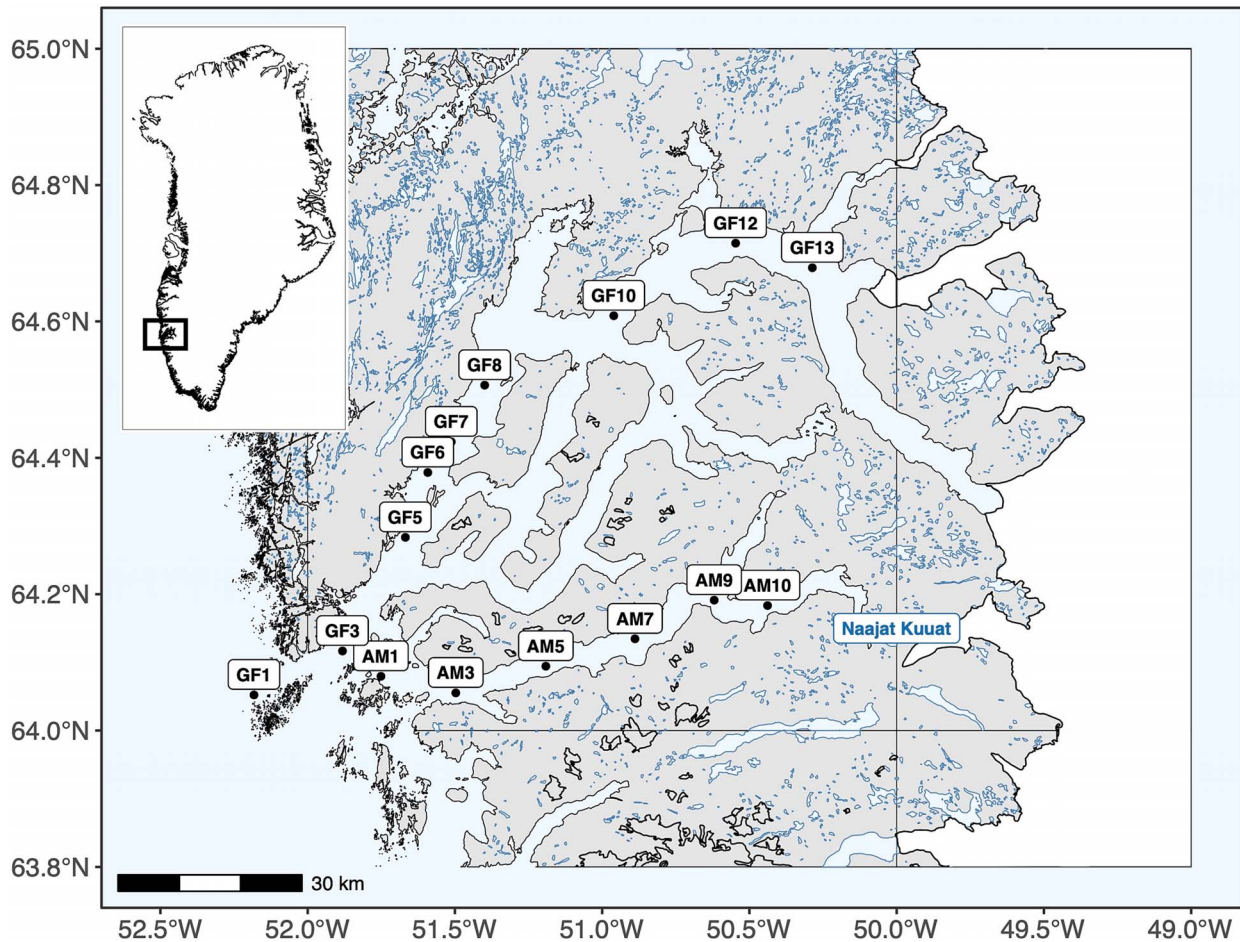


Fig. 1. Map of the study site showing the sampling stations (circles) in Nuup Kangerlua (GF) and Ameralik (AM) in southwest Greenland. Stations are annotated GFx for Nuup Kangerlua and AMx for Ameralik and numbered sequentially from outer to inner fjord, as per prior work. Naajat Kuuat is the glacial river entering Ameralik. The inset shows the location of the fjord system in Greenland.

Table I: Species-specific length (μm or mm) to carbon weight (mg C ind^{-1}) conversion values used for biomass estimates and feeding preferences

Species	a	b	Length Unit	Source	Feeding Preference
<i>Acartia</i> spp.	1.11×10^{-11}	2.92	μm	Berggreen <i>et al.</i> (1988)	Omnivore
<i>Calanus finmarchicus</i>	4.8×10^{-03}	3.5687	mm	Madsen <i>et al.</i> (2001)	Herbivore
<i>Calanus glacialis</i>	4.8×10^{-03}	3.5687	mm	Madsen <i>et al.</i> (2001)	Herbivore
<i>Calanus hyperboreus</i>	1.4×10^{-03}	3.3899	mm	Hirche and Mumm (1992)	Herbivore
<i>Calanus</i> spp.	4.45×10^{-03}	3.3838	mm	Hirche and Mumm (1992)	Herbivore
<i>Centropages</i> spp.	1.78×10^{-02}	2.451	mm	Hay <i>et al.</i> (1991)	Omnivore
<i>Metridia longa</i>	0.605×10^{-03}	3.0167	mm	Hirche and Mumm (1992)	Omnivore
<i>Microcalanus</i> spp.	9.468×10^{-10}	2.16	μm	Sabatini and Kiørboe (1994)	Omnivore
<i>Microsetella norvegica</i>	2.65×10^{-09}	1.95	μm	Uye (2002)	Omnivore
<i>Oithona</i> spp.	9.467×10^{-10}	2.16	μm	Sabatini and Kiørboe (1994)	Omnivore
<i>Oncaea</i> spp.	2.511×10^{-11}	2.9	μm	Satapoomin (1999)	Omnivore
<i>Pareuchaeta</i> spp.	4.8×10^{-03}	3.5687	mm	Madsen <i>et al.</i> (2001)	Carnivore
<i>Pseudocalanus</i> spp.	6.12×10^{-11}	2.7302	μm	Klein Breteler <i>et al.</i> (1982)	Herbivore
<i>Scolecithricella minor</i>	9.467×10^{-10}	2.16	μm	Sabatini and Kiørboe (1994)	Omnivore
<i>Calanus</i> spp. & <i>Metridia</i> spp. nauplii	4.29×10^{-09}	2.05	μm	Hygum <i>et al.</i> (2000)	Omnivore
Other nauplii	3.18×10^{-12}	3.31	μm	Berggreen <i>et al.</i> (1988)	

The values "a" and "b" are those used in the biomass estimate (Equation 1).

As our focus is on consequences for the food web, we use biomass as basis for comparison between fjords instead of abundance. Biomass estimates were calculated using length to carbon weight regressions from the literature (Table I) using the equation:

$$CW = aL^b \quad (1)$$

where CW is carbon weight (mg C ind^{-1}), a and b are conversion factors, and L is the mean prosome length (mm or μm) of the measured individuals.

Ingestion rates of large and small copepods feeding on phytoplankton were estimated for the upper 50 m of each station using Equations 1–3 of Hansen *et al.* (1997). *Oncaea* spp. and *M. norvegica* were excluded from the ingestion rate estimates for small copepods as their feeding behaviors differ from the generalizations made here, with detritus (as opposed to phytoplankton) forming a large part of their diets (Koski *et al.*, 2021). Chl-*a* concentrations were converted to phytoplankton biomass estimates using a carbon to Chl-*a* w:w ratio of 30 (Booth and Horner, 1997; Behrenfeld *et al.*, 2016). Copepod biomass was converted to volume estimates using a Carbon:volume ratio for fixed zooplankton of 0.13 g C cm^{-3} (Berggreen *et al.*, 1988). A Q_{10} (temperature coefficient) factor of 2.8 was used for correcting the ingestion rates to *in situ* temperatures (Hansen *et al.*, 1997).

All statistical analysis was done using the open-source programming language R (R Core Team, 2013). Statistical comparisons of groups in non-parametric data were carried out in base R using the “coin” package v1.4–3 (Hothorn *et al.*, 2008), and applying a combination of Wilcoxon rank-sum tests (W statistic) and Kruskal-Wallis tests (H statistic) according to the type of comparison (significance level = 0.05).

RESULTS

Hydrography and Chl-*a* fluorescence

In May, both fjords were characterized by relatively high surface salinities and weak to no stratification (Fig. 2). The potential temperature was around $0\text{--}2^\circ\text{C}$ throughout the upper 100 m of the water column, particularly at the mouth regions (Fig. 2a and b). In the surface water layer, the potential temperature increased from around $1\text{--}2^\circ\text{C}$ in May up to around 6°C in July and salinity decreased from around 34 in May to around 25 in July. While Chl-*a* concentrations increased in Nuup Kangerlua between May and July, there was an overall decline between May and July in Ameralik, though high concentrations remained at station AM9 (Fig. 2d). In September, stratification had weakened and salinity in the inner parts of the fjords was reduced (Fig. 2e and f). Chl-*a* concentrations declined from July levels in Ameralik, but in the inner fjord of Nuup Kangerlua some concentrated areas of high Chl-*a* remained at $\sim 10 \text{ m}$ depth (Fig. 2e).

Zooplankton abundance and biomass

Copepods accounted for 70% of the total zooplankton abundance measured across both fjords with a mean depth integrated abundance of $1.6 \times 10^6 \text{ ind m}^{-2}$ (Fig. S1). The majority of the remaining abundance was represented by bivalve larvae ($5.7 \times 10^5 \text{ ind m}^{-2}$), appendicularians (*Oikopleura* spp., $1.5 \times 10^4 \text{ ind m}^{-2}$), krill ($8.4 \times 10^3 \text{ ind m}^{-2}$), echinoderm larvae

($3.0 \times 10^3 \text{ ind m}^{-2}$) and the chaetognaths *Sagitta* spp. and *Eukronhia* spp. ($1.2 \times 10^3 \text{ ind m}^{-2}$).

In May, copepod biomass was higher in Ameralik than in Nuup Kangerlua (Fig. 3a and b). The mean integrated biomass across all stations was 1.34 g C m^{-2} for Nuup Kangerlua (SD = 0.92 g C m^{-2}) and 2.67 g C m^{-2} for Ameralik (SD = 2.07 g C m^{-2}). The outer fjord stations (GF1–5, AM1–3) generally had lower integrated biomasses than the inner fjord stations ($W = 927$, $P < 0.001$, $r = 0.53$). The most dominant copepod in both fjords at this time was *Metridia longa*, which contributed 47.1% of the total copepod biomass in Nuup Kangerlua, and 52.8% in Ameralik (Fig. 4a and b). Many species reached peak density in July, when overall copepod biomass was highest (mean value across stations of 4.20 g C m^{-2} for Nuup Kangerlua, SD = 1.34 g C m^{-2} , and 5.44 g C m^{-2} for Ameralik, SD = 3.42 g C m^{-2}). The most notable exceptions were *M. norvegica*, for which biomass was highest in September in both fjords, and *Metridia longa* in Ameralik, for which biomass peaked in May (Fig. 3a and b). Integrated biomass remained higher in Ameralik than Nuup Kangerlua in September, with mean values across the stations of 3.17 g C m^{-2} (Nuup Kangerlua, SD = 1.01 g C m^{-2}) and 3.95 g C m^{-2} (Ameralik, SD = 1.23 g C m^{-2}).

Community composition and feeding preferences

The dominant species by total integrated biomass in Nuup Kangerlua were *Metridia longa*, *C. glacialis*, *C. finmarchicus* and *Pseudocalanus* spp. and in Ameralik these were *Metridia longa*, *M. norvegica*, *Pseudocalanus* spp. and *C. finmarchicus* (Fig. 4). Between the two fjords, the mean biomass of the larger *Calanus* copepod *C. glacialis* was higher in Nuup Kangerlua ($W = 248$, $P < 0.05$, $r = 0.35$). In Ameralik, higher representations of *M. norvegica* and *Oncaea* spp. were found (Fig. 4; $W = 29$, $P < 0.001$, $r = 0.72$ for *M. norvegica*; $W = 55$, $P < 0.001$, $r = 0.61$ for *Oncaea* spp.).

The most dominant omnivorous species by biomass were *Metridia longa*, *M. norvegica* and *Oncaea* spp., and each of these represented a higher proportion of the copepod community in Ameralik than in Nuup Kangerlua throughout the observation period (with one exception of *Metridia longa* in September, Fig. 4). The strongest contrast in feeding preferences was in July, when there was a large increase in herbivory in both fjords, but to a greater extent in Nuup Kangerlua. This was driven by the most dominant herbivores *Pseudocalanus* spp., *C. glacialis*, *C. finmarchicus* and *C. hyperboreus* (Fig. 4c and d). Across all sampled seasons, herbivores represented a higher proportion of the total biomass than omnivores at outer fjord stations GF1–5 and AM1, and in July, this extended to station GF10 in Nuup Kangerlua. At the central and inner fjord stations, omnivores generally represented a higher proportion of the sampled communities. Carnivores (*Pareuchaeta* spp.) represented a very small proportion of the total copepod biomass.

Along-fjord and depth gradients

Generalizing along the transects from the May and July campaigns, some species were more abundant at the central and inner stations of both fjords compared to the outer regions, most notably *Metridia longa* and *M. norvegica* (Fig. Sf and g). In Ameralik, *Oncaea* spp. was also more abundant at the inner fjord

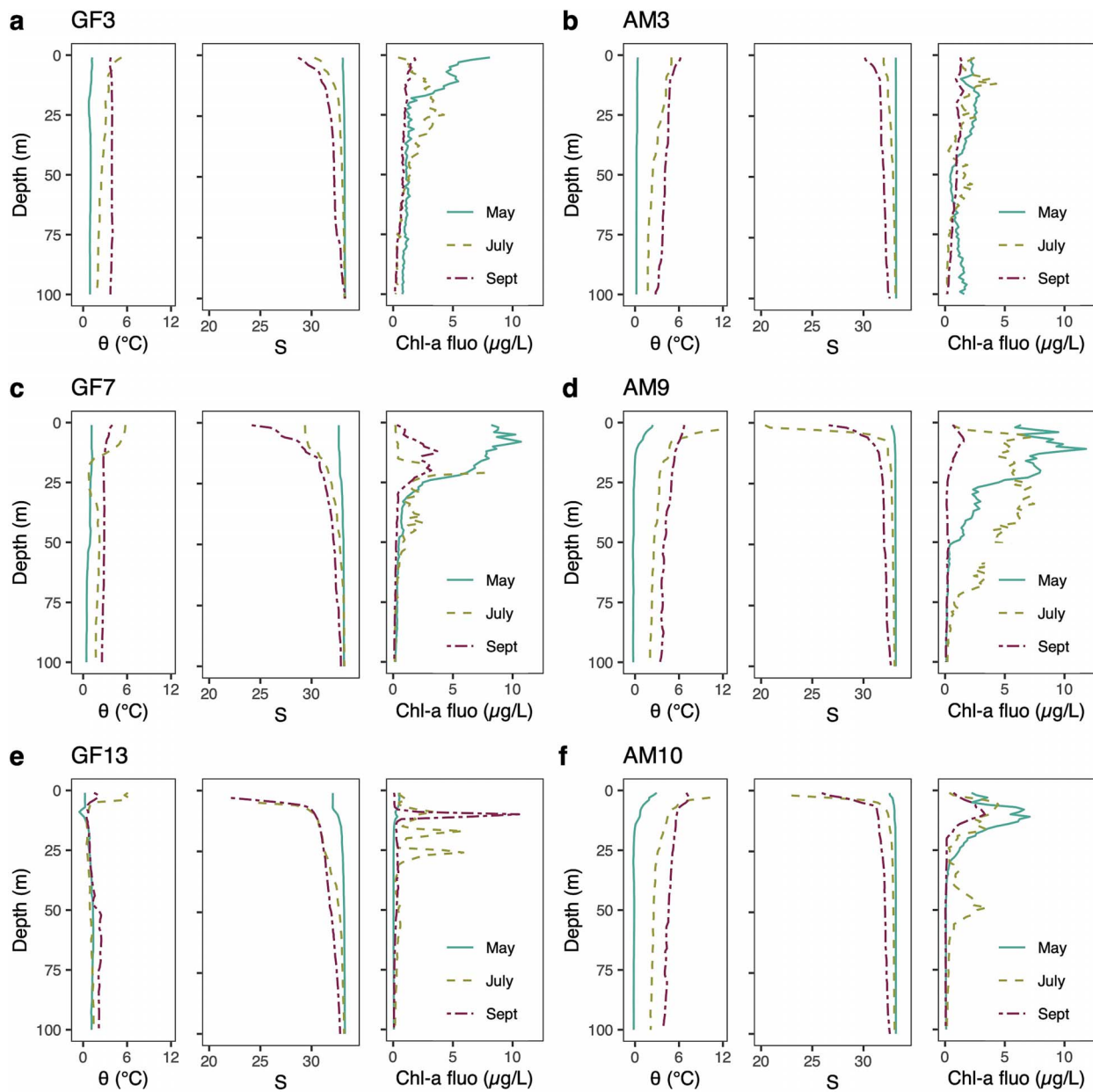


Fig. 2. Upper 100 m seasonal profiles of potential temperature, salinity, and calibrated Chl-a fluorescence from mouth to inner fjord stations (a) GF3, (b) AM3, (c) GF7, (d) AM9, (e) GF13 and (f) AM10.

stations (Fig. 5i). Others were observed more often towards the outer fjord regions, including *C. glacialis* (Fig. 5c). The compositions of outer fjord stations (GF1–5, AM1–3) were often comparable to one another, while overall differences between the fjords were greater when considering the inner fjord stations (Fig. 3c and d). This can be seen, for example, in July, when the outer fjord stations of Ameralik (AM1, AM3) showed very low representations of *M. norvegica* and *Oncaea* spp. (in similarity to outer stations of Nuup Kangerlua), while these species are much more dominant in-fjord. Similarly, in September, the outer fjord station GF3 had a notable proportion of *M. norvegica* (as in Ameralik), which was almost absent further in-fjord (Fig. 3).

Regarding vertical distributions, *A. longiremis*, *C. finmarchicus*, *M. norvegica* and *Oithona* spp. were most concentrated in the

upper 100 m, while the highest biomasses of *C. glacialis*, *C. hyperboreus*, *Metridia longa*, *Oncaea* spp., *Pareuchaeta* spp. *Pseudocalanus* spp. and *S. minor* were typically found below this depth range (Fig. 5). Across both fjords, there were significant differences in the proportion of total biomass that was found in the top 100 m of the water column between months, as determined by the Kruskal–Wallis test ($H = 11.3$, $df = 2$, $P < 0.001$). In July, the proportion of total biomass sampled in the upper 100 m was 46% (compared to 16% in May and 19% in September).

Sizes and stage composition

In Nuup Kangerlua there was a greater representation of large species (those with mean lengths of adult and stage CV individuals ≥ 2.5 mm) in the copepod community than small species

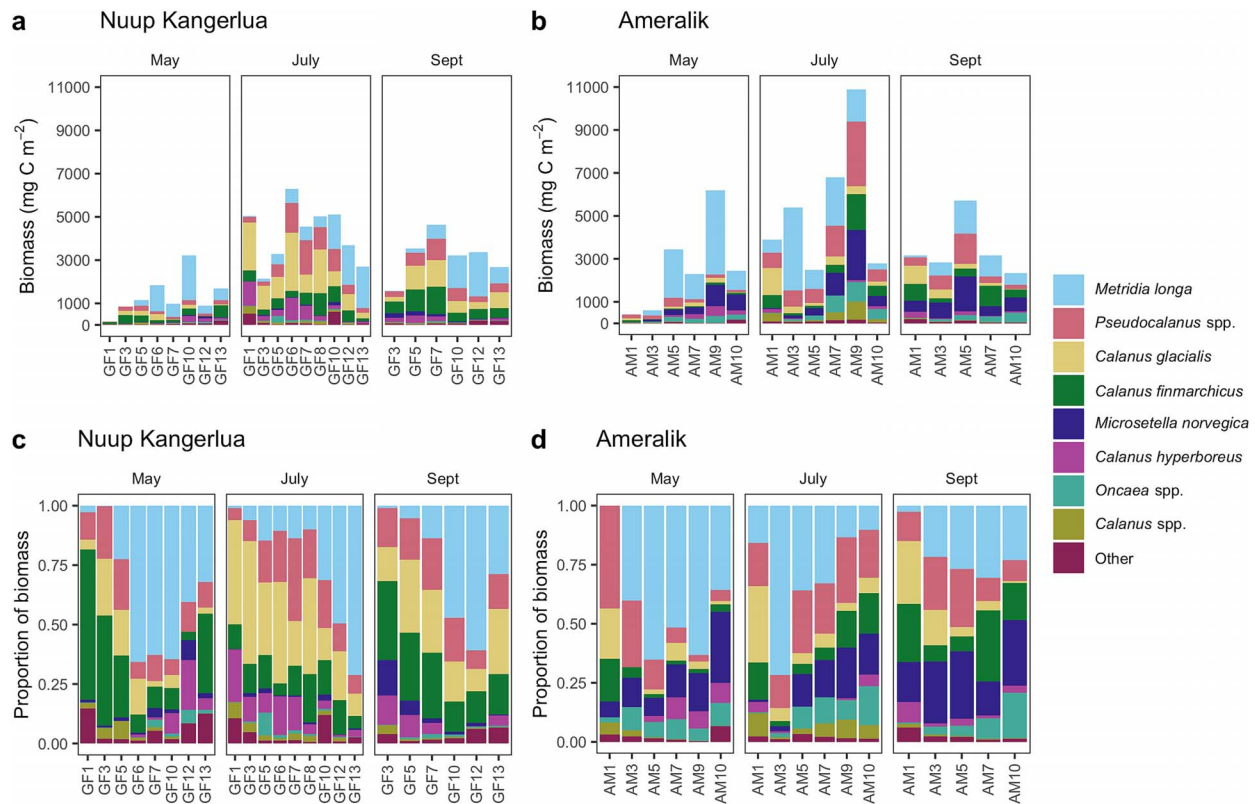


Fig. 3. Seasonal copepod species distributions in both fjord systems. **(a,b)** Integrated copepod biomass (mg C m⁻²) for the sampled water column (sum of the 5 depth intervals for each station) in Nuup Kangerlua and Ameralik. **(c,d)** Relative proportions of species across the total copepod biomass sampled at each station in Nuup Kangerlua and Ameralik. The legend is ordered by decreasing total biomass across the observation period. Corresponding abundance data are presented in Fig. S1.

(< 2.5 mm), in contrast to Ameralik ($W = 6589$, $P < 0.01$, $r = 0.40$; Figs 4 and 6). The difference in mean lengths between fjords was greatest in July (Table II). The largest species were *C. hyperboreus*, *Pareuchaeta* spp. and *C. glacialis*, with mean adult and stage CV lengths across all seasons of 6520, 6310 and 3760 μm , respectively. The smallest species were *Oncaea* spp. (393 μm), *M. norvegica* (506 μm) and *Oithona* spp. (537 μm).

In both fjords, the *Calanus* community followed clear seasonal patterns. Adults dominated in May, with females far outnumbering males (Fig. S2a). July showed a surge in stage CV and smaller copepodites (CIII and CIV). In September, a high biomass of *Calanus* CV remained, but the smaller copepodites had declined. The non-hibernating species *Metridia longa* was dominated by adult females in all seasons, though the proportion of adults was lowest in September and there were larger numbers of the CV stage at this time (Fig. S2b).

A higher overall biomass of *Calanus* spp. nauplii was observed in Nuup Kangerlua than in Ameralik (Fig. 6), although the difference was found to be significant only in September ($W = 400$, $P < 0.05$). Throughout the sampled period, integrated biomasses were comparable in the mouth region (GF1–3, AM1–3; Fig. 6). The nauplii of *M. norvegica*, and *Oncaea* spp. were better represented in Ameralik ($W = 450$, $P < 0.01$ for *M. norvegica*; $W = 70$, $P < 0.01$ for *Oncaea* spp.), and the largest difference in biomass between fjords occurred in July for both

these species. Of these, the nauplii of *M. norvegica* were the most dominant, peaking in July with an increasing in-fjord gradient towards the maximum biomass at station AM9 of 506 mg C m⁻². The representation of *M. norvegica* nauplii in September was very low in comparison, and they were not observed in May. In Nuup Kangerlua, the most dominant nauplii was that of *Calanus* spp., for which the maximum integrated biomass of 86 mg C m⁻² was observed at station GF5 in May.

Copepod grazing

Estimates of copepod ingestion rates for the upper 50 m of the water column, an indicator of phytoplankton turnover, reached their maxima for both large and small copepods in July (Fig. 7a). The peak for large copepods was higher in Nuup Kangerlua at 2.4 $\mu\text{g C L}^{-1} \text{d}^{-1}$ (station GF12), compared to 1.3 $\mu\text{g C L}^{-1} \text{d}^{-1}$ in Ameralik (station AM9). These rates correspond to 3.2% and 0.8% of the respective phytoplankton biomass estimates (Fig. 7b). Estimates for small copepods were more comparable between fjords, with maxima found at station GF7 in Nuup Kangerlua (1.4 $\mu\text{g C L}^{-1} \text{d}^{-1}$, 1.8%) and at station AM9 in Ameralik (1.7 $\mu\text{g C L}^{-1} \text{d}^{-1}$, 1.1%). Grazing potential by small copepods in July was highest in the mid-fjords, with ingestion rates for small copepods greater than those for large copepods at stations GF5–GF7 and AM5–AM9.

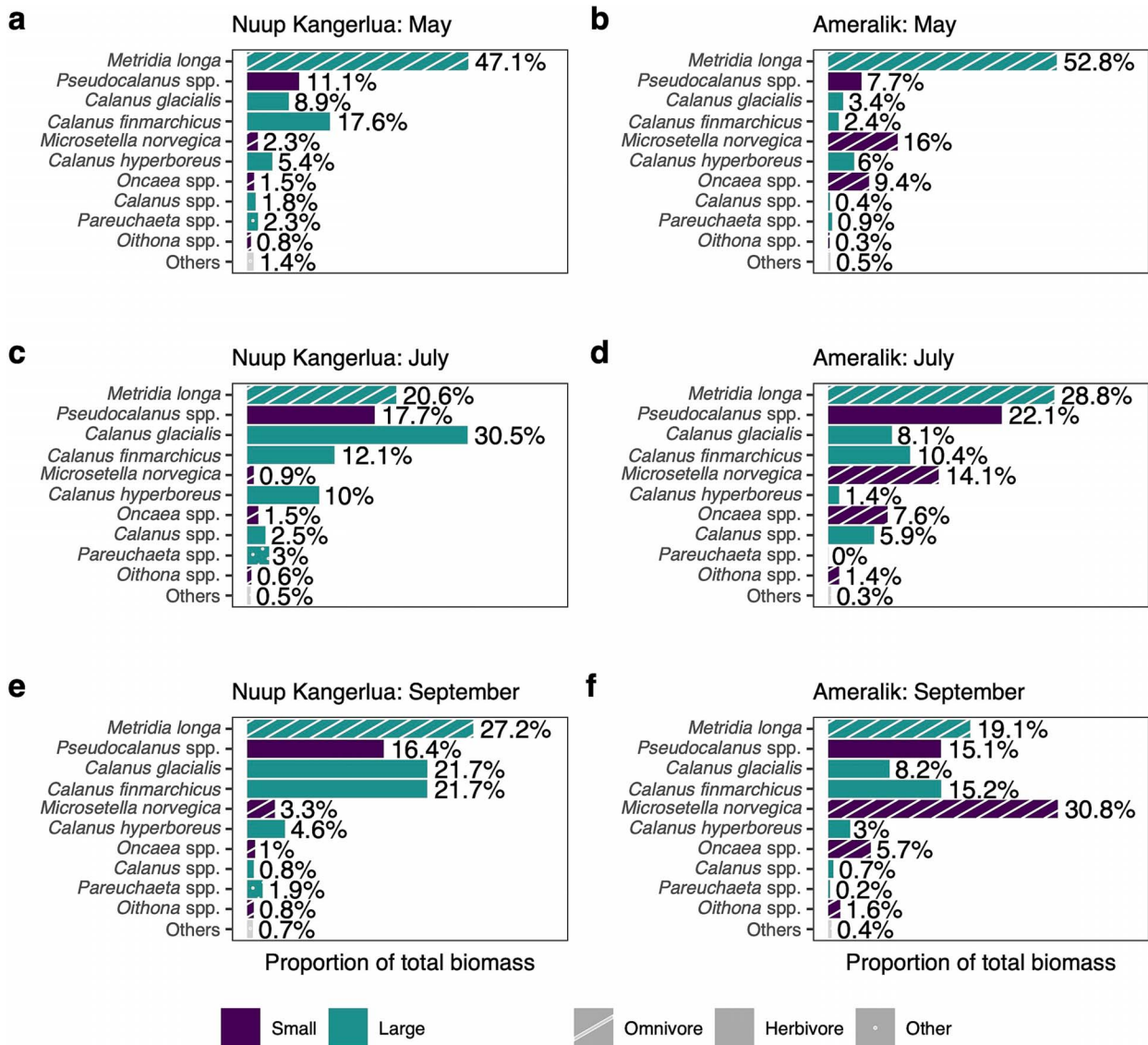


Fig. 4. Proportional representations by season of the 10 most dominant copepod species by relative biomass (g C m⁻²) in each fjord. May, July and September 2019 are shown for Nuup Kangerlua (a,c,e) and Ameralik (b,d,f), respectively. Species are listed in decreasing order of overall fjord biomass across all seasons. Species with mean adult female length < 2.5 mm are designated as small, and the remaining ones are designated as large.

Table II: Mean lengths (μm) of the copepod community by fjord and month

	Mean length (μm)	Std dev	Number of measured individuals (n)	Total abundance (ind)
May				
Nuup Kangerlua	492	411	8295	2.94×10^5
Ameralik	437	267	4981	1.19×10^6
July				
Nuup Kangerlua	464	492	9290	7.62×10^5
Ameralik	350	239	7045	3.51×10^6
September				
Nuup Kangerlua	544	435	6925	4.23×10^5
Ameralik	494	185	5563	1.96×10^6

For each species and stage combination per sample, up to 10 individuals were measured.

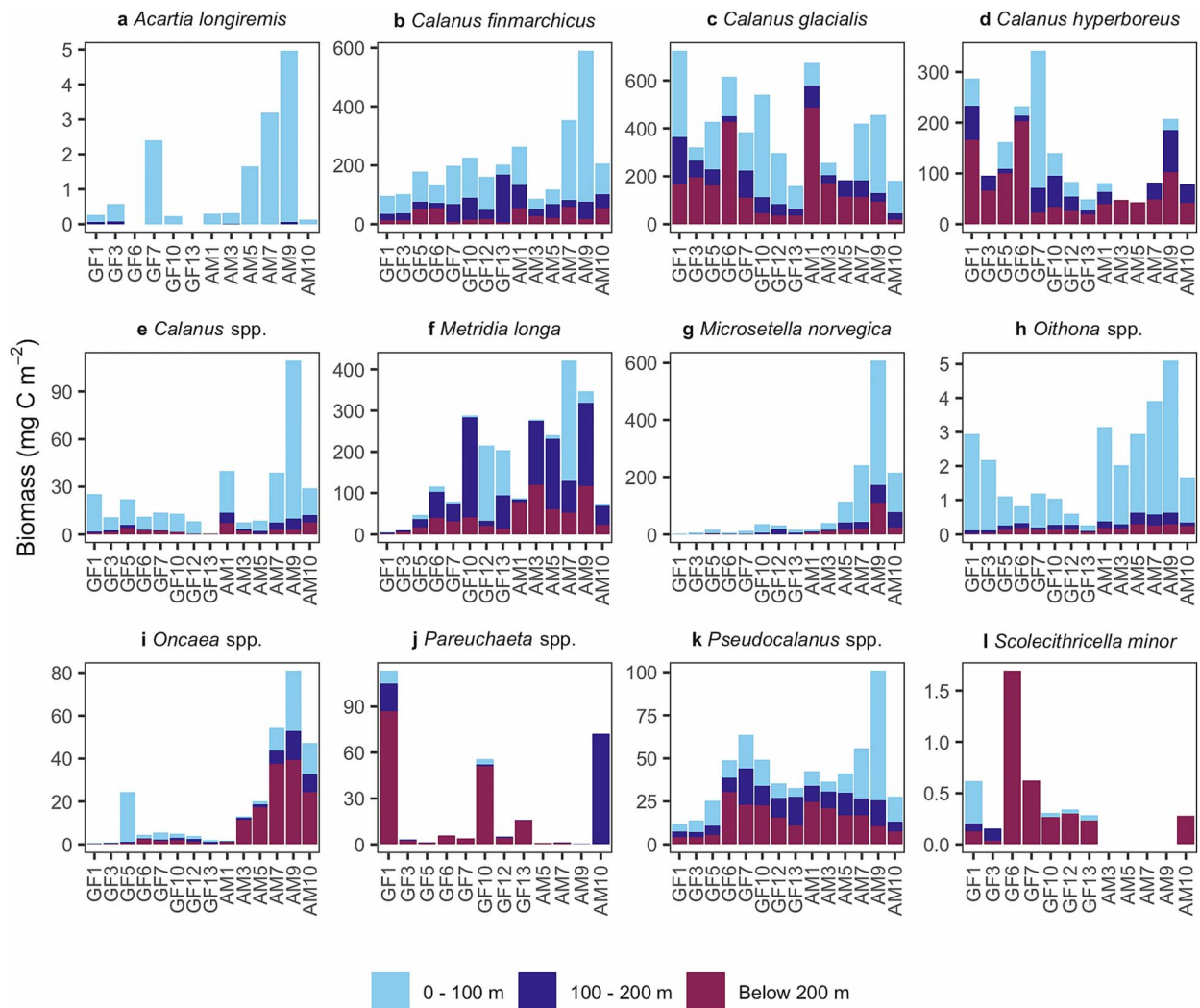


Fig. 5. Mean integrated biomass (mg C m^{-2}) from the May and July campaigns of selected copepod species at each station. Stations displayed were sampled in both campaigns. Shading indicates the vertical distribution.

DISCUSSION

During spring, the impact of glacial meltwater was still limited, resulting in saline and well-mixed water columns in both Ameralik and Nuup Kangerlua. At this time, copepod biomass was at its lowest of the studied period (Fig. 3a and b) and *Metridia longa* dominated in both fjords (Fig. 4a and b). In Ameralik, the mean integrated copepod biomass across all stations was 2.76 g C m^{-2} , compared to 1.34 g C m^{-2} for Nuup Kangerlua. Ameralik maintained a higher overall biomass throughout the observation period (Fig. 3a and b), though the difference between the fjords in May was much larger than in July or September. The larger difference in May may be connected to the different bloom conditions in the fjord. Prior work shows that Ameralik was likely in a more advanced phase of the spring bloom than Nuup Kangerlua during May sampling (Stuart-Lee *et al.*, 2023), which would imply that the build-up of copepod biomass was more advanced.

The end of the spring bloom is typically marked by a transition from new to regenerated production (i.e. nitrate- to ammonium-based), the latter being more reliant on the microbial loop. The

effects on microbial communities translate to zooplankton, as the food web structure shifts from a dominance of herbivory more towards the microbial loop (Legendre and Rassoulzadegan, 1995; Shilova *et al.*, 2017; Svensen *et al.*, 2019). Small copepods, such as *Oithona* spp. have been observed to be key beneficiaries of the post-bloom transition in the Arctic, potentially because their omnivorous diets are less strictly tied to the spring bloom and allow them to use post-bloom regenerated production for reproduction as well as reproduce year-round (Hansen *et al.*, 1999; Svensen *et al.*, 2019). Changes in the copepod community in Ameralik reflect this seasonal transition. With each sampling campaign we observed a reduction in the ratio of large to small copepod biomass (from 2.0 in May to 1.2 in July, and 0.9 in September), driven mostly by an increase in the small copepods *Pseudocalanus* spp. and *M. norvegica* (Fig. 3b and d). Prior work from the same campaigns shows a corresponding reduction in mean phytoplankton cell sizes between May and September alongside higher abundances of cyanobacteria (Meire *et al.*, 2023; Stuart-Lee *et al.*, 2023), which

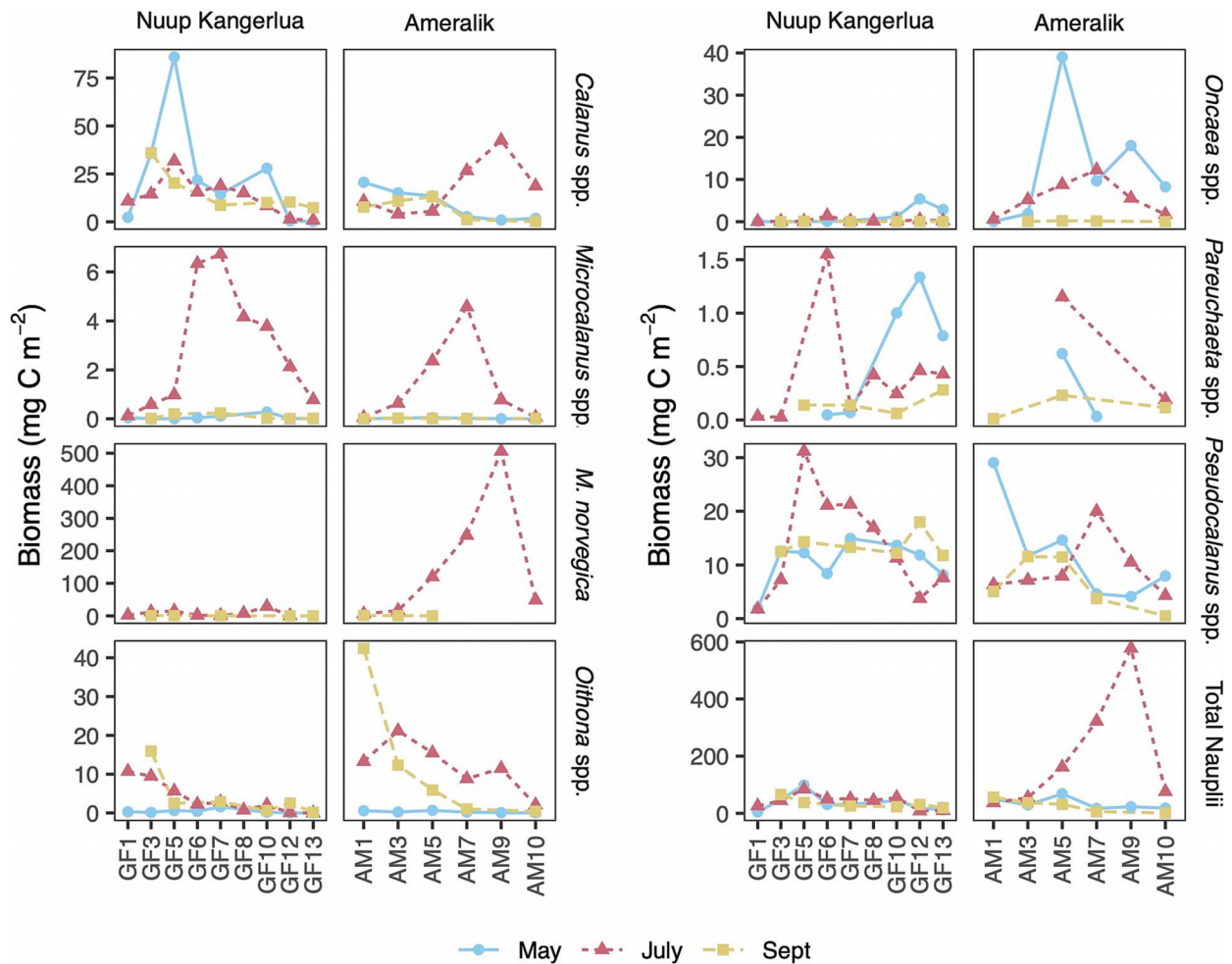


Fig. 6. Integrated Nauplii biomass (mg C m^{-2}) for each station and sampling campaign. All identified species are shown except for *Acartia longiremis* and *Centropages* spp., which represent few data points (included in the 'Total Nauplii' category).

offers less favorable grazing conditions for larger zooplankton (Haney, 1987).

Nuup Kangerlua is known to support a productive summer bloom stimulated by increased nutrient availability in the euphotic zone. This is associated with the upwelling of nutrient-rich bottom water by subglacial discharge plumes from marine-terminating glaciers (Meire et al., 2017). Prior work identified the summer bloom in 2019 and showed that there were no signs of significant cyanobacteria growth from May to July, and limited growth by September (Stuart-Lee et al., 2023). We observe here that mean integrated biomass of large copepods (3.31 g C m^{-2}) exceeded that of Ameralik (2.97 g C m^{-2}) in July, though not in May. While small copepods had the higher estimated grazing potential in the mid-fjord region (stations GF5 to GF7), large copepods represented a higher grazing pressure on phytoplankton for Nuup Kangerlua overall. This is in contrast to Ameralik, where small copepods represented the higher overall grazing potential throughout the fjord (Fig. 7b). The difference in large copepod biomass between the two fjords grew by September, with a mean biomass of 2.47 g C m^{-2} in Nuup Kangerlua, compared to 1.83 g C m^{-2} in Ameralik. This is in line with studies showing that the summer bloom (as observed in

Nuup Kangerlua) provides favorable feeding conditions for large copepods (Lydersen et al., 2014; Grønckjær et al., 2019), which likely delays and minimizes the post-spring bloom zooplankton community shift that would otherwise be observed in a land-terminating glacier system, such as in Ameralik.

Seasonal changes in the relative biomass of the *Calanus* complex were found in Nuup Kangerlua, with a greater dominance of *C. finmarchicus* in May and September, compared to July, when *C. glacialis* was the most dominant *Calanus* copepod by biomass (Fig. 3c). This pattern can be connected to the life cycles of these species. The life cycle of *C. glacialis* in Arctic regions is linked to the timing of mid-summer phytoplankton blooms (Falk-Petersen et al., 2009). With a longer development time than *C. finmarchicus*, *C. glacialis* often takes two years to complete its life cycle, peaking in population during the summer months (Hirche and Bohrer, 1987). In contrast, *C. finmarchicus* typically has a one-year life cycle, with population peaks in spring and autumn (Hirche, 1996).

The summer copepod community in Nuup Kangerlua demonstrated an along-fjord change in species composition. At station GF1, located just outside of the fjord mouth, the larger Arctic *Calanus* species *C. hyperboreus* and *C. glacialis*,

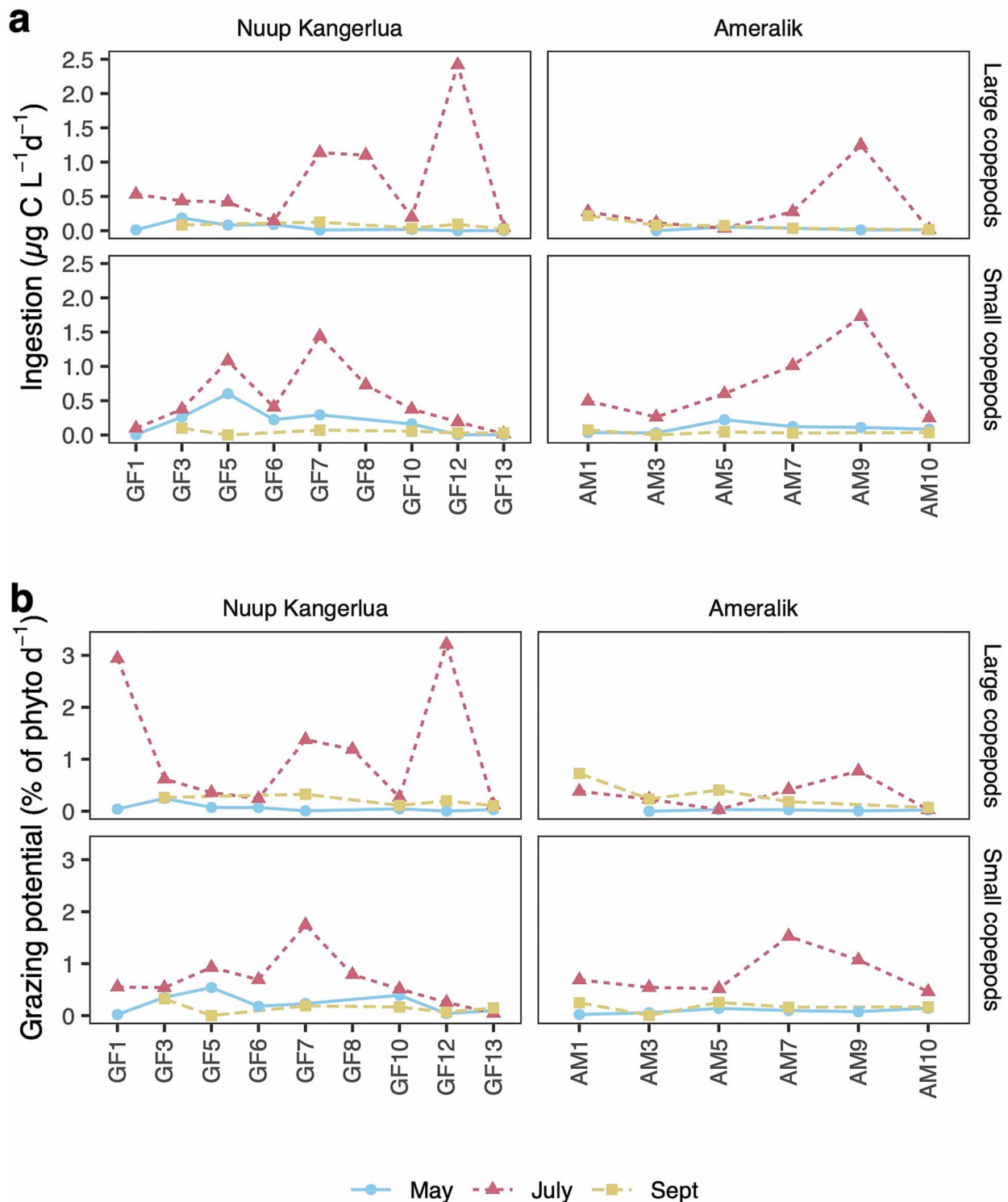


Fig. 7. (a) Ingestion rate ($\mu\text{g C L}^{-1} \text{d}^{-1}$) estimates of large and small copepod communities respectively in the upper 50 m water column of each station, and (b) the equivalent values expressed as the grazing potential of the phytoplankton biomass (% d^{-1}). Note the scale differences between 'Large copepods' and 'Small copepods'. *Oncaea* spp. and *Microsetella norvegica* are excluded from the calculations for small copepods.

typically associated with shelf waters, made up the majority of the biomass observed, while *Metridia longa* made a negligible contribution. Moving to the inner fjord, there was a reduction in the proportion of *Calanus* spp. and an increase in *Metridia longa* (Fig. 3a and c). This distribution corresponds to earlier studies

from the summers of 2008, 2010 and 2013 (Tang *et al.*, 2011; Swalethorp *et al.*, 2015; Grønkjær *et al.*, 2019). A high abundance of *Metridia longa* has also been observed in a Svalbard fjord (Lischka & Hagen, 2016). It is hypothesized that this detritus- and particle-associated, omnivorous species feeds on pelagic

carbon at greater depth and is linked to food webs characterized by high levels of nutrient recycling (Levinsen *et al.*, 2000).

By September, overall biomass in the two fjords converged, with mean values for integrated biomass across the stations of 3.95 g C m^{-2} (Ameralik) and 3.17 g C m^{-2} (Nuup Kangerlua). Both fjords showed reduced Chl-*a* concentrations (Fig. 2) and an increasing proportion of small omnivorous copepods (Fig. 4e and f), in line with expected early autumn zooplankton transitions in the Arctic (e.g. Blachowiak-Samolyk *et al.*, 2007). *M. norvegica* exhibited growth in both fjords, though to a much greater extent in Ameralik where *M. norvegica* dominated the early autumn copepod community (Fig. 4f). In contrast, *Metridia longa* represented the greatest biomass in Nuup Kangerlua, followed by *C. glacialis* (Fig. 4e). *C. finmarchicus* and *Pseudocalanus* spp. were also well represented in both fjords.

Copepod biomass was particularly high at inner-fjord station AM9 in July (Fig. 3b). Station AM9 presented sampling difficulties due to stormy conditions, and it is possible that the resulting drift of the ship may have resulted in a longer sampling distance traveled by the net, thus inflating the counts. Despite these conditions, evidence suggests that the high biomass was not an anomaly. In July, the high biomass at station AM9 corresponded to high Chl-*a* concentrations ($> 5 \mu\text{g L}^{-1}$) throughout the upper 50 m (Fig. 2d) and high picophytoplankton counts based on flow cytometry from Niskin bottle samples (Stuart-Lee *et al.*, 2023). We also observed that copepod biomass in May was considerably higher at station AM9 than elsewhere in Ameralik (Fig. 3b). This suggests that this location was indeed very biologically active in July, as opposed to being an anomalous result. The high biological activity could be related to the location of this station at a branching point in the fjord, where water from a fjord arm meets the innermost part of the fjord containing plume water from the river (Fig. 1). This convergence of water masses may result in a region where biomass builds up, as reflected in the elevated Chl-*a* in the upper 50 m, providing favorable feeding conditions for zooplankton.

Looking to the species composition of station AM9 in July, the non-nauplii component was proportionally similar to that of neighboring stations (Fig. 3d). The composition of nauplii, however, was unique (Fig. 6). Nauplii of *M. norvegica* increased with the along-fjord gradient from station AM1 to AM9, reaching a maximum biomass at AM9 of 506 mg C m^{-2} . Hence, station AM9 appears to be a key reproduction area for *M. norvegica*, as apparent from the increasing representation of *M. norvegica*, from 14% of the copepod biomass in July to 31% in September (Fig. 4d and f).

As annual primary production is higher due to subglacial discharge (Meire *et al.*, 2017, 2023), we expected higher copepod production in Nuup Kangerlua during the meltwater season. In this study, biomass estimates provide one indicator of production. Perhaps surprisingly, our values reveal a higher mean integrated copepod biomass in Ameralik than in Nuup Kangerlua in each sampled season (Fig. 3a and b). However, this doesn't necessarily also mean higher secondary production in Ameralik. Biomass estimates from Nuup Kangerlua may well have been underestimated through the use of a $50 \mu\text{m}$ mesh multinet, as larger zooplankton and krill have a better ability to avoid the net (Eriksen *et al.*, 2016). Indeed, earlier surveys in Nuup Kangerlua

have also shown high abundances of krill in spring and summer months in the central and inner fjord regions (Agersted *et al.*, 2011; Agersted and Nielsen, 2014). While marine-terminating glaciers are associated with a mechanism known to enhance summer primary production, our study does not provide evidence for large differences in summer copepod biomass in connection with this effect, and uncertainty remains for true figures of secondary production.

While overall copepod biomass estimates between the two fjords were comparable in magnitude, a contrast is seen in the species composition and size structure (Figs 4 and 6). The outer fjord stations GF1–3 and AM1–3 are located in the shared mouth region and therefore influenced by similar water masses. This is reflected in their similarity in species compositions, slightly diluting the differences observed between the two main fjord branches. We nonetheless see that, overall, Ameralik hosted a higher proportion of small and omnivorous copepods than Nuup Kangerlua, the latter being dominated by the large, herbivorous *Calanus* spp. (Fig. 4c and d). The respective food webs thus represent a classic distinction between a dominance of small copepods/omnivory and that of larger copepods/herbivory.

The smaller copepods *M. norvegica* and *Oncaea* spp. are both aggregate-colonizing copepods, feeding more on marine snow than on suspended phytoplankton, and are characterized by relatively low metabolic and mortality rates (Koski *et al.*, 2005, 2021). The biomass of these copepods was higher in Ameralik than in Nuup Kangerlua and they were found in all seasons and throughout Ameralik. *M. norvegica* were found mostly in the upper 100 m, while *Oncaea* spp. were found deeper in the water column (Fig. 5g and i). The high turbidity in inner Ameralik (Stuart-Lee *et al.*, 2023) may favor their particle-feeding preference. Although the biology of these species is distinct and they respond differently to environmental changes (Koski *et al.*, 2021), in general, higher temperatures, increased stratification, and lower nutrient availability are factors that may favor smaller, omnivorous copepods that are better able to utilize marine aggregates (e.g. Middelbo *et al.*, 2017). Of these factors, there is a particularly strong contrast in surface water temperature between the two fjords, with the upper 100 m water column being warmer in Ameralik than in Nuup Kangerlua in July and September (Fig. 2). This temperature difference during the meltwater period has been associated with the higher glacial meltwater and ice input in Nuup Kangerlua, which cools the surface waters (Stuart-Lee *et al.*, 2021), and we suggest that it is a key factor in the species composition. The abundance and wide distribution of *M. norvegica* in high-latitude ecosystems make it a key player in transferring energy through the food web. *M. norvegica* not only contributes to the vertical flux of organic material by feeding on marine snow but also serves as an important prey for a variety of fish, supporting higher trophic levels and overall ecosystem function (Svensen *et al.*, 2018). Svensen *et al.* (2018) suggest that fluctuations in *M. norvegica* populations could have significant implications for the broader marine food web and carbon cycling processes in these regions.

High biomass observations of *M. norvegica* and *Oncaea* spp. have also been reported in Nuup Kangerlua, but primarily in the southern Kapisigdlit and Uummannap branches (Swaethorpe *et al.*, 2015; Malanski *et al.*, 2020; Koski *et al.*, 2021). These

areas are less influenced by marine-terminating glaciers than the main branch sampled in this study. This suggests that the communities in Kapisigdlit and Uummannap could be more comparable to those in Ameralik. Moreover, the community of the main fjord branch might develop similarly to its lower branches if the glaciers retreat onto land in the future.

In addition to changes in size composition as a result of glacial retreat, shifts towards smaller species are expected as a result of continued atlantification of zooplankton communities with climate warming. This has been observed in Disko Bay (West Greenland) for the *Calanus* complex, with recent increases in the proportion of *C. finmarchicus* relative to the larger *C. glacialis* and *C. hyperboreus* (Møller and Nielsen, 2020). In general, a greater role has been predicted for small copepods as a result of hydrographic changes related to climate change, including those related to glacial retreat (Middelbo *et al.*, 2018).

A key implication of increased energy transfer through smaller copepods is the lower quality food source available to higher trophic levels in the spring and summer, due to their lower lipid content or to the different timing of lipid accumulation (Kattner and Hagen, 2009; Møller and Nielsen, 2020). This has been demonstrated for capelin (*Mallotus villosus*) in Nuup Kangerlua, for which a strong negative correlation was demonstrated between small copepods and quality of diet as indicated by stomach contents (Grønkjær *et al.*, 2019). Not only is capelin a major grazer of zooplankton in these systems, exerting a top-down control, it is also an important prey for many fish and marine mammals (Friis-Rødel and Friis, 2002). In this way, the effects of lower lipid content of smaller copepods are transferred throughout the food web.

CONCLUSIONS

We investigated copepod community structure in fjord systems influenced by predominantly marine- (Nuup Kangerlua) and land-terminating (Ameralik) glaciers. The integrated biomass estimates were similar between the fjords, yet clear differences were found in the copepod species composition during the summer period. In Nuup Kangerlua, zooplankton community was characterized by the presence of large, herbivorous copepods, particularly in summer. The larger Arctic *Calanus* species (*C. hyperboreus* and *C. glacialis*) made up the majority of the biomass in the fjord mouth, while the inner fjord was dominated by *Metridia longa*. This indicates that the high primary production in Nuup Kangerlua favors herbivorous species that rely on abundant phytoplankton.

In contrast, the copepod biomass in Ameralik was characterized by smaller and omnivorous copepods, in particular the aggregate-colonizing *M. norvegica* and *Oncaea* spp., although the large copepod *Metridia longa* was represented as well. Potentially these species were associated with particles from the more turbid inner fjord. Additionally *M. norvegica* and *Oncaea* spp. may also benefit from the higher upper water temperatures in Ameralik during summer and autumn. This suggests that, with a total copepod biomass similar to Nuup Kangerlua, Ameralik likely supports a community better able to utilize the regenerated production.

In this study, the highest biomass was estimated for the central part of Ameralik in July. This is a frontal zone area where water masses from an outer fjord meet the innermost water masses containing riverine discharge. We hypothesize that this site is biologically rich due to the convergence of water masses resulting in biomass build-up and favorable feeding conditions for zooplankton. It also seems to be a key reproduction site for *M. norvegica*, as suggested by the high abundance of nauplii.

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SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author, A. Stuart-Lee, upon reasonable request.

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