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Spatial occurrence and abundance of marine zooplankton in Northeast Greenland

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Abstract

We present a large-scale survey of mesozooplankton (size range 0.2–20 mm) across coastal, shelf, and slope locations in Northeast Greenland (latitudes 74–79° N, August 2015 and September 2017). Our study is centred on the Video Plankton Recorder (VPR) for non-invasive in situ observations of taxa distribution and abundance while simultaneously recording oceanographic profiles. A modified WP-2 plankton net (85-μm mesh size) was used primarily not only to verify taxa detected by the VPR but also to make a preliminary comparison of abundance estimates by the two gears. A total of 35 zooplankton taxa were identified with 10 genera alone among copepods (Hexanauplia). Selected taxa from the VPR (N=16) were associated with the temperature-salinity spaces and the chlorophyll a-depth profiles in the study area. From surface to > 900 m depth, the overall temperature and salinity ranged between −1.9 and 6.8 °C and 26.6 and 35.3, respectively. Two copepod genera dominated, i.e. *Pseudocalanus* prevailed in the upper sub-zero layers in coastal waters whereas *Calanus* was omnipresent, but mainly abundant in the warmer Atlantic waters at the shelf break. Chlorophyll a levels were in general very low (< 2 mg m^{-3}) and peaked at 30–50 m depth, suggesting post-bloom conditions. Overall, zooplankton abundances tended to increase from the coast towards the slope (9–344×10^3 individuals m^{-2}). Biodiversity in terms of taxon richness, on the other hand, showed the opposite trend and decreased from 16 taxa at the coast to 5 taxa further offshore.

Keywords Copepods · Arctic biogeography · Taxon richness · Environmental spaces · Fine-scale distribution · Video Plankton Recorder

Introduction

Zooplankton link primary producers and higher trophic levels and so play a key role in ecosystem functioning through the cycling of carbon and nutrients in the water column and subsequent export to benthic communities (Piepenburg et al. 1997; Mayor et al. 2020; Tarrant 2020; Lomatire et al. 2021). Zooplankton species may position themselves on a fine scale in the water column to occupy optimal habitat spaces near the peak of their food resource (Herman 1983; Norrbin et al. 2009; Basedow et al. 2010) but often without directly matching their prey distribution (Greer et al. 2013). Predatory

zooplankton are often positioned below their prey (Jacobsen and Norrbin 2009) but e.g. doliolids (Thaliacea) may aggregate directly within diatom layers which constitute their main food source (Greer et al. 2020). However, currents, sea ice, and other abiotic conditions, such as temperature, salinity, and depth, strongly influence the distribution of Arctic zooplankton, both vertically in the water column through stratification and shear, and over geographic distances through advection (Gallager et al. 1996; Willis et al. 2008).

Zooplankton communities are well studied for some Euro-Arctic locations, such as the Svalbard Archipelago (Daase and Eiane 2007; Willis et al. 2008; Weydmann-Zwolicka et al. 2021), the Fram Strait (Blachowiak-Samolyk et al. 2007; Svensen et al. 2011), and West Greenland (Pedersen and Smidt 2000; Madsen et al. 2008). In Northeast Greenland, on the other hand, the coastline and shelf between latitudes 70°N and 80° N are little known, mainly because the southward drift of heavy pack ice from the Central Arctic Ocean hampers scientific surveys.

Locally in Northeast Greenland, Young Sound (latitude 74° N) has become an Arctic key site for marine research

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(Middelbo et al. 2018), and further north in the seasonally recurring Northeast Water Polynya (latitudes 80–81° N), zooplankton have been intensively studied, especially the copepod species in the genus *Calanus* (Hirche et al. 1994; Ashjian et al. 1995; Schneider and Budéus 1997). Between these two Arctic sites, a long stretch of secluded fjords and a topographically complex shelf remains little investigated and warrants further studies (Christiansen 2012; Møller et al. 2019).

The Northeast Greenland coast and shelf are covered by fast-ice inshore and glacial ice and sea-ice on the shelf for more than 10 months of the year (October–August; Christiansen et al. 2016). Seasonal freshwater runoffs from the Greenland ice sheet create low-salinity surface waters in the fjords (Aagaard and Carmack 1989; Gjelstrup 2021). Freshwater discharges into coastal areas are common for the Arctic shelf seas—they build up strong salinity gradients and create water masses with different properties and thus distinct habitat spaces for zooplankton (Søgaard et al. 2021). Freshwater runoff may either benefit or limit the organic production. They are not only usually rich in terrigenous nutrients necessary for primary producers to thrive, but may also be loaded with shading sediments such as silt and thereby impede light penetration and subsequent photosynthesis (Seifert et al. 2019).

Because Northeast Greenland is affected mainly by the cold East Greenland Current moving southward on the shelf, and by the warmer Return Atlantic Current crossing the Fram Strait from Spitsbergen towards the Northeast Greenland shelf break (Straneo et al. 2012; Arndt et al. 2015; Gjelstrup 2021), we may expect both Arctic and boreal species in the area (Christiansen 2017; Andrews et al. 2019). Small-sized copepod genera like *Pseudocalanus*, *Triconia*, and *Oithona* appear to dominate the coastal area, and they also constitute the highest biomass of zooplankton in the East Greenland Current (Møller et al. 2006, 2019). Other copepod genera, like *Calanus*, *Metridia*, *Acartia*, *Microcalanus*, and *Microsetella*, are reported from Young Sound (Nielsen et al. 2007). Especially when advection is relatively low and local production substantial, resident populations of zooplankton may persist in fjords (Aksnes et al. 1989). One example of this phenomenon is the *Calanus* populations in Billefjorden, an inner basin of the Isfjorden fjord system, Spitsbergen (Arnkværn et al. 2005).

The Northeast Greenland shelf acts as the node for downstream Polar Water from the Central Arctic Ocean and upstream Atlantic Water of the West Spitsbergen Current. Hence, changes in biota and hydrography in downstream and upstream waters are readily detected in this Arctic key region. Our large-scale survey in Northeast Greenland waters aims to estimate biodiversity (i.e. taxon richness) and abundance of selected mesozooplankton taxa (size range 0.2–20 mm) in late summer. Their distribution is associated with coastal, shelf, and slope locations and environmental spaces comprising temperature, salinity, chlorophyll-*a*, and depth. All estimates are based on recordings by a Video Plankton

Recorder (VPR) because this gear, in contrast to conventional plankton nets, captures footage of single organisms directly within their environmental space. Finally, a preliminary comparison between the VPR and a WP-2 plankton net is included primarily to raise a flag of uncertainty in estimates of zooplankton abundance based on different sampling gears.

Material and methods

Study area

Northeast Greenland belongs to the largest national park in the world, and the coast and adjacent shelf are characterised by very diverse oceanographic, bathymetric, and topographic features. As part of the TUNU Programme (Christiansen 2012), we visited 16 locations (Fig. 1) during the TUNU-VI (2015, *N*=7) and TUNU-VII (2017, *N*=9) expeditions to
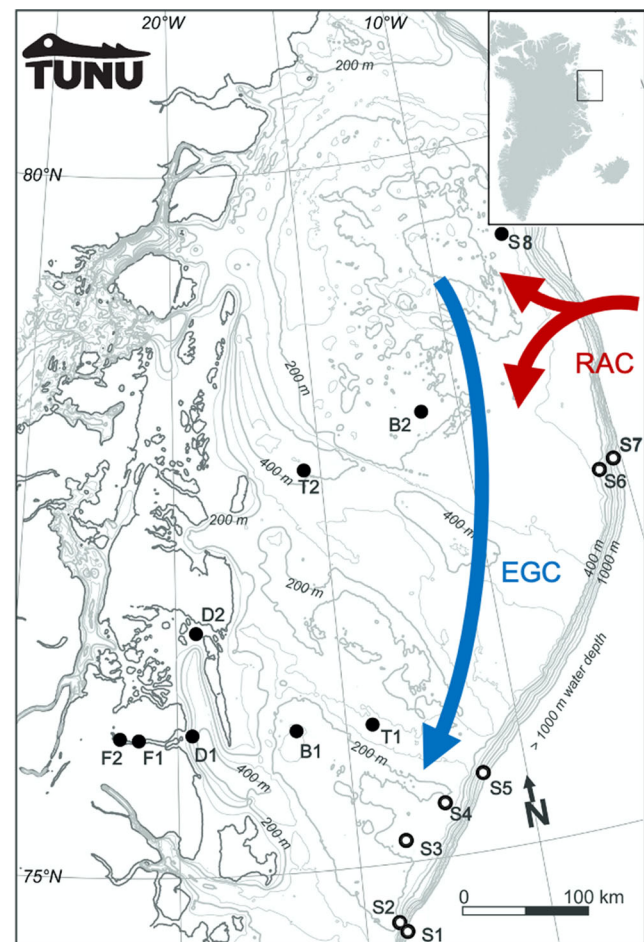
Fig. 1 Study area and the 16 locations sampled during the TUNU-VI (August 2015, open circles) and TUNU-VII (September 2017, filled circles) expeditions to Northeast Greenland. Letters and numbers identify locations (Table 1). Currents are based on Bourke (1987) and Håvik et al. (2017, 2019)—EGC in blue is the East Greenland Current and RAC in red is the Return Atlantic Current. Contoured map—courtesy of T. A. Rydningen at UiT The Arctic University of Norway

Northeast Greenland with the R/V Helmer Hanssen (UiT The Arctic University of Norway). Sampling took place in August 2015 and September 2017, mainly during daytime, and covered the area between latitudes 74° N and 79° N and longitudes 5° W and 21° W (Table 1). The entire survey area encompasses more than 65,000 NM^2 (about 223,000 km^2).

Habitats and water masses

Locations differed from west to east, i.e. from the coast, across the shelf proper to the shelf break and slope, and were grouped a priori into six distinct habitats (Table 1). Habitats comprised coastal areas with (1) Fjord and (2) Bay (bugt), the shelf area with (3) Banks and (4) Troughs, and, finally, the shelf break with (5) Shelf locations < 500 m depth and (6) Slope locations > 500 m depth.

The Northeast Greenland shelf is completely dominated by the southward outflow of cold, less saline water masses, and drift ice from the Central Arctic Ocean via the East Greenland Current (EGC). In the Fram Strait to the east, the Return Atlantic Current (RAC) also brings warmer and more saline water of Atlantic origin to the shelf and shelf break (Fig. 1; Christiansen et al. 2016; Håvik et al. 2017; Gjelstrup 2021).

We coupled our observations of zooplankton to the five main water masses identified for Northeast Greenland (Table 2), each one with a specific oceanographic profile— (1) the less saline and sub-zero Polar Surface Water (PSW); (2) the Polar Surface Water warm (PSWw); (3) the warm and saline Atlantic Water (AW); (4) the colder Modified Atlantic

Water (MAW); and (5) the sub-zero Arctic Intermediate Water (ArIW)—as given in Bourke (1987); Pickard and Emery (1990); Rudels et al. (2000 and 2002); Svendsen et al. (2002); Straneo et al. (2012); Håvik et al. (2017); Richter et al. (2018); Håvik et al. (2019), and Gjelstrup (2021).

Sampling of zooplankton

At each of the 16 locations (Table 1), we deployed a VPR for non-invasive in situ observations of zooplankton distribution, abundance estimates, and sampling of concomitant oceanographic profiles. A WP-2 plankton net was then deployed at the same site (except location S7, Table 1) to sample zooplankton, mainly not only for taxa verification and voucher specimens, but also to preliminarily compare estimates of zooplankton abundance obtained from VPR vs. WP-2 sampling. In the following, however, we focus on the VPR-data, because they present high-resolution in situ snapshots of the organisms in their surrounding environment (i.e. environmental space).

Video Plankton Recorder

An autonomous, digital Video Plankton Recorder (VPR, Seascan Inc., USA) was used to register the vertical distribution and abundance of the zooplankton. The VPR had a 1.4 MP B/W UNIQ UP-900DS-CL camera (UNIQ Vision Inc., USA) synchronized to a Xenon strobe, and an external flash drive for data capture. In addition, a SBE49 FastCAT CTD (Sea-Bird Scientific, USA) and an ECO Puck fluorometer-turbidimeter

Table 1 Overview of locations and corresponding habitats sampled by Video Plankton Recorder (VPR) and WP-2 plankton net during the TUNU-VI (2015) and TUNU-VII (2017) expeditions to Northeast Greenland (cf. Fig. 1). WP-2 samples from S5 and S6 were partially counted (Suppl. 2) and no S7 net sample was collected.

Location	Code	Date (local time)	Latitude ° N	Longitude ° W	Echo depth (m)	Habitat
Bessel Fjord	F1	17 Sep 2017 (09:24)	75.98	21.15	374	Fjord
Bessel Fjord	F2	17 Sep 2017 (18:17)	75.97	21.70	237	Fjord
Dove Bugt	D1	18 Sep 2017 (14:57)	76.01	19.57	511	Bay
Dove Bugt	D2	19 Sep 2017 (13:52)	76.74	19.32	228	Bay
76N Bank	B1	21 Sep 2017 (17:11)	76.00	16.45	73	Bank
Belgica Bank	B2	23 Sep 2017 (08:01)	78.17	11.32	190	Bank
Store Koldewey Trough	T1	21 Sep 2017 (07:20)	76.00	14.23	345	Trough
Norske Trough	T2	22 Sep 2017 (10:27)	77.86	15.58	414	Trough
74N Shelf Break	S2	09 Aug 2015 (07:47)	74.57	14.10	298	Shelf
75N Shelf Break	S3	10 Aug 2015 (07:34)	75.16	13.64	214	Shelf
75N Shelf Break	S4	11 Aug 2015 (19:30)	75.39	12.41	176	Shelf
77N Shelf Break	S6	14 Aug 2015 (07:22)	77.49	05.82	379	Shelf
79N Shelf Break	S8	24 Aug 2017 (07:47)	79.27	07.13	264	Shelf
74N Shelf Break	S1	08 Aug 2015 (15:24)	74.51	13.95	1009	Slope
76N Shelf Break	S5	12 Aug 2015 (06:13)	75.55	11.23	1005	Slope
77N Shelf Break	S7	14 Aug 2015 (13:26)	77.48	05.19	1017	Slope

Table 2 Physical properties of the five main water masses met in Northeast Greenland: Polar Surface Water (*PSW*), Polar Surface Water warm (*PSWw*), Atlantic Water (*AW*), Modified Atlantic Water (*MAW*), and Arctic Intermediate Water (*ArIW*). Water mass properties are delineated and abbreviated according to references in "Material and methods"

Water mass	PSW	PSWw	AW	MAW	ArIW
Temperature (°C)	≤ 0	> 0	> 2	0–2	< 0
Salinity	-	-	> 34.92	-	-
Density (σ_θ, ppt)	≤ 27.70	< 27.97	> 27.70	27.70–29.97	27.97–28.05

(Sea-Bird Scientific, USA) were attached to the tow frame. All parts and sensors are certified to a depth of 1000 m (Seascan, Inc., USA). We used the "S2" camera setting, with each frame recording a 22 × 32 mm field of view (FOV) and 35.2 ml water volume, at a frequency of ca. 20 image frames s^{-1}. The VPR was deployed at each location for ca. 1 h in repeated vertical profiles from the surface to 5–10 m above the bottom, at a speed of 0.8–0.9 ms^{-1}, resulting in a total sample volume of ca. 2 m^3. All data were saved in a compressed file on the flash drive, which was uploaded and processed after each deployment.

This camera setting of the VPR is best suited to detect the larger fraction of mesozooplankton (size range 1.5–20 mm), including many copepods, appendicularians, and gelatinous species. The typical abundance of this fraction of mesozooplankton in shelf seas also makes the "S2" magnification setting appropriate for mapping their distribution (comparable to the 2-cm FOV of the VPR prototype for shelf copepods, cf. Table 1 in Davis et al. 1992). However, the identification of smaller zooplankton to species (e.g. copepods with a prosome length < 1.5 mm) is impaired because the image resolution does not allow us to reliably distinguish body features. More accurate imaging of smaller species at a higher VPR magnification is possible, but that would involve an imaging volume ca. 7% of that used here, and thus result in a considerably lower sampling volume per unit time.

Plankton net (WP-2)

Zooplankton samples were generally taken from ca. 10 m above the bottom to the surface with a modified WP-2 plankton net (opening area: 0.25 m^2 as in the original gear, but total length: 3.45 m and mesh size: 85 μm, resulting in a similar porosity as the standard net towed at 0.25 ms^{-1}) (UNESCO 1968). Note that the deep Slope stations (S1 and S5 in Table 1) were sampled only in the upper 200 m.

No flowmeter was used, but sampling took place in calm waters and there was no clogging of the net. Samples were fixed in 34% formaldehyde and 1,2-propanediol (1:1), buffered with sodium tetraborate and diluted to a concentration of 4% formalin. Aliquots (subsamples) of 1.7–3.4% were taken from each sample, sorted and identified under a Leica M125C stereo microscope. For each subsample, we counted at least 300 individuals in total and 100 individuals of the most abundant taxon.

For the majority of the 2015 locations, we analysed the entire sample for the larger zooplankton taxa such as amphipods, krill, and chaetognaths. Moreover, for all locations, the prosome lengths (μm) of *Calanus* (N_{tot} = 1761 specimens) were measured under the stereomicroscope for a size-based estimate of species composition following Daase and Eiane (2007) and Daase et al. (2018), i.e. *C. hyperboreus* > *C. glacialis* > *C. finmarchicus* within each of the six copepodite stages CI–CVI (Suppl. 3). Although the species overlap in size, the overall distribution of life stage-specific length classes provides a rough appraisal of the *Calanus* species present in given habitats. These data, however, are only briefly discussed here because molecular analyses are warranted to properly discriminate between the *Calanus* species of concern (e.g. Nielsen et al. 2014; Choquet et al. 2018).

Data analyses

We used the software packages Autodeck (Seascan, Inc., USA) and Visual Plankton (C.S. Davis, WHOI; USA), as well as own Matlab (MathWorks Inc., USA) scripts, to extract the environmental data and plankton images (ROIs, regions of interest). The ROIs were automatically classified with Visual Plankton to major groups, before being sorted manually to the lowest practical taxonomical level (usually class or genus) according to WoRMS (http://marinespecies.org/). All selected taxa had more than 45 observations unambiguously identified from the VPR frames, except in the cases of *Acartia* and *Paraeuchaeta*, with 7 and 14 observations, respectively.

The VPR observations were verified by the WP-2 samples, and further analysis was done in Rstudio 2.5 (Rstudio Inc. USA) with the oce package (Kelley 2018).

The distribution patterns for the 16 selected zooplankton taxa and their association with particular water masses (Table 2) were visualised by temperature-salinity spaces for the six habitats (Fig. 2a). These spaces were depicted by point clouds representing all temperature and salinity combinations throughout the water column both within given habitats and for all locations combined—in total above one million data points in the entire point cloud. Similarly, an equal number of data points was used in a point cloud depicting chlorophyll *a* fluorescence vs. depth to illustrate the vertical profile for the

same taxa within given habitats and for all locations combined (Fig. 2b). Chlorophyll *a* (Chl-*a*) fluorescence from the Ecopuck sensor on the VPR corresponded well with Chl-*a* extracted from water samples (Beroujon 2019). Finally, the counts for a single taxon (Table 3) were superimposed on the point clouds of the temperature-salinity space (Fig. 3) and the chlorophyll *a* fluorescence-depth profile (Fig. 4).

Because of the exploratory nature of the TUNU expeditions and the opportunistic sampling in ice-laden waters, we decided to base our biodiversity estimates simply on the number of taxa (i.e. taxon richness) rather than the commonly used Shannon-Wiener or Simpson indexes, which require ample sample sizes and comprehensive abundance data (Magurran 2004).

Abundance estimates for given taxa (*A*) are presented in numbers per unit sea surface area (m^{-2}) and were obtained from counts in the VPR footage according to the equation:

$$A = \frac{N}{V} \times D$$

where *N* is the number of individuals, *V* is the total volume (m^3) imaged, and *D* is the maximum depth (m) sampled at each location. Abundance estimates are given both for the entire water column and for the upper 70 m because this depth corresponds to that of the shallowest location (i.e. 76N-Bank (B1), Table 1). In the case of Table 3, average abundance per

cubic metre is given, which is calculated as number (*A*), but without the multiplication with depth (*D*).

Zooplankton counts from the WP-2 net were converted into abundance estimates for a single taxon based on the volume sampled (UNESCO 1968) and compared with those estimates obtained from the VPR sampling.

A canonical-correspondence analysis (CCA) was done to illustrate how taxa are associated with given habitats (ellipses in Fig. 5). The graph was made in Rstudio using the Vegan package (Oksanen et al. 2014). Prior to running the CCA, the dataset was weighted by total volume sampled for each habitat to compensate for more offshore than coastal locations being sampled. Habitat delineations represent the 95% confidence interval for which taxa occur within given habitats. The overall power of the analysis is given by the sum of values for each CCA axis, here 66.23% (Fig. 5).

Results

Habitats and water masses

Bottom depth varied greatly across the 16 locations and ranged from 73 m at the 76N-Bank (B1) to 1017 m on the slope (S7, Table 1). The six habitats, i.e. Fjord, Bay, Bank, Through, Shelf, and Slope, also differed markedly in overall
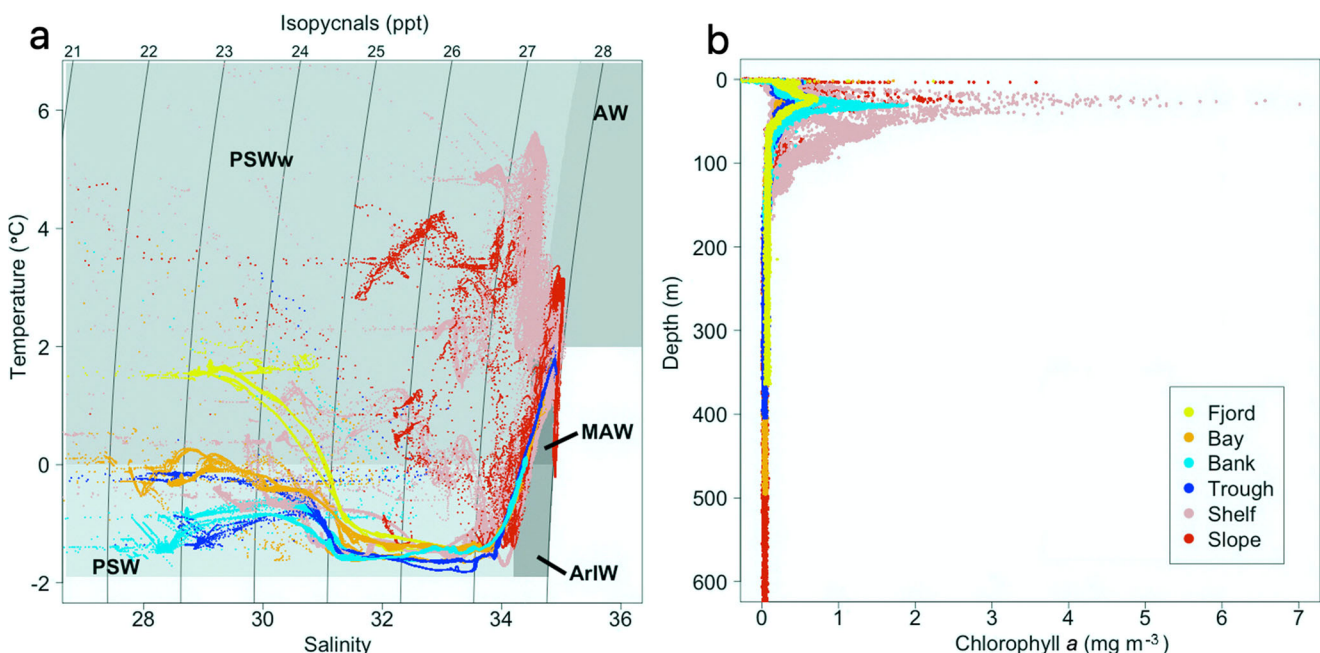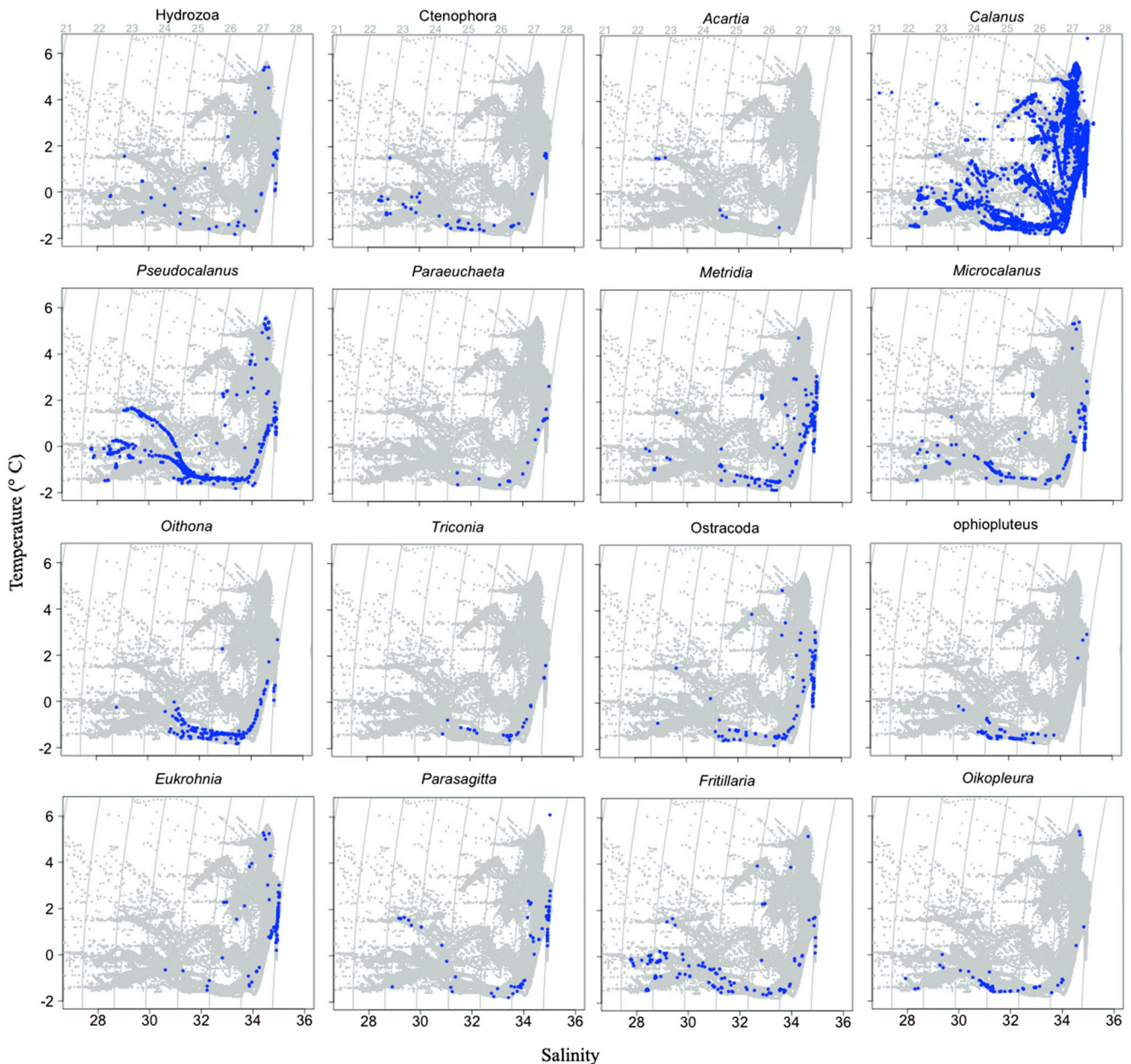

Fig. 2 Water mass properties recorded by Video Plankton Recorder (VPR) across locations during the TUNU-VI (August 2015) and TUNU-VII (September 2017) expeditions to Northeast Greenland (Fig. 1). Locations are grouped according to the corresponding habitats (Table 1). **a** The overall temperature-salinity plot together with isopycnic lines (density, ppt). Delineations and abbreviations of water masses are from Table 2; **b** the overall chlorophyll *a* fluorescence-depth profile for the same locations and habitats. The point clouds of **a** and **b** form the background in Figs. 3 and 4, respectively. Zooplankton were found at salinities between 26.95 and 35.24 and temperatures between −1.81 and 6.64 °C

Table 3 Zooplankton taxa (N=16) detected by Video Plankton Recorder (VPR) across locations and corresponding habitats during the TUNU-VI (August 2015) and TUNU-VII (September 2017) expeditions to Northeast Greenland (cf. Fig. 1 and Table 1). Taxa are listed and named following WoRMS (http://marinespecies.org). Abundance per m^3 of specimens for given locations and taxa as identified from the VPR footage (cf. Figs. 3 and 4). The mean abundance of specimens for each habitat and taxon is shown in bold. ND denotes undetected taxa. Note the overall decrease in taxon richness and the concomitant increase in total abundance from the coast towards the shelf and slope locations (cf. Table 3)

| Habitat Taxa	Hydrozoa	Ctenophora	Acartia	Calanus	Pseudocalanus	Paraeuchaeta	Metridia	Microcalanus	Oithona	Triconia	Ostracoda	ophiopluteus	Eukrohnia	Parasagitta	Fritillaria	Oikopleura	Total abundance
Fjord	3	2	1	58	45	1	21	4	15	10	10	<1	<1	2	4	ND	176
F1	5	2	<1	36	28	1	13	4	11	8	5	<1	<1	1	6	ND	120
F2	ND	1	2	93	70	1	34	3	21	15	18	ND	ND	5	2	ND	265
Bay	5	ND	2	45	113	2	6	15	12	2	3	4	1	4	16	1	233
D1	3	ND	2	14	10	<1	3	9	3	1	5	1	<1	4	11	1	68
D2	12	ND	3	117	352	5	14	29	31	3	1	11	2	6	26	2	615
Bank	6	ND	1	30	9	<1	1	1	6	2	3	7	1	2	12	10	90
B1	14	ND	ND	43	18	ND	ND	ND	8	ND	3	15	1	ND	25	2	129
B2	3	ND	1	25	5	<1	1	1	5	3	3	4	1	2	6	13	75
Trough	<1	ND	2	23	2	<1	3	1	4	ND	2	<1	<1	2	1	<1	43
T1	1	ND	3	31	3	1	4	2	4	ND	2	ND	1	1	3	ND	55
T2	ND	ND	<1	17	1	ND	3	1	3	ND	2	1	ND	3	ND	<1	33
Shelf	1	ND	1	438	7	ND	5	1	1	<1	2	1	4	<1	1	2	463
S2	ND	ND	ND	714	2	ND	1	ND	ND	ND	2	ND	ND	<1	ND	ND	720
S3	ND	2	2	208	2	ND	11	ND	ND	ND	2	ND	4	ND	1	ND	229
S4	ND	6	6	1554	26	ND	13	2	1	ND	1	1	14	ND	5	2	1624
S6	ND	ND	ND	104	ND	ND	2	ND	ND	ND	1	ND	5	ND	<1	ND	113
S8	3	<1	<1	80	17	ND	3	1	3	2	2	ND	2	ND	2	7	129
Slope	ND	1	1	212	3	<1	4	3	<1	<1	4	<1	3	4	1	ND	236
S1	ND	1	1	325	3	1	4	5	ND	<1	9	1	5	5	1	ND	360
S5	ND	1	1	122	4	ND	4	1	ND	ND	2	ND	2	4	1	ND	141
S7	ND	1	1	190	3	ND	4	2	1	ND	2	ND	3	2	ND	ND	207

Fig. 3 The 16 selected zooplankton taxa detected by Video Plankton Recorder (VPR) across locations and corresponding habitats during the TUNU-VI (August 2015) and TUNU-VII (September 2017) expeditions to Northeast Greenland (cf. Table 3 and Fig. 4). Temperature and salinity affinities for single specimens in given taxa were identified from the VPR footage and superimposed (blue points) on the temperature-salinity plot for the entire study area (grey point cloud, cf. Fig. 2a)

temperature (range, −1.9 to 6.8 °C) and salinity (range 26.6–35.3) (Fig. 2a). The temperature-salinity space of the secluded Bessel Fjord (F1 and F2) was 2.0 °C and salinity 28.0 near the surface, and −1.4 °C and salinity 33.5 in the deepest part of the water column. In the open Dove Bugt (D1 and D2), we observed a similar increase in salinity with depth, but the temperature did not exceed 0.5 °C. Bessel Fjord and Dove Bugt were both associated mainly with the oceanographic profiles of Polar Surface Water warm and Polar Surface Water, respectively (Table 2, Fig. 2a).

On the shelf, the Banks (B1 and B2) had much lower temperatures (−1.9 to 0.1 °C) and a wider salinity range (27.5–34.5) compared to the coastal locations. The temperature-salinity space of the two Troughs, on the other hand, differed near the surface. The Store Koldeway Trough (T1) had higher temperatures (−0.2 °C) and lower salinities (28.0) compared to the strong sub-zero temperatures (−1.6 °C) and somewhat higher salinities (28.8) in the Norske Trough (T2). For both Troughs, maximum temperatures of 1.9 °C and salinities of 34.7 were reached near the bottom. The water masses for both
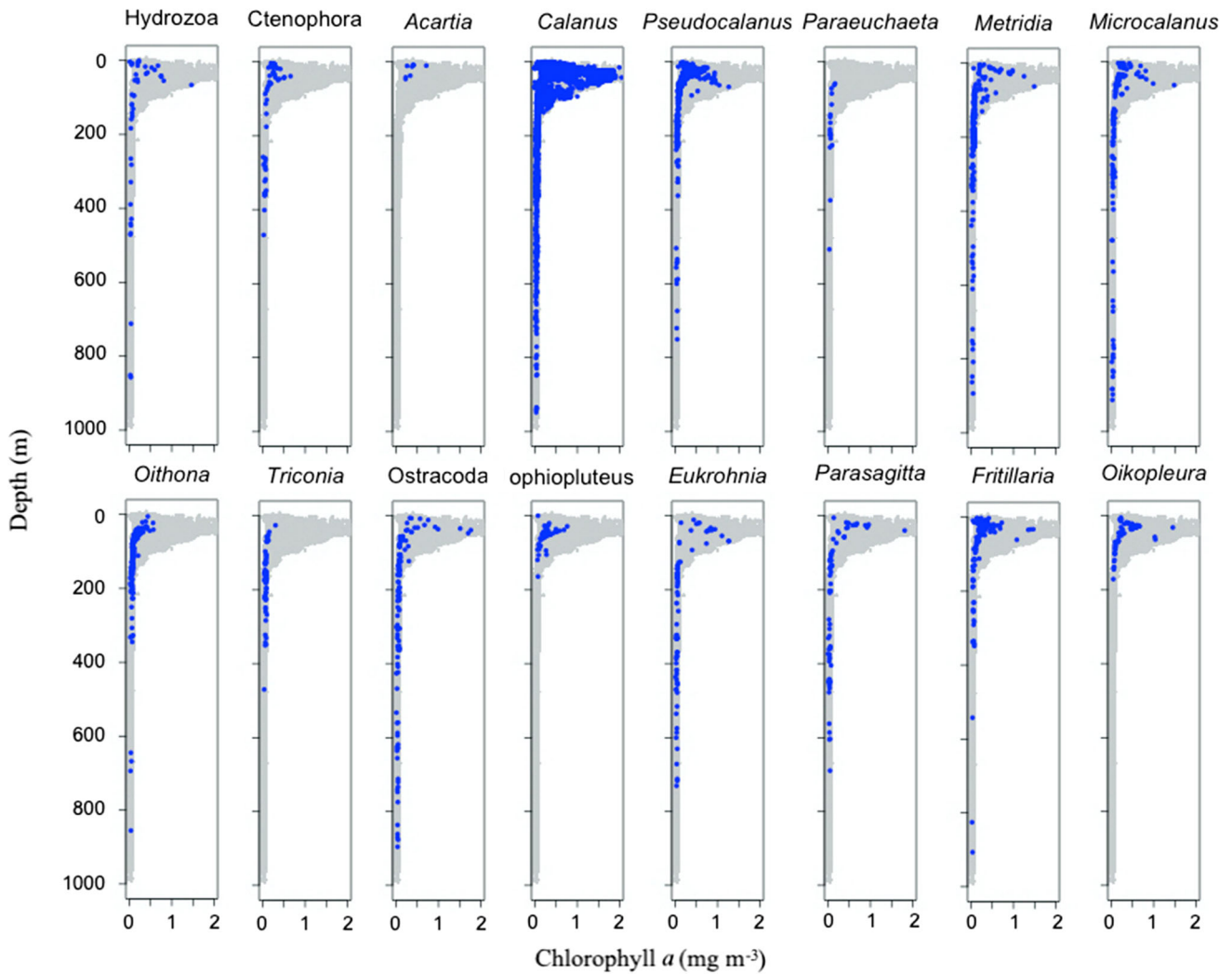
Fig. 4 The 16 selected zooplankton taxa detected by Video Plankton Recorder (VPR) across locations and corresponding habitats during the TUNU-VI (August 2015) and TUNU-VII (September 2017) expeditions to Northeast Greenland (cf. Table 3 and Fig. 3). Depth and chlorophyll a fluorescence affinity for single specimens in given taxa were identified from the VPR footage and superimposed (blue points) on the chlorophyll a fluorescence-depth profile for the entire study area (grey point cloud, cf. Fig. 2b). No taxa were detected at chlorophyll values > 2 mg m^{-3}

Banks and Troughs were associated mainly with Polar Surface Water and Modified Atlantic Water (Table 2, Fig. 2a).

The temperature-salinity spaces at the shelf break, i.e. Shelf (S2-S4, S6 and S8) and Slope (S1, S5 and S7) locations, were not as distinct as for those in the coastal habitats and they were dominated mainly by Polar Surface Water warm and Polar Surface Water. In the deeper part, Modified Atlantic Water dominated on the Shelf, whereas warmer (> 2.0 °C) and more saline (> 34.9) Atlantic water dominated the Slope (Table 2, Fig. 2a).

The chlorophyll a fluorescence-depth profiles for locations within given habitats are shown in Fig. 2b. Overall, the Chl-a values ranged from near 0 to 7.32 mg m^{-3} across depths from surface to 989 m with a mean Chl-a maximum of < 2 mg m^{-3} at 30–50 m depth. The Chl-a maxima varied markedly across habitats from the Troughs (0.70 mg m^{-3}) and the Banks (1.90 mg m^{-3}), via Dove Bugt (1.71 mg m^{-3}) and Bessel

Fjord (2.23 mg m^{-3}) toward the Shelf (7.32 mg m^{-3}) and Slope (3.57 mg m^{-3}). The Shelf and Slope areas appear to have the highest Chl-a values, but note that most of these locations (S1–S7) were sampled in August 2015, whereas the other locations were sampled in September 2017 (Table 1, cf. "Discussion").

Spatial occurrence of zooplankton

We identified 35 zooplankton taxa in total (Suppl. 1), with 10 genera in class Hexanauplia (subclass Copepoda) alone. In Suppl. 1, traits were assigned to taxa according to Benedetti et al. (2016). The gelatinous ctenophores (Ctenophora) were detected only by the VPR and not in the WP-2 net. On the other hand, 13 taxa were identified only from the WP-2 net and went largely undetected by the VPR (Suppl. 1). Among those were the sea-ice associated amphipods *Gammarus*

Fig. 5 Canonical-correspondence analysis (CCA) shows the association between taxa and habitats recorded by Video Plankton Recorder (VPR) during the TUNU-VI (August 2015) and TUNU-VII (September 2017) expeditions to Northeast Greenland (cf. Table 3 and Fig. 3). Coloured ellipses represent habitats. Taxa, identified with three-letter codes, are located according to their degree of association with given habitat. Note: Habitats and taxa distant from the origin (0.0) are more distinctive than those near the origin (cf. "Discussion")
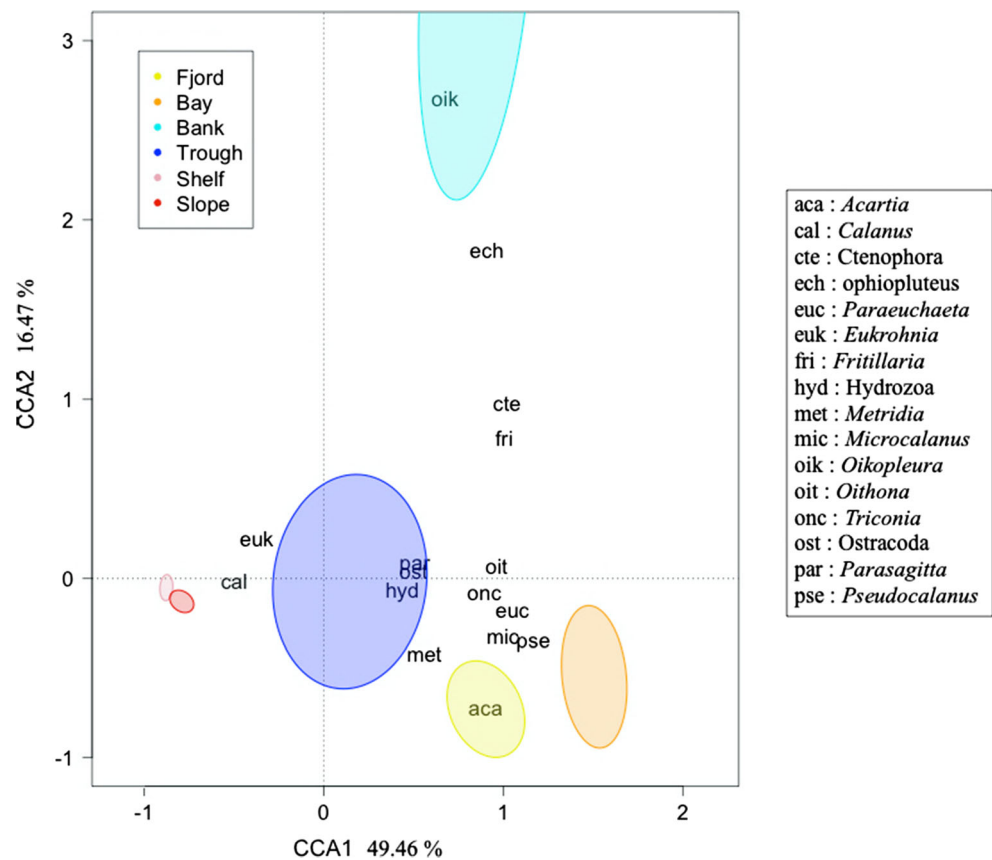
wilkitzkii and *Apherusa glacialis* (Crustacea) which were observed near the marginal sea-ice zone, fish eggs (Chordata), the krill genera *Meganyctiphanes* and *Thysanoessa* (Euphausiidae), decapod larvae (Crustacea), hyperiid amphipod *Themisto* (Crustacea), and molluscs, i.e. bivalve veligers and pteropods. Only two taxa belonged to meroplankton, i.e. the larval stages of bivalves (veliger, Mollusca) and decapod crustaceans (zoea).

The temperature-salinity space and the chlorophyll *a* fluorescence-depth profile for each of the 16 selected zooplankton taxa are shown in Figs. 3 and 4. The copepod *Pseudocalanus* occurred mostly at temperatures < 2.0 °C. Many taxa were present in cold water, usually below 0 °C. This was the case for the copepods *Oithona* and *Triconia*, the appendicularians *Fritillaria* and *Oikopleura*, and for the ctenophores. The chaetognaths *Parasagitta* and *Eukrohnia* were present at salinities above 29.0 and 30.5, respectively. The copepods *Metridia* and *Paraeuchaeta*, and ostracods were present at salinities above 31.0. The ophioplutei were mainly present in very cold waters (< −1.0 °C), and at salinities ranging from 30.5 to 34.0. Other taxa, such as the hydrozoans and the copepod *Microcalanus* and especially the *Calanus* species, occurred across a wide range of temperatures and salinities (Fig. 3).

Similarly, the chlorophyll *a* fluorescence-depth profiles (Fig. 4) showed that the copepods *Acartia* and *Paraeuchaeta*, the appendicularian *Oikopleura*, and ophioplutei were present mainly in the upper 200 m of the water column. The copepod *Paraeuchaeta* was found only deeper than 30 m, while all other taxa also occurred throughout the water column. The copepods *Oithona, Pseudocalanus, Triconia*, the appendicularian *Fritillaria*, and ctenophores occurred mostly from the surface to 400 m depth. The chaetognaths *Parasagitta* and *Eukrohnia*, the copepods *Calanus, Metridia*, and *Microcalanus*, the hydrozoans, and ostracods were present also in deeper waters (0–947 m). Some taxa, such as the copepods *Calanus* and *Pseudocalanus* and the appendicularian *Fritillaria*, tended to occur around the Chl-*a* peak. In September 2017 (TUNU-VII), all locations but the 76N bank had Chl-*a* maxima below 0.5 mg m^{-3} (ca 1.5 mg m^{-3} for location B1), while higher values were recorded on the Shelf and Slope stations in August 2015 (Figs. 2b and 4).

Zooplankton abundance and taxon richness

Across the 16 locations, zooplankton abundances obtained by the VPR ranged between $9×10^3$ (B1) and $344×10^3$ (S1) individuals m^{-2}, and the corresponding taxon richness ranged

between 5 (S6) and 15 (F1, D1, D2, B2) taxa (Table 4). The Shelf and Slope locations had by far the highest abundances compared to the other locations with a mean of 118×10^3 and 228×10^3 individuals m^{-2}, respectively, and were completely dominated by copepod species in the genus *Calanus*. These offshore locations were also lowest in taxon richness, ranging from 5 (S2 and S6) to 13 (S8) taxa (Table 4). Banks and Troughs had the lowest mean abundances with 11×10^3 and 16×10^3 individuals m^{-2}, respectively. Bessel Fjord and Dove Bugt, on the other hand, had mean abundances of 52×10^3 and 83×10^3 individuals m^{-2}, respectively, and the latter location was dominated by the copepod *Pseudocalanus*. In contrast to the relatively low taxon richness at the Shelf and Slope, the four other habitats revealed a marked taxon heterogeneity, with a taxon richness ranging from 9 (B1) to 15 (F1, D1, D2, B2) taxa. The copepod genus *Calanus* was by far the most common taxon across the entire study area with abundances corresponding to 20% of all mesozooplankton counts in Dove Bugt (D2) and up to 99% of the counts on the Shelf (S2; Table 4).

The zooplankton abundances in the upper 70 m relative to the entire depth varied from 31% for the Troughs to 70% for the Shelf locations. The apparently high proportion in the upper 70 m for the Banks is strongly biased by the shallow waters on the 76N-Bank (Tables 1 and 3). Although the modified WP-2 net was used primarily for taxon validation of the VPR-footage, abundance estimates were done as well (Suppl. 2).

Based on the WP-2 counts and prosome length measurements, the composition of *Calanus* species is shown in Suppl. 3. In August 2015, *C. finmarchicus* (stages CI–CIV) was the most abundant copepod at the southernmost shelf break and slope location (S1, S2) and comprised 88–95% of the three *Calanus* species considered here. An incursion of *C. glacialis* (17%) and *C. hyperboreus* (19%) occurred further north (S3). In September 2017, a similar assemblage of *Calanus* species, dominated by *C. finmarchicus* CIII, was seen at the shelf break (S8). Older copepodites (CV) of *C. finmarchicus* also dominated the Store Koldewey Trough (63%, T1) but *C. hyperboreus* was not detected here. The *C. glacialis* was the most abundant copepod (53–91%) in the Norske Trough (T2; stage CV), at both banks (B1, B2; stages CIV–CV), in Bessel Fjord (F1, F2; stages CIV–CV) and Dove Bugt (D1, D2; stages CIII–CIV), with contributions from the other two *Calanus* species, and in Bessel fjord especially *C. hyperboreus* CV and adults.

Table 4 Zooplankton taxa (*N*=16) detected by Video Plankton Recorder (*VPR*) across locations and corresponding habitats during the TUNU-VI (August 2015) and TUNU VII (September 2017) expeditions to Northeast Greenland (cf. Fig. 1, Table 1). Total abundances (individuals m^{-2} in thousands) were calculated from abundances at given locations (Table 3) and the relative abundance as the proportion of total abundance from surface to 70 m depth (i.e. the shallowest location). Similarly, the proportions of total abundance are shown for the prominent copepod genera *Calanus* and *Pseudocalanus*, and the other 14 taxa combined. Percentages are rounded to add up to 100%. Taxon richness for given locations is indicated also in Table 3. Mean abundances and taxon richness ranges for given habitats are shown in bold

Location and habitat	Total abundance	Relative abundance (%) in 0–70 m	VPR depth (m)	*Calanus* (%)	*Pseudocalanus* (%)	Other taxa (%)	Taxon richness
Fjord	**52**	**40**	**297**	**33**	**25**	**42**	**12–15**
F1	44	35	364	30	24	46	15
F2	61	44	230	35	27	38	12
Bay	**83**	**57**	**355**	**19**	**49**	**32**	**15**
D1	33	50	495	21	15	64	15
D2	132	64	214	19	57	24	15
Bank	**11**	**78**	**119**	**33**	**10**	**57**	**9–15**
B1	9	100	68	34	14	52	9
B2	13	56	170	33	7	60	15
Trough	**16**	**31**	**364**	**55**	**5**	**40**	**10–12**
T1	18	49	323	56	6	38	12
T2	13	13	404	53	4	43	10
Shelf	**118**	**70**	**255**	**94**	**2**	**4**	**5–13**
S2	205	90	285	99	0	1	5
S3	47	41	204	91	1	8	6
S4	265	91	163	95	2	3	11
S6	42	64	372	92	0	8	5
S8	33	66	252	62	13	25	13
Slope	**228**	**65**	**968**	**90**	**1**	**9**	**9–12**
S1	344	58	955	90	1	9	12
S5	136	57	961	86	3	11	9
S7	205	81	989	92	1	7	9

Zooplankton associated with habitats

Most of the 16 taxa, identified in the VPR footage, revealed an apparent link to the given habitats (Table 3). The copepods *Triconia* and *Acartia* occurred mostly in Bessel Fjord, whereas other copepods, like *Pseudocalanus*, *Microcalanus*, and *Oithona*, occurred in both Bessel Fjord, Dove Bugt, and the Troughs. The appendicularian *Oikopleura* and ophioplutei, on the other hand, occurred mostly on the Banks. Ctenophores and the appendicularian *Fritillaria* appeared to occur closer to the coast (Bessel Fjord, Dove Bugt, Banks). In contrast, calanoid copepods (*Calanus*) and the chaetognath *Eukrohnia* dominated the Shelf and Slope habitats. The chaetognath *Parasagitta* was mainly concentrated in Slope locations, whereas the copepod *Metridia* was not only mainly present in Fjord locations but also present in high abundance on the Shelf, Trough, and Slope (Table 3). Ostracods (Ostracoda) and hydrozoans (Hydrozoa) occurred in all habitats, albeit in low abundances (Table 3). Finally, the copepod *Paraeuchaeta* occurred in all habitats except the Shelf.

In general, the smaller-sized copepods were more closely associated with the inshore habitats, while the larger species were closer associated with offshore habitats (Fig. 5). Thus, the copepod *Calanus* and the chaetognath *Eukrohnia* were linked to the Shelf, Slope, and Trough habitats, while the chaetognath *Parasagitta*, Ostracoda, and Hydrozoa were linked to the Trough habitat (Fig. 5). The copepod *Metridia* appeared to have an affinity for both Trough and Fjord habitats (Fig. 5). Several copepods, i.e. *Microcalanus*, *Oithona*, *Paraeuchaeta*, *Pseudocalanus*, and *Triconia*, seemed to be associated with both Fjord, Bay, and Trough habitats. The copepod *Acartia* and the appendicularian *Oikopleura* revealed the strongest habitat association of any of the taxa (CCA 95% evidence, Fig. 5), whereas Ctenophores and the appendicularian *Fritillaria*, and to some extent also ophiopluteus larvae, did not appear to be strongly associated with any particular habitat (Fig. 5). Please note, for this type of analysis (Fig. 5), taxa close to the origin are less habitat specific and may in fact occur across several habitats.

Potential gear bias in abundance estimates of zooplankton

Our study is centred on the 16 selected zooplankton taxa detected by the VPR (Table 3). Gear and sampling methods may render different outcomes (cf. Discussion) and the use of VPR vs. WP-2 net may potentially bias abundance estimates for given habitats (Table 5) and zooplankton taxa (Table 6).

The total abundance estimates (individuals m^{-2}) differed markedly between the VPR and the WP-2 net across habitats (Table 5). Overall, the WP-2 net gave higher abundances than the VPR—especially for the Trough where the WP-2 net disclosed abundance more than six times higher. In the Bay

and on the Slope, the abundance estimates were quite similar for the two gear types. The taxon richness detected by the VPR, on the other hand, was in general higher than that disclosed by the WP-2, irrespective of habitat (Table 5).

Nevertheless, abundance and taxon richness showed similar trends across habitats for both gear types employed, i.e. a lower abundance and a higher taxon richness nearer the coast and, inversely, a higher abundance and a lower taxon richness at the shelf break. Also, the abundance estimates for given taxa were affected by the gear employed (Table 6). The small-sized copepods (*Triconia*, *Pseudocalanus*, *Microcalanus*, and *Acartia*) were underestimated by the VPR by a factor of 2 compared to the modified WP-2 net, while the discrepancy was even larger for *Oithona*, with more than 26 times higher average abundance in the WP-2 net. *Oithona* in fact revealed 65% of the abundance of the large-sized *Calanus* in the WP-2-net, but only 3% of the *Calanus* abundance as deduced from the VPR sampling (Table 6). In contrast, large-sized and gelatinous or fragile zooplankton taxa, such as hydrozoans, the chaetognaths *Parasagitta* and *Eukrohnia*, ostracods, and the appendicularian *Fritillaria*, were all substantially underestimated by the WP-2 net (Table 6). Other taxa such as the copepods *Paraeuchaeta*, *Calanus* and *Metridia*, the appendicularian *Oikopleura*, and the ophioplutei showed similar abundance estimates and thus appeared little affected by the gear employed.

Discussion

Compared to Arctic locations on the eastern side of the Fram Strait, the fjords and shelf of the Svalbard Archipelago (Hegseth et al. 2019), Northeast Greenland experiences a later start of the productive season (Arendt et al. 2016, Mayot et al. 2018). This is caused by ice flux from the Arctic Ocean and the East Greenland Current carrying cold water southwards, resulting in lingering sea ice on the shelf (Vernet et al. 2021). In the fjords, the seasonal ice-cover does not break up until mid- to late July (Holding et al. 2019). Productivity in the fjords is enhanced by glacial runoff (Arendt et al. 2016, Meire et al. 2017), while the shelf receives varying nutrient loads depending on the water mass composition of the East Greenland Current (S. Kristiansen, pers. comm.) and may experience under-ice blooms (Mayot et al. 2018). Net primary production on the shelf peaks in July and may remain high until September (Mayot et al. 2018, Vernet et al. 2021), while the fjords may have a spring bloom peak after ice break-up with sustained primary production until September (Holding et al. 2019).

The general trend for mesozooplankton revealed a higher taxon richness in the fjords than on the shelf, and vice versa for total abundance. Likewise, the prevalence of smaller-sized zooplankton taxa decreased from fjord to shelf habitats.

Table 5 Habitats visited during the TUNU-VI (August 2015) and TUNU-VII (September 2017) expeditions to Northeast Greenland (Fig. 1, Table 1). Overall total mean abundance (individuals m⁻² in thousands) for the 16 selected taxa detected by Video Plankton Recorder (VPR) are combined for each habitat and shown for both sampling gears, i.e. the VPR and the modified 85 μm WP-2 plankton net (cf. Tables 4 and Suppl. 2). A gear ratio (WP-2/VPR) close to 1 signifies that both gears estimate similar abundances. Habitats underestimated by the WP-2 show values < 1 and those underestimated by the VPR show values > 1. Taxon richness is shown as the range of taxa encountered for the specific gear across locations within given habitats (cf. Table 4)

Habitat	Total mean abundance, VPR	Total mean abundance, WP-2	Gear ratio WP-2/VPR	Taxon richness, VPR	Taxon richness, WP-2
Fjord	52	98	1.9	12–15	10–11
Bay	83	77	0.9	15	11–13
Bank	11	43	3.9	9–15	10–13
Trough	16	107	6.7	10–12	13
Shelf	118	290	2.4	5–13	2–12
Slope*	344	293	0.9	9	11

*For the Slope, we obtained data from only one WP-2 haul (S1, 200-0 m; Table 1)

Habitats and water masses

Depth, temperature, and salinity are the main environmental drivers that determine the spatial distribution of marine zooplankton in Northeast Greenland. The bathymetry varies considerably between the Fjord, Shelf, and Slope locations (Table 1; Arndt et al. 2015; Laberg et al. 2017; Olsen et al. 2020). Bathymetry and seabed features may redirect water currents on a small geographic scale, thus affecting both the extent of sea-ice cover, freshwater runoff from melting glaciers, and primary production by advection. In the coastal area, Bessel Fjord and Dove Bugt were strongly influenced by freshwater runoff in the upper 20 m, and this low-salinity layer became gradually thinner further offshore. Differences in salinity and temperature with depth may lead to strong stratification of the water body and so create environmental barriers and structure distinct temperature-salinity spaces, within which zooplankton taxa may thrive (Gjelstrup 2021).

The warm water masses we observed at the Shelf and Slope locations (Table 1, Fig. 2a) are brought to the Northeast Greenland shelf by the Return Atlantic Current (Håvik et al. 2019) and the Modified Atlantic Water, i.e. water masses of Atlantic origin deflecting from the eastern Fram Strait. As a consequence, boreal biota such as the northern shrimp

Table 6 Zooplankton taxa sampled during the TUNU-VI (August 2015) and TUNU-VII (September 2017) expeditions to Northeast Greenland (Fig. 1, Table 1). Overall mean abundance (individuals m⁻²) for each of the 16 selected taxa detected by Video Plankton Recorder (VPR) and all locations combined are shown for both sampling gears, i.e. the VPR and the modified 85 μm WP-2 plankton net (cf. Tables 4 and Suppl. 2). Taxa are listed from the lowest to the highest gear ratio (WP-2/VPR). A gear ratio close to 1 signifies that both gears estimate similar abundances. Taxa underestimated by WP-2 show values < 1 and those underestimated by VPR show values > 1

Taxa	Total mean abundance VPR	Total mean abundance WP-2	Gear ratio, WP-2/VPR
Ctenophora	3739	0	0
Hydrozoa	3208	134	~ 0
Eukrohnia	5021	528	0.1
Ostracoda	9781	1828	0.2
Fritillaria	9890	2588	0.3
Parasagitta	6704	3013	0.4
Paraeuchaeta	1160	718	0.6
Metridia	14,822	12,226	0.8
ophiopluteus	2812	2953	1.0
Calanus	362,202	440,529	1.2
Oikopleura	2045	2672	1.3
Pseudocalanus	60,386	116,882	1.9
Acartia	468	1000	2.1
Triconia	4178	9511	2.3
Microcalanus	9873	24,016	2.4
Oithona	10,996	290,120	26.4

Pandalus borealis, beaked redfish *Sebastes mentella*, and Atlantic cod *Gadus morhua* may spread from the Barents Sea to Northeast Greenland waters (Christiansen et al. 2016; Strand et al. 2017; Andrews et al. 2019; Gjøsæter et al. 2020). However, the major water mass overflowing the Northeast Greenland shelf is undoubtedly the cold and less saline East Greenland Current coming from the Central Arctic Ocean (Table 2; Håvik et al. 2017; Richter et al. 2018; Gjelstrup 2021).

The temperature-salinity spaces in the Store Koldeway Trough and the Norske Trough tended to differ in the upper part of the water column (Fig. 2a). The Store Koldewey Island, partly closing Dove Bugt, directs low-salinity glacial waters from Dove Bugt through the Store Koldewey Trough, whereas the Norske Through further north is less affected by freshwater and has colder and more saline waters (Arndt et al. 2015; Olsen et al. 2020).

Spatial occurrence of zooplankton

Overall, the zooplankton composition did not differ between the two TUNU expeditions conducted in August 2015 and September 2017. Unsurprisingly, the major taxon was the copepod genus *Calanus* (Fig. 3, Tables 3 and 4, Suppl. 3). In Arctic regions, the genus *Calanus* comprises three major species, the arctic *C. hyperboreus* and *C. glacialis*, and the boreal *C. finmarchicus*, and together they may represent more than 87% of the zooplankton biomass (Kosobokova and Hirche 2009; Daase et al. 2021). Similarly, for the Northeast Greenland Shelf and Slope locations, the VPR counts of *Calanus* dominated with 62–99% of the total zooplankton abundance resulting in an overall low taxon richness for these locations (Table 4).

We can roughly group copepod taxa in Arctic waters according to their adult body size (Lane et al. 2008). Copepods with a prosome length < 1.5 mm are considered small-sized and here comprised the genera *Acartia*, *Microcalanus*, *Oithona*, *Triconia*, and *Pseudocalanus*, whereas *Calanus*, *Metridia*, and *Paraeuchaeta* represented the large-sized ones above this size limit. For the coastal locations in Bessel Fjord and Dove Bugt, the abundance of the small-sized copepod *Pseudocalanus* either equalled or outnumbered that of the large-sized *Calanus*, and here the concomitant taxon richness was the highest in the entire study area (Tables 3 and 4).

Even though VPR likely underestimates the abundance of *Pseudocalanus* (Table 6), the numerical importance of this taxon in coastal waters was well supported by the abundance estimates of the WP-2 net samples (Suppl. 2). High densities of *Pseudocalanus* seem a typical feature during the productive season in Arctic and subarctic coastal waters (Norrbin 1991; Tang et al. 2011). Small-sized copepod taxa were associated with the coastal habitats (Tables 3 and 4, Fig. 5). This phenomenon may relate to both the tight trophic

coupling of small-sized zooplankton grazing on dinoflagellates, ciliates, and protists present in fjords (Levinsen and Nielsen 2002) and bioenergetic limitations. That is, small-sized neritic zooplankton species cannot store large amounts of energy and therefore require a continuous supply of food (Dagg 1977).

Due to wind-borne nutrients and freshwater runoff from land, a substantial primary production may allow a range of small herbivorous zooplankton and omnivorous appendicularians to thrive in coastal areas (Rowe et al. 1975; Aagaard and Carmack 1989; Smith Jr, 1995) and, notably, in inner basins of fjords (Matthews and Heimdal 1980; Lydersen et al. 2014). Also, the appendicularian *Fritillaria* and the ctenophores were more abundant in the coastal areas than further offshore (Table 3). In contrast, the shelf further offshore is less affected by terrigenous nutrients (Polis and Hurd 1996). The carnivorous ctenophores consume large amounts of the smallest zooplankton, which is consistent with the presence of their potential prey of small-sized copepods. The omnivorous appendicularians feed on nano- and pico-plankton (Conley et al. 2018), and thereby constitute an important part of the microbial loop, as well as serve as prey for higher trophic level organisms in the classical food chain (Gorsky et al. 1998; Purcell et al. 2005; Sato et al. 2008). Appendicularians tend to be abundant in productive areas and so enhance the benthic-pelagic coupling by frequently producing and shedding fast-sinking mucous houses (Alldredge 2005; Berline et al. 2011). This corresponds well with the tight association of the appendicularian *Oikopleura* with the Banks and the presence of high biomasses of benthic fauna in these habitats (Table 3, Fig. 5; Fredriksen et al. 2020).

The depth of occurrence for zooplankton may partly be explained by feeding ecology and proximity to food sources (Fig. 5; Folt and Burns 1999; Jacobsen and Norrbin 2009; Norrbin et al. 2009; Greer et al. 2013). In Northeast Greenland, herbivores tended to accumulate in the upper part of the water column and were often associated with the Chl-*a* peak at 30–50 m (Figs. 2b and 4). Omnivorous zooplankton, on the other hand, occurred across a wide range of habitats from surface to great depths of > 900 m and at very different temperatures and salinities (Fig. 4; Norrbin et al. 2009). Predatory zooplankton tended to assemble in high-salinity waters across a range of temperatures. They were mainly situated right below the Chl-*a* peak, probably to feed on small herbivores performing vertical migrations (Jacobsen and Norrbin 2009, Greer et al. 2013). Predatory zooplankton also feed on small omnivores which may explain their presence in deeper waters. For example, the carnivorous chaetognaths *Eukrohnia* and *Parasagitta* feed on herbivorous copepods such as *Calanus* and *Pseudocalanus* as well as on the omnivorous copepod *Microcalanus* (Grigor et al. 2015 and 2017) and they may even feed on phytoplankton (Grigor et al. 2020). Ctenophores and hydrozoans can prey on several size groups

of zooplankton and their occurrence matched the peak distribution for herbivorous copepods (Fig. 4).

In Bessel Fjord and Dove Bugt, the taxon richness was higher compared to the Shelf and Slope, probably due to the more heterogeneous, nutrient-rich, and secluded habitats inshore (Middelbo et al. 2018). The southward East Greenland Current passes along the east coast of the Store Koldewey Island and the 76N-Bank (Laberg et al. 2017). Given the high rugosity of the seabed, eddies may develop in shallow waters and advect zooplankton from offshore areas towards the coast. The shallow 76N-Bank is interesting. Here, not only was the taxon richness high with 12 zooplankton taxa, but also the poorest location in terms of a total abundance of about 9×10^3 individuals m^{-2} (Table 4). We suggest that the East Greenland Current may deflect before it reaches the shallow 76N-Bank and so decrease the amount of advected zooplankton to the bank proper, but that needs to be verified by detailed vertical profiling of the ocean currents, as well as repeated plankton sampling.

Echinoderm larvae, i.e. the pluteus of brittle stars (Ophiuroidea), were found mainly on the shallow Banks where a tight pelagic-benthic coupling appears to be established (Fig. 5; Fredriksen et al. 2020). On the other hand, bivalve veligers (Mollusca) were abundant in Bessel Fjord but were not recorded on the Banks (Suppl. 2). Decapod crustacean larvae (zoea) were abundant only in the entrance to Dove Bugt (D1 in Fig. 1; Suppl. 2) and they may represent the shrimps *Sclerocrangon ferox* and/or *Lebbeus polaris*. These two shrimp species, together with the northern shrimp *Pandalus borealis* further offshore, constitute part of the epibenthic fauna in Northeast Greenland (Fredriksen et al. 2020). The ophioplutei, veligers, and zoea were the only meroplankton taxa recorded during the TUNU expeditions (Suppl. 2). However, in light of ocean warming and species shifts, the meroplanktonic stages of, for example, the introduced Kamchatka red king crab *Paralithodes camtschaticus* and the invasive snow crab *Chionoecetes opilio*, may likely advect from the Barents Sea and settle on the Northeast Greenland shelf (Christiansen et al. 2015; Gjøsæter et al. 2020).

The apparent lack of veligers on the Banks is notable because the settled stages of the pectinoid (Bivalvia) *Similipecten greenlandicus* were the most dominating species in the epibenthic fauna on the 76N-Bank, in terms of both abundance and biomass (Fredriksen et al. 2020). Larvae of bivalves (Mollusca) are common in Subarctic and Arctic plankton from mid-July to September or later (Stübner et al. 2016; Michelsen et al. 2017; Weydmann-Zwolicka et al., 2021), but the reproduction peak of *Similipecten* is not known for Northeast Greenland and may have been missed during our brief visits to the area.

Our findings of low Chl-*a* levels (Fig. 2b) are well supported by other studies in Northeast Greenland such as the North

East Water Polynya (Smith Jr. 1995) and Young Sound (Arendt et al. 2016). In our study, and for the 16 locations combined, the maximum Chl-*a* value was recorded on the shelf break in August 2015 (7.32 mg m^{-3}), while the mean for the entire study was < 2 mg m^{-3} (Fig. 2b). Thus, primary production at the shelf break and slope was still ongoing in August (2015) but was in decline by mid-September (2017). A survey from the Greenland Sea, partly overlapping our study area, reported a phytoplankton peak in early July at the marginal ice-zone, with a net primary production in open water continuing through August (Mayot et al. 2018). The East Greenland Current extends to the 1000-m iso-depth contour at the shelf break (Fig. 1) and very little nutrients are delivered to the shelf, explaining the low potential for primary production (Mayot et al. 2018). The Chl-*a* levels in the fjords and inner shelf in September 2017 are at least a magnitude lower than those of the Kongsfjorden fjord (Spitsbergen, latitude 79° N) during the same season. In September 2017 (TUNU-VII), nitrogen was depleted in surface waters (S. Kristiansen, pers. comm.) and the deep (30–50 m) Chl-*a* fluorescence peak suggested post-bloom conditions. Long-term satellite observations of surface Chl-*a* revealed blooms from April to August in the high seas of the Northeast Atlantic. In Northeast Greenland, on the other hand, blooms were delayed, began in coastal areas, and peaked in July and August (Cherkasheva et al. 2014), i.e. a month earlier than our sampling in 2017 (TUNU-VII). Although situated at similar latitudes as our study area, Kongsfjorden is heavily affected by the warm West Spitsbergen Current with summer Chl-*a* levels ranging between 30 and 160 mg m^{-2} (Hop et al. 2002).

The zooplankton distribution with depth revealed some interesting patterns (Fig. 4). The copepod genus *Calanus* was present throughout the water column from the surface to 947 m depth but was particularly abundant at depths around the Chl-*a* peak (30–50 m). This suggests continued feeding by younger stages, while older stages have begun their overwintering descent. The ophioplutei and the appendicularian *Oikopleura* occurred strictly in the upper part of the water column (< 200 m depth) irrespective of echo depth. This can be explained by their prime prey consisting of nanoplankton and microscopic particles (e.g. Fernández et al., 2004; Lobón et al., 2013; Conley et al. 2018). In contrast, more than half the observations of the chaetognath *Eukrohnia* and the ostracods were made deeper than 200 m (Fig. 4). This is consistent with earlier observations of deep-dwelling ostracod species such as *Discoconchoecia elegans*, *Boroecia borealis*, and/or *B. maxima* (Richter 1994).

Bias in abundance and biodiversity measures

The small-sized copepods and other microplankton emerge as essential in ecosystem functioning (Gallienne and Robins, 2001; Koski et al. 2020; Tarrant 2020; Olofsson and Wulff

2021). Range distributions of small-sized copepods are still little studied compared to the large-sized *Calanus* because the former are comparatively difficult to sample and record. The large-sized copepods, on the other hand, are well retained by conventional plankton nets (mesh size 200–1000 μm) and are readily quantified by optical plankton counters (OPC/LOPC) and acoustic methods (Wiebe and Benfield 2003) and even by remote sensing using satellites (Basedow et al. 2019).

Accurate abundance estimates are needed for a variety of biodiversity measures (Magurran 2004) and quantitative analyses. However, abundance estimates are also affected by the sampling gear used (e.g. Hopcroft et al. 2001; Skjoldal et al. 2013; Wiebe et al. 2015). Our study is first and foremost based on VPR sampling because this instrument gives exact in situ resolution of the spatial distribution of zooplankton in their ambient environment, which no plankton net can achieve. On the other hand, the modified WP-2-net with a reduced mesh size (85 μm) resulted in better sampling of the small-sized plankton taxa, which were not well detected by the VPR at our chosen camera setting.

To sum up Tables 5 and 6, the modified, 85 μm, WP-2 net underestimated the abundance of macrozooplankton (> 20 mm), and the large-sized mesozooplankton (1.5–20 mm), whereas the VPR underestimated the small sized mesozooplankton (0.2–1.5 mm) and most of the microzooplankton (20–200 μm). A WP-2 net with a conventional 200-μm mesh size (UNESCO 1968) would likely render similar abundance estimates as those of the VPR, i.e. a WP-2/VPR-ratio closer to 1 for all habitats and taxa (Tables 5 and 6). Thus, care is called for in comparative studies of zooplankton diversity and abundance using different sampling techniques (Harris et al. 2000, Skjoldal et al. 2013).

The omnipresent genus *Calanus* in Northeast Greenland waters

The copepod species in the genus *Calanus* have been at the centre of zooplankton research for more than a century because their high and energy-rich biomass drives food webs and serves as food for a range of predators worldwide, among those many of commercial interest.

Nonetheless, the large-sized *Calanus* may constitute less than 50% of the zooplankton abundance in the coastal waters of Northeast Greenland (Møller et al. 2006). This makes it important to study also the small-sized zooplankton taxa with the same dedication as *Calanus*. The genus *Calanus* was presented at all locations in our study area. But three species of *Calanus* may occur in Northeast Greenland waters (Hirche and Kwasniewski 1997; Daase et al. 2021): the arctic and larger-sized *C. glacialis* and *C. hyperboreus* and the boreal and smaller-sized *C. finmarchicus* (Kwasniewski et al. 2003). *Calanus finmarchicus* was most abundant at the shelf break, which suggests that the species advects across the Fram Strait via the Return Atlantic Current (Chust et al. 2014; Christiansen et al. 2016; Gjøsæter et al. 2020). *Calanus glacialis* and *C. hyperboreus*, on the other hand, were prominent near the coast as well as in Trough and Bank locations (Suppl. 3). This is consistent with previous studies from Northeast Greenland and, in particular, the Svalbard Archipelago and Fram Strait (Hirche et al. 1994; Ashjian et al. 1995; Schneider and Budéus 1997).

Although *C. finmarchicus* is widely spread in the Greenland Sea, the younger life stages (CI–CIII) appear to be present mainly in the warmer waters of Atlantic origin. So, this copepod species is considered an Atlantic expatriate to the Arctic Ocean (Hirche and Kosobokova 2007). Choquet et al. (2017) reviewed the distribution of *Calanus* species in the North Atlantic and Arctic Ocean. Based on morphological characters, this general view places *C. finmarchicus* in the deep waters of the Greenland Sea east of the Northeast Greenland shelf although the species may also reach the shelf break area (Choquet et al. 2017). *Calanus glacialis*, on the other hand, is restricted to shelf and coastal areas including the Northeast Greenland fjords, whereas *C. hyperboreus* ranges across the deep waters of the North Atlantic and the Central Arctic Ocean (Choquet et al. 2017).

Given these general zoogeographic ranges, it is interesting to note that all three *Calanus* species co-existed in the cold, innermost parts of coastal Northeast Greenland (Suppl. 3). Simple morphological characters such as prosome length, however, may not reliably discriminate the *Calanus* species of concern, especially *C. finmarchicus* and *C. glacialis* (Choquet et al. 2017). In light of the ongoing warming of the Nordic Seas (Tsubouchi et al. 2021) and the concomitant redistribution of biota, molecular techniques, and better use of environmental DNA are warranted to identify proper range extensions of the *Calanus* species and other zooplankton in the North Atlantic and Arctic Ocean (Djurhuus et al. 2018; Laakmann et al., 2020; Sasaki and Dam 2021; Novotny et al. 2021).

Conclusion

This large-scale study in Northeast Greenland waters disclosed a total of 35 mesozooplankton taxa across coastal, shelf, and slope habitats in August and September. Copepods were the most prominent zooplankton with 10 taxa. Based on the high-resolution on-spot measurements of the Video Plankton Recorder, zooplankton were clearly structured according to the prevailing water masses and habitats. Two copepod genera were particularly abundant, i.e. *Pseudocalanus* prevailed in the upper sub-zero layers in the coastal waters, whereas *Calanus* was omnipresent albeit most abundant in the warmer Atlantic influenced waters at the shelf break. Overall, zooplankton abundances tended to increase from the coast

towards the offshore locations and the shelf break. Biodiversity in terms of taxon richness, on the other hand, showed the opposite trend.

The use of different sampling gears for comparative studies of zooplankton is problematic. Taxon richness and abundance estimates are potentially biased because the VPR and the WP-2 net record zooplankton taxa unequally. The small-sized and gelatinous zooplankton need further attention, and future studies of *Calanus* assemblages in Northeast Greenland should employ molecular markers to increase the taxon resolution and to track arctic and boreal species and populations.

Declarations

Conflict of interest   The authors declare no competing interests.

Ethical approval   All applicable international, national, and/or institutional guidelines for animal testing, animal care and use of animals were followed by the authors.

Sampling and field studies   All necessary permits for sampling and observational field studies have been obtained by the TUNU programme from the Government of Greenland (documents C-15-17 & C-17-129).

Data availability   The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Author contributions   T. Beroujon: conceptualization, methodology, investigation, writing–original draft, formal analysis J. S. Christiansen: conceptualization, methodology, investigation, writing–review and editing, funding acquisition, supervision. F. Norrbin: conceptualization, methodology, investigation, writing–review and editing, supervision.

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