

The under-ice habitat constitutes a critical survival hub for zooplankton in the Central Arctic Ocean

Astrid Cornils

Astrid.Cornils@awi.de

Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung <https://orcid.org/0000-0003-4536-9015>

Hauke Flores

Alfred Wegener Institute <https://orcid.org/0000-0003-1617-5449>

Kim Wermeyer

Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany

Philipp Anhaus

German Aerospace Center (DLR e. V.), Institute for the Protection of Maritime Infrastructures, Bremerhaven, Germany

Carin Ashjian

Woods Hole Oceanographic Institution, Woods Hole, MA, USA

Robert Campbell

University of Rhode Island Graduate School of Oceanography, Narragansett, RI, USA
<https://orcid.org/0000-0002-3710-9750>

Giulia Castellani

University of Bremen, Institute of Environmental Physics (IUP), Bremen, Germany

Celia Gelfman

University of Rhode Island Graduate School of Oceanography, Narragansett, RI, USA

Nicole Hildebrandt

Alfred Wegener Institute <https://orcid.org/0000-0003-0555-3096>

Clara Hoppe

1 Alfred-Wegener-Institut - Helmholtz-Zentrum für Polar- und Meeresforschung <https://orcid.org/0000-0002-2509-0546>

Christian Katlein

Alfred Wegener Institute for Polar and Marine Research

Nadine Knüppel

Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany

Serdar Sakinan

Wageningen Marine Research, Den Helder, The Netherlands

Fokje Schaafsma

Wageningen Marine Research

Katrin Schmidt

University of Plymouth <https://orcid.org/0000-0002-6488-623X>

Katyanne Shoemaker

University of Rhode Island Graduate School of Oceanography, Narragansett, RI, USA

<https://orcid.org/0000-0002-5129-2387>

Martina Vortkamp

Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research

MOSAIC Teams ECO, ICE & OCEAN

Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung

Barbara Niehoff

Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany

Article

Keywords:

Posted Date: March 4th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-8853601/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: There is **NO** Competing Interest.

The under-ice habitat constitutes a critical survival hub for zooplankton in the Central Arctic Ocean

Astrid Cornils^{1*}, Hauke Flores^{1*}, Kim Julie Wermeyer¹, Philipp Anhaus²³, Carin J. Ashjian⁴, Robert G. Campbell⁵, Giulia Castellani^{1,6}, Celia Gelfman⁵, Nicole Hildebrandt¹, Clara J. M. Hoppe⁷, Christian Katlein², Nadine Knüppel¹, Serdar Sakinan⁸, Fokje L. Schaafsma⁸, Katrin Schmidt⁹, Katyanne M. Shoemaker⁵, Martina Vorkamp¹, MOSAiC TEAMs ECO, ICE & OCEAN, Barbara Niehoff¹

*These authors contributed equally to the work.

Affiliations

¹Polar Biological Oceanography, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany

²Sea Ice Physics, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany

³German Aerospace Center (DLR e. V.), Institute for the Protection of Maritime Infrastructures, Bremerhaven, Germany

⁴Woods Hole Oceanographic Institution, Woods Hole, MA, USA

⁵University of Rhode Island Graduate School of Oceanography, Narragansett, RI, USA

⁶University of Bremen, Institute of Environmental Physics (IUP), Bremen, Germany

⁷Marine Biogeoscience, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany

⁸Wageningen Marine Research, Den Helder, The Netherlands

⁹School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK

Abstract

The consequences of sea-ice decline for zooplankton survival in the Central Arctic Ocean (CAO) remain poorly understood, limiting predictions of ecosystem resilience. During the MOSAiC expedition (November 2019 - September 2020), we conducted the first year-round sampling of under-ice zooplankton (Ice-water interface and 10 m depth) along the Transpolar Drift using a remotely operated vehicle equipped with a zooplankton net (ROVnet). Multivariate analyses identified three spatio-seasonal community regimes: autumn and winter regimes in the Amundsen Basin, and a spring regime in both the Amundsen and Nansen Basin. Variations in taxon-specific abundances and biomass patterns indicate that the under-ice habitat shifts in function from a feeding and sheltering habitat in autumn and winter to a nursery habitat in spring. During the polar night, estimated particulate carbon supply, likely originating from sea ice, only marginally met community carbon demand. This deficit was partly offset by high trophic transfer efficiency inferred by normalized biomass size spectra (NBSS). This implies that the under-ice habitat enables zooplankton survival during the polar night at their very energetic limit, suggesting that changes in the duration and extent of sea-ice coverage will be critical for sustaining the future ecosystem functionality of the CAO.

MAIN

Introduction

In the Arctic Ocean, rising temperatures and altered ocean circulation have led to a significant decline in sea-ice extent, shifting the system from a perennial to seasonal ice cover and changing its properties¹. The ‘under-ice habitat’² between the ice-water interface and a strong density gradient at 20 to 50 m depth sustains an abundant zooplankton community year-round^{3,4} which is particularly susceptible to shifts in the physical and chemical properties of sea ice and the underlying water column^{4,5}. Organic matter produced by microalgae growing in sea ice (‘ice algae’) may provide a critical ‘food bank’ from autumn to spring^{6,7}. Longer open water seasons and enhanced under-ice light alter the magnitude and timing of primary production, and thus food availability^{8,9}. Thinner and shorter sea-ice coverage also impacts vertical zooplankton distribution^{2,10}. Changes in this habitat can profoundly affect biodiversity, food web structure, and carbon cycling in the Arctic Ocean, as zooplankton transfer energy to higher trophic levels and contribute significantly to the biological carbon pump^{11,12}.

Despite the importance of zooplankton, projections of ecosystem change remain limited by sparse data from the deep basins of the Central Arctic Ocean (CAO). The taxonomic composition, habitat use, and role of the under-ice community in carbon turnover during the polar night are largely unknown, as most seasonal studies focus on shelves and slopes^{4,13}. Sampling the underside of sea ice remains technically challenging. Previous methods, including diver-operated nets, video transects, pumps, and under-ice trawls, vary in taxonomic resolution and targeted size range^{3,4,6,13–15}.

The Multidisciplinary Drifting Observatory for the Study of Arctic Climate (MOSAiC) expedition provided a unique opportunity to overcome some of these limitations. Using a Remotely Operated Vehicle (ROV)¹⁶ equipped with a zooplankton net (ROVnet)¹⁷ we sampled zooplankton and sympagic (ice-associated) fauna along the Transpolar Drift, paired with environmental parameters¹⁸. Through consistent sampling effort and high-resolution data collection over nearly one year, this study contributes to the monitoring of ecosystem changes essential for future management of marine resources and biodiversity conservation identified as a priority by international fora, including the *Convention of Biological Diversity*¹⁹ and the *Agreement to Prevent Unregulated High Seas Fisheries in the Central Arctic Ocean*²⁰. By analyzing samples collected with a novel under-ice sampling device, we aim to (1) determine the taxa using the under-ice habitat with particular focus on the polar night and adjacent twilight; (2) resolve seasonal changes in food web structure and carbon transfer efficiency, and (3) quantify biomass and potential carbon provision of the under-ice community. Together, these analyses yield new insights into the functioning of the Arctic under-ice ecosystem and provide critical data to project how continued sea-ice decline may alter biodiversity, trophic interactions, and carbon cycling at the basin scale.

Results

During the MOSAiC drift expedition with the RV Polarstern, we deployed the ROV net at 22 stations between 10 November 2019 and 12 September 2020 at the ice-water interface (IWI) and at 10 m depth (Fig. 1, suppl. Table 1) to sample the zooplankton in the under-ice habitat² of the Central Arctic Ocean (CAO). All zooplankton samples were processed using a scanning system (ZooScan²¹), and the resulting images were semi-automatically identified utilizing the deep-learning algorithm in EcoTaxa²². We identified 43 taxa from 8 phyla (suppl. Table 2). Abundances ranged between 20 ind. m⁻³ in March and 4880 ind. m⁻³ in August. Numerically, copepods accounted for more than 90% of the organisms.

Spatio-seasonal community structure and drivers

Hierarchical clustering and non-metric multidimensional scaling (nMDS; stress = 0.087) based on Bray-Curtis identified three spatio-seasonal clusters in the Central Arctic under-ice community: an ‘autumn’ regime (August - September), a ‘winter’ regime (November – February) and a ‘spring’ regime (March – May) (Fig. 2A, suppl. Fig. 1A). While the nMDS separated the IWI from the 10 m communities in winter, spring samples showed regional subclustering, with the Nansen Basin communities being distinct from the Amundsen Basin and Gakkel Ridge communities. Environmental vector fitting identified chlorophyll *a* (sea-ice and water) and mixed layer depth (MLD) as strongest predictors, while particulate organic carbon (POC) contributed less strongly.

PERMANOVA confirmed significant effects from spatio-seasonal regime ($F = 21.54$, $R^2 = 0.45$, $p = 0.001$), depth strata ($F = 5.88$, $R^2 = 0.06$, $p = 0.001$) and their interaction ($F = 4.13$, $R^2 = 0.09$, $p = 0.002$), together explaining ~60% of the community variation (suppl. Table 4). The significant interaction reflects the effect of sampling depth mirrored in the nMDS subclusters. Homogeneous multivariate dispersion across regimes and depths (suppl. Table 5) suggests that these differences were driven by composition rather than variance. Due to uneven sampling coverage, the regional effect was excluded from the final model (see Methods).

The environmental principal component analysis (PCA) mirrored the spatio-seasonal patterns of the zooplankton community but with a slight temporal lag, as community shifts tended to precede environmental changes. The PCA’s first two axes explained 74.5% of the variance, separating the autumn/early winter, winter/early spring, and late spring periods (Fig. 2B, suppl. Fig. 1). As in the nMDS, chlorophyll *a*, POC and MLD were the main drivers of this environmental variation.

The autumn regime

To highlight seasonal transitions along the spatial drift from the eastern CAO to the Nansen Basin, our results are presented following the spatial-seasonal trajectory (late summer/autumn 2020 through winter-spring 2019/2020) rather than the strict chronological order. The autumn regime in the Amundsen Basin (late August - September) was characterized by ongoing sea-ice melt, indicated by a drop in surface salinity (32.3 to 28.9, Fig. 1) and a shallow mixed surface layer (10-20 m) stabilized by a strong pycnocline²³. Sea surface temperatures ranged between -1.6 and -1.5 °C. As light declined, integrated chlorophyll *a* decreased rapidly in the upper 20 m water column (12 to 4.5 mg m⁻²; Fig. 1). The nMDS ordination linked the 10 m samples to elevated chlorophyll *a* in the water column and the IWI samples to relatively high sea-ice chlorophyll *a*; both indicating an association of the autumn regime under-ice community with productivity (Fig. 2A). Copepod abundances reached median values of 589 ind. m⁻³ (IWI) and 1115 ind. m⁻³ (10 m layer), dominated by *Oithona* spp. (70%), followed by Oncaeidae (Fig. 3). *Calanus glacialis* was primarily represented by young copepodites (CI-CIV; suppl. Fig. 4). Among non-copepods, larvaceans and polychaete larvae were abundant at 10 m, while the IWI was characterised by sea-ice associated (sympagic) taxa, including the ice amphipod *Apherusa glacialis*, the copepod *Cyclopina* spp. and unidentified harpacticoids (Fig. 3; suppl. Fig. 3).

The winter regime

The winter regime in the Amundsen Basin (November – February) was characterized by relatively uniform conditions, with low sea surface temperatures (-1.8 to -1.7°C) and surface salinities (31.5 to 32.8). Integrated chlorophyll *a* remained low in the 20 m water column (<0.01 to 1.1 mg m⁻²) compared to autumn, while it decreased in the sea ice from 0.76 mg m⁻² in November to 0.01 mg m⁻² in December (Fig. 1). This decline aligned with the environmental PCA, which distinguished the early winter transition from the stable late-winter period (Fig. 2B). A strong pycnocline separated the 20–50 m surface mixed layer from deeper waters (Fig. 1). Copepod abundances were considerably lower than in the autumn regime. In both depth layers, communities were dominated by *Oithona* spp., *Microcalanus* spp., *Metridia longa* late copepodites (CV) and *C. glacialis* females (Fig. 3). Non-copepod abundances were higher at the IWI, mainly driven by chaetognaths (*Eukrohnia hamata*) and appendicularians (*Oikopleura* spp.), while ostracods dominated the 10 m depth layer (Fig. 3). Although the ice amphipod *A. glacialis* was largely absent, the remaining sympagic fauna resembled the autumn assemblages (suppl. Fig. 3).

The spring regime

At the onset of the spring regime (March - May), light levels and surface salinity increased. The mixed layer deepened from ~50 m (March) to 150 m (May) as the pycnocline weakened.

Chlorophyll *a* concentrations increased first in the sea ice, followed by the water column (Fig. 1). During this period the MOSAiC ice floe drifted across the Gakkel Ridge, moving from the Amundsen into the Nansen Basin. Copepod abundances increased to medians of 353 ind. m⁻³ (IWI) and 196 ind. m⁻³ (10 m), primarily due abundances of copepod nauplii (Fig. 3). Conversely, abundances of the large copepods *M. longa* and *C. glacialis* dropped by an order of magnitude (suppl. Fig. 4). The population structure of the few remaining *M. longa* changed from a dominance of females and CV stages in winter to a higher proportion of younger copepodites in spring (CI-CIV) (suppl. Fig. 4). Non-copepod dynamics were characterized by the disappearance of ostracods by April and an increase in amphipod abundance, which comprised ~25% of the non-copepods by May (Fig. 3). This shift was driven by sympagic amphipods (*A. glacialis*, *Eusirus holmii*, *Onisimus* spp.) at the IWI, and pelagic *Themisto libellula* at 10 m depth. In contrast, the abundance of the sympagic copepod *Cyclopina* sp. at the IWI decreased considerably (suppl. Fig. 3).

Vertical distribution and community size structure

Beyond the spatio-seasonal regimes, the under-ice community exhibited distinct vertical preferences. *Cyclopina* sp. resided directly at the IWI, while *M. longa*, *C. glacialis* and ostracods, preferred the 10 m depth layer (Fig. 4). Other taxa, including Aetideidae, Heterorhabdidae, and Cnidaria occurred consistently across both depths (suppl. Fig. 5). Polar day (spring, autumn) taxa included *A. glacialis* at the IWI and *Calanus hyperboreus* and Oncaeidae at 10 m, while larvae (nauplii, molluscs and polychaetes) were present at both depths (Fig. 4). Some taxa shifted their depth preference from the IWI to 10 m across regimes, including Ectinosomatidae, the chaetognath *E. hamata*, and Oikopleuridae. In contrast, ubiquitous taxa including *Oithona* spp. and *Microcalanus* spp. showed no clear seasonal or vertical preference (Fig. 3, 4).

These taxonomic shifts were reflected in the Normalized Biomass-Size Spectra (NBSS). Small organisms dominated during spring and autumns regimes, whereas larger size classes contributed more during winter (Fig. 5A). The NBSS slope, which serves as a proxy for trophic transfer efficiency²⁴, was consistently flatter during the winter regime compared to autumn and spring (suppl. Table 6), reflecting a higher relative biomass of large individuals. To ensure a robust signal despite unequal sampling sizes, we used bootstrap resampling to estimate confidence intervals for seasonal mean slopes. The resulting winter regime confidence intervals were clearly separated from those of the other two regimes (Fig. 5b), confirming the statistical distinctness of the winter community structure.

Carbon biomass and demand

To quantify the energetic role of the under-ice zooplankton community, zooplankton carbon biomass was estimated from ZooScan derived biovolumes using established conversion formulas^{25–27} (suppl. Table 2). Integrated biomass (IWI-10 m) was comparable between the autumn (50.6 mg C m^{-2}) and winter regimes (62 mg C m^{-2}) but was an order of magnitude lower during spring (6.0 mg C m^{-2} ; Table 1). Zooplankton community carbon demand, modelled from respiration rates at ambient temperature^{28,29}, followed the patterns observed in carbon biomass: the carbon demand was high in the autumn ($2.3 \text{ mg C m}^{-2} \text{ d}^{-1}$) and winter regimes ($2.2 \text{ mg C m}^{-2} \text{ d}^{-1}$), but declined in spring ($0.7 \text{ mg C m}^{-2} \text{ d}^{-1}$; Table 1). To accurately reflect seasonal physiology, the model was adjusted for polar night conditions by assuming that the metabolism was primarily based on lipid reserves rather than active ingestion with the respiratory quotient (RQ) reduced from 0.97 to 0.75³⁰.

From these values we derived two key ecological ratios: (1) daily turnover (d^{-1}), defined as fraction of the POC stock required to meet community carbon demand, and (2) the POC/zooplankton biomass ratio, providing a proxy for relative food supply (Table 1). To account for the integration depth mismatch between POC (0–20 m) and biomass (IWI-10 m), we used 50% of the POC stock, assuming relatively homogeneous mixing in the upper 20 m. Turnover rates reached their maximum during the winter regime (0.015 d^{-1}), followed by autumn regime (0.012 d^{-1}) and lowest in the spring regime (0.002 d^{-1}). Conversely, the POC/biomass ratio was the highest in spring (46.1), intermediate in the autumn regime (6.4) and lowest in the winter regime (2.7; Table 1). Together, these ratios highlight a strong contrast between food surplus in the spring regime and food-limited conditions during the polar night.

Discussion

While it is well known that the surface layer (0–100 m) of the Central Arctic Ocean (CAO) holds the bulk of zooplankton biomass during the polar day³¹, its distribution remains largely unknown in the under-ice habitat during polar night and twilight periods. Using a newly developed ROVnet, we obtained the first eight-month record of the under-ice habitat (IWI–10 m) under undisturbed sea ice. This approach minimized shipboard illumination bias³² and captured fine-scale patterns typically obscured by vertically integrated net hauls (0–50/100m). Our findings provide evidence that the under-ice habitat is inhabited by diverse zooplankton from autumn twilight through the polar day, providing taxonomic context to hydroacoustic measurements suggesting under-ice zooplankton aggregations during this period^{2,10}. Furthermore, the ROVnet during MOSAiC enabled the first standardized trans-seasonal record of rarely sampled sympagic fauna. These data fill a critical winter gap, highlighting small-scale vertical shifts (IWI vs. 10 m) in zooplankton that are often overlooked in polar regions³³. The under-ice zooplankton community showed quasi-seasonal changes along the Transpolar Drift driven by life-cycle dynamics, vertical migration and oceanographic processes³⁴.

Acknowledging that seasonal and spatial processes are inherently coupled, we consider the three statistically defined regimes as a continuum of seasonal progression and spatial connectivity – transitioning from autumn (2020) and winter (2019/20) in the Amundsen Basin to spring (2020) in the Nansen Basin (Fig. 1, Fig. 2).

Between successive polar days, the under-ice habitat served different ecological functions. The autumn regime was characterized by high phytoplankton biomass and a strong pycnocline at 20 - 30 m depth, which restricted vertical exchange of particles with deeper waters (Fig. 1)²³. This period exhibited the highest zooplankton abundances and biovolumes compared to the other two regimes (Fig. 3, suppl. Fig. 2). Copepods, the sympagic amphipod *Apherusa glacialis*, and other grazers likely exploited remnant primary production in both the water column and sea ice while light was available. Hence, the under-ice habitat during autumn played a critical role for building up carbon reserves essential for winter survival.

Despite the decline of phytoplankton and ice algae biomass to very low values (Fig. 1), the under-ice zooplankton biomass during winter remained comparable to autumn (Table 1). While *A. glacialis* likely descended into deeper layers, and was transported back to the origin of the Transpolar Drift off the Siberian shelf³⁵, other taxa typically found at intermediate depths, such as *Metridia longa*, Aetideidae and Ostracoda³⁶, emerged in the under-ice habitat. These joined year-round residents like the omnivorous *Oithona similis* and *Microcalanus* spp. and predators such as the *Paraeuchaeta* spp. and *Eukrohnia hamata* (Fig. 4, suppl. Fig. 5). Unlike dormant species (e.g., *Calanus* spp.), these winter-active taxa require a minimum food intake to sustain basic metabolism³⁷. Their broad feeding spectra likely enabled them to exploit the ‘sea-ice food bank’^{2,6} – a persistent supply of suspended particles, including sea-ice biota, and detritus released during periods of high sea-ice dynamics (e.g. ridge formation), retained above the shallow pycnocline. Furthermore, protection of visual predators during the polar night reduces the advantage of vertical migration. Consequently, the under-ice habitat functioned as both a refuge and a low but critical carbon supply ensuring the survival of active zooplankton during the polar night.

The spring regime was marked by rapid environmental change: the onset of the polar day triggered primary production³⁸ and the pycnocline disintegrated in May, mixing Atlantic Water and its biota to the surface (Fig 1)²³. During this transition, taxa associated with polar day, including the Oncaeidae, and the sympagic *A. glacialis*, increased in abundance at the IWI (Fig. 4). *A. glacialis* likely returned to the IWI to feed on ice algae^{7,13}. The most striking change, however, was the disappearing of large calanoid copepods (*Calanus* spp., *M. longa*) and ostracods, coupled with an increase of *O. similis* and copepod nauplii. The accumulation of nauplii was likely linked to the hatching of *Calanus hyperboreus* eggs^{14,15,34}. This concurrent reduction of large calanoids in spring is consistent with observations from the Yermak Plateau and the Barents Sea^{4,13}, and may reflect a general seasonal life-cycle pattern rather than a

response to local hydrography. The peak in nauplii and the arrival of *A. glacialis* at the IWI coincided with the onset of the ice algae bloom³⁸, suggesting that the reproductive timing of *C. glacialis* and the arrival of *A. glacialis* at the IWI align with the seasonal phenology of their primary food source^{7,39,40}. Thus, the spring under-ice habitat served predominantly as a feeding and nursery ground for the next generation.

Since the under-ice community maintained its biomass level throughout the autumn and winter regimes, metabolic demand remained nearly constant despite a declining supply of particulate organic carbon (POC) as the polar night progressed (Table 1). Arctic under-ice food webs are broadly consistent with ecological theory suggesting that a POC/zooplankton biomass ratio of approximately 10 is required to sustain metabolic needs over longer periods^{11,41}. In our study, this ratio declined from 6 during the autumn regime to only 3 in the winter regime, indicating an increasing food limitation during the progressing polar night (Table 1).

Besides feeding on the ‘sea-ice food bank’, the community’s carbon demand may have been balanced by reduced metabolic rates, paused food intake with reliance on storage lipids⁴², and high trophic transfer efficiency through predation and microbial recycling of carbon. In our NBSS analysis, the slopes for the autumn and winter regimes were significantly shallower than the -1 value typically indicative of marine ecosystems in equilibrium²⁴. This suggests a high trophic transfer efficiency within the under-ice habitat during these periods (Fig. 5). While our analysis was restricted to the size range captured by the ROVnet and ZooScan ($\log_{10}$ individual biovolume $\approx$ -2.5 to 2.4), this range spans several orders of magnitude and includes the dominant secondary producers in the CAO. Although absolute slope values are not directly comparable to whole-plankton studies, our approach robustly detects relative changes in size structure and energy transfer^{43,44}. Similarly shallow size spectra have recently been reported for the Central Arctic basins⁴³, suggesting that these flat slopes represent a consistent ecological signal in the High Arctic rather than a methodological bias. During the polar night, however, these shallow slopes were likely not caused solely by efficient transfer, but also by the presence of large copepods (*Calanus* spp.) utilizing lipid reserves rather than active feeding⁴². In the spring regime, the under-ice community switched from food limitation to a food surplus, with the POC/zooplankton biomass ratio reaching 46 (Table 1). Since POC levels remained stable, this change was largely caused by the considerable reduction in zooplankton biomass after large *C. glacialis* had emigrated from the under-ice habitat. The resulting dominance of smaller copepods and nauplii caused a steepening of the NBSS slope toward -1, indicating lower trophic transfer efficiency and a diminished dependency on storage lipids compared to the autumn and winter regimes^{44,45}.

Carbon limitation makes the polar night the most critical period for sustaining the future functionality of the CAO ecosystem. Our findings underscore that the under-ice habitat is vital during this period, providing a stable carbon supply via the ‘sea-ice food bank’ and enabling

the community to survive with high trophic transfer efficiency and reliance on storage lipids. However, current CMIP6 Earth System Model scenarios suggest that this balance is at risk⁴⁶. Later sea-ice formation may reduce autumn ice algae production, i.e. the ‘sea-ice food bank’, while rising temperatures increase metabolic costs⁴⁷, and consequently carbon demand. Furthermore, zooplankton populations may enter the polar night in a weakened state, arriving later in an under-ice habitat with diminished food stocks². Finally, northward expansion of boreal predators such as jellyfish and fish, may diminish the refuge value of the under-ice habitat⁴⁸.

Increasing primary production due to thinning sea ice may partially alleviate carbon limitation. Recent projections suggest that net primary production in the CAO could increase by 50 – 100% by the end of the 21st century, potentially supporting enhanced zooplankton production, although model divergence remains substantial⁴⁹. However, these changes will be heterogeneous: while increased light availability may foster more frequent under-ice blooms⁵⁰, shorter sea-ice coverage and habitat loss are projected to limit total ice-algal production⁹. Beyond magnitude, the phenology of primary production is shifting. CMIP-6 projections estimate that under-ice and ice-algal spring blooms may occur 1-7 days earlier per decade⁵¹. This shift can lead to trophic mismatches⁵², such as decoupling the emergence of *Calanus* spp. nauplii from their algal resource. The extremely high POC/zooplankton biomass ratio observed in our spring regime may be an early indication of mismatch dynamics at the community level.

Even in a more productive future Arctic, the polar night will continue to suppress primary production for several months, remaining a major seasonal constraint on zooplankton survival. The future state of the under-ice habitat will be an important factor in determining whether a more productive CAO translates into a resilient food web or into amplified mismatches and reduced winter survival - ultimately weakening secondary production and the efficiency of the biological carbon pump.

ONLINE METHODS

Sampling period and drift trajectory

During the MOSAiC (Multidisciplinary drifting Observatory for the Study of Arctic Climate) drift expedition, the research icebreaker *Polarstern* drifted attached to an ice floe from October 2019 to May 2020 (cruise legs 1 - 3) following the Transpolar Drift from the Amundsen Basin to the Nansen Basin. The Transpolar Drift transports surface water and sea ice from the Laptev Sea and the East Siberian Sea towards the Fram Strait and is thus a major gateway for sea-ice export. For August – September 2020 (cruise leg 5) the ship was moored to a new ice floe in the Amundsen Basin^{18,53}.

At the beginning of the drift the core of the MOSAiC ice floe was consistent of ice that had already survived one summer. The approximate ice age was estimated as 318 days in September 2019. Backtracking analysis suggested that most of the ice of the MOSAiC floe was formed in November 2018 on the shallow Eastern Siberian shelf⁵³. Thickness of the floe varied from 0.78 – 1.11 m in October 2019⁵³. The floe was carried by the Transpolar Drift, which was faster than anticipated and thus not only seasonal differences were observed but also regional aspects as the floe drifted from the Amundsen Basin across the Gakkel Ridge to the Atlantic influenced waters of the Nansen Basin in spring.

Environmental data

Daily average sea surface temperature, salinity values as well as daily average mixed layer depth (MLD) values have been calculated from the measurements of the various CTDs and buoys deployed during the MOSAiC drift^{54–57}. Chlorophyll *a* concentration ($\mu\text{g l}^{-1}$) was obtained from the upper ≤ 20 m of the water column and from the lower 10 cm of the sea-ice^{58,59}. For each sampling station the chlorophyll *a* values were integrated over the upper 20 m (± 2 m) of the water column using the trapezoidal rule: $(\text{Integrated chl}a = \sum_{i=1}^{n-1} ((\text{chl}a_i + \text{chl}a_{i+1})/2 \cdot \Delta z))$ where $\text{chl}a_i$ is the concentration at depth i , and Δz is the difference between adjacent depth (m). If only one single depth value was available, the concentration was assumed to be constant throughout the upper 20 m. When the deepest available chlorophyll *a* value was shallower than 20 m, this value was duplicated and added as a value at 20 m depth, thus ensuring consistent vertical integration. This integration yields chlorophyll *a* concentrations in units of mg m^{-2} . The same procedure was applied to the sea-ice chlorophyll *a*. Particulate organic carbon (POC) concentrations from discrete depth were obtained⁶⁰ and integrated over the upper 20 m of the water column in the same procedure as described for chlorophyll *a*.

Under-ice sampling

A remotely operated vehicle (ROV) equipped with environmental sensors was deployed from the ROV sites on the ice^{16,61}. Incident and transmitted PAR through sea ice (W m^{-2}) and sea-

ice draft were obtained during most ROV dives⁶². Mean values of each parameter were calculated for each ROV deployment. Attached to the ROV was also a custom-made plankton net (ROVnet) to sample the under-ice fauna^{17,63}. The ROVnet had an aperture of 0.24 m² and a mesh size of 150 µm. From November to May sampling yielded an almost weekly resolution for under-ice zooplankton sampling. After the relocation of the vessel to a new ice floe, additional samples were taken in August and September 2020. The majority of the under-ice samples were taken at a similar local daytime (7 – 10 am). However, in December and January during polar night the sampling time deviates from this pattern (suppl. Table 1). Generally, two depth layers were sampled: the ice-water interface (IWI) and the 10 m depth layer (10 m; suppl. Table 1). The net was towed horizontally along linear or triangular transects at the two depth horizons for approximately 15 minutes with an average speed of 0.26 m/s (calculated from the positioning recordings and duration of sampling; see below). All ROV net samples were preserved with a 4% formaldehyde seawater solution buffered with hexamethylenetetramine and stored at room temperature until processed in the lab.

Due to the cold environment directly under the sea ice flowmeters did not record the filtered water volume properly. Instead, the volume of filtered water was calculated from position recordings of the ROV dive and the net opening area. An acoustic Long Base Line (LBL) positioning system (LinkQuest Pinpoint) measured the horizontal position of the ROV in floe-fixed, relative coordinate system (x,y) with the starting point at the ROV site (x=0, y= 0). To take into account the vertical movement of the ROV during the dive the depth (Z) was recorded by a pressure sensor (Keller A-21, Keller AG). All recorded positions are available in PANGAEA⁶². With this information we calculated the 3D distances between recorded positions and added them together to obtain the total distance of each ROV net tow. For the stations 30-069 and 33-083 no position recordings existed. Hence, mean filtered volumes based on the duration of the ROV dive and the average speed of the ROV were used.

ZooScan analyses of net samples

Prior to scanning all net samples were rinsed to remove the formaldehyde and were size fractionated in three size fractions: 150 – 500 µm, 500 – 1000 µm and >1000 µm to prevent overlapping of small and large objects on the scanning frame. The size fractions were split with a Motoda plankton splitter if necessary to aliquots of max. 1/128 in order to obtain an optimal number of specimens (<2000 specimens) for the scanning procedure. The aliquots were each digitized with the ZooScan system²¹ (Hydroptic, version Biotom), with a scanning resolution of 2400 dpi. The resulting scans were processed with ZooProcess (version 7.29), a macro in ImageJ⁶⁴ (version 1.41) to first extract images with single specimens (threshold to retain images 150 µm²⁶), and second to attach metadata to each image. A detailed description of the scanning and processing procedure that was used is available in Cornils et al. (2022)²⁶. Images

with more than one specimen were separated manually and reprocessed in ZooProcess. All extracted images were uploaded to the web application EcoTaxa²² for semi-automated annotation. For an initial prediction of the taxonomic categories previously classified images from the Arctic Ocean were used²⁶. Predicted classifications were then manually validated or corrected. The copepod specimens were identified to the lowest taxonomic level (species). In some cases, the orientation of the specimens on the image and blurred specimens hampered the identification, and these specimens were grouped at higher taxonomic categories (Phylum, Class, Order, Family). Finally, 390 images contained two or more overlapping specimens that were identified and counted manually. For these, metadata were generated from the same taxon and stations to enable quantitative analysis. The three *Calanus* species were separated according to their prosome length²⁶. Additionally, the copepodite stages and adults of each *Calanus* species and *Metridia longa* were separated manually (copepodite stage 1 to 5 (CI-CV), adult female, adult male).

Adjustments of quantitative samples analysis

Due to time constraints during some MOSAiC cruise legs certain organisms were sorted onboard from the samples for experiments. Each specimen was identified and photographed. Their numbers were added to the ZooScan dataset. In order to be able to calculate size-based parameters it is assumed that these organisms have the average size of the corresponding taxon at the same station measured from the ZooScan images. From two surface hauls (21-125, 32-078) subsamples of 10% were removed onboard for genetic analysis (Table 1). The counts of the organisms have been adjusted for these two samples.

Abundance, Biovolume, Biomass (Dry mass) and Carbon estimation

Each image is associated with image parameters defining shape and size of the organisms²¹. Of these the primary (major) and secondary (minor) axis of the best fitting ellipse of the organisms can be used to calculate the biovolume (mm^3) of each organism: $BV = 4/3 \cdot \pi \cdot (\text{major}/2 \cdot (\text{minor}/2)^2)$. Individual biovolume can be transferred to wet mass (WM) under the assumption that preserved zooplankton organisms are neutrally buoyant (specific density of 1 g m^{-3})²⁷. Dry mass and carbon content for each individual was estimated from published conversion factors translating WM to DM and C^{25,26} (supp. Table 3). A previous investigation has shown that the conversion factor for Arctic copepods overestimated the dry mass of *C. hyperboreus*²⁶. We have adjusted the conversion factor accordingly (supp. Table 3). Abundances (number of individuals m^{-3}), Biovolume ($\text{mm}^3 \text{ m}^{-3}$), Biomass (mg DM m^{-3}) and Carbon biomass (mg C m^{-3}) for each taxon were calculated as the sum of all organisms from each taxon for each sample divided by the volume of filtered water. To gain the equivalent

quantitative measures per square meter the values per cubic meter were multiplied by the height of the net (0.4 m).

Respiration rates and carbon demand

For an estimate of respiration rates oxygen consumption for each individual was calculated (R_o ; $\mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}$) using taxon-specific equations dependent on body mass (as mg DM) and ambient temperature (T ; Kelvin), using taxon-specific components (RF_t ; suppl. Table 3). This model assumes that body mass and temperature effects on all taxa are the same as that of copepods²⁸: $\ln(R_o) = 18.775 + 0.766 * \ln(\text{DM}) - 5.256 * 1000/T - 0.113 * \ln(\text{depth}) + RF_t$. As temperature the average temperature obtained from the ROV CTD at the sampling time and depth horizon (0 m, 10 m) was used.

The respiration rates were converted to carbon units (R_c) ($\mu\text{g C ind}^{-1} \text{ d}^{-1}$) under the assumption that (i) 1 ml of oxygen corresponds to 0.44 mg C, and (ii) the respiration quotient (RQ) in ammonotelic organisms (Many aquatic organisms excrete ammonia directly.) is 0.97⁶⁵, while in winter, when metabolism is based on lipid reserves, it is reduced to 0.75³⁰: $R_c (\mu\text{g C ind}^{-1} \text{ d}^{-1}) = R_o * 24\text{h} * 0.44 * RQ$. Respiratory community carbon production ($\mu\text{g C m}^{-2} \text{ d}^{-1}$) was then calculated as the sum of all taxa per sample divided by their carbon biomass (mg C m^{-2}). Individual ingestion rate (I , $\mu\text{g C ind}^{-1} \text{ d}^{-1}$) was calculated using an average digestive efficiency of 0.7 and a gross growth efficiency of 0.3 in marine zooplankton^{29,66}: $I = R_c * 1/(0.7-0.3)$. The individual ingestion rate was then summed up for each taxon per sample to calculate the carbon demand of the under-ice fauna per day ($\mu\text{g C m}^{-2} \text{ d}^{-1}$).

Normalized biomass size spectra (NBSS)

The normalized biomass size spectra (NBSS) analysis was conducted with individual biovolume (mm^3) derived from the ZooScan analysis (see above). All images containing only body parts and their sizes were excluded from the analysis. Size classes are octave scaled; after the smallest size class each following size class is doubled. The total biovolume of each size was calculated as the sum of all individual biovolumes per size class, divided by the width of the size classes and normalized using $\log_2$ transformation (y axis). The midpoint of the corresponding size class was normalized (x axis)^{26,67}. The smallest size classes obtained with the ZooScan showed minima indicating the detection limit of the instrument⁴⁵. In our case, we excluded the two smallest size classes for the calculation of the least-squares linear regressions. For each sample, least-squares linear regressions of $\log_2$ -normalized biomass against $\log_2$ -midpoint size were fitted to estimate the slope and intercept of the NBSS. The slope reflects the relative dominance of small versus large organisms and is inversely related to the efficiency of carbon transfer to higher trophic levels, while the intercept approximates the total biomass of the community at a standardized size. To account for sampling uncertainty,

95 % confidence intervals (CI) of slopes and intercepts were estimated by non-parametric bootstrapping (1000 resamples per sample).

Data analysis

All data analyses were conducted in the scientific R programming language in the Rstudio environment^{68,69}. To investigate the similarity among stations a principal component analysis (PCA) was performed based on scaled environmental variables (Figure 1) using the *prcomp()* function from the *vegan* R-package⁷⁰. To account for missing data in the environmental variables, the functions from the R package *missMDA*⁷¹ were applied (1) to estimate the number of components for the PCA for the imputation (*estim_ncpPCA()*) and (2) to carry out a PCA-based imputation (*imputePCA()*) before conducting the PCA. Non-metric multidimensional scaling (nMDS) was performed using the *metaMDS()* function from the *vegan* package to visualize the similarity among stations using log-transformed abundances (*log1p* function). This analysis was based on Bray-Curtis similarity matrices, which are well-suited to assess community composition based on abundance data. Environmental vectors were fitted to the ordination using the *envfit()* function, which included the parameters from Figure 1. The fit (R_2) for each environmental variable to the ordination was assessed with a Monte Carlo analysis of 999 permutations. nMDS was performed using the *metaMDS()* function to explore community structure. To assess, whether the predefined regimes winter (WIN), spring (SPR), summer (SUM) and autumn (AUT) correspond to meaningful data structure in both PCA and nMDS analyses, we applied hierarchical clustering using Ward's method and Euclidean distances (*hclust()*) with k-means clustering (*kmeans()*) to the first three PCA and nMDS axes, respectively. The number of clusters was evaluated based on visual inspection of dendrograms and within-cluster sum of squares. A PERMANOVA (Bray-Curtis dissimilarity, 999 permutations) was chosen to assess the differences among regimes and depth strata and their interaction using the *adonis2()* function. We evaluate the homogeneity of the multivariate dispersion with *betadisper()* to ensure robust inference. Sampling in the Amundsen Basin (AB) covered multiple seasons, while in the Gakkel Ridge and Nansen Basin areas only single seasonal regimes were sampled. Although 'region' appeared significant in preliminary PERMANOVA tests (suppl. Table 4b), higher within-group dispersion in the AB (average distance to centroid = 0.28; suppl. Table 5) compared to the Gakkel Ridge (0.19) and Nansen Basin (0.13) samples suggests that regional differences mostly reflect differences in seasonal coverage rather than true geographic variation. Therefore, although a region effect cannot entirely be disproven, 'region' was excluded from the final model, which tested only season (regime), depth and their interaction.

To test for differences in the NBSS slopes across spatial and seasonal gradients, we performed non-parametric Kruskal-Wallis and pairwise Wilcoxon tests. We tested the effects

of Region, Regime (seasonal phase), and Depth (ICI vs. 10 m) on slope values. To explore environmental controls beyond these categorical factors, we related NBSS slopes to continuous predictors ($\log_{1+}$ ice-chlorophyll *a*, MLD, and integrated POC) using generalized additive models (GAMs) with Gaussian errors and thin-plate regression splines, using the *mgcv* R package⁷². Model selection was based on restricted maximum likelihood, and residual diagnostics were inspected to confirm adequate fit. To account for sampling uncertainty, 95 % confidence intervals for slopes were estimated by non-parametric bootstrapping (1000 resamples per sample) using the R package *boot*⁷³.

TABLE

Table 1: Integrated POC stocks, carbon biomass and -demand with turnover and food-consumer ratios of the under-ice zooplankton community. Presented are average values and ranges of POC integrated over 0 - 20 m, integrated zooplankton carbon biomass (mg C m⁻²) from the IWI to 10 m depth, and carbon demand. For the calculation of the turnover, the POC was divided by 2 to account for the larger integrated depth interval.

Regime	Unit	Autumn		Winter		Spring	
		mean	range	mean	range	mean	range
POC, 0 - 20 m	mg C m ⁻²	529	326 - 1097	323	174 - 1140	366	114 - 1072
Biomass, 0 - 10 m	mg C m ⁻²	50.6	20.2 - 104.4	62.1	14.7 - 137.6	6.0	2.6 - 10.6
Carbon demand	mg C m ⁻² d ⁻¹	2.3	1.8 - 8.1	2.2	0.7 - 4.6	0.7	0.1 - 1.1
Turnover (demand/50% POC)	d ⁻¹	0.012	0.010 - 0.046	0.015	0.003 - 0.071	0.002	0.001 - 0.005
Relative food supply (50% POC/Biomass)		6.4	2.0 - 8.1	2.7	0.6 - 14.6	46.1	13.3 - 84.8

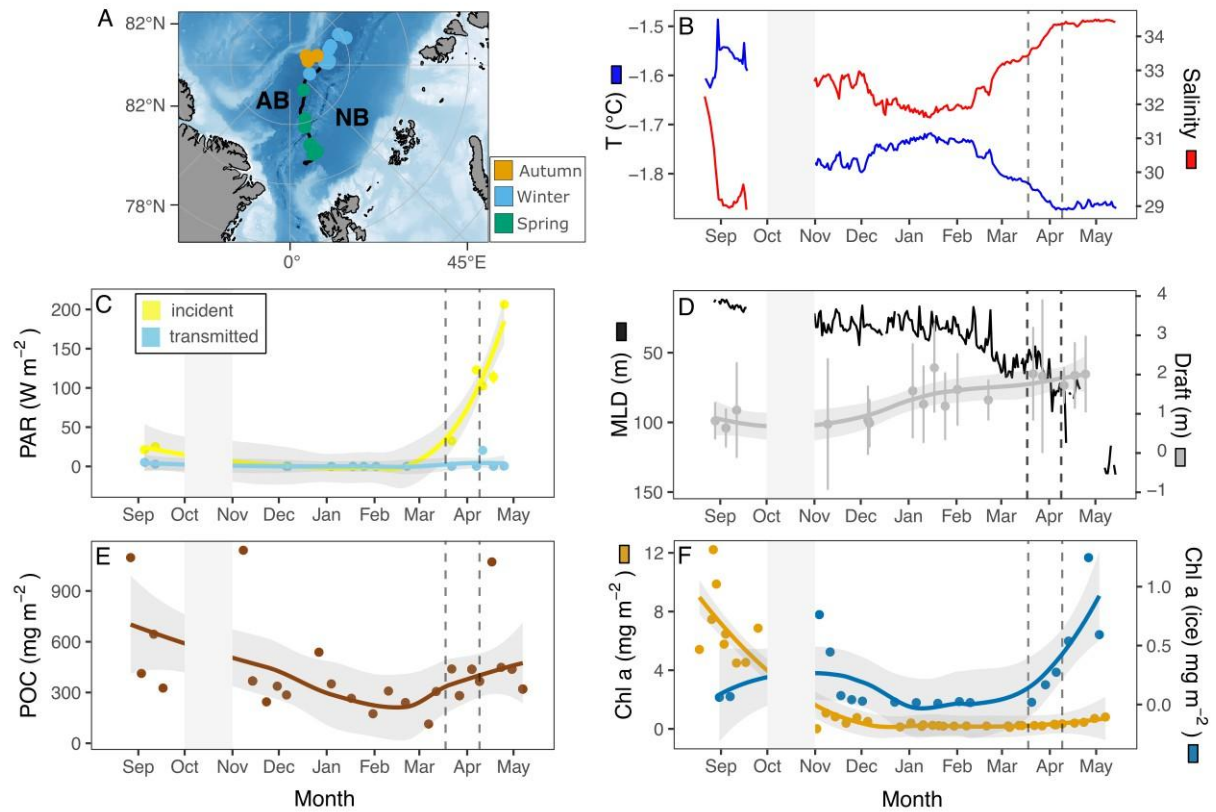


Fig. 1: Station map and environmental conditions at MOSAiC ice floes 2 (August - September 2020) and 1 (November 2019 - May 2020, separated by grey area). (A) Map - stations colored according to regimes identified by cluster analysis (Figure 2); (B) daily averages of surface water temperature (°C) and salinity⁵⁷; (C) incident and transmitted photosynthetic active radiation (PAR, W m⁻²) from ROV surveys⁶²; (D) mixed layer depth (MLD, m) and sea-ice draft obtained during ROV surveys^{57,62}; (E) particulate organic carbon (POC) concentration (mg m⁻²) integrated over 0 – ~20 m⁶⁰; (F) chlorophyll a concentration (mg m⁻²) integrated over 0 – ~20 m⁵⁸ and in the bottom 10 cm of the sea ice⁵⁹; dashed vertical lines mark transitions from the Amundsen Basin across the Gakkel Ridge to the Nansen Basin.

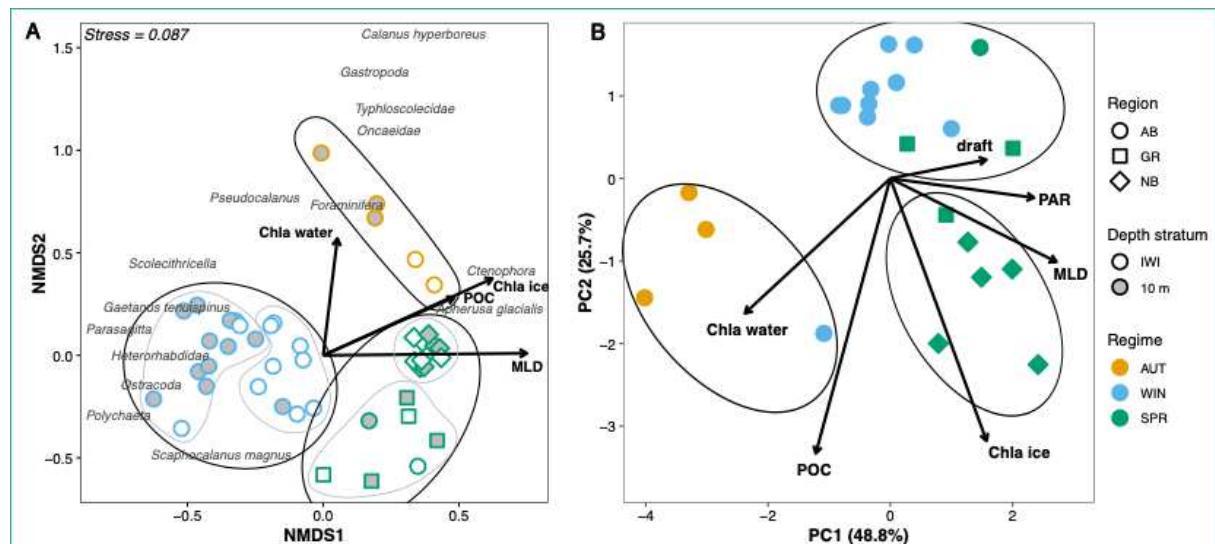


Fig. 2: Non-metric multidimensional scaling (nMDS) of zooplankton community composition and principal component analysis (PCA) of environmental variables during the MOSAiC drift (2019–2020). (A) nMDS based on log-transformed abundances (ind. m^{-3}) at ROV stations. (B) PCA of scaled environmental variables. Round frames mark clusters (black) and subclusters (grey) derived from hierarchical clustering. Symbol colours indicate the seasonal regimes autumn (AUT), winter (WIN) and spring (SPR); shapes denote the three regions Amundsen Basin (AB), Gakkel Ridge (GR), and Nansen Basin (NB). In the nMDS, filled symbols represent samples from 10 m depth and open symbols samples from the ice–water interface (IWI). Environmental variables were overlaid onto the ordination space (only significant variables for nMDS, $p < 0.01$): mixed layer depth (m, MLD), chlorophyll *a* concentration (mg m^{-2}) in the lower 10 cm of sea ice (Chl *a* (ice)), chlorophyll *a* concentration (mg m^{-2}) integrated over the upper 20 m of the water column (Chl *a*), particulate organic carbon concentration (mmol m^{-2}) integrated over the upper 20 m (POC), transmitted photosynthetically active radiation (PAR) and sea-ice draft (m, draft). Taxon names in (B) refer to the 15 taxa contributing most to spatial variation in community composition.

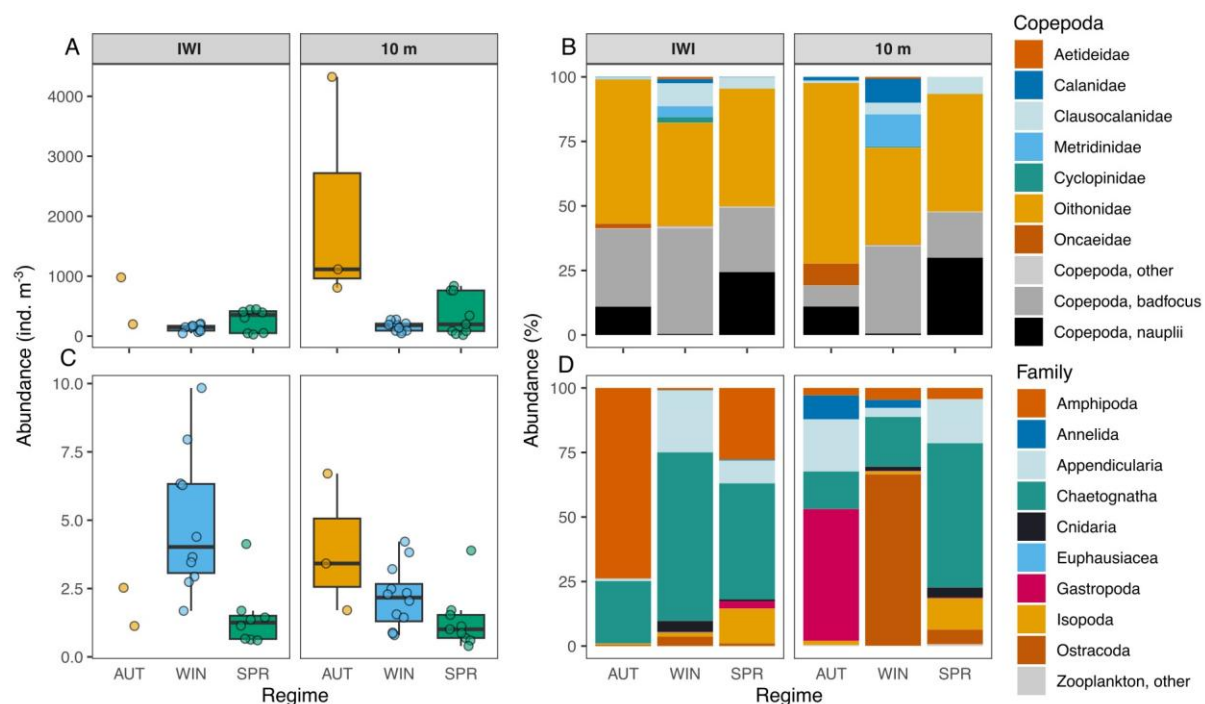


Fig. 3: Abundances (ind m⁻³) of the under-ice fauna at the Ice-Water-Interface (IWI) and at 10 m depth (10 m) during the MOSAiC drift for (A) Copepoda and (C) other zooplankton coloured by regime (autumn, winter, spring), and the relative composition of (B) copepod families (%) and (D) non-copepod taxa (%) of the under-ice fauna during the four regimes.

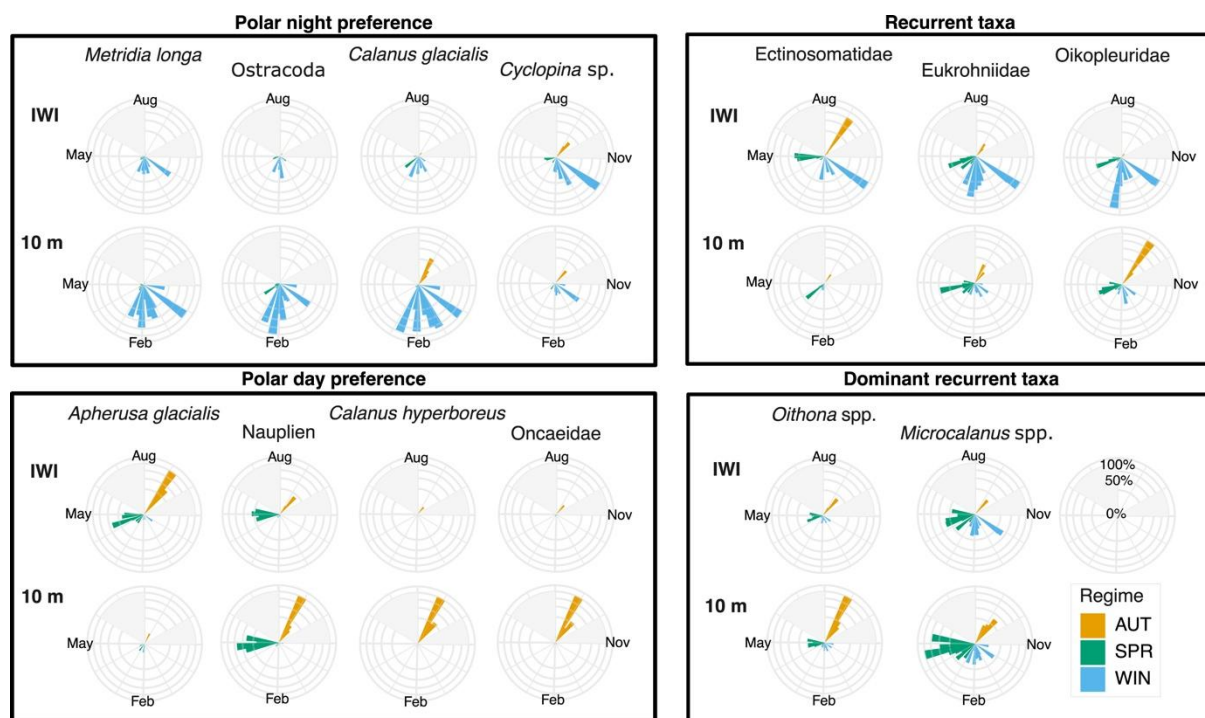


Fig. 4: Normalized abundances (% of max. abundance per taxon) of selected taxa at the Ice-Water-Interface (IWI) and at 10 m depth (10 m) during the MOSAiC drift for taxa (A) preferring polar night, (B) preferring polar day, (C) shifting preference across regimes and (D) dominant taxa. Grey areas represent periods with no samples.

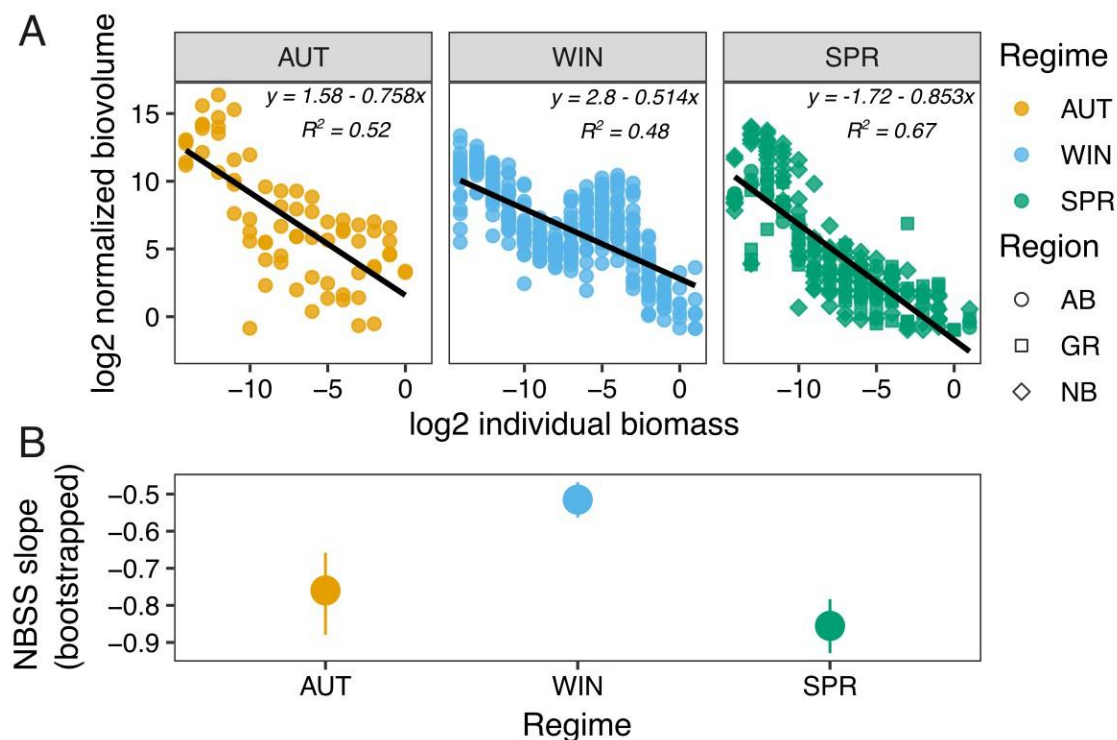


Fig. 5: Normalised biomass size spectra (NBSS) of mesozooplankton from ROV net samples. (A) NBSS per season (summer/autumn (AUT), winter (WIN), spring (SPR)), showing linear regression fits; (B) Seasonally averaged NBSS slopes with $\pm$ 95% confidence intervals derived from bootstrapping resampling (n=10,000 iterations). Symbols indicate the three regions Amundsen Basin (AB), Gakkel Ridge (GR) and Nansen Basin (NB).

Acknowledgements

The results of the present manuscript are part of the international Multidisciplinary drifting Observatory for the Study of the Arctic Climate (MOSAiC) with the tag MOSAiC20192020 and the Project ID: AWI_PS122_00. We thank the crew, the participants and the logistics support during the RV Polarstern expeditions and everyone else involved as listed in Nixdorf et al. (2021): <https://zenodo.org/record/5541624#.YXru8dIBzX0>. HF, BN, PA, CK, GC, NH, CJMH, NK, MV and BN were funded by the Helmholtz Association's Programme Oriented Research period 4 (POF-4), Topic 2 and Topic 6. AC was funded through the German Ministry for Education and Research (BMBF; Grant 03F0917A MOSAiC 3). SS and FLS were funded by the Dutch Research Council grant 866.18.003, with contributions of the European Commission (EC), European Climate, Infrastructure and Environment Executive Agency (CINEA), Framework Contract EASME/EMFF/2018/003, Specific Contract EASME/EMFF/2018/1.3.2.2/03/SI2.805469 (Project EFICA), and of the Netherlands Ministry of Agriculture, Fisheries, Food Security and Nature (LVVN) grant WOT04-009-047.04. PA was funded through the internal project AWI_ROV of the AWI, through the German Ministry of Education and Research (BMBF) project MOSAiC 3 - IceScan (03F0916A), through additional funds from the project DiatomARCTIC (03F0810A), part of the Changing Arctic Ocean Programme, jointly funded by the UKRI Natural Environment Research Council (NERC) and the BMBF, and through the institutional funding of the German Aerospace Center (DLR e. V.) RGC, CG, and KMS were funded through the NSF Office of Polar Programs award OPP-1824414, and CJA through OPP-1824447. KS was funded through the UK Natural Environment Research Council's (NERC) contribution to MOSAiC, the SYM-PEL project (NE/S002502/1).

Contributions

HF, BN, CJA, RGC and FLS conceived the research and designed the study
PA, CJA, RGC, GC, CG, NH, CJMH, CK, SS, FLS and KMS performed the field work during MOSAiC
NK and MV contributed materials/analysis tools, organized samples
AC, KJW and NK analysed the samples
AC, BN and HF analysed the data
AC HF and BN drafted the manuscript
All authors participated in writing the paper, discussed, interpreted results and drew conclusions.
Corresponding author: Astrid Cornils (astrid.cornils@awi.de)

Ethics declaration

Competing interest

The authors declare no competing interests.

Data availability

All ROV related data from the MOSAiC expedition are available in PANGAEA⁶². These specific datasets have been used:

Anhaus P, Katlein C, Matero I, Nicolaus M, Arndt S, Krampe D, Lange BA, Regnery J, Rohde J, Schiller M (2022) Absorbance and spectral absorption coefficient (SAC) parameters from remotely operated vehicle (ROV) surveys during the MOSAiC expedition 2019/20.

PANGAEA. doi: 10.1594/pangaea.952801

Anhaus P, Katlein C, Matero I, Nicolaus M, Arndt S, Krampe D, Lange BA, Regnery J, Rohde J, Schiller M (2022) Single-beam sea-ice draft from remotely operated vehicle (ROV) surveys during the MOSAiC expedition 2019/20. PANGAEA. doi: 10.1594/pangaea.952801

Anhaus P, Katlein C, Matero I, Nicolaus M, Arndt S, Krampe D, Lange BA, Regnery J, Rohde J, Schiller M (2023) Positioning and telemetry from remotely operated vehicle (ROV) surveys during the MOSAiC expedition 2019/20. PANGAEA. doi: 10.1594/pangaea.952676

All zooplankton data are available at PANGAEA:

Cornils A, Flores H, Wermeyer KJ, Anhaus P, Katlein C, Ashjian CJ, Campbell RG, Castellani G, Gelfman C, Hildebrandt N, Knüppel N, Sakinan S, Schmidt K, Svenson A, Schaafsma FL, Shoemaker KM, Vortkamp M, Niehoff B (in revision) Zooplankton abundance, biovolume, biomass and respiration from ROV net samples during the MOSAiC expedition (PS122) in the Central Arctic Ocean. PANGAEA, doi:10.1594/PANGAEA.968897

ZooScan images will made publicly available on EcoTaxa: <https://ecotaxa.obs-vlfr.fr/prj/9968>

Code availability

The R code is available upon request. Essential code will be published on Zenodo.

References

1. Krumpen, T. *et al.* Smoother sea ice with fewer pressure ridges in a more dynamic Arctic. *Nat. Clim. Chang.* **15**, 66–72 (2025).
2. Flores, H. *et al.* Sea-ice decline could keep zooplankton deeper for longer. *Nat. Clim. Chang.* **13**, 1122–1130 (2023).
3. David, C., Lange, B., Rabe, B. & Flores, H. Community structure of under-ice fauna in the Eurasian Central Arctic Ocean in relation to environmental properties of sea-ice habitats. *Mar. Ecol. Prog. Ser.* **522**, 15–32 (2015).
4. Hop, H. *et al.* Winter-spring development of the zooplankton community below sea ice in the Arctic Ocean. *Front. Mar. Sci.* **8**, 609480 (2021).
5. Flores, H. *et al.* Sea-ice properties and nutrient concentration as drivers of the taxonomic and trophic structure of high-Arctic protist and metazoan communities. *Polar Biol.* **42**, 1377–1395 (2019).
6. Hobbs, L., Banas, N. S., Cottier, F. R., Berge, J. & Daase, M. Eat or sleep: availability of winter prey explains mid-winter and spring activity in an Arctic *Calanus* population. *Front. Mar. Sci.* **7**, 541564 (2020).
7. Kohlbach, D. *et al.* The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: Food web relationships revealed by lipid and stable isotope analyses. *Limnol. Oceanogr.* **61**, 2027–2044 (2016).
8. Tedesco, L., Vichi, M. & Scoccimarro, E. Sea-ice algal phenology in a warmer Arctic. *Sci. Adv.* **5**, eaav4830 (2019).
9. Lannuzel, D. *et al.* The future of Arctic sea-ice biogeochemistry and ice-associated ecosystems. *Nat. Clim. Chang.* **10**, 983–992 (2020).
10. Hobbs, L., Cottier, F., Last, K. & Berge, J. Pan-Arctic diel vertical migration during the polar night. *Mar. Ecol. Prog. Ser.* **605**, 61–72 (2018).
11. Ehrlich, J. *et al.* Sea-ice associated carbon flux in Arctic spring. *Elem. Sci. Anth.* **9**, (2021).
12. Darnis, G. *et al.* Zooplankton fecal pellet flux drives the biological carbon pump during the winter–spring transition in a high-Arctic system. *Limnol. Oceanogr.* **69**, 1481–1493 (2024).
13. Werner, I. Living conditions, abundance and biomass of under-ice fauna in the Storfjord area (western Barents Sea, Arctic) in late winter (March 2003). *Polar Biol.* **28**, 311–318 (2005).
14. Werner, I. & Arbizu, P. M. The sub-ice fauna of the Laptev Sea and the adjacent Arctic Ocean in summer 1995. *Polar Biol.* **21**, 71–79 (1999).
15. Horner, R. & Murphy, D. Species composition and abundance of zooplankton in the nearshore Beaufort Sea in winter-spring. *ARCTIC* **38**, (1985).

16. Anhaus, P. *et al.* Under-ice environment observations from a remotely operated vehicle during the MOSAiC expedition. *Sci. Data* **12**, 944 (2025).
17. Wollenburg, J. E. *et al.* New observations of the distribution, morphology and dissolution dynamics of cryogenic gypsum in the Arctic Ocean. *Cryosphere* **14**, 1795–1808 (2020).
18. Fong, A. A. *et al.* Overview of the MOSAiC expedition: Ecosystem. *Elem. Sci. Anth.* **12**, 00135 (2024).
19. United Nations. Convention on Biological Diversity. <https://www.cbd.int/convention/text> (1992).
20. Arctic Council. Agreement to prevent unregulated High Seas Fisheries in the Central Arctic Ocean. <https://arctic-council.org/document/agreement-to-prevent-unregulated-high-seas-fisheries-in-the-central-arctic-ocean/> (2018).
21. Gorsky, G. *et al.* Digital zooplankton image analysis using the ZooScan integrated system. *J. Plankton Res.* **32**, 285–303 (2010).
22. Picheral, M., Colin, S. & Irisson, J.-O. EcoTaxa, a tool for the taxonomic classification of images. <http://ecotaxa.obs-vlfr.fr> (2017).
23. Schulz, K. *et al.* The Eurasian Arctic Ocean along the MOSAiC drift in 2019–2020: An interdisciplinary perspective on physical properties and processes. *Elem. Sci. Anth.* **12**, (2024).
24. Sprules, W. G. & Munawar, M. Plankton size spectra in relation to ecosystem productivity, size, and perturbation. *Can. J. Fish. Aquat. Sci.* **43**, 1789–1794 (1986).
25. Kiørboe, T. Zooplankton body composition. *Limnol. Oceanogr.* **58**, 1843–1850 (2013).
26. Cornils, A. *et al.* Testing the usefulness of optical data for zooplankton long-term monitoring: Taxonomic composition, abundance, biomass, and size spectra from ZooScan image analysis. *Limnol. Oceanogr.* **20**, 428–450 (2022).
27. Postel, L., Fock, H. & Hagen, W. Biomass and abundance. In *ICES Zooplankton Methodology Manual* (eds Harris, R. *et al.*) 83–192. (Academic Press, 2000).
28. Ikeda, T. Respiration and ammonia excretion by marine metazooplankton taxa: synthesis toward a global-bathymetric model. *Mar. Biol.* **161**, 2753–2766 (2014).
29. Bode, M., Koppelman, R., Teuber, L., Hagen, W. & Auel, H. Carbon budgets of mesozooplankton copepod communities in the Eastern Atlantic Ocean - regional and vertical patterns between 24°N and 21°S. *Global Biogeochem. Cyc.* **32**, 840–857 (2018).
30. Darnis, G. & Fortier, L. Zooplankton respiration and the export of carbon at depth in the Amundsen Gulf (Arctic Ocean). *J. Geophys. Res.* **117**, C04013 (2012).
31. Kosobokova, K. & Hirche, H.-J. Biomass of zooplankton in the eastern Arctic Ocean – A base line study. *Prog. Oceanogr.* **82**, 265–280 (2009).
32. Berge, J. *et al.* Artificial light during the polar night disrupts Arctic fish and zooplankton behaviour down to 200 m depth. *Commun. Biol.* **3**, 102 (2020).

33. Flores, H. *et al.* Seasonal changes in the vertical distribution and community structure of Antarctic macrozooplankton and micronekton. *Deep Sea Res. Part I* **84**, 127–141 (2014).
34. Schmidt, K. *et al.* Seasonal vertical migration of large polar copepods reinterpreted as a dispersal mechanism throughout the water column. *Commun. Earth Environ.* **6**, 431 (2025).
35. Berge, J. *et al.* Retention of ice-associated amphipods: possible consequences for an ice-free Arctic Ocean. *Biol. Lett.* **8**, 1012–1015 (2012).
36. Kosobokova, K. N., Hopcroft, R. R. & Hirche, H.-J. Patterns of zooplankton diversity through the depths of the Arctic's central basins. *Mar. Biodiv.* **41**, 29–50 (2011).
37. Lischka, S. & Hagen, W. Seasonal lipid dynamics of the copepods *Pseudocalanus minutus* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). *Mar. Biol.* **150**, 443–454 (2007).
38. Hoppe, C. J. M. *et al.* Photosynthetic light requirement near the theoretical minimum detected in Arctic microalgae. *Nat. Commun.* **15**, 7385 (2024).
39. Niehoff, B., Madsen, S., Hansen, B. & Nielsen, T. Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. *Mar. Biol.* **140**, 567–576 (2002).
40. Søreide, J. E., Leu, E., Berge, J., Graeve, M. & Falk-Petersen, S. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob. Chang. Biol.* **16**, 3154–3163 (2010).
41. Lindeman, R. L. The Trophic-dynamic aspect of ecology. *Ecology* **23**, 399–417 (1942).
42. Mayor, D. J. *et al.* Biomass turnover rates in metabolically active and inactive marine calanoid copepods. *Front. Mar. Sci.* **9**, 907290 (2022).
43. Dugenne, M. *et al.* First release of the Pelagic Size Structure database: global datasets of marine size spectra obtained from plankton imaging devices. *Earth Syst. Sci. Data* **16**, 2971–2999 (2024).
44. Sato, K., Matsuno, K., Arima, D., Abe, Y. & Yamaguchi, A. Spatial and temporal changes in zooplankton abundance, biovolume, and size spectra in the neighboring waters of Japan: analyses using an optical plankton counter. *Zool. Stud.* **54**, 18 (2015).
45. García-Comas, C. *et al.* Mesozooplankton size structure in response to environmental conditions in the East China Sea: How much does size spectra theory fit empirical data of a dynamic coastal area? *Prog. Oceanogr.* **121**, 141–157 (2014).
46. Lebrun, M., Vancoppenolle, M., Madec, G. & Massonnet, F. Arctic sea-ice-free season projected to extend into autumn. *Cryosphere* **13**, 79–96 (2018).
47. Grote, U., Pasternak, A., Arashkevich, E., Halvorsen, E. & Nikishina, A. Thermal response of ingestion and egestion rates in the Arctic copepod *Calanus glacialis* and possible metabolic consequences in a warming ocean. *Polar Biol.* **38**, 1025–1033 (2015).
48. Snoeijs-Leijonmalm, P. *et al.* Unexpected fish and squid in the central Arctic deep scattering layer. *Sci. Adv.* **8**, eabj7536 (2022).

49. Champiot-Bayard, L. L., Kwiatkowski, L. L. & Vancoppenolle, M. M. Heterogeneous future Arctic Ocean primary productivity changes projected in CMIP6. *EGUsphere* (2025) doi:10.5194/egusphere-2025-4296].
50. Assmy, P. *et al.* Leads in Arctic pack ice enable early phytoplankton blooms below snow-covered sea ice. *Sci. Rep.* **7**, 40850 (2017).
51. Heorton, H. DBS., Stroeve, J. C. & Veyssi re, G. Future under sea ice light availability and algal bloom timing from CMIP6 model simulations. *Front. Mar. Sci.* **12**, 1642506 (2025).
52. Renaud, P. E. *et al.* Extreme mismatch between phytoplankton and grazers during Arctic spring blooms and consequences for the pelagic food-web. *Prog. Oceanogr.* **229**, 103365 (2024).
53. Krumpen, T. *et al.* The MOSAiC ice floe: sediment-laden survivor from the Siberian shelf. *Cryosphere* **14**, 2173–2187 (2020).
54. Hoppmann, M., Kuznetsov, I., Fang, Y.-C. & Rabe, B. Processed data of CTD buoys 2019O1 to 2019O8 as part of the MOSAiC Distributed Network. *PANGAEA* (2022) doi:10.1594/pangaea.940320.
55. Tippenhauer, S. *et al.* Physical oceanography based on ship CTD during POLARSTERN cruise PS122. *PANGAEA* (2023) doi:10.1594/pangaea.959963.
56. Tippenhauer, S. *et al.* Physical oceanography based on Ocean City CTD during POLARSTERN cruise PS122. *PANGAEA* (2023) doi:10.1594/pangaea.959964.
57. Schulz, K., Koenig, Z. & Muilwijk, M. The Eurasian Arctic Ocean along the MOSAiC drift (2019-2020): Core hydrographic parameters. *Arctic Data Center* (2023) doi:10.18739/a21j9790b.
58. Hoppe, C. J. M. *et al.* Water column Chlorophyll a concentrations during the MOSAiC expedition (PS122) in the Central Arctic Ocean 2019-2020. *PANGAEA* (2023) doi:10.1594/pangaea.963277.
59. Hoppe, C. J. M. *et al.* Chlorophyll a concentrations in first year sea ice during the MOSAiC expedition (PS122) in the Central Arctic Ocean 2019-2020. *PANGAEA* (2026) doi:10.1594/pangaea.990053.
60. Hoppe, C. J. M. *et al.* Concentrations and stable isotopic composition of particulate organic carbon and nitrogen from water column samples collected in the central Arctic Ocean in 2019/2020 during the MOSAiC campaign. *PANGAEA* (2025) doi:10.1594/pangaea.980518.
61. Nicolaus, M. *et al.* Overview of the MOSAiC expedition: Snow and sea ice. *Elem. Sci. Anth.* **10**, 000046 (2022).
62. Anhaus, P. *et al.* Under-ice environment surveys using a remotely operated vehicle (ROV) during the MOSAiC expedition 2019/20 [dataset bibliography]. *PANGAEA* (2023) doi:10.1594/pangaea.951077.

- 792 63. Katlein, C. *et al.* A New Remotely Operated Sensor Platform for Interdisciplinary
793 Observations under Sea Ice. *Front. Mar. Sci.* **4**, (2017).
- 794 64. Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. NIH Image to ImageJ: 25 years of
795 image analysis. *Nat. methods* **9**, 671–675 (2012).
- 796 65. Gnaiger, E. Polarographic Oxygen Sensors, Aquatic and Physiological Applications.
797 *Polarographic Oxygen Sensors* 337–345 (1983) doi:10.1007/978-3-642-81863-9_30.
- 798 66. Ikeda, T. & Motoda, S. Zooplankton production in the Bering Sea calculated from 1956-
799 1970 Oshoro Maru data. *Mar. Sci. Commun.* **4**, (1978).
- 800 67. Plum, C. *et al.* Mesozooplankton trait distribution in relation to environmental conditions
801 and the presence of krill and salps along the northern Antarctic Peninsula. *J Plankton Res*
802 **43**, 927–944 (2021).
- 803 68. R CoreTeam. R: A Language and Environment for Statistical Computing. R Foundation
804 for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> (2025).
- 805 69. Posit team. RStudio: Integrated Development Environment for R. Posit Software, PBC,
806 Boston, MA. <http://www.posit.co> (2025).
- 807 70. Oksanen, J. *et al.* vegan: Community Ecology Package. *CRAN: Contrib. Packag.* (2025)
808 doi:10.32614/cran.package.vegan.
- 809 71. Josse, J. & Husson, F. missMDA : A package for handling missing values in multivariate
810 data analysis. *J. Stat. Softw.* **70**, (2016).
- 811 72. Wood, S. N. Fast stable restricted maximum likelihood and marginal likelihood estimation
812 of semiparametric generalized linear models. *J. R. Stat. Soc.: Ser. B (Stat. Methodol.)* **73**, 3–
813 36 (2011).
- 814 73. Canty, A. & Ripley, B. boot: Bootstrap Functions. *CRAN: Contrib. Packag.* (1999)
815 doi:10.32614/cran.package.boot.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementCornilsFloresetalROVnet20260205.docx](#)