



Zooplankton communities across the Nansen and Amundsen Basins of the Arctic Ocean

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Abstract

The Arctic Ocean remains one of the least studied ecosystems due to its remoteness and persistent sea ice. Ongoing warming and Arctic amplification may lead to an ice-free 'blue ocean' by 2050. In the Eurasian sector, the Nansen and Amundsen Basins, separated by the Gakkel Ridge, host distinct water masses that shape pelagic habitats. We examined zooplankton diversity across both basins, sampling a broad size range from meso- to macrozooplankton at five depths. Mesozooplankton diversity did not differ significantly between stations but varied by depth in relation to water-mass structure, with generally higher diversity at depth, especially in the Amundsen Basin. Abundance peaked in the southern Nansen Basin near the continental slope and Atlantic inflow. Small cyclopoid copepods, particularly *Oithona similis* and Oncaeididae, dominated across basins. *Calanus* copepods accounted for over 50% of mesozooplankton biomass, with the Arctic species *Calanus hyperboreus* and *Calanus glacialis* contributing far more than the North Atlantic *Calanus finmarchicus*, which was largely confined to the Nansen Basin. The northern Amundsen Basin supported fewer, less biomass-rich mesozooplankton but showed greater taxonomic diversity. Macrozooplankton communities also differed: chaetognaths were more abundant in the Nansen Basin, while amphipods and euphausiids dominated the Amundsen Basin. Gelatinous zooplankton biomass was similar between basins, though species composition varied. Historical comparisons (1975–2007) indicate small shifts in community structure, including the presence of previously unobserved Atlantic taxa such as *Themisto compressa* and *Triconia conifera*, and the absence of ice-associated species such as *Gammarus wilkitzkii* and *Eusirogenes arctica*. Our results provide a snapshot of present-day zooplankton communities in a rapidly changing Arctic gateway, highlighting the influence of water-mass origin and shelf-slope transitions on community structure.

Keywords: Atlantification; Zooplankton; Arctic Ocean; Nansen Basin; Amundsen Basin; Pelagic ecosystem

Introduction

The Arctic Ocean is characterized by low temperatures, consolidated sea ice, and strong seasonality in light climate with a 6-month dark season. The short window of primary production facilitates a highly specialized ecosystem where energy captured by primary producers is effectively passed to higher trophic levels through zooplankton (Wassmann et al. 2020, Schmidt et al. 2025). The Arctic Ocean is undergoing significant environmental changes due to climate warming and the escalating process of Atlantification over the last decade (Ingvaldsen et al. 2021, Thomas et al. 2022, Polyakov et al. 2023). Atlantification, a set of interrelated processes influencing the ecosystem in the European sector of the Arctic Ocean, is driven by the inflow of warm and saline Atlantic water (AW), which enters the Nansen Basin through the eastern Fram Strait and the Barents Sea (Rudels et al. 2015, Rudels and Carmack 2022). This inflow is forced by the large-scale atmospheric pattern called the Arctic Dipole, in which winds affect North Atlantic water inflows across Fram Strait and within the Barents Sea, resulting in variations in the Arctic Ocean circulation that follows a ~15-year climatic cycle (Polyakov et al. 2020, 2023, Muilwijk et al. 2023). Between 2007 and 2021, a

predominantly positive Arctic Dipole phase reduced inflow of AW through the Fram Strait, while enhancing inflow through the Barents Sea. This slowed down the sea-ice loss in the Arctic Ocean over the past decade (Polyakov et al. 2023). However, during the 2024–2025 winter, a record-low ice distribution was observed (www.met.no), potentially indicating ice-free summers in the relatively near future (Heuzé et al. 2024).

The Eurasian sector of the Central Arctic Ocean is divided into two deep basins, the Nansen Basin and the Amundsen Basin, separated by the Gakkel Ridge. Studies by Rudels et al. (2013, 2015) and Rudels and Carmack (2022) revealed a complex circulation system in which currents transporting water masses of different origins follow different paths within basins and at different depths, suggesting that pelagic environments within basins may provide different microhabitats. The southern part of the Nansen Basin is influenced by the warm, nutrient-rich AW mass, which reaches the surface near the continental slope north of Svalbard (Rudels et al. 2013, Renner et al. 2023), resulting in reduced sea ice and high productivity compared to further north in the Nansen and Amundsen basins (Castellani et al. 2020). In the Amundsen Basin, however, the AW signal is much weaker due to the distance

from the sources of origin, and the transformation into Arctic Atlantic Water (AAW). Additionally, the transpolar drift (TPD) transports sea ice and river water across the Arctic Basin from Siberia. These combined factors create a pelagic environment in the Amundsen Basin with characteristics different from those of the Nansen Basin (Charette et al. 2020, Wassmann et al. 2020). In both basins, the primary production is minimal compared to the shelf seas surrounding the Arctic Ocean (Nöthig et al. 2020). The spring bloom occurs late in the season (late June–early August) due to extensive sea-ice cover, and the ice algae production equals or exceeds the phytoplankton production in areas with consolidated sea ice, particularly in the Amundsen Basin (Ardynia and Arrigo 2020). It can therefore be assumed that these differences in environmental conditions may create preconditions for differences in the zooplankton communities inhabiting these mid-ocean basins.

The increased inflow of warmer and saltier AW into the Arctic Ocean, coupled with reduced sea ice, may have profound implications for the pelagic ecosystem by altering its physical and chemical characteristics and facilitating a possible northward expansion of boreal zooplankton (Wassmann et al. 2015, Ingvaldsen et al. 2021, Snoeijs-Leijonmalm et al. 2021, Kohlbach et al. 2025). Based on extensive studies in the Eurasian and Makarov Basins of the Arctic Ocean conducted during the period 1993–1998, it was revealed that the zooplankton biomass varies considerably in association with the water-mass circulation pattern and food availability (Kosobokova and Hirche 2009). At the same time, the boreal copepod *Calanus finmarchicus* has expanded northward (Tarling et al. 2022), but the short productive season limits the species from reaching diapause (Ji et al. 2012). The long winter is hence a bottleneck for the smaller *C. finmarchicus* to fulfil its life cycle and expand further north in the Central Arctic Ocean. The observed shift in copepod species composition may significantly affect Arctic food webs, as Atlantic species are generally smaller and less calorie-rich per individual than their Arctic counterparts (Falk-Petersen et al. 2009), making it harder for predators to obtain sufficient food for the same effort.

Understanding the potential impacts of Atlantification on zooplankton communities in the Amundsen and Nansen Basins is crucial for predicting broader ecological consequences of climate change for the unique Arctic Ocean ecosystems. Changes in zooplankton dynamics may have cascading effects on higher trophic levels, including fish and marine mammals, impacting the overall resilience and stability of the Arctic marine ecosystem (MacKenzie et al. 2022, Kuletz et al. 2024). This study expands knowledge of zooplankton composition in two basins of the Eurasian Arctic Ocean and establishes a baseline for future monitoring. Building on the multidisciplinary work of Kohlbach et al. (2025), it provides more detailed information on zooplankton distribution and taxonomy. As an incentive for upcoming ecosystem studies, it extends previous research by collecting zooplankton using a wider set of nets with mesh sizes 64, 180, and 1500 μm , compared to prior studies that often used only one type of net (usually 150–200 μm ; Kosobokova and Hirche 2009, Kosobokova et al. 2011, Ershova et al. 2021a, Hop et al. 2021b). This broader approach allowed us to assess size-fractionated diversity, especially smaller zooplankton whose role in deep layers remains poorly understood. By sampling the full water column to the bottom of

deep basins, we also gained rare insights into deep-water communities.

The main aim of this study was to complement and compare results on the zooplankton community status in 2021 with previous work on zooplankton in the Arctic Ocean from 1993 to 2007 (Kosobokova and Hirche 2009, Kosobokova et al. 2011).

Materials and methods

Study area

Samples and measurements for this study were collected from 24 August to 24 September 2021, aboard RV *Kronprins Haakon* as part of the Norwegian Nansen Legacy project (cruise number 2021 710, <https://arvenetternansen.com>). Hydrographic measurements were conducted at 15 stations along a transect from 81.8°N to 87.5°N, with repeated CTD casts at some stations, and zooplankton samples were collected at five of these 15 stations, namely P7–P11 (Figs. 1 and 2). A detailed description of the cruise and associated research is provided in Kohlbach et al. (2025). All stations, except for the southernmost station (P7), were covered by sea ice during sampling. Stations P7 and P8 were situated in the Nansen Basin, and stations P9–P11 were located in the Amundsen Basin.

Environmental variables

A shipboard conductivity, temperature, and depth profiler (Seabird 911plus CTD), attached to a 24-bottle rosette system, was deployed at 15 stations (Figs. 1 and 2). For inclusion in the multivariate analyses, average values of potential temperature (T), practical salinity (S), and potential density anomaly (σ_θ) were calculated for each layer from which separate zooplankton samples were collected. We used the definitions by Schulz et al. (2024) for water mass classification. Seawater samples for chlorophyll *a* concentrations were taken from water bottles mounted on the rosette system. Samples of 100–500 ml were filtered through 25 mm GF/F filters (Whatman), extracted in 100% methanol for 12 h at 4°C and measured with a Trilogy Laboratory Fluorometer (Turner Design, San Jose, CA) according to the method of Holm-Hansen and Riemann (1978).

Zooplankton sampling

Mesozooplankton sampling was conducted at five plankton stations (P7–P11) by stratified vertical hauls using two Multi-Net Midi plankton nets (Hydro-Bios Apparatebau, opening: 0.25 m², net length: 2.50 m). To collect mesozooplankton across a broader range of sizes, nets with two mesh sizes were used: 64 μm and 180 μm , and sampling covered five standard depth intervals: Bottom–2000 m, 2000–600 m, 600–200 m, 200–50 m, and 50–0 m. The nets were hauled with a speed of 0.3 m s^{−1} and 0.5 m s^{−1} for the 64 μm and 180 μm nets, respectively. Upon retrieval of the nets, the collected zooplankton were concentrated on sieves (64 μm and 180 μm , respectively), gently flushed with filtered seawater, transferred into 125 ml plastic bottles, and preserved in 4% acid-free formaldehyde for later taxonomical identification in the laboratory.

Macrozooplankton was sampled from the upper 1000 m of the water column using a MIK net (Method Isaacs-Kidd Midwater Trawl, opening 3.14 m², 1500 μm net aperture in

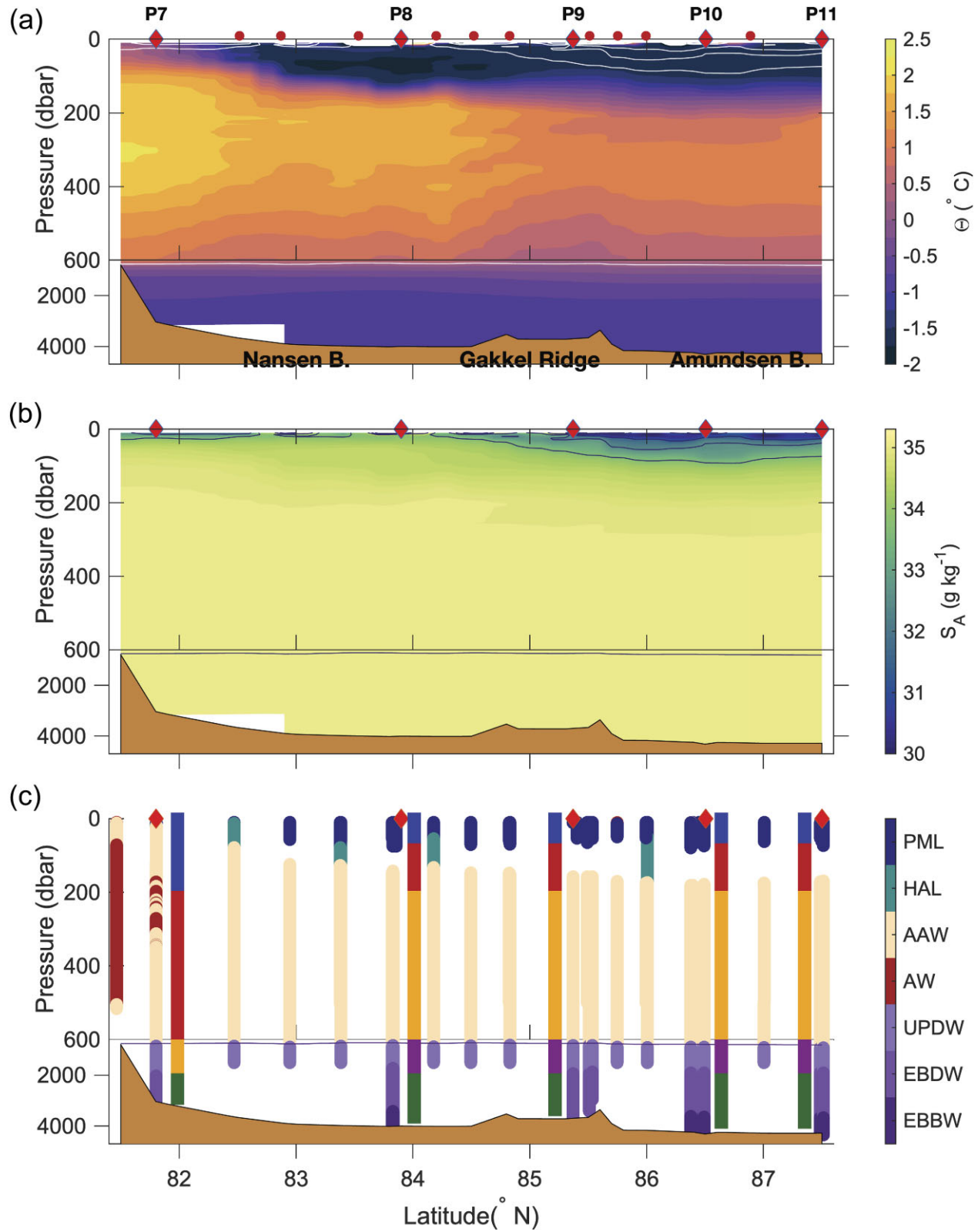


Figure 1. Distribution along the section (from South, to the left, to North) of (a) Conservative temperature, (b) Absolute salinity, and (c) Water masses; Polar Mixed Layer (PML), Halocline Water (HAL), AAW, Atlantic Water (AW), Upper Deep Water (UPDW), Eurasian Basin Deep Water (EBDW), and Eurasian Bottom Basin Water (EBBW) based on water-mass classification from Schulz et al. (2024). The black lines are isopycnals. Bathymetry is shown at the bottom of each panel, and the x-axis is the latitude. The red diamonds indicate the locations of the zooplankton stations and the red circles indicate the CTD stations. The columns in the lower panel show the main zooplankton groups revealed by the PCA: Epi_U = Epipelagic upper layer, Epi_L = Epipelagic lower, Meso = Mesopelagic, Deep = Deep, Bathy = Bathypelagic.

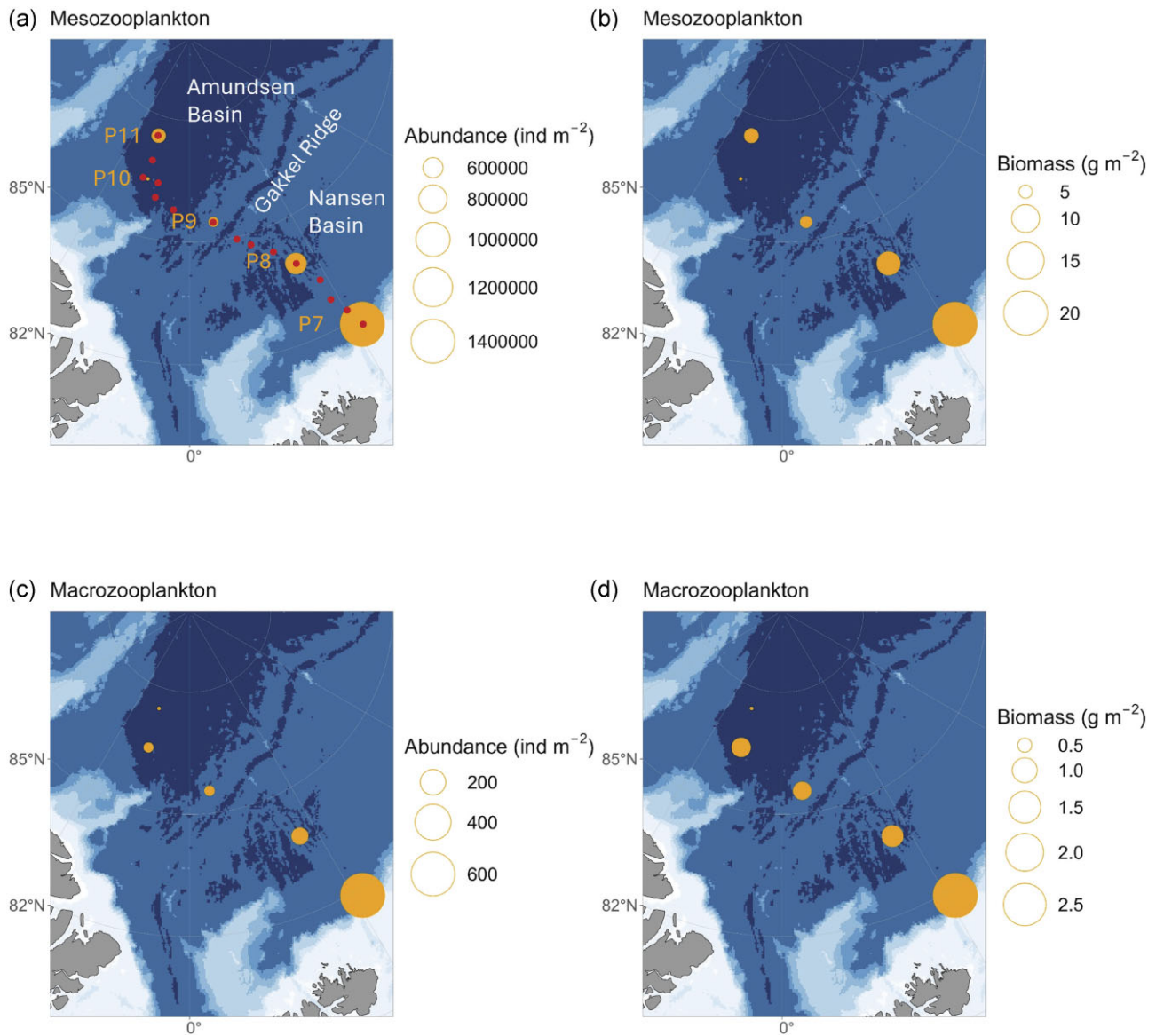


Figure 2. Total abundance (ind. m⁻²) and biomass (mg DM m⁻²) of mesozooplankton (a, b) and macrozooplankton (c, d) in the Nansen Basin (P7 and P8) and Amundsen Basin (P9–P11). Yellow circle size corresponds to the magnitude of abundance and biomass at sampling location. The red circles indicate the CTD stations. The background colour gradient indicates ocean depth, with darker blue representing deeper areas and lighter shades indicating shallower regions.

the main net and 500 μm aperture in the rear 1 m of the net). A hauling speed of $\sim 1.5 \text{ m s}^{-1}$ was applied. Gelatinous zooplankton were carefully removed from the catch using riddled spoons or wide-mouthed pipettes, placed in seawater and kept at 2°C for identification, enumeration, size measurement, and weighing. Afterwards, the specimens were transferred to separate jars, preserved in $>96\%$ non-denatured ethanol and stored at -20°C for subsequent genetic identification. A known portion of the remaining MIK sample (typically a half, separated by a Motoda splitter) was preserved in 4% acid-free formaldehyde for taxonomical identification.

Zooplankton taxonomical analysis

Mesozooplankton was analysed following standard procedures outlined by Postel (2000) and described in Wold et al.

(2023) at the Institute of Oceanology, Polish Academy of Sciences (IO PAN, Sopot, Poland). Organisms were identified and counted using a stereomicroscope equipped with an ocular micrometre. Zooplankters of total size $<5 \text{ mm}$, including most Copepoda and juvenile stages of Pteropoda, Euphausiacea, Ostracoda, Amphipoda, and Chaetognatha, were identified and counted in subsamples extracted from a fixed sample volume using an automatic macro pipette in which the tip opening was widened to a width of $>5 \text{ mm}$. In this process, no fewer than 500 individuals from at least five subsamples were consistently identified and counted. Zooplankters of total size $>5 \text{ mm}$, including large Copepoda, Pteropoda, Euphausiacea, Ostracoda, Amphipoda, Decapoda, Appendicularia, Chaetognatha, and Pisces larvae were sorted and identified from the entire sample. Species were identified to the lowest possible taxonomic level, distinguishing developmental stages based on morphology and, when useful, body size. In some cases,

identification was limited to adults or older stages (CIV–CVI) or to larger individuals. *Calanus* spp. were identified to species and stage using morphology and prosome length of individual copepodids (Kwasniewski et al. 2003). For *Pseudocalanus*, females were classified as *Pseudocalanus minutus* based on morphology (Frost 1989) or as *Pseudocalanus* spp. (likely *Pseudocalanus acuspes* and/or *Pseudocalanus moultoni*; Aarbakke et al. 2011, Ershova et al. 2021b). Males and copepodids CI–CV were identified only to the genus. For other copepods, younger stages (CI–CIII for Calanoida; CI–CIII or CI–CV for Cyclopoida and Harpacticoida) were generally identified only to genus or family, due to underdeveloped or missing characters. For Oithonidae, CI–CIII were recorded as *Oithona* spp., while older stages were identified as *Oithona similis* or *Oithona atlantica* (CIV–CVI AF/AM). For Oncaeidae, copepodids CI–CV were recorded as *Oncaeidae* indet., whereas adults were identified as *Triconia borealis* AF, *Triconia conifera* AF, or *Oncaea* spp. AF. *Triconia borealis* males were identified only when attached to conspecific females; unattached *Triconia/Oncaea* males were recorded as *Oncaea* spp. AM.

In some cases, species- or genus-level identification was impossible due to specimen damage or missing diagnostic features. Similar restrictions applied to other taxa, and the resulting identifications are listed in Table 1. Samples from 64- and 180- μ m gauze meshes were analysed separately, but the data used are merged with small specimens based on results from 64 μ m and large specimens from 180 μ m. Complete information on which mesh-size sample data were included as representative of which organisms and stages in the final data is provided in Supplementary Table 1.

Macrozooplankton was analysed at the Institute of Marine Research (IMR, Bergen, Norway). All organisms in a subset (1/2 or 1/4 of the total sample) were identified to the highest possible taxon, counted and weighed. Length measurements were conducted on randomly selected samples of euphausiids and amphipods.

Identification of gelatinous zooplankton

The EtOH-preserved gelatinous zooplankton individuals from the MIK-net samples were later identified to the highest taxonomic level possible under a stereomicroscope. Tissue samples were taken for DNA analysis from specimens that could not be confidently identified, all of which were ctenophores. DNA was extracted using the Chelex rapid-boiling procedure (Granhag et al. 2012), and PCR was conducted following protocols specific to ctenophores as outlined by Majaneva and Majaneva (2013). PCR products were purified using the Cytiva GFXtm PCR DNA and gel purification kit following the protocol recommended by the manufacturer. Sequencing was carried out by MacroGen Sequencing Service (MacroGen Inc., The Netherlands). The resulting nucleotide sequence electropherograms were checked by eye for poor base calls and sequence quality using Chromas Lite 2.1 (Technelysium Pty Ltd). The good-quality sequences were assembled using BioEdit software (Hall 1999). They were meticulously analysed using the BLAST (Basic Local Alignment Search Tool) algorithm available on the NCBI (National Center for Biotechnology Information) platform. The sequences reported in this paper have been deposited in the European Nucleotide Archive.

Zooplankton biodiversity and distribution analysis

Original zooplankton data include the abundance of zooplankters (individuals per cubic metre, ind. m^{-3}) in each sampled depth layer. Abundance values were converted to biomass estimates (milligrams of dry mass per cubic metre, mg DM m^{-3}) using species-specific dry mass values from published sources (Supplementary Table 1). In case of ctenophores and cnidarians we used a conversion factor from wet mass to dry mass of 0.041 according to Kiørboe, 2013. The abundance and biomass of each organism at a station (ind. m^{-2} and mg DM m^{-2} , respectively) were calculated by summing the abundance or biomass across all layers for the entire water column.

The mesozooplankton diversity at different stations and depths was evaluated based on the Simpson diversity index (D), which accounts for both the number of taxa (richness) and their relative abundance (evenness) in the sample.

$$\text{Simpson Diversity Index } D = 1 - \sum [(p_i^2)] \quad (1)$$

$$p_i = \frac{n}{N} \quad (2)$$

where p_i represents the proportion of individuals of the i th taxon in a community at a given station and depth layer (here represented as a sample), n is the number of individuals of this taxon, and N is the total number of individuals of all taxa in a community at a given station and depth layer (in a sample). Since the assumption for parametric analysis was violated according to Shapiro–Wilk test for normality ($p < 0.05$) and Levene’s test for homogeneity of variance ($p < 0.05$), we used the nonparametric Kruskal–Wallis test to determine significant differences in diversity across stations and depth layers, illustrated by boxplots.

The difference in zooplankton species composition between the stations and depth layers was analysed using a dissimilarity matrix based on the Bray–Curtis index. The abundance data (ind. m^{-3}) were fourth root transformed to reduce the influence of highly abundant taxa while preserving information about community composition. The results of the dissimilarity analysis were visualized using a hierarchical cluster diagram using the average linkage method and tested using a PERMANOVA test.

A detailed examination of the structure and diversity of the mesozooplankton community was performed using principal component analysis (PCA). Species abundance data were fourth root transformed to reduce the influence of dominant taxa. Results were visualized through two PCA biplots: one illustrating sample scores, with samples colour-coded by depth layer, and another for species scores. Both analyses were conducted in R (version 4.4.2) utilising the *vegan* and *ggplot2* packages.

The division of the water column into layers corresponding to hypothetical depth-related habitats follows the description of Kosobokova et al. (2011). It distinguishes epipelagic (0–200 m), mesopelagic (200–600 m), bathypelagic (600–3000 m), and abyssopelagic (>3000 m) layers. The boundary between mesopelagic and bathypelagic layers is shallower in our study than in Kosobokova et al. (2011), because it was established to match the boundary of Atlantic water masses known from earlier studies (Hop et al. 2019), as not only the absolute depth but also the type of water masses determine the specificity of the habitat.

The species composition of copepods in the bar graphs has been simplified to enhance the display of results in the illus-

Table 1. Copepod taxa present in the Nansen basin and Amundsen basin based on multinet (64 and 180 μm)

Order/family	Species	Abbrev. Fig. 5	Nansen Basin	Amundsen Basin
Calanoida				
Aetideidae	Aetideidae indet.	Aetide	*	*
	<i>Aetideopsis minor</i>		*	**
	<i>Aetideopsis rostrata</i>		**	**
	<i>Chiridiella abyssalis</i>		**	**
	<i>Chiridius obtusifrons</i>		**	**
	<i>Gaetanus brevispinus</i>		***	***
	<i>Gaetanus tenuispinus</i>		***	**
	<i>Jaschnovia brevis</i>		*	*
	<i>Pseudochirella spectabilis</i>	PseSpe	*	*
Augaptilidae	Augaptilidae indet.		**	**
	<i>Augaptilus glacialis</i>		**	**
	<i>Haloptilus acutifrons</i>	HalAcu	**	**
Bathypontiidae	<i>Temorites brevis</i>		**	***
Calanidae	<i>Calanus finmarchicus</i>	CalFin	****	**
	<i>Calanus glacialis</i>	CalGla	****	**
	<i>Calanus hyperboreus</i>	CalHyp	****	**
Clausocalanidae	<i>Microcalanus</i> spp.	Microc	****	****
	<i>Pseudocalanus</i> spp.		****	**
	<i>Pseudocalanus minutus</i>		*	—
Discoidae	Discoidae indet.		***	***
	<i>Pertsovius</i> spp.	Pertso	***	***
	<i>Disco</i> spp.	Discoi	**	**
Heterorhabdidae	<i>Heterorhabdus norvegicus</i>	HetNor	***	**
	<i>Paraheterorhabdus compactus</i>		**	**
Euchaetidae	<i>Paraeuchaeta</i> spp.	Paraeu	***	***
	<i>Paraeuchaeta barbata</i>		*	*
	<i>Paraeuchaeta glacialis</i>		*	**
	<i>Paraeuchaeta norvegica</i>		**	—
Lucicutiidae	<i>Lucicutia</i> spp.	Lucicu	**	**
	<i>Lucicutia anomala</i>		**	**
	<i>Lucicutia polaris</i>	LucPol	*	**
Metridinidae	<i>Metridia longa</i>	MetLon	****	***
	<i>Metridia lucens</i>		**	—
Scolecitrichidae	Scolecitrichidae indet.		**	**
	<i>Brodskius arcticus</i>		*	*
	<i>Scaphocalanus</i> spp.		***	***
	<i>Scaphocalanus brevicornis</i>	ScaBre	***	***
	<i>Scaphocalanus magnus</i>	ScaMag	***	***
	<i>Scaphocalanus polaris</i>	ScaPol	**	**
	<i>Scolecithricella minor</i>		**	**
Spinocalanidae	<i>Mimocalanus damkaeri</i>		—	*
	<i>Spinocalanus</i> spp.	Spinoc	****	****
	<i>Spinocalanus antarcticus</i>		***	***
	<i>Spinocalanus horridus</i>	SpiHor	***	***
	<i>Spinocalanus magnus</i>		*	*
Tharybidae	Tharybidae indet.		**	**
	<i>Tharybis groenlandica</i>		**	**
	<i>Undinella oblonga</i>		*	**
Cyclopoida				
Oithonidae	<i>Oithona atlantica</i>		***	—
	<i>Oithona similis</i>		****	****
Oncaeidae	Oncaeidae indet.	Oncaei	**	****
	<i>Triconia borealis</i>	TriBor	****	***
	<i>Triconia conifera</i>		*	—
	<i>Oncaea</i> spp.		**	**
Lubbockiidae	Lubbockiidae indet.		—	*
Harpacticoida				
Ectinosomatidae	<i>Microsetella norvegica</i>	MicNor	****	**
	Harpacticoida indet.		*	*
Mormonilloida				
Mormonillidae	<i>Neomormonilla minor</i>	NeoMin	***	***
Siphonostomatoida				
Megapontiidae	<i>Hyalopontius typicus</i>		*	*
Bradfordian families	Species indet.	Bradfo	**	***

The abbreviation of species names used in Fig. 5 is included. The number of stars (*) indicates the magnitude of abundance (**** > 1000 ind. m^{-2} , *** 100–1000 ind. m^{-2} , ** 10–100 ind. m^{-2} , and * < 10 ind. m^{-2}).

trations. The taxonomic composition of zooplankton in the figures is presented simplified to ensure a clear presentation of the most important results. In particular, for Copepoda, results for highly abundant zooplankters such as nauplii (occurring in the abundance range 1–1000 ind. m⁻³) and small cyclopoid copepods (100–1500 ind. m⁻³), and for major mesozooplankton components such as *Calanus* spp. (0.1–35 ind. m⁻³) and *Metridia* spp. (0.1–5 ind. m⁻³), were presented separately from results for less abundant small copepods (0.02–140 ind. m⁻³) and other large copepods (0.005–2 ind. m⁻³), because otherwise details of less abundant groups would be masked.

Results

Physical and biological environment

Our study area spanned from the continental slope (P7) North of Svalbard into the Nansen Basin (P8), across the Gakkel Ridge (P9) into the Amundsen Basin (P10 and P11) (Fig. 1). The southern part of the Nansen Basin, with its relative proximity to the continental slope, marks a key region where warm Atlantic waters (AW) flows into the Arctic (Fig. 1c). In this region at P7, there was no distinct halocline in the water column, and the warm waters originating from the Atlantic were found close to the surface. Cold and fresh Polar Mixed Layer (PML) water dominated the surface layer (0 to ~100 m) across the deep basins. Between the PML and the AAW at 50–100 m depth, there was a layer of halocline water (HAL). At some stations, gaps between PML and AAW in the figure reflect water masses that did not strictly meet the HAL definition but were close. The halocline layer was thicker in the Amundsen Basin than in the Nansen Basin. The AAW, a derivative of the Atlantic Water and therefore a relatively warm water mass in the Arctic Ocean, occupied a large part of the water column in the study area. However, in the Nansen Basin, this water reached closer to the surface, to a depth of about 150 m, and was slightly warmer, while in the Amundsen Basin, it occurred deeper, only to 200 m, and its core was colder (Fig. 1a and c). Deep Arctic water [Eurasian Basin Deep Water (EBDW) and Eurasian Bottom Basin Water (EBBW), Fig. 1c] remained below 1000 m, with particularly cold saline water below 2000 m depth.

The phytoplankton biomass measured as chlorophyll *a* was low in the surface 50 m throughout the transect (0.09–0.24 µg l⁻¹), with an increase to 0.85 µg l⁻¹ at P7 in the southern Nansen Basin (Supplementary Table 2, Kohlbach et al. 2025).

Zooplankton biodiversity

Copepods were the most diverse component of the zooplankton, with 60 taxa identified, of which 42 were identified at the species level, nine at genus level, seven at the family level, and two at a higher level (Table 1). *Mimocalanus damkaeri* was the only copepod species exclusive to the Amundsen Basin. Also, representatives of Lubbockiidae were found only in the samples from this basin. Conversely, *Metridia lucens*, *P. minutus*, *Paraeuchaeta norvegica*, *O. atlantica*, and *Triconia conifera* were solely found in the Nansen Basin. *Calanus finmarchicus* and *Microsetella norvegica* were found in high numbers in the southern part of the Nansen Basin and were few in the northern Nansen and in the Amundsen basins. *Triconia conifera* was reported for the first time in the Arctic Ocean (Nansen Basin only, Supplementary Table 2). We found *Spinocalanus*

magnus in both basins, a species whose presence in the Arctic Ocean was expected. The actual number of copepod species in the Nansen and Amundsen Basins is likely higher, as individuals that were identified only to genus or family may include several different species that require genetic confirmation. Thus, a comprehensive assessment of species diversity in both basins will require further research.

Amphipods were the second-most numerous crustaceans after copepods (Table 2), with ten taxa identified. *Andaniexis abyssi*, *Eusirus holmii*, and *Onisimus* spp. were found exclusively in the Amundsen Basin, while *Scina borealis* was restricted to the Nansen Basin. Other crustaceans included decapods (*Hymenodora glacialis* and other unidentified juvenile Caridea), euphausiids (four taxa), with *Meganyctiphanes norvegica* and *Thysanoessa inermis* found only in the Nansen Basin, *Hansarsia megalops* only in the Amundsen Basin, and *Thysanoessa longicaudata* found in both basins. Mysids, ostracods, and isopods were also recorded, the latter ones including larval forms of parasitic taxa (e.g. Bopyridae postlarvae) and single specimens of the free-living *Ilyarachna*, which were too damaged to allow for unambiguous species identification. Crustaceans other than copepods, recorded for the first time in the Nansen and Amundsen basins, included the Atlantic amphipod *Themisto compressa*, which was confirmed for nine individuals at P7 in the Nansen Basin and 14 individuals at P9 in the Amundsen Basin. Three different polychaete species were identified, with *Tomopteris septentrionalis* only found in the Amundsen Basin. The pteropods *Limacina helicina* and *Clione limacina* were present in both basins, as well as were the appendicularians *Fritillaria borealis* and *Oikopleura* spp.

The gelatinous zooplankton comprised the representatives of phylum Cnidaria (both Hydrozoa and Scyphozoa) and Ctenophora (both Nuda and Tentaculate), with hydrozoans constituting the most diverse group, encompassing 18 species and two taxa identified to higher ranks (*Lensia* spp. and one other representative of Calycophorae (Table 3). Three of the hydrozoan taxa were exclusive to the Amundsen Basin: *Crossota norvegica*, *Lensia* spp., and *Marrus orthocanna*, while *Plotocnide borealis* and *Nectadamas diomedae* were only found in the Nansen Basin. Two species of Scyphozoa were identified, with *Atolla* cf. *tenella* exclusively present in the Amundsen Basin. Three species were recorded among the ctenophores, with *Beroë abyssicola* only present in the Amundsen Basin. Chaetognaths, comprising the three species *Parasagitta elegans*, *Pseudosagitta maxima*, and *Eukrohnna hamata*, were present at all stations, but in much higher quantities at P7 than at any other station.

Regional patterns in zooplankton abundance and biomass

The total mesozooplankton abundance and biomass were considerably higher in the southern Nansen Basin (P7), close to the continental slope, than elsewhere (Fig. 2a and b). At all stations, smaller copepod species dominated in abundance, while larger species (most notably *Calanus*) had a larger share of biomass (Fig. 3a and b). The 'other zooplankton' group included various zooplankton occurring in small numbers, such as ostracods, appendicularians, chaetognaths, amphipods, and euphausiids. The higher mesozooplankton biomass at P7 was due to greater numbers of the relatively large copepods *C. finmarchicus*, *Calanus glacialis*, and *Metridia longa*. Further

Table 2. Crustacea, chaetognatha, echinodermata, annelida, and mollusca present in the Nansen Basin and Amundsen Basin based on multinet (64 and 180 μm) and MIK net 1500 μm .

Phylum/class	Order/species	Abbr. Fig. 5	Nansen Basin	Amundsen Basin	Reported in Barents Sea or Svalbard waters
Crustacea					
Malacostraca	Amphipoda				
	<i>Andaniexis abyssii</i>		—	*	Artsdatabanken
	<i>Apherusa glacialis</i>		*	*	
	<i>Cyclocaris guilelmi</i>	CycGui	*	**	
	<i>Eusirus holmii</i>		—	*	Artsdatabanken
	<i>Lanceola clausii</i>		*	**	
	<i>Onisimus</i> spp.		—	*	Artsdatabanken
	<i>Scina borealis</i>		*	—	
	<i>Themisto abyssorum</i>	TheAby	**	**	
	<i>Themisto compressa</i>		**	*	
	<i>Themisto libellula</i>		*	*	
	Decapoda				
	Caridea indet.		*	*	
	<i>Hymenodora glacialis</i>		*	*	
	Euphausiacea				
	Euphausiacea indet.		**	—	
	<i>Meganyctiphanes norvegica</i>		**	—	
	<i>Thysanoessa inermis</i>	ThyIne	*	—	
	<i>Thysanoessa longicaudata</i>		*	*	
	<i>Hansarsia megllops</i>		—	*	Artsdatabanken
	Isopoda				
	Bopyridae indet.		***	***	
	Isopoda indet.		***	***	
	<i>Ilyarachna</i> sp.		*	*	
	Mysida				
	Mysidae indet.		**	—	
Ostracoda	Ostracoda indet.	Ostrac	***	***	
Cirripedia	Cirripedia indet.		**	—	
Chaetognatha					
Sagittoidea	Aphragmophora				
	<i>Parasagitta elegans</i>	ParEle	***	**	
	<i>Pseudosagitta maxima</i>	PseMax	**	**	
	Phragmophora				
	<i>Eukrohnia hamata</i>	EukHam	**	**	
Echinodermata	Echinodermata indet.	EchInd	****	*	
Annelida					
Polychaeta	Phyllodocida				
	Polychaeta indet.		**	**	
	<i>Pelagobia longicirrata</i>	PelLon	**	**	
	<i>Tomopteris septentrionalis</i>		*	—	
	<i>Typhloscolex muelleri</i>	TypMue	**	*	
Mollusca					
Gastropoda	Gymnosomata				
	<i>Clione limacina</i>		**	**	
	Thecosomata				
	<i>Limacina helicina</i>		***	**	
Bivalvia	Bivalvia indet.		****	*	
Appendicularia					
	<i>Fritillaria borealis</i>	FriBor	****	****	
	<i>Oikopleura</i> spp.		****	****	

The abbreviation of species names used in Fig. 5 is included. The number of stars indicates the magnitude of abundance (**** > 100 ind. m^{-2} , *** 10–100 ind. m^{-2} , ** 1–10 ind. m^{-2} , * < 1 ind. m^{-2}). For species not present in the Nansen Basin, it is indicated if they have previously been reported from the Barents Sea or Svalbard waters in either Artsdatabanken (<https://www.artsdatabanken.no>) or WoRMS (<https://www.marinespecies.org>).

north in the Nansen Basin (P8), over the Gakkel Ridge (P9) and in the Amundsen Basin (P10 and P11), mesozooplankton had considerably lower total abundance and biomass for most taxonomic groups, particularly those associated with Atlantic water (Fig. 3a and b).

Macrozooplankton abundance and biomass peaked at P7 along the continental slope, primarily due to the contribution of chaetognaths and euphausiids (Fig. 2c and d), and the main chaetognath species at P7, as well as at the other locations, was *E. hamata*. Euphausiids were nearly absent in the

Table 3. Cnidaria and ctenophora present in Nansen Basin and Amundsen Basin based on Multinet (64 and 180 μm) and MIK net 1500 μm .

Phylum/class	Order/species	Abbr. Fig. 5	Nansen Basin	Amundsen Basin	Reported in Barents Sea or Svalbard waters
Cnidaria					
Hydrozoa	Anthoathecata				
	<i>Paragotoea bathybia</i>		**	**	
	<i>Plotocnide borealis</i>		*	—	
	Narcomedusae				
	<i>Aeginopsis laurentii</i>		*	**	
	<i>Bathykoros bouilloni</i>	BatBou	**	**	
	<i>Solmundella bitentaculata</i>	SolBit	**	***	
	Siphonophorae				
	<i>Calycophorae</i>		*	*	
	<i>Crystallophytes amygdalina</i>		*	**	
	<i>Dimophyes arctica</i>	DimArc	***	**	
	<i>Gilia reticulata</i>		*	*	
	<i>Lensia</i> spp.		—	*	
	<i>Marrus orthocanna</i>		—	*	WoRMS
	<i>Muggiaea bargmannae</i>		—	*	
	<i>Nectadamas diomedae</i>		*	—	
	<i>Rudjakovia plicata</i>	RudPli	***	***	
	Trachymedusae				
	<i>Aglantha digitale</i>		***	***	
	<i>Botrynema brucei</i>		*	**	
	<i>Botrynema brucei ellinorae</i>	BotEll	*	**	
	<i>Crossota norvegica</i>		—	*	
	<i>Homoeonema platygonon</i>	HomPla	***	***	
	<i>Sminthea arctica</i>	SmiArc	**	***	
Scyphozoa	Coronatae				
	<i>Atolla</i> spp.		*	*	
	<i>Atolla cf. tenella</i>		—	*	WoRMS
Nuda	Beroidea				
	<i>Beroe cf. cucumis</i>		*	*	
	<i>Beroe abyssicola</i>		—	*	WoRMS
Tentaculata	Cydiippida				
	<i>Mertensia ovum</i>	MerOvu	**	***	

The abbreviation of species names used in Fig. 5 is included. The number of stars indicates the magnitude of abundance (**** > 100 ind. m^{-2} , *** 10–100 ind. m^{-2} , ** 1–10 ind. m^{-2} , * < 1 ind. m^{-2}). For species not present in the Nansen Basin, it is indicated if they have previously been reported from the Barents Sea or Svalbard waters in either Artsdatabanken (<https://www.artsdatabanken.no>) or WoRMS (<https://www.marinespecies.org>).

Amundsen Basin. On the other hand, amphipods and cnidarians contributed relatively more to the total biomass, which resulted in a more even share of different groups at the deep basin stations than in the case of the shelf P7 station (Fig. 3c and d).

The biomass of gelatinous zooplankton (cnidarians, ctenophores) was comparable in the two basins (Fig. 3c and d), but the species composition was different; ctenophores *Mertensia ovum* and *Beroe* spp. were common in the Nansen Basin, while scyphozoan *Atolla cf. tenella* dominated in the Amundsen Basin (Table 3).

Mesozooplankton vertical distribution and diversity

The mesozooplankton diversity, according to the Simpson diversity index, did not differ significantly among stations ($H = 2.40$, $P = .663$, Fig. 4). However, it was slightly higher at the stations in the Nansen Basin (P7 and P8) compared to the Amundsen Basin (P9–P11, Fig. 4). In contrast, diversity varied significantly across depth layers ($H = 17.08$, $p = 0.0019$), with the lowest diversity in the surface layer (50–0 m) and the highest in the lower epipelagic and mesopelagic layer (200–50 m and 600–200 m), followed by the deepest layers (Supplementary Table 4).

The PCA analysis revealed distinct zooplankton communities with depth, with P7 differing from the other stations.

The surface epipelagic and lower epipelagic layers extended deeper at P7 than at the other stations (Figs. 1 and 5, and Supplementary Table 5). PERMANOVA analysis further confirmed a significant difference in mesozooplankton species composition with depth ($p = 0.001$, $R^2 = 0.62$) but not between stations ($p = 0.775$, $R^2 = 0.13$, Supplementary Fig. 1, Supplementary Table 6). The bathypelagic communities were clearly distinct from the meso- and epi-pelagic communities. The deepest samples (bottom–2000 m, green) clustered together across stations and were associated with bottom layers influenced by EBDW and EBBW. Dominant taxa included the bathypelagic and abyssopelagic copepods *Scaphocalanus polaris* (ScaPol), *Lucicutia polaris* (LucPol), Bradfordian copepods (Bradfo), Discoidae family copepods (Discoi), including genus *Pertsovius* (Pertsovius), and the hydrozoan medusae *Bathykoros bouilloni* (BatBou). Samples collected from depths of 2000–600 m (purple) formed a distinct cluster of deep basin stations (P8–P11), associated with Upper Polar Deep Water (UPDW). Characteristic species included bathypelagic and mesopelagic copepods *Spinocalanus horridus* (SpiHor), also small *Spinocalanus* species (Spinoc), *Neomormonilla minor* (NeoMin), hydrozoans *Homoeonema platygonon* (HomPla) and *Solmundella bitentaculata* (SolBit), and the amphipod *Cyclocaris guilelmi* (CycGui). Samples from 600 to 200 m (yellow) in the deep basins represented the mesopelagic community. The 2000–600 m sample from P7 clustered with

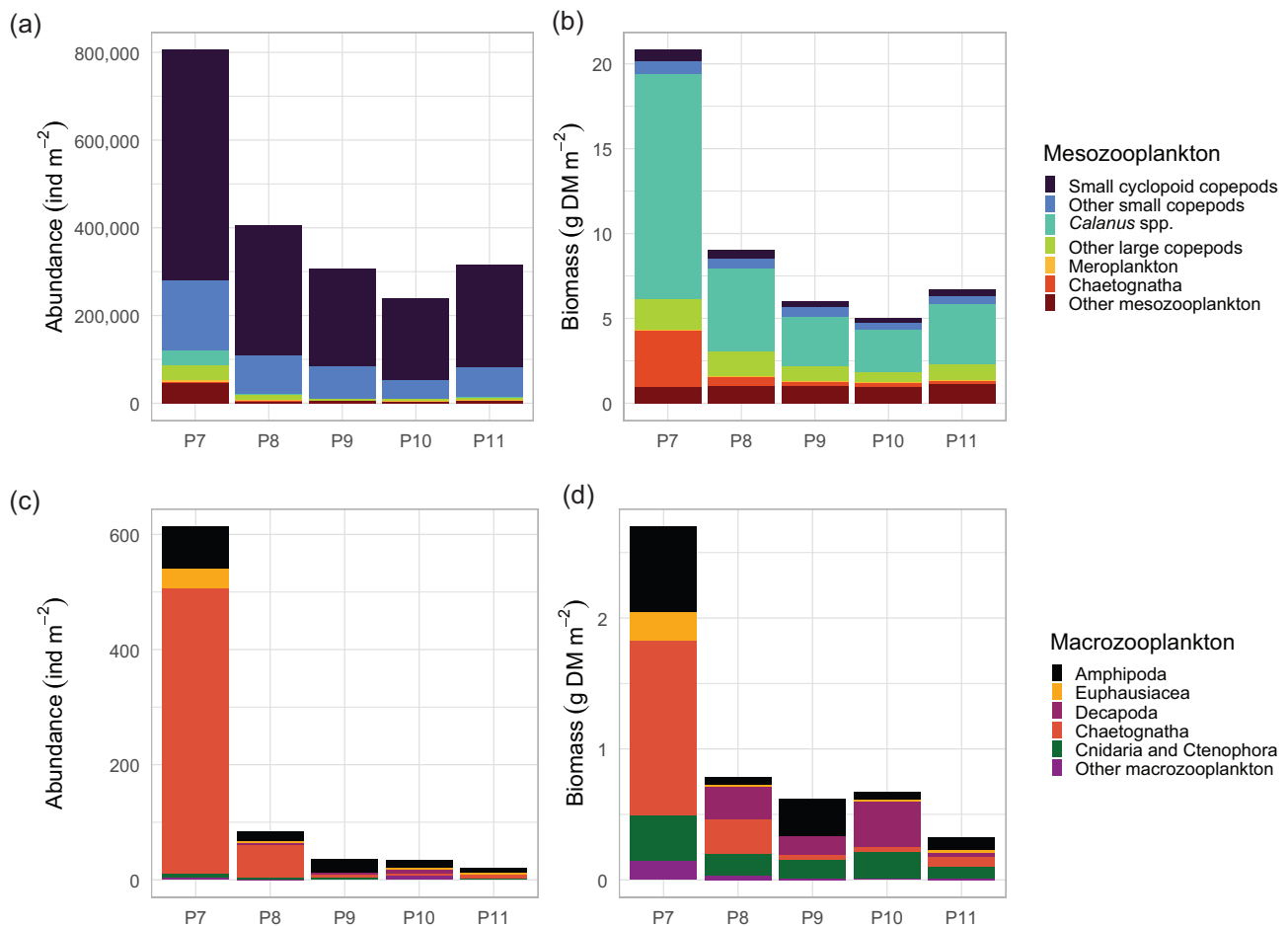


Figure 3. Abundance (ind. m^{-3}) and biomass (mg DM m^{-2}) of mesozooplankton (a, b) at stations, based on Multinet 64 and 180 μm and of the macrozooplankton (c, d) based on MIK net in Nansen (P7 and P8) and Amundsen Basin (P9–P11). Different colours represent various taxonomic groups within mesozooplankton (*Calanus* spp., large copepods, small copepods, meroplankton).

this group due to its similarly high abundances. This layer was characterized by AAW, except at P7 where UPDW also influenced the layer. Key taxa included mesopelagic and bathypelagic copepods such as *Scaphocalanus brevicornis* (ScaBrev), *S. magnus* (ScaMag), and *Heterorhabdus norvegicus* (HetNor), younger copepodids of the family Aetideidae (Aetide), amphipod *Themisto abyssorum* (TheAby) and polychaete *Typhloscolex muelleri* (TypMue). The 200–50 m layer (red) formed a lower epipelagic cluster, associated with Halocline Layer (HAL) water, and it also included the 600–200 m layer from P7. This community featured copepods *Calanus hyperboreus* (CalHyp), *C. finmarchicus* (CalFin), *M. longa* (MetLon), *Microcalanus* (Microc), *Calanoida nauplii* (CalNau), and the chaetognath *E. hamata* (EukHam). Surface samples (50–0 m, blue) formed a coherent group, indicating a distinct surface zooplankton community. This included *C. glacialis* (CalGla) and *O. similis* (OitSim), and at P7 also *M. norvegica* (MicNor), meroplankton and the chaetognath *P. elegans* (ParEle). Surface water at stations P8–P11 were dominated by PML water, while AAW water was also present in the associated deeper layer (200–50 m) at P7.

A closer look at the vertical distribution of selected copepod taxa revealed that among small copepods the cyclopoid *O. similis* (AF/AM and CI–CV stages) dominated the upper 200 m at all stations and that the Atlantic water indicator species *O. atlantica* was only present at P7 (Fig. 6a and b).

Among other small copepods, *Microcalanus* spp. was common and mainly restricted to the upper 200 m. *Microsetella norvegica* was confined to P7 and P8. *Neomormonilla minor* was found at greater depths from P8 northward (Fig. 6c). Cyclopoid nauplii were the most abundant copepod taxa. They were copious in surface waters at all locations (Fig. 6d). Among the larger copepod taxa, the three *Calanus* species were relatively abundant, with P7 being particularly rich in *C. glacialis* and *C. finmarchicus* in the upper 200 m (Fig. 7a). *Calanus finmarchicus* and *C. glacialis* were restricted to the upper 200 m, except at P7, where they were also found deeper (Fig. 7a). *Calanus hyperboreus* had low abundance at all stations and was present from surface to 2000 m depth, with the highest concentration at P8 in the surface (Fig. 7a). Among other larger copepods *M. longa* was common, with relatively high abundances in the upper 200 m at all stations and extending down to 2000 m at P7 (Fig. 7b). It is boreal counterpart *M. lucens* was only present at P7 at deeper depths (Fig. 7b). Adult Euchaetidae were generally rare, with *Paraeuchaeta barbata* most abundant at P9–P11, whereas *P. glacialis* and *P. norvegica* were only recorded at P7 and P8 (Fig. 7c). *Heterorhabdus norvegicus* dominated at intermediate depths at P7 and P8. Adults of the Scolecitrichidae family were more common from P8 northward, with *S. brevicornis* and *S. magnus* as the most numerous, while *Brodskius arcticus* and *S. polaris* were restricted to deeper layers (Fig. 7d). Other large

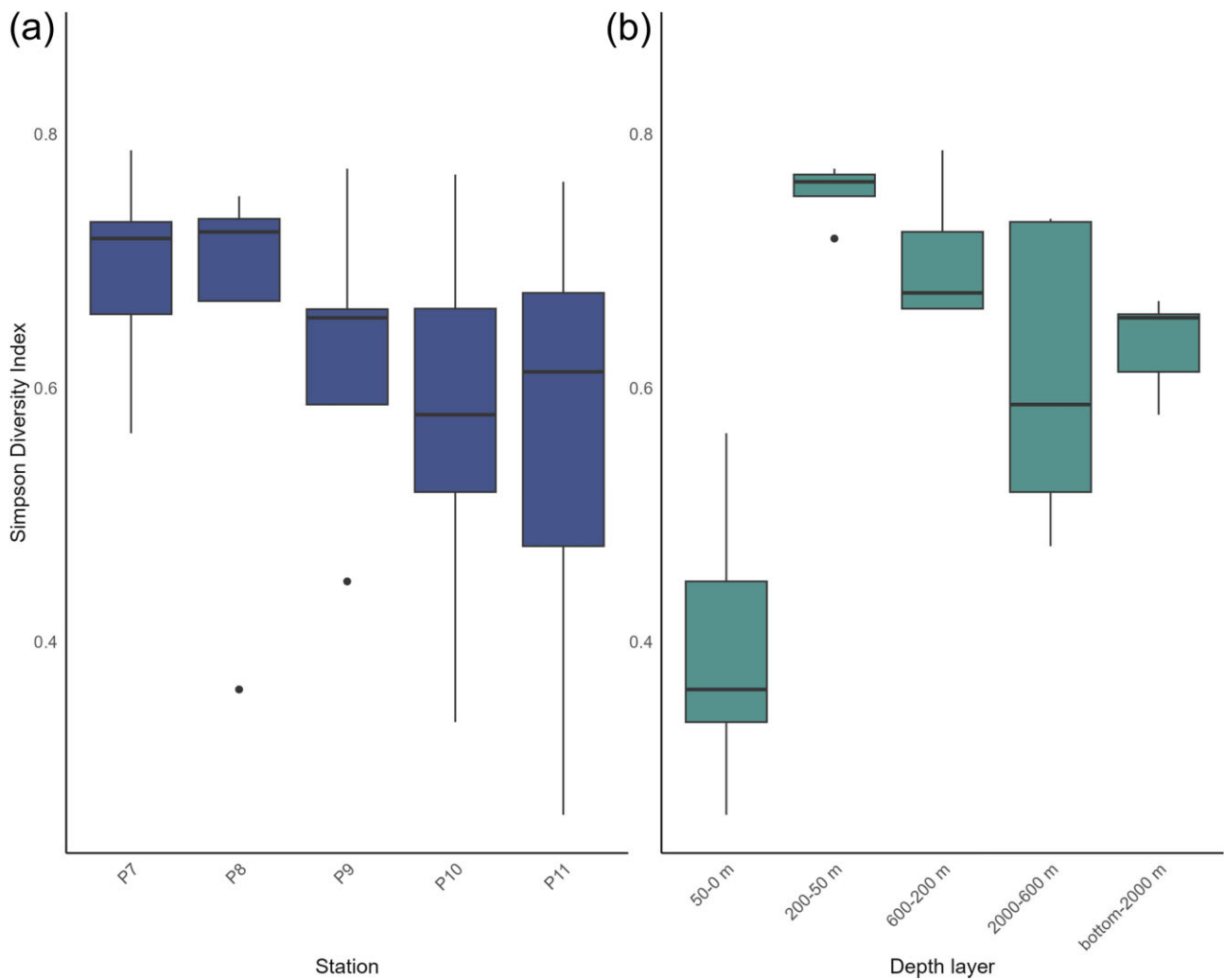


Figure 4. Boxplots showing the Simpson Diversity Index of mesozooplankton communities across (a) stations and (b) depth layers. The Simpson Diversity Index (y-axis) represents species diversity, with values ranging from 0 (low diversity) to 1 (high diversity). The box represents the interquartile range (IQR, 25th to 75th percentile). The horizontal line within the box indicates the median diversity value. The whiskers extend to the minimum and maximum values within 1.5 times the IQR. The dots represent outliers, data points outside 1.5 times the IQR.

copepods, such as *Spinocalanus* spp. (*S. antarcticus* and *S. horridus*), *Gaetanus* spp. (*G. tenuispinus*, *G. brevispinus*), and *Chiridiu obtusifrons* were more evenly distributed across the transect than the boreal species (Fig. 7e).

Calanus population structure

Calanus spp. occurred mainly in the upper 200 m and in low abundance, except at station P7, where a large number of younger developmental stages were present (Fig. 8). *Calanus finmarchicus* was concentrated in the southern part of the Nansen Basin, with only a few records further north (Fig. 8a). Copepodids CI, CIII, and CV were abundant in the upper 200 m at P7. In contrast, CV and adult females (AF) occurred in the deeper layers, but in low abundance (<0.001 ind. m^{-3}). In the Amundsen Basin, only females of *C. finmarchicus* were found. None of the females showed signs of maturity when live specimens were examined under the stereomicroscope during the cruise (C. Svensen pers. obs.).

Calanus glacialis was present at all stations but was less abundant north of P7 (Fig. 8b). Copepodids CI and CII and females were plentiful in the surface waters at P7. In

contrast, deeper, the main stages present were CIII—CV, and they were found in low abundances. Further north, *C. glacialis* was predominantly found in the upper 200 m, and adult females were the most abundant life stage, followed by CV.

Calanus hyperboreus showed a broad vertical distribution at all stations with highest abundance in the surface at P8. Different developmental stages dominated in different layers, with the most abundant stages being CIV, CV, and females (Fig. 8c). At the northernmost station P11, a significant proportion of CIII was also recorded.

Discussion

With Arctic sea ice rapidly declining, understanding shifts in pelagic communities is increasingly urgent. This study updates zooplankton inventories from the Nansen and Amundsen basins, which were last surveyed more than two decades ago (Kosobokova et al. 2011). This study was conducted as part of a broader study of the Arctic Ocean's physical, chemical, and biological compartments (Kohlbach et al. 2025). It provides new information on zooplankton diversity and dis-

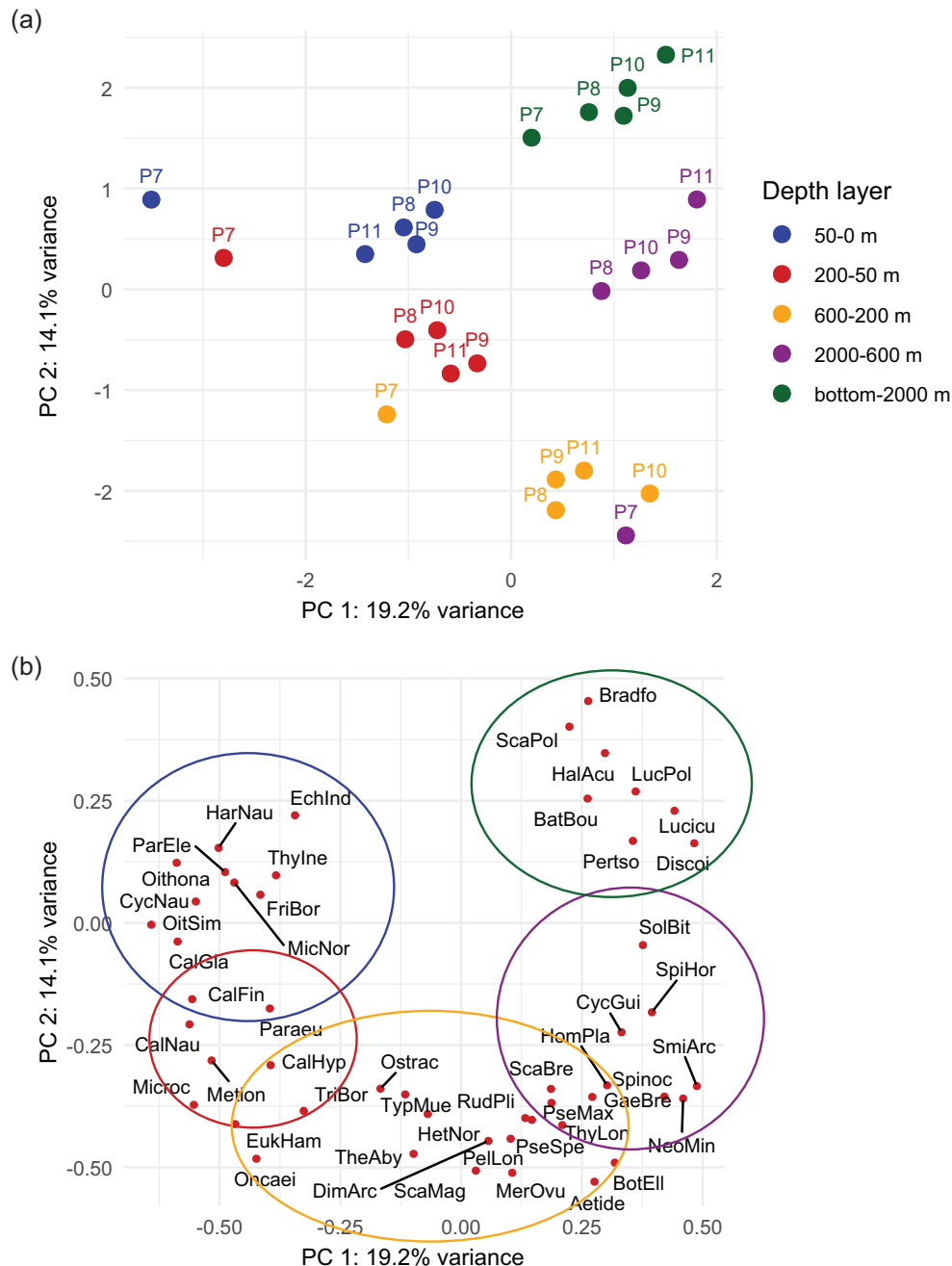


Figure 5. PCA biplot showing zooplankton community composition along the first two PCA axes. (a) Sample distribution, colour-coded by depth layer, (b) the 50 species contributing most to variation, with coordinates reflecting their association with sample position. Species clustering suggests shared ecological preferences or responses to water mass conditions. PCA axis 1 explains 19.2% of variation, and PCA axis 2 explains 14.1%. The full species name of the abbreviation used are listed in [Tables 1–3](#).

tribution. Zooplankton communities showed greater variability with depth than along the transect, highlighting the importance of water mass origin, the hydrodynamic structure of the Arctic Ocean, and shelf-to-slope transition phenomena in shaping the biodiversity and structure of Arctic zooplankton.

Regional differences in zooplankton abundance and biomass

The Southern Nansen Basin, influenced by Atlantic Water, is a hotspot for mesozooplankton and macrozooplankton biomass and diversity compared to areas further north in

the Arctic Ocean. Atlantic inflow facilitates nutrient transport across the pycnocline, supporting higher bacterial and protist biomass, likely sustaining zooplankton in this area (Kohlbach et al. 2025). The Atlantic current also transports zooplankton, forming a high-biomass belt along the Eurasian slope and into the southern Nansen Basin, a pattern already observed over two decades ago (Kosobokova and Hirche 2000, 2009). The results of this study show that despite the weakening of Atlantic water inflow through the Fram Strait over the past 15 years, caused by the positive phase of the Arctic Dipole (Polyakov et al. 2023), the northward expansion of Atlantic zooplankton species continues. This indicates that Atlantic



Figure 6. Vertical distribution (abundance, ind. m^{-3}) of (a) juvenile cyclopoid copepods, (b) adult female and male cyclopoid copepods, (c) other small copepods, and (d) nauplii in the Nansen Basin (P7 and P8) and Amundsen Basin (P9–P11). Colours indicate individual taxa within each group. The group «Other taxa» includes: Discoidæ indet., *Pertsovius* spp., *Pseudocalanus* spp., *Scolecithricella minor*, *Temorites brevis*, *Tharybis groenlandica*, and *Harpacticoida* indet. Note the different scales for different taxa and stations. *Harpacticoida* nauplii were found in very low abundance only in the upper two layers at P7. They are not visible in the figure because they are masked by other nauplii, but their locations are indicated by asterisks.

water advection, even if physically reduced, remains an essential phenomenon for the Arctic Ocean system, especially in combination with the observed decrease in sea-ice cover, creating favourable living conditions and increasing the survival of local and influent species (e.g. Tarling et al. 2022). Because the Arctic Dipole follows a cycle of ~ 15 years (Polyakov et al. 2023), its subsequent entry into its negative phase, with stronger inflows through the Fram Strait, will most likely further intensify Atlantification and its effects (Polyakov et al. 2023). Increased biomass in the upper epipelagic zone in the southern Nansen Basin was due to high abundances of *C. finmarchicus*, *C. glacialis*, *M. longa*, and chaetognaths, taxa that at present form the basis of zooplankton also in the northern Barents Sea and west of Spitsbergen (Skjoldal and Sperfeld 2024). In the central Nansen and Amundsen Basins, which were less affected by Atlantic inflow, zooplankton abundance and biomass were lower, reflecting lower biomass and production of pelagic and ice-associated algae in these regions (Kohlbach et al. 2025), similarly to the central Eurasian Basin (Kosobokova et al. 2011, Snoeijs-Leijonmalm et al. 2021).

The key difference in species composition between the two basins was the presence of Atlantic expatriates (*C. finmarchicus*, *O. atlantica*, *M. lucens*, *M. norvegica*, *Aglantha digitale*) and neritic expatriates (*P. borealis*), in the Nansen Basin. This is linked to the Atlantic inflow from the Fram Strait and through the Barents Sea and the Siberian shelf (Kosobokova and Hirche 2000, Kosobokova et al. 2011, Bluhm et al. 2015) and fits to the water-mass circulation through these basins proposed by Rudels et al. (2013), with separate current flows in the Nansen Basin and the Amundsen Basin, probably maintained primarily by the existence of two separate Atlantic water transport paths (the Fram Strait path and the Barents Sea path), and less controlled by the bottom topography and the presence of structures such as the Gakkel Ridge, especially in the epi or mesopelagic layers. The copepods *T. conifera*, the euphausiids *M. norvegica* and *T. inermis*, the amphipod *S. borealis*, and the hydrozoan *N. diomedea* were exclusively found in the Nansen Basin. The presence of these species associated with the Atlantic biome has previously been recorded in the fjords of western Spitsbergen (Balazy et al. 2021), Fram Strait (Weydmann et al. 2014, Wassmann et al. 2015, Gluchowska et al. 2017, Mańko et al. 2020), and the Barents Sea (ICES 2020),

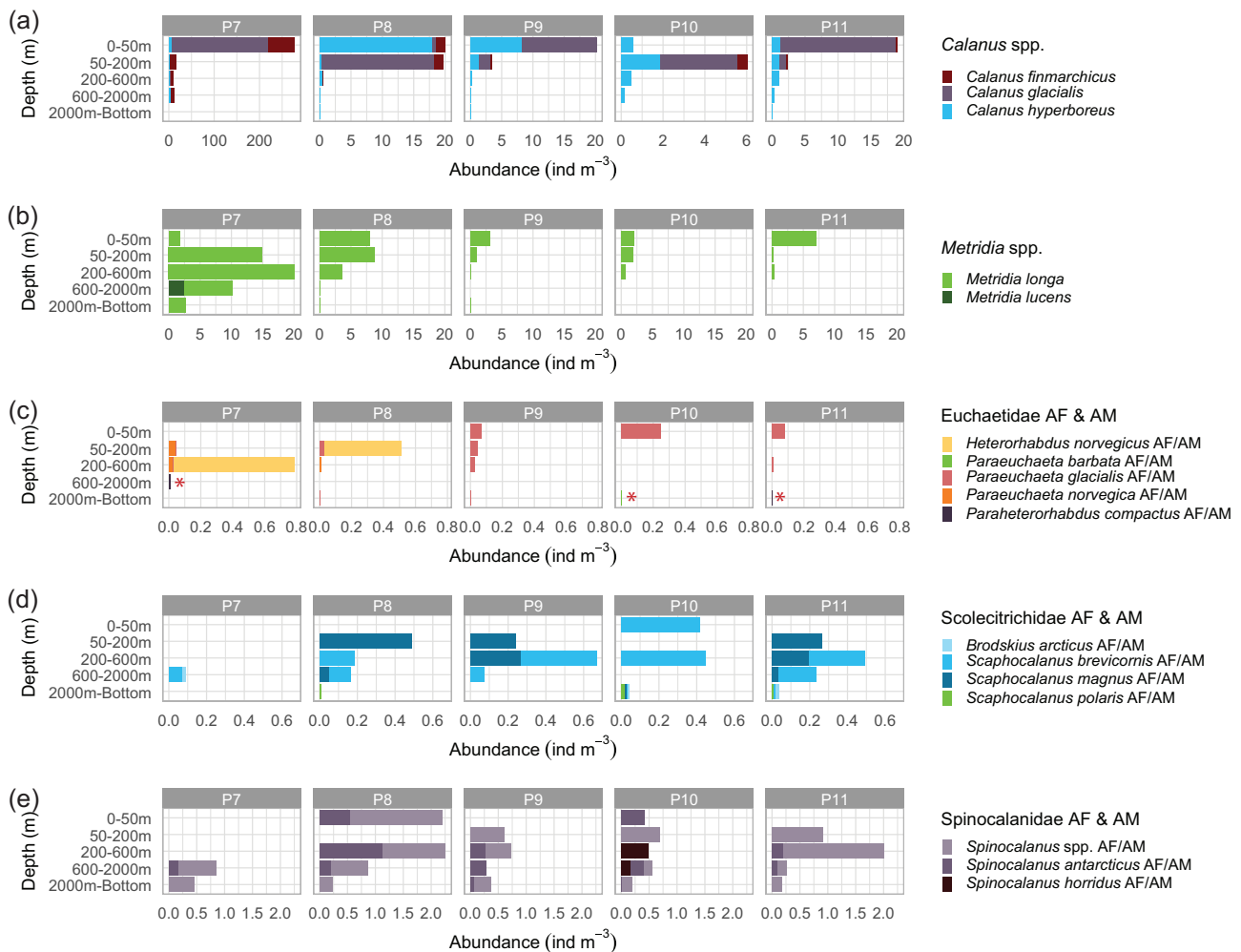


Figure 7. Vertical distribution (abundance, ind. m⁻³) of *Calanus* species (all stages found) (b) *Metridia* species (all stages found) (c) adult females and males of *H. norvegicus* and Euchaetidae, (d) adult females and males of Scolecitrichidae, and (e) adult females and males of Spinocalanidae family. *Paraeuchaeta barbata* and *Paraheterorhabdus compactus* were found in very low abundance in the deep layers at P7, P10, and P1. They are not visible in the figure, but their locations are indicated by asterisks.

confirming the ongoing Atlantification. The shelf-dwelling neritic hydrozoan *P. borealis* has been found in both the Nansen Basin (Kosobokova et al. 1998) and the Amundsen Basin (Kosobokova et al. 2011), indicating exchange between shelf and open ocean environments. In both basins, in samples from greater depths (>1000 m), we also found *S. magnus*, a species whose presence in the Arctic Ocean was previously suggested (Damkaer 1975, Brodsky et al. 1983), but which was not listed among the species found by Kosobokova et al. (2011). On the other hand, only in the Amundsen Basin we found the copepod *M. damkaeri*, the amphipods *A. abyssi* and *E. holmii*, the hydrozoans *Lensia* spp., *M. orthocanna*, and *C. norvegica*, the scyphozoan *Atolla* cf. *tenella*, and the ctenophore *B. abyssicola*. All these species likely have a wide distribution in the Arctic Ocean, having been recorded in all four deep Arctic Ocean basins (Kosobokova pers. comm.), and some (*M. damkaeri* and *E. holmii*) have even been indicated as Arctic endemic pelagic or ice-associated species (Kosobokova et al. 2011). The discovery of new taxa and the absence of others compared to previous studies highlight the need for continued research on zooplankton biodiversity in the Nansen and Amundsen basins to better understand the region's fauna.

The small number of recorded cnidarian and ctenophore species and their moderate biomasses, similar in both basins, do not provide evidence in support of the notion that a warmer climate (e.g. in the Nansen Basin) will favour a richer and more abundant gelatinous zooplankton as predicted in recent studies (Ingvaldsen et al. 2021). In the Nansen Basin, the main components of gelatinous zooplankton were the ctenophores *M. ovum* and *Beroe* spp. (tentatively considered *B. cf. cucumis* and *B. abyssicola*, Peters et al. 2025), while the Scyphozoa *Atolla* sp. (tentatively *A. cf. tenella*, Matsumoto et al. 2022, Pantiukhin et al. 2023) was more common in the Amundsen Basin. All three taxa (*M. ovum*, *Beroe* spp., and *Atolla* cf. *tenella*) are known to be widely distributed in the northern polar waters (<https://www.gbif.org/>). Other gelatinous zooplankton taxa we recorded in the study area were less abundant. While our limited number of observations prevents definitive conclusions, the influence of differing environmental conditions across basins suggests that variation in zooplankton composition is likely. The absence of some species may reflect both limited sampling effort (Hosia et al. 2017) and uneven species distribution, as gelatinous zooplankton is known to be very patchy (Majaneva et al. 2013). Future studies should prioritize increased trawling efforts, use

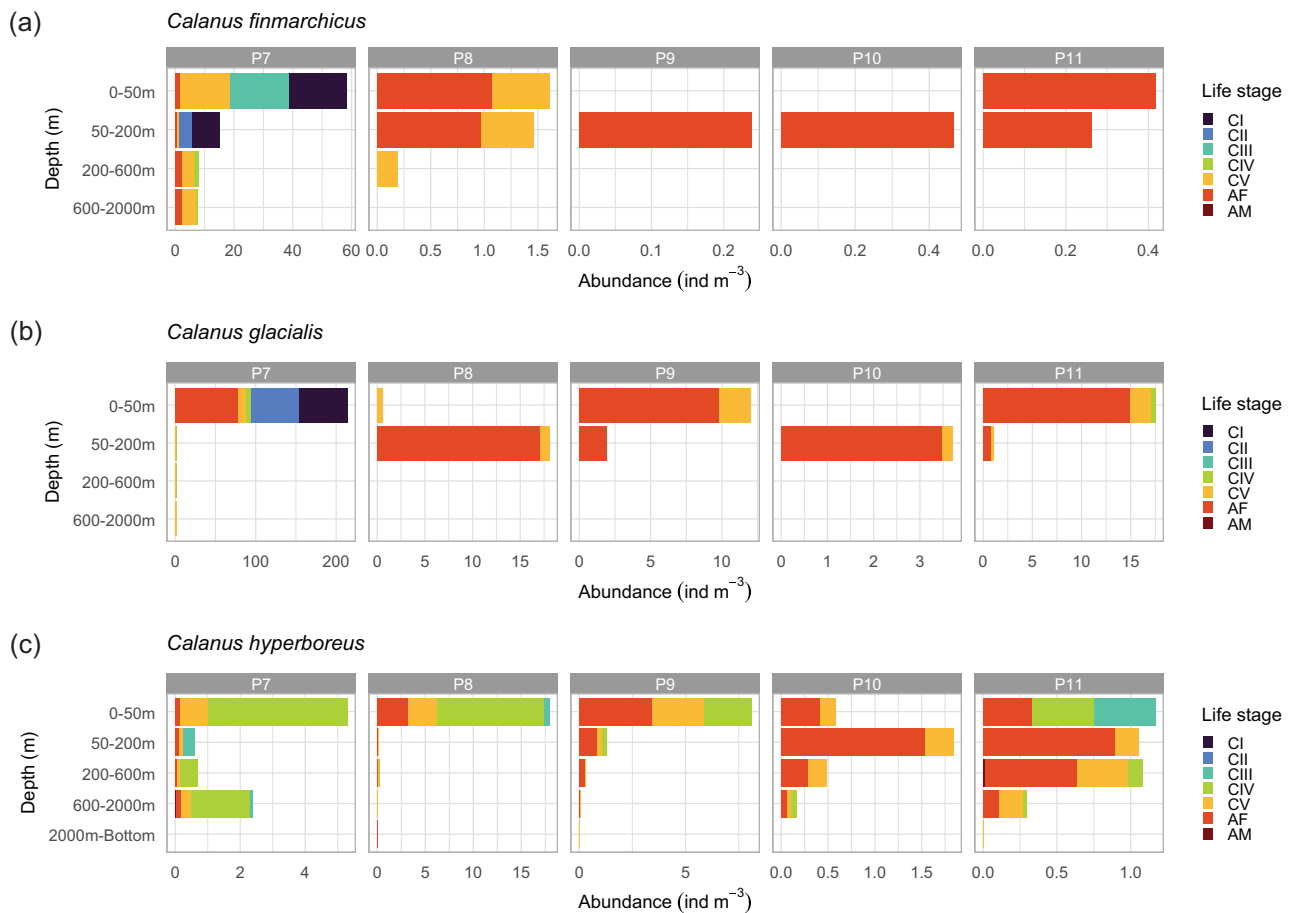


Figure 8. Vertical distribution (abundance, ind. m^{-3}) of different life stages of (a) *C. finmarchicus*, (b) *C. glacialis*, and (c) *C. hyperboreus* in stations in Nansen Basin (P7 and P8) and Amundsen Basin (P9, P10, and P11). Note the different scales for various groups and stations.

of dedicated gelatinous zooplankton sampling gear, and replicate sampling to better capture rare species and macrozooplankton. Overall, knowledge of gelatinous zooplankton distribution in the high Arctic remains scarce, with many species known from only a few or single observations (Majaneva et al. 2024).

Vertical and regional community structure

The Arctic Ocean exhibits strong vertical stratification driven by hydrography and current dynamics, which in turn shape zooplankton distribution (Kosobokova et al. 2011, Smoot and Hopcroft 2017, Ershova et al. 2021a, Kohlbach et al. 2025). As expected, we observed distinct depth-related communities, with vertical patterns reflecting hydrographic structuring, particularly in the Atlantic-influenced slope region. The biomass in surface waters in September was dominated by *Calanus* spp., forming the core of both upper and lower epipelagic communities. Green gut contents and early developmental stages, in the southernmost stations, suggest continued feeding and development into autumn in Atlantic-influenced waters. *Calanus hyperboreus* was the exception, occurring deeper in the Amundsen Basin, a pattern typical of this oceanic species (Conover 1988, Hirche et al. 2024). *Calanus* spp. adults and CVs persisted in surface waters farther north, despite low chlorophyll concentrations. These populations were likely sustained by autotrophic protists or microzooplankton (Svensen et al. 2019, Schmidt et al. 2025) or were potentially

awaiting a delayed protist bloom to enhance egg reproduction, as suggested by recent studies on *Calanus* life strategies in the Arctic Ocean (Feng et al. 2017, Kvile, 2019, Hirche et al. 2024).

Oithona similis, a key epipelagic species known for its year-round presence (Kosobokova 1983, Ashjian et al. 2003, Darnis and Fortier 2014), was abundant across both Atlantic-influenced and polar regions. Its dominance in the southern part of the Nansen Basin and the Amundsen Basin highlights its important position in the pelagic ecosystem. *Oithona* copepodid CI–CIII were not identified to species, but *O. atlantica* females occurred only at the Atlantic-influenced station P7, comprising around 4% of *Oithona* females. This suggests that the juveniles observed further north were likely all *O. similis*. The high proportion of juveniles in polar surface waters confirms previous observations that *O. similis* increases relative dominance later in the year when *Calanus* spp. descend to deeper waters for overwintering (Svensen et al. 2019, Balazy et al. 2021).

Statistical analyses confirmed significant differences between station P7 (region with Atlantic inflow) and more northern stations (P8–P11), in both community structure and abundance. Notable taxa at P7 included *C. finmarchicus*, *M. norvegica*, and *P. elegans*. The concentration of *Microsetella norvegica* in the upper 50 m likely reflects the influence of fjord outflows from northern Svalbard, which provide detritus-rich conditions favourable to this harpacticoid (Svensen et al. 2018, 2024). The elevated zooplankton abun-

dance and distinctive composition at P7 underscore the ecological importance of the northern Barents Sea shelf and Atlantic inflow areas as key productivity zones in the Arctic Ocean. This role, predicted in both conceptual and modelling studies (Wassmann et al. 2015, 2020, Årthun et al. 2025), is increasingly supported by observational data (Wold et al. 2023, this study).

A key vertical feature observed at P7 was the downward extension of community depth ranges. The upper epipelagic community extended below 50 m, the lower epipelagic community was observed at 600–200 m, and the mesopelagic community occupied depths beyond 600 m. These shifts reflect the subduction of Atlantic-origin water masses, which descend due to higher salinity and density along the slope (Wassmann et al. 2020). The presence of *M. lucens* in the 2000–600 m layer and *O. atlantica* in the 200–50 m layer further supports this interpretation.

Distinct zooplankton communities were found at different deep-water layers associated with specific water masses. The 600–200 m layer (AAW) hosted mesopelagic species such as *S. brevicornis*, *H. norvegicus*, and *T. abyssorum*, while the 2000–600 m layer (UPDW) supported a different community, including *S. horridus*, *N. minor*, *H. platygonon*, and *C. guilelmi*. The deepest layer (4000–2000 m), linked to EBDW and EBBW, was characterized by deep-sea copepods *S. polaris*, *L. polaris*, and Discoidae family and the hydrozoan *B. bouillonii*. Although based on single observations, these vertical and regional patterns align with earlier studies (Kosobokova et al. 2011, Yamaguchi et al. 2020) and provide complementary insights into the lesser-known community structure below the epipelagic zone.

Calanus distribution and population dynamics

Identifying *Calanus* species by prosome length alone is imperfect, especially for early copepodids (CI–CIII) of *C. finmarchicus* and *C. glacialis* (Gabrielsen, 2021, Choquet, 2018, Ershova et al. 2021a). Ongoing genetic studies from Nansen Legacy (2021) and SUDARCO (2022–2023) material, however, indicate that *C. finmarchicus* was present in the southern Nansen Basin and formed a significant part of the local gene pool (J. E. Søreide, pers. comm.). In this study, we applied the established size-based method used in earlier work on *Calanus* distributions in the Nansen and Amundsen Basins (Mumm et al. 1998, Kosobokova and Hirche 2000, 2009, Hirche and Kosobokova 2007), as well as adjacent regions such as the Fram Strait (Weydmann et al. 2014, Gluchowska et al. 2017, Basedow et al. 2018), the Barents Sea (Unstad and Tande 1991, Dvoretzky 2011, Wold et al. 2023), and Baffin Bay/Greenland (Madsen et al. 2001). While error-prone, this method yields ecologically meaningful results when combined with hydrography, currents, and co-occurring zooplankton data. Given the consistency of our results with previous studies and their interpretation in an environmental context, we consider them a reliable representation of *Calanus* distribution in the system.

Studies indicate that the Atlantic *C. finmarchicus* is advected northward into the Arctic Ocean (Aarflot et al. 2018, Wassmann et al. 2020). However, its ability to establish populations in the Arctic Ocean proper, outside the areas strongly influenced or shaped by Atlantic water inflow, remains uncertain. Warmer temperatures, retreating sea ice and increased habitat suitability in the Fram Strait, west of Svalbard, have

led to higher *C. finmarchicus* abundance, with evidence of local reproduction (Tarling et al. 2022). Basedow et al. (2018) estimated that ~500 000 metric tons of *C. finmarchicus* enter the Arctic Basin annually via the Fram Strait. Our findings confirm that *C. finmarchicus* contributes substantially to zooplankton abundance and biomass as far north as the southern Nansen Basin, consistent with modelling studies (Ji et al. 2012, Wassmann et al. 2020) and previous observations (Kosobokova and Hirche 2009, Hop et al. 2019). The presence of young copepodids (CI and CIII) and late stages (CV) in the upper 50 m at P7 indicates a thriving new generation, originating from females spawning in the Fram Strait area. However, the scarcity of *C. finmarchicus* and the absence of females and young copepodids further into the Arctic Ocean, suggest that its reproductive potential remains confined to the Atlantic Water inflow region.

Calanus glacialis shows a similar spatial pattern to *C. finmarchicus* but at higher abundance. At P7, we observed numerous *C. glacialis*, including early stages copepodids, while later stages (CV, AF) dominated further north, consistent with previous studies (Ershova et al. 2021a, Hirche et al. 2024). Hirche et al. (2024) reported that reproduction and early stages were restricted to the southern basin margins, with late-stage copepodids and adult females occurring throughout their study area. Similarly, Ershova et al. (2021a), analysing samples from 1993 to 2016, documented high spatial and interannual variability in *C. glacialis* abundance, spanning three orders of magnitude. The absence of young stages beyond P7, together with the scarcity of overwintering stages of *C. finmarchicus* and *C. glacialis* below 200 m, suggests that the Arctic Ocean acts as a continuous sink for advected populations of these boreal and Arctic shelf-sea species (Daase et al. 2013, Wassmann et al. 2020, Hirche et al. 2024). The lack of CI–CIII stages further indicates that *C. glacialis* does not reproduce north of P7. This aligns with model studies showing that its long developmental period from nauplius III (NIII) to copepodid CIII prevents colonization of most central Arctic basins (Feng et al. 2016, 2018). However, future ocean warming, longer growth seasons, and greater phytoplankton availability may promote development and enable a poleward expansion of *C. glacialis* (Feng et al. 2016).

Calanus hyperboreus displayed a broader vertical distribution across all stations, with all life stages present from surface to deep waters and a predominance of CIV and CV stages, except at station P11 in the Amundsen Basin where CIII dominated. Previous studies have suggested that *C. hyperboreus* is an expatriate in the central Arctic basins due to low abundances and a dominance of late developmental stages (Kvile et al. 2019). A modelling study by Ji, 2012 indicated that they cannot develop from the first feeding stage (NIII) to the critical overwintering stage (CIII) within 1 year. However, the wide distribution and presence of CIII at the northernmost station P11 in our study suggest that *C. hyperboreus* is well adapted to deep Arctic basin conditions (Conover 1988, Wassmann et al. 2020, Hirche et al. 2024, Schmidt et al. 2025).

Changes in zooplankton communities over time

Kosobokova et al. (2011) provided a comprehensive inventory of zooplankton across the Arctic Ocean, covering the Nansen, Amundsen, Makarov, and Canadian basins over an extended period. Their data include samples from Russian drifting ice

stations (1975–1977) and cruises with RV *Polarstern* (1993–2007) and the USCGC *Healy* (2005). Thus, their zooplankton inventories are more extensive than the present study, which focuses only on the western parts of the Nansen and Amundsen basins and is based on samples from one summer season. A comparison of species identified in both studies for these basins is provided in [Supplementary Table 4](#). Atlantic species, such as the euphausiid *H. megalops* and the amphipod *T. compressa*, were found in the Nansen and Amundsen basins in 2021 but were not reported in the 1975–2007 inventory (Kosobokova et al. 2011). *Themisto compressa* began appearing in high abundances in the long-term sediment trap record in Fram Strait (79°N, 4°E) in 2004, with reproduction observed for the first time in 2011 (Kraft et al. 2012, Havermans et al. 2019). *Hansarsia megalops* have also been observed in Kongsfjorden (Huenerlage and Buchholz 2015). However, neither species had been recorded in the Nansen or Amundsen basins before 2021. This northward expansion of Atlantic species aligns with broader trends of Atlantification of the Arctic Ocean system and borealization of the Arctic fauna (Descamp and Strøm 2021, Ingvaldsen et al. 2023, Husson et al. 2024). Although our study took place in the central Arctic Ocean, we did not record ice-associated amphipods such as *Gammarus wilkitzkii*, *Onisimus glacialis*, or *O. nanseni* in the zooplankton samples. Their distribution is highly heterogeneous (Arndt and Swadling 2006), and their absence may reflect low sample numbers or the lack of under-ice sampling specifically targeting them. *Onisimus glacialis* and *O. nanseni* have shorter lifespans than *G. wilkitzkii* and may be better adapted to changing ice conditions but remain vulnerable to overall sea-ice loss. *Gammarus wilkitzkii* has shown declining abundance in the Arctic since the mid-1990s, closely linked to the reduction of multiyear sea ice (Hop et al. 2021a). In contrast, we found the ice-associated amphipod *Apherusa glacialis* in samples from both basins; this species appears less sensitive to ice loss as it also occurs pelagically (Kosobokova et al. 2011, Kunisch et al. 2020). Kosobokova et al. 2011 identified 78 copepod taxa in the Nansen and Amundsen basins, of which 76 were identified at the species level, while this study found 60 taxa, of which 42 were identified to species, nine to genus and seven to family level. The higher number of taxa in earlier studies likely reflects a more detailed taxonomic identification and a larger sample size and a larger geographical area investigated. The less complete species lists for some zooplankton taxa, including primarily Calanoida or Cyclopoida species, but also Hydrozoa, Polychaeta and Appendicularia stem from these differences. Species identification based on morphology remains challenging, especially for deep-water taxa, due to limited descriptions and subtle diagnostic traits (e.g. sensory setae on mouth appendages). This concerns species from families such as Phaennidae (*Xanthocalanus* spp.), Tharybidae (*Tharybis* spp.), Scolecitrichidae (*Scaphocalanus* spp.), and Diaixidae (*Byrathis* sp.), grouped in this study as Bradfordian families (Bradford 1973, Boxshall and Halsey 2004, Andronov 2014, Laakmann et al. 2019). Identification is further complicated by the lack of descriptions for developmental stages, as many specimens were immature and lacked fully developed characteristics. Consequently, Augaptilidae indet. may include *Euaugaptilus hyperboreus* and *Pseudaugaptilus polaris*, while Aetideidae indet., in addition to younger stages of widely distributed species of genera *Gaetanus* (e.g. *G. tenuispinus* and *G. brevispinus*) or *Aetideopsis* (*A. rostrata* and *A. minor*), may comprise cope-

podids of *Chiridiella* spp., *Jaschnovia* spp. or *Pseudochirella* spp. Similarly, *Xanthocalanus* spp. may contain copepodids of *X. polarsternae*, *X. profundus*, or *X. spinodenticulatus*. Some copepods recorded in this study were included in the 1975–2007 inventory only at the genus (*Brodskius* spp., likely our *B. arcticus*) or family (Discoidae spp., likely our *Pertsovius* spp.) levels. *Tharybis groenlandica* has a species name correction, whereas *T. conifera* was not recorded in previous studies at all. On the other hand, some species (*Arctokonstantinus hardingi*, *Eurytemora richingsi*, *Lucicutia pseudopolaris*, *Mimocalanus crassus*) were recorded in the 1975–2007 study only in the Nansen Basin. Thus, some species absent from our collection may be due to less numerous sample collection, shorter study period or not sampling all the same habitats (e.g. shelf or neritic waters). The presence of advected species from outside the Arctic biome (including *C. finmarchicus*, *M. lucens*, *O. atlantica*, *T. borealis*, *T. abyssorum*, *T. compressa*, *H. megalops*) indicates the emergence of competition or need for coexistence with native Arctic zooplankton in the future system (Ershova et al. 2021a). As Atlantification progresses, Arctic endemics may struggle with warming, and reduced sea ice, while expanding boreal species may establish and reshape zooplankton communities. Given the Arctic Ocean's vast unexplored regions, particularly at depth, new species discoveries remain likely, but some species may also disappear, emphasizing the need for further studies.

Conclusion

This study provides insights into the zooplankton composition and pelagic ecosystem characteristics of the Central Arctic Ocean, confirming the significant role of advection from the Atlantic domain and revealing differences in zooplankton communities between Nansen and Amundsen basins as well as across depths. The southern Nansen Basin, influenced by Atlantic inflow, supports higher mesozooplankton and macrozooplankton abundances, mainly driven by copepods (*C. finmarchicus*, *C. glacialis*, and *M. longa*), chaetognaths (*P. elegans* and *E. hamata*) and euphausiids (*M. norvegica* and *T. inermis*) and adds to the secondary production along the continental shelf-slope regions. In contrast, the Amundsen Basin, influenced by the TPD and where the AW signal is significantly weakened, is characterized by lower zooplankton biomass but greater species diversity at depth. Comparisons with historical data suggest a continued northward expansion of Atlantic species, such as the cyclopoid copepod *T. borealis*, the amphipod *T. compressa*, the euphausiid *H. megalops*, while reducing the role of ice-associated species such as *G. wilkitzkii* and *Onisimus* spp.. These changes are likely driven by climate change and sea-ice loss creating increased survival or mortality depending on species. Further monitoring of zooplankton communities is essential to confirm potential community changes and to understand the impacts of environmental change on pelagic ecosystems and Arctic marine food webs.

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Author contributions

Anette Wold (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Investigation [lead], Methodology [equal], Project administration [equal], Writing – original draft [lead]), Haakon Hop (Conceptualization [equal], Funding acquisition [equal], Project administration [equal], Writing – review & editing [equal]), Camilla Svensen (Conceptualization [equal], Funding acquisition [equal], Methodology [equal], Writing – original draft [equal]), Janne E. Søreide (Conceptualization [equal], Funding acquisition [equal], Project administration [equal], Writing – review & editing [equal]), Sanna Majaneva (Conceptualization [equal], Formal analysis [equal], Writing – review & editing [equal]), Mateusz Ormanczyk (Formal analysis [equal], Writing – review & editing [equal]), Sławomir Kwasniewski (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Writing – review & editing [equal]).

Supplementary data

Supplementary data are available at *ICES Journal of Marine Science* online.

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Data availability

The mesozooplankton data used for this study are available at the Norwegian Polar Data Centre (<https://data.npolar.no>):

Mesozooplankton biodiversity Nansen Legacy JC2-2:

DOI: 10.21334/npolar.2024.667911e4

Macrozooplankton biodiversity Nansen Legacy JC2-2:

DOI: 10.21334/npolar.2024.11c1595f

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