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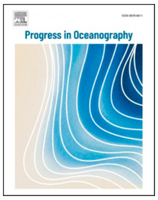

Synthesis of spatiotemporal variability in western Arctic zooplankton communities from summer to fall during 2008–2021

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ABSTRACT

The Arctic marine ecosystem is undergoing a major, rapid transformation driven by climate change, resulting in complex and unpredictable shifts in zooplankton communities, which are key pelagic food web components. We synthesized extensive multi-year zooplankton datasets (2008–2021) collected by a Korean icebreaker research vessel (IBRV Araon; August 2016–2021) and a Japanese research vessel (RV Mirai; September 2008, 2010, 2012–2017, and 2021) in the western Arctic Ocean to examine the effects of environmental factors on zooplankton distribution. We determined the effect of key environmental variables, including integrated mean temperature, mean salinity, and fluorescence, on zooplankton community structure. We identified six distinct zooplankton communities shaped by regional characteristics and interannual oceanographic variability. The pronounced seasonal transition of zooplankton communities from summer to autumn, particularly in the Chukchi Sea and the Chukchi Borderland in 2017 and 2021, was the major finding. During summer, Pacific water inflow into the Chukchi Sea significantly increased Pacific species (e.g., Metridia pacifica) and meroplankton (e.g., barnacle larvae), with barnacle larvae extending into the Chukchi Borderland in 2017 and 2021. Although small species (e.g., *Pseudocalanus* spp.) remained dominant during the summer, but no clear increasing trend was observed in total abundance within the Chukchi Sea. By September, these Pacific Ocean–influenced communities had decreased rapidly, suggesting their high environmental dependency and incomplete establishment in the region. This study integrates multi-year, seasonally diverse datasets collected across a broad spatial range, providing a comprehensive understanding of how Arctic zooplankton respond to climate-induced environmental changes.

1. Introduction

Rapid changes in Arctic marine ecosystems driven by climate change not only affect human populations but also have substantial effects on the survival of many species. In recent years, numerous studies have examined how changes in the Arctic marine environment affect harvestable marine resources (Christiansen et al., 2014; Haug et al., 2017) and the zooplankton communities that constitute their primary food source and play a key role in transferring energy from primary producers to higher trophic levels, thereby shaping the pelagic food web (Carstensen et al., 2019; Matsuno et al., 2016b; Stige et al., 2019; Xu et al., 2018). The Chukchi Sea—where Pacific Summer Water enters the Arctic—poses substantial challenges for predicting ecosystem responses because of the strong seasonal and interannual variability in water mass properties (Brugler et al., 2014; Corlett and Pickart, 2017; Matsuno et al., 2011; Matsuno et al., 2012; Pickart et al., 2023). Synthesizing the patterns of zooplankton community shifts in this dynamic environment is crucial for understanding overall ecosystem changes and predicting adaptive strategies among species.

The Arctic ecosystem is sensitive to environmental changes, with

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zooplankton communities playing a crucial role in the trophic structure. The region experiences considerable interannual and seasonal variability due to changing oceanographic and climatic conditions. In the Chukchi Sea, species originating from the Pacific Ocean are introduced during the summer through the inflow of Pacific water, further complicating the prediction of ecosystem dynamics (Ershova et al., 2015; Kim et al., 2020). Previous studies on zooplankton responses to changes in sea ice concentration have primarily focused on near-coastal waters (Dezutter et al., 2019; Feng et al., 2018; Søreide et al., 2010). However, these studies failed to capture the full complexity of zooplankton growth and distribution in regions experiencing substantial external inflows, such as the Chukchi Sea. In addition, recent studies have demonstrated that zooplankton communities are influenced by hydrographic conditions associated with inflows from the Pacific Ocean; however, these studies have primarily focused on ice-free regions (Abe et al., 2020; Hibino et al., 2025; Spear et al., 2019).

The influence of Pacific water inflow on the Arctic zooplankton community structure extends beyond immediate seasonal effects, potentially driving long-term shifts in species composition. Warm Pacific waters have been shown to facilitate the northward expansion of boreal copepods, which may compete with native Arctic species and alter the regional food web dynamics (Mueter et al., 2017). Variations in sea ice coverage and timing are associated with fluctuations in phytoplankton productivity, which in turn affect zooplankton biomass and species distribution (Huntington et al., 2020). Because the timing and extent of the Pacific water inflow are becoming more variable with climate change, understanding how these hydrographic changes translate into shifts in the zooplankton community structure is important for predicting broader ecosystem responses (Gong and Pickart, 2015; Woodgate et al., 2006).

Data collection in the Arctic region is often constrained by limited accessibility because of sea ice, short field seasons, and high operational costs (Lynch et al., 2022). These challenges, coupled with variations in research methodologies and survey designs, have made it difficult to effectively integrate datasets and achieve a comprehensive understanding of Arctic zooplankton communities (Ershova et al., 2015; Kim et al., 2022; Skjoldal et al., 2013; Weydmann-Zwolicka et al., 2021). The present study addresses these limitations by systematically integrating extensive, multi-year datasets (2008–2021) collected by the Korean IBRV Araon and the Japanese RV Mirai in overlapping regions of the western Arctic Ocean. In contrast to previous studies, the combined analysis of long-term surveys conducted in August (Araon) and September (Mirai) across the Chukchi Sea and Chukchi Borderland uniquely captures the pronounced seasonal transition of zooplankton communities from summer to autumn. Furthermore, by incorporating the most recent 2021 survey data, this study provides insights into regional and seasonal variability, confirming an increase in Pacific species (*Metridia pacifica*) in the Chukchi Sea and an increase in meroplankton (barnacle larvae) in the Chukchi Borderland during the summer, while also showing no clear increasing trend in total zooplankton abundance in the Chukchi Sea. Observing mesozooplankton assemblage response to summer and fall hydrographic changes provides valuable but understudied insights into a critical ecological transition in the Arctic marine ecosystem (Ershova et al., 2021; Kimura et al., 2020).

Based on the observed seasonal and interannual fluctuations, we hypothesized that Arctic warming may not only promote an increase in Pacific species but also favor smaller, opportunistic zooplankton species over larger, energy-rich taxa, with cascading consequences for higher trophic levels. By combining datasets from multiple research vessels, this study offers a comprehensive perspective on Arctic zooplankton dynamics, reinforcing the need for sustained field-based monitoring. A key challenge in integrating long-term datasets, including those analyzed in the present study, is distinguishing seasonal variability from climate-driven changes while identifying persistent long-term trends within this variability.

2. Materials and methods

2.1. Study area

This study focuses on the western Arctic Ocean, encompassing the highly dynamic regions of the Bering Strait, Chukchi Sea, Chukchi Borderland, and East Siberian Sea. This area serves as a critical gateway for Pacific Ocean waters entering the Arctic, resulting in pronounced seasonal and interannual variability in oceanographic and climatic conditions (Corlett and Pickart, 2017; Gong and Pickart, 2015; Woodgate et al., 2006). The general oceanography of this region is primarily shaped by the inflow of Pacific Summer Water, which includes distinct Pacific-origin Alaskan Coastal Water and Bering Shelf Water (also known as Bering Summer Water) (Corlett and Pickart, 2017; Gong and Pickart, 2015). These water masses enter the Chukchi Sea through the Bering Strait, establishing a clear latitudinal temperature gradient, with the warmest waters near the strait gradually cooling northward (Kim et al., 2020; Pickart et al., 2019). Northward circulation continues through key conduits such as Barrow Canyon and the Chukchi Slope Current, eventually reaching the Chukchi Borderland (Boury et al., 2020).

Water masses in the western Arctic are characterized by distinct temperature and salinity profiles. Higher salinity is typically observed in areas directly influenced by Pacific inflow, especially near the Bering Strait, whereas lower salinity occurs in coastal regions due to freshwater input or in parts of the Chukchi Sea and eastern Chukchi Borderland where warm inflow accelerates sea ice melt (Corlett and Pickart, 2017; Pickart et al., 2019). The summer inflow of Pacific water not only brings warmer temperatures and variable salinity (Corlett and Pickart, 2017; Pickart et al., 2019) but also profoundly affects nutrient availability (Danielson et al., 2017; Whitney et al., 2005), upwelling processes (Lin et al., 2019), and water column stratification (Zhuang et al., 2016). These dynamic hydrographic conditions are recognized as primary drivers of zooplankton community structure and distribution in the region (Abe et al., 2020; Ershova et al., 2015; Kim et al., 2020; Kim et al., 2022). The bathymetry of the study area ranges from the relatively shallow Chukchi Sea shelf to deeper zones such as the Chukchi Borderland and Northwind Abyssal Plain, influencing the pathways of water masses and the habitats of diverse zooplankton taxa (Pickart et al., 2023).

2.2. Hydrographic measurements

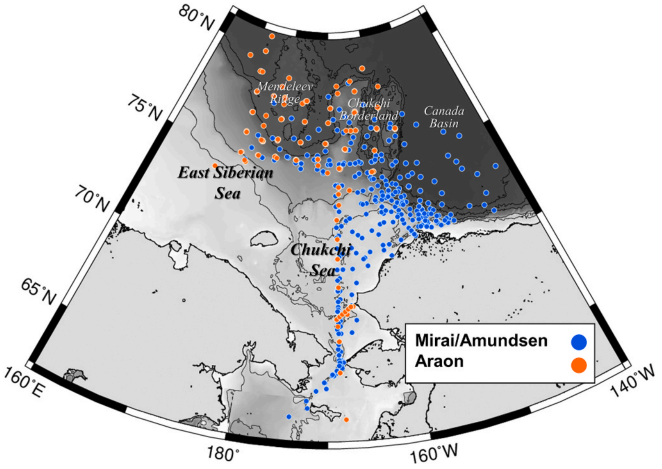

Fig. 1. Location of sampling stations in the Pacific Arctic Ocean during 2008–2021. Blue and orange circles indicate the sampling conducted by RV Mirai or IBRV Araon, respectively.

To characterize hydrographic conditions at the sampling stations

(Fig. 1), vertical profiles of water temperature, salinity, and chlorophyll *a* (Chl *a*) were obtained using a Conductivity, Temperature, and Depth (CTD) profiler. A Sea-Bird Electronics SBE911 plus CTD was used aboard *RV Mirai*, while an SBE32 carousel water sampler equipped with an SBE 9 plus CTD profiler was deployed aboard *IBRV Araon*. Water mass properties were analyzed using temperature and salinity profiles to assess oceanographic variability across survey years. The spatial distribution of integrated mean temperature (IMT), integrated mean salinity (IMS), and integrated fluorescence (Iflu) during the study period is illustrated in Fig. 2. Historical hydrographic and zooplankton abundance data from 2008 to 2017 were sourced from Abe et al., 2020 for comparative analysis.

2.3. Filed sample collection

Zooplankton sampling was conducted in the Pacific Arctic Ocean aboard the RV Mirai and IBRV Araon, spanning latitudes 64–81°N and longitudes 169°E–133°W. The surveys were carried out over multiple years, covering different seasonal and regional conditions. The total number of sampling stations was 606 (Fig. 1). Sampling aboard RV Mirai took place during August–October 2008, September–October 2010, September–October 2012, August–October 2013, September 2015, August–September 2016, August–September 2017, and August–October 2021 (Fig. 1). Field sampling was also carried out by Canadian icebreaker Amundsen in September 2014. The IBRV Araon surveys were conducted primarily during August (2015–2020) and July–August (2021), covering oceanographic transects from the Bering Strait through the Chukchi Sea and extending into the East Siberian Sea (Fig. 1). The cruise information is summarized in Supplementary **Table S1**. Zooplankton samples collected aboard RV Mirai utilized a NORPAC net (45c m mouth diameter, 335 μm mesh) deployed in vertical tows. For stations with depths greater than 150 m, the net was towed from 150 m to the surface, while in shallower waters, the sampling depth extended from 7 m above the seafloor to the surface. In contrast, mesozooplankton sampling aboard IBRV Araon employed a bongo net (60 cm mouth diameter, 330 μm mesh) towed vertically from the 200 m depth (where depths greater than 200 m) or about 8 m above the seafloor to the surface. Both net systems were equipped with a one-way flow meter (Araon: hydro-bios, German; Mirai: Rigosha Co., Ltd., Japan) to calculate the volume of seawater filtered and estimate zooplankton abundance (ind. M^{-3}). Immediately after collection, all samples were preserved in 5 % buffered formalin for subsequent laboratory analysis.

2.4. Filed sample analysis

Zooplankton samples were subsampled using a Motoda plankton splitter (Motoda, 1959), with each sample divided into 1/4 to 1/8 fractions for analysis. Subsamples were examined under dissecting microscopes (Mirai: SMZ-10, Nikon; Araon: SMZ1500, Nikon), with magnification adjusted as needed for accurate taxonomic identification and enumeration. Copepod specimens were identified to the genus or species level according to the taxonomic framework established by Brodskii (1950), as shown in Table 1. Due to morphological similarities between *Calanus glacialis* and *Calanus marshallae* (Frost, 1974), these taxa were grouped as *C. glacialis/marshallae*. To maintain consistency in long-term monitoring across sampling years and platforms, other morphologically similar or developmentally indistinct taxa were also grouped where necessary. For example, early copepodite stages of *Pseudocalanus* spp. were not distinguished to the species level and were reported as a single taxonomic group.

For quantitative compilation between the Mirai and Araon cruises, zooplankton abundance (ind. m^{-2}) was estimated using the following equation:

$$\text{Abundance}= N \times L / F \times s$$

where N represents the number of individuals per taxon, L is the tow distance, F is the filtered water volume (m^3) calculated from flowmeter

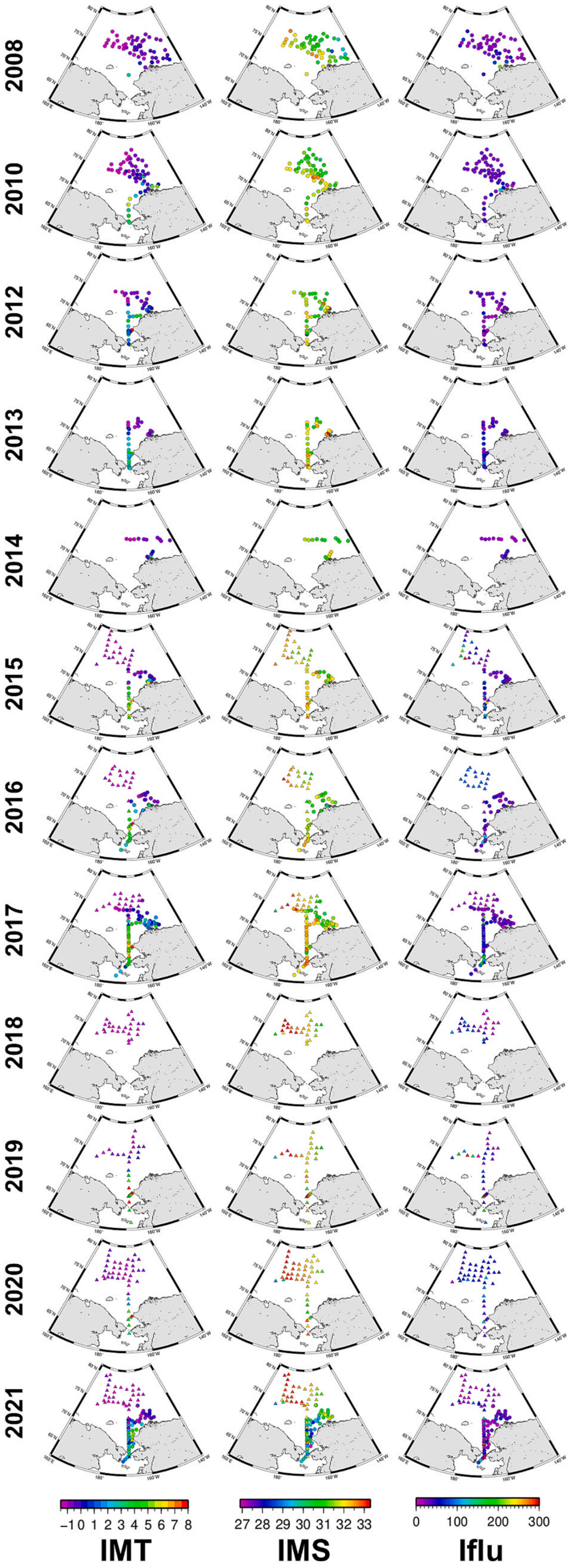

Fig. 2. Horizontal distribution of in-situ hydrographical data in the Pacific Arctic Ocean during 2008–2021. Circles and triangles indicate the data collected by RV Mirai/CCGS Amundsen and IBRV Araon, respectively. IMT: integrated mean temperature, IMS: integrated mean salinity, Iflu: Integrated fluorescence.

Table 1
Mean abundance of mesozooplankton in the groups identified by cluster analysis using the 2008–2021 data set (cf. Fig. 3) from the Pacific Arctic Ocean.

Species/Taxon	A (240)	B (9)	C (17)	D (221)	E (68)	F (32)
Copepoda						
Acartia spp.	90	–	–	**1,435**	173	522
Aetideopsis spp.	1	–	–	11	–	–
Calanus glacialis/marshallae	8,187*	1,786*	**15,501***	9,261*	2,870*	9,903*
Calanus hyperboreus	**263**	**357***	42	83	8	–
Centropages spp.	3	–	–	**2,330**	34	311
Chiridius spp.	3	–	–	20	–	9
Cyclopoida	**2,452***	68	840	**2,729**	190	357
Epilabidocera longipedata	–	–	–	6	1	–
Eucalanus bungii	3	–	14	462	102	**3,079**
Eurytemora spp.	0.1	–	–	108	5	12
Gaetanus tenuispinus	3	–	–	4	–	–
Gaidius brevispinus	0.1	–	–	6	–	–
Heterorhabdus spp.	32	–	17	5	2	–
Lucicutia anomala	0.1	–	–	–	–	–
Metridia longa	**1,358***	440	**1,040**	890	12	2
Metridia pacifica	11	–	–	1,897	43	**1,092**
Microcalanus spp.	**767**	103	95	353	34	119
Neocalanus cristatus	2	–	–	8	3	**340**
Neocalanus flemingeri	11	–	–	43	34	14
Neocalanus plumchrus	12	–	–	23	40	17
Oncaea spp.	7	–	–	7	1	2
Paraeuchaeta glacialis	135	**294***	7	45	–	–
Pseudocalanus spp.	2,084*	55	4,630*	**24,610***	3,284*	**15,687***
Racovitzanus antarcticus	0.1	–	–	0.2	–	–
Scaphocalanus spp.	7	–	14	1	0.4	–
Scolecithricella minor	28	–	63	19	–	11
Spinocalanus spp.	4	–	–	4	8	–
Temorites brevis	7	–	–	8	0.2	–
Tortanus discaudatus	0.1	–	–	2	1	–
Undinella oblonga	1	–	–	0.4	–	–
Amphipoda	57	58	62	33	18	88
Appendicularia	627	350	1,735*	**3,222***	1,668	809
Barnacle larvae	84	–	**7,843**	**5,468***	515	1,503
Bivalvia	84	–	**660**	614	8	–
Chaetognatha	458*	144	412	**1,231***	619*	663*
Echinodea larva	12	–	192	**3,950**	33	9
Eubrachyura zoea	5	–	36	7	12	51
Euphausiacea	6	–	–	244	40	**1,225**
Evadne spp.	1	–	–	139	–	–
Hydrozoa	312	105	245	**1,598**	111	176
Isopoda	4	21	–	9	1	8
Ostracoda	**170**	82	42	39	2	–
Podon spp.	0.2	–	–	271	–	–
Polychaeta	51	–	589	**1,688**	55	166
Pteropoda						
Clione limacina	3	1	–	25	6	0.4
Limacina helicina	157	39	–	359	543	167
Total abundance	17,497	3,902	34,082	63,268	10,477	36,342

*Represents the top 50 % of species for each group based on the SIMPER analysis. Bold indicates an IndVal > 25 % for that group.

data, and *s* denotes the sample split ratio.

2.5. Data analysis

To investigate the community structure characteristics of zooplankton communities in the Pacific sector of the Arctic Ocean, we performed a cluster analysis and present the mean abundances of key taxa within the identified zooplankton groups. After the fourth-roots transformation of the zooplankton abundances, similarities between zooplankton samples were calculated using the Bray-Curtis index, which measures compositional differences between stations (Fig. 3). The resulting similarity matrix was subsequently analyzed through hierarchical agglomerative clustering using a complete linkage method and the unweighted pair-group method with arithmetic mean (UPGMA). The statistical significance of the resulting clusters was assessed using similarity profile analysis (SIMPROF) at a 5 % significance level. Additionally, a similarity percentage (SIMPER) analysis was applied to identify the species most responsible for the similarity between zooplankton groups (Table 2).

The relationship between zooplankton community structure and environmental parameters was evaluated using distance-based linear modeling (DistLM) and redundancy analysis (RDA). To compare the zooplankton and environmental data, the mean values of hydrographic variables, including water temperature, salinity, and chlorophyll-*a* fluorescence were calculated for the water column from the surface down to either 10 m above the seafloor or 150/200 m depth, depending on station depth. Environmental predictors included water temperature, salinity, chlorophyll-*a* fluorescence, and sampling date. Prior to analysis, all environmental variables were normalized by subtracting the mean and dividing by the standard deviation to ensure comparability. DistLM was performed using a stepwise selection procedure with the Akaike Information Criterion corrected for small sample sizes (AICc) as the selection metric, and 999 permutations were used to assess the model's significance (Table 3). All clustering, DistLM, and RDA analyses were conducted using PRIMER v7 (PRIMER-E Ltd., Albany, New Zealand). To test for significant differences in environmental parameters (e.g., water temperature, salinity, and chlorophyll-*a* fluorescence) among the groups defined through the cluster analysis, a heteroscedastic-

Fig. 3. Heat map of zooplankton abundance in the Pacific Arctic Ocean during 2008–2021 with Q and R mode cluster dendrograms based on Bray–Curtis similarity.

Table 2
Ranking of taxa based on their relative contribution (%) to the multivariate similarities between pairs of zooplankton groups (A–E, cf. Fig. 3), as defined by the cluster analysis in the Pacific Arctic Ocean during 2008–2021.

	A	B	C	D	E
B	Cyclopoida (11.46) *Pseudocalanus* spp. (10.75) *Microcalanus* spp. (8.37)				
C	Barnacle (9.33) *C. glacialis/marshallae* (6.86) *Microcalanus* spp. (6.13)	*Pseudocalanus* spp. (11.07) Barnacle (10.03) Appendicuralian (7.19)			
D	*Pseudocalanus* spp. (8.16) Barnacle (7.08) *Acartia* spp. (5.52)	*Pseudocalanus* spp. (12.73) Barnacle (7.36) *Acartia* spp. (5.98)	*Pseudocalanus* spp. (7.42) *Acartia* spp. (7.23) Barnacle (6.97)		
E	*M. longa* (9.18) *Microcalanus* spp. (6.63) Cyclopoida (6.30)	*Pseudocalanus* spp. (12.65) *C. hyperboreus* (8.34) *P. glacialis* (7.72)	Barnacle (9.43) *M. longa* (8.92) *C. glacialis/marshallae* (8.50)	*Pseudocalanus* spp. (6.90) Barnacle (6.85 %) Polychaeta (6.31 %)	
F	*Pseudocalanus* spp. (7.65) *M. longa* (7.30) *M. pacifica* (6.44)	*Pseudocalanus* spp. (14.23) *M. pacifica* (7.08) Euphausiidae (6.63)	Barnacle (7.44) *M. pacifica* (7.35) *M. longa* (7.12)	Barnacle (6.14 %) *M. pacifica* (5.94) Echinodeamata (5.66)	*M. pacifica* (8.84) *Pseudocalanus* spp. (7.48) Euphausiidae (7.44)

consistent covariance estimation (HC3) was applied using the Max-*t* test, as outlined by (Herberich et al., 2010, Table 4). The statistical computations were carried out using R software (version 4.4.2; R Core Team, 2024) with the “multcomp” and “sandwich” packages.

3. Results

3.1. Hydrography

The hydrographic conditions in the Pacific Arctic Ocean exhibited significant spatial, seasonal, and interannual variability, as evidenced by in situ measurements (Fig. 2). The integrated mean temperature (IMT) exhibited a distinct latitudinal gradient, with the highest temperatures

Table 3
Summary of the results of the DistLM sequential tests. The results are for the model with the lowest AICc values for each response variable, based on field data by RV Mirai/CCGS Amundsen and IBRV Araon in the Pacific Arctic Ocean during 2008–2021. IMT: Integrated mean temperature; IMS: Integrated mean salinity; Iflu: Integrated fluorescence.

Variables	AICc	SS	Pseudo-*F*	P-value	Prop.	Cumul.	Res.df
IMT	4205.8	127,450	123.78	0.001	0.17007	0.17007	604
Sampling date	4172.5	35,224	36.202	0.001	0.047004	0.21708	603
IMS	4154.4	19,237	20.408	0.001	0.025671	0.24275	602
Iflu	4141.2	14,031	15.236	0.001	0.018723	0.26147	601

Table 4
Comparison of environmental factors between the zooplankton groups identified by cluster analysis (cf. Fig. 3) in the Pacific Arctic Ocean during 2008–2021. Different superscript numbers indicate significant ($p < 0.05$) differences between the groups. The superscript letters are included only for significant variables determined by the Max-*t* test, and the order is from high to low alphabetically. Values represent the mean. Numbers in parentheses are the number of sampling dates for each group. IMT: Integrated mean temperature; IMS: Integrated mean salinity; Iflu: Integrated fluorescence.

Parameters	Groups					
	A (240)	**B (9)**	**C (17)**	**D (221)**	**E (68)**	**F (32)**
IMT	-0.79^{c}	-1.03^{d}	-1.10^{d}	1.44^{b}	2.57^{a}	3.06^{a}
IMS	31.74^{a}	31.53^{a}	31.76^{a}	31.68^{a}	30.57^{b}	31.88^{a}
Iflu	39.53^{a}	20.48^{b}	52.67^{a}	49.04^{a}	$36.33^{a,b}$	73.84^{a}

recorded near the Bering Strait (maximum 7.8°C) and progressively decreasing further north (Fig. 2). Seasonal variations were evident, as the IBRV Araon and RV Mirai surveys conducted in 2017 and 2021 enabled a direct comparison of the temperature changes. August (IBRV Araon surveys) generally yielded higher IMT values than September (RV Mirai surveys), reflecting the cooling effect of seasonal progression. Interannual trends in IMT varied significantly, with specific years, such as 2017, 2019, and 2021, exhibiting pronounced temperature anomalies associated with Pacific Summer Water inflow.

The salinity patterns, represented by the integrated mean salinity (IMS), showed regional differences reflecting hydrographic variability (Fig. 2). Higher salinity was observed in the Pacific-influenced regions, particularly near the Bering Strait, whereas lower salinity was observed in coastal areas with freshwater input and in the Chukchi Sea and eastern Chukchi Borderland, where warm water inflow accelerates sea ice melt (Fig. 2). Seasonal differences in IMS were particularly evident in 2021. In August, the salinity was relatively high (31.88 psu) at stations in the Northwind Abyssal Plain (74.52° N, 161.95°–162.18° W); however, by September, freshwater input and increased mixing resulted in a decrease to 30.54 psu (Fig. 2).

Integrated fluorescence (Iflu) data revealed spatial heterogeneity in biological activity (Fig. 2). In regions affected by the Pacific water inflow, particularly in August, Iflu values were higher, whereas in the ice-dominated northern areas, they were relatively lower (Fig. 2). A comparison in 2021 revealed that fluorescence values were higher in August (316.0) than in September (24.19) at stations in the hotspot of Point Hope (67.5°–67.67° N, 168.74°–168.96° W), indicating a decrease in biological productivity as the Arctic transitioned into autumn.

3.2. Interannual variations in zooplankton communities

Zooplankton communities in the Pacific Arctic Ocean showed distinct spatial and interannual variability, as determined by cluster analysis (Figs. 3, 4). Based on the species composition and abundance, the community was classified into six distinct groups (A–F, Figs. 3, 5; Table 1). The temporal distribution of these communities from 2008 to 2021 indicated interannual shifts in the community structure and regional variability, reflecting changes in the hydrographic conditions and the effect of Pacific water (Figs. 4, 6).

Community A was primarily observed in the northern Chukchi Sea and Arctic shelf regions, where it was associated with colder, low-salinity water, and likely represents a stable Arctic zooplankton assemblage (Fig. 4). Community B was occurred mainly in the central Chukchi Sea and showed the lowest total abundance among the six communities (Figs. 4, 5). Community C was present around the Chukchi Borderland during periods of strong Pacific-origin water inflow (Fig. 4). It included Arctic and Pacific species and was characterized by an abundance of barnacle larvae (Fig. 5; Table 1). In contrast, communities D, E, and F were distributed in the Bering Sea and Chukchi Sea and were associated with summer Pacific water inflow, unlike communities A, B, and C. *Pseudocalanus* spp. was the dominant taxon in these communities (Fig. 4). Community D was the most abundant in areas experiencing strong Pacific inflow, such as Barrow Canyon, with a high total abundance and continued dominance of barnacle larvae (Figs. 4, 5). Community E was also distributed in a similar area as Community D; however, its total abundance was lower (Figs. 4, 5). Finally, Community F was predominantly found near the Bering Strait, heavily influenced by Pacific-origin waters, and characterized by an abundance of Pacific copepods, *Metridia pacifica* (Fig. 4; Table 2).

Interannual variations in zooplankton community distribution were closely associated with changes in temperature and salinity associated with Pacific water inflow and sea ice retreat. Community A was dominant in the Chukchi Borderland (Fig. 4**a, b, f–l**), whereas Community D was prevalent under typical Arctic conditions in the Chukchi Sea (Fig. 4**a–d, f–h, j**). However, during periods of strong Pacific water inflow and increased temperatures, particularly in years 2017 and 2021, Community A in the Chukchi Borderland was replaced by Community C (Figs. 4h, l). In contrast, in the Chukchi Sea, Community D shifted to either community E or F (Figs. 4c, f, g, k, l). Community E emerged in reduced salinity environments compared with Community D, whereas Community F appeared under higher temperature conditions (Fig. 4; Table 4).

The 2021 dataset provided further insight into community shifts associated with hydrological changes. During that year, the survey covered the broadest spatial extent, offering a more comprehensive view of how regional zooplankton communities respond to interannual hydrographic variability (Fig. 4l). The hydrographic variability in 2021, including changes in temperature and salinity, demonstrated its effects on zooplankton assemblages and their spatial distribution. In the Chukchi Sea, the presence of communities E and F was most pronounced, indicating a strong influence of Pacific water extending into the region (Fig. 4l). In the Chukchi Borderland, Community C, which was characterized by a high abundance of barnacle larvae, displaced Community A (Fig. 4l).

3.3. Seasonal variations in zooplankton communities from summer to autumn

A comparison of the RV Mirai (September) and IBRV Araon (August) surveys revealed seasonal differences in the zooplankton community structure. In August, Pacific-origin communities, particularly Community C and F, were dominant and reflected strong summer inflows of warm Pacific water (Figs. 4h, l). By September, the Arctic-origin communities, such as Community A and D, became more prevalent, indicating a shift toward colder water conditions as the influence of Pacific

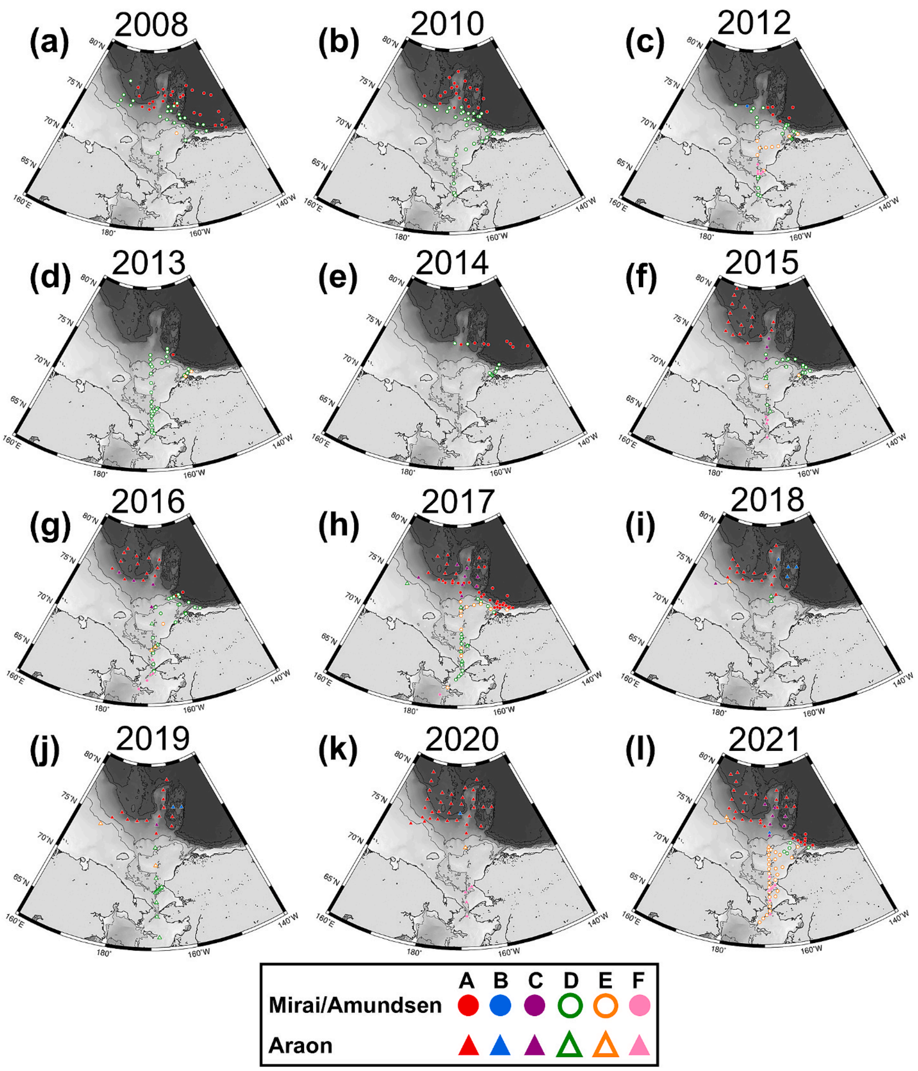

Fig. 4. Interannual changes of zooplankton community distribution in the Pacific Arctic Ocean during 2008–2021. Symbols indicate sampling cruises.

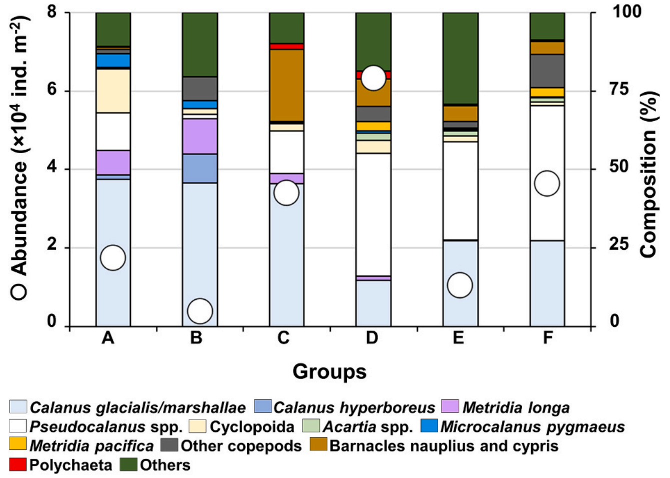

Fig. 5. Comparison of zooplankton community structure among groups identified by cluster analysis in the Pacific Arctic Ocean during 2008–2021.

inflow weakened (Fig. 4). This seasonal transition was especially pronounced in the Chukchi Sea, where Community F was dominant in August, whereas Communities D and E were more prevalent in September (Figs. 4, 7).

The effect of hydrographic variability was notable in 2017 and 2021, when IBRV Araon and RV Mirai conducted surveys in the Chukchi Sea and the Chukchi Borderland during August and September. This revealed a distinct transition in the zooplankton communities from summer to autumn (Figs. 4h, l). In the Chukchi Sea in 2017, both the IBRV Araon and RV Mirai surveys were dominated by Community D, with Community E appearing to some extent during summer, while Community F was not observed (Figs. 4h, 7). In the Chukchi Borderland, Community C shifted to Community A in September as the influence of Pacific water weakened (Fig. 4h). In 2021, the Chukchi Sea showed a clear change, with the community F shifting entirely to Community E by September. (Figs. 4l, 7). Community F was associated with higher temperatures than Community E and comprised a greater proportion of Pacific species (Tables 2, 4). The shift in zooplankton community composition in 2021 reflects a significant seasonal transition, with a pronounced change in community structure observed in the Chukchi Sea from August to September (Figs. 4l, 5, 7). The inflow of Pacific water in August resulted in hydrological changes in temperature and salinity, promoting an increase in small copepod–dominated communities (e.g., *Pseudocalanus* spp.), meroplankton (e.g., Barnacle larvae), and Pacific species (e.g., *M. pacifica*) (Fig. 5). However, as the season transitioned into early autumn, the abundance of these communities decreased as the effect of the Pacific water decreased and was replaced by Community E, which showed a lower total abundance (Figs. 4l, 7).

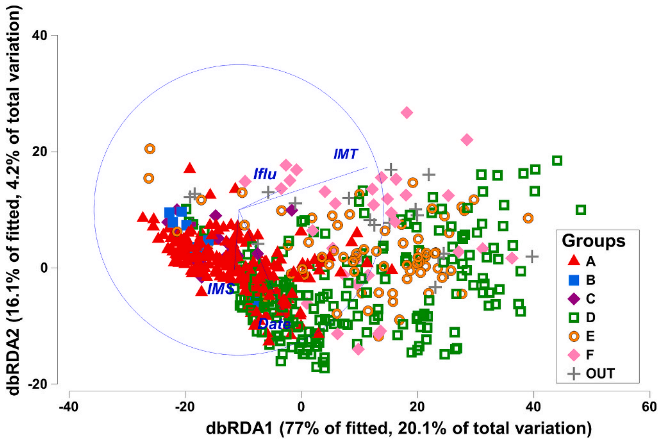

Fig. 6. Distance-based redundancy analysis (dbRDA) plot for the six zooplankton groups with environmental parameters based on field data from RV Mirai/CCGS Amundsen and IBRV Araon in the Pacific Arctic Ocean during 2008–2021. The parameters were selected using distance-based linear modeling procedures, which consisted of step-wise, AICc (Akaike information criterion corrected for small samples), and 999 permutations. The direction of the lines indicates the relationship between the groups and parameters. Date: sampling date; IMT: Integrated mean temperature; IMS: Integrated mean salinity; Iflu: Integrated fluorescence.

3.4. Influence of key environmental factors on zooplankton community distribution

Environmental factors strongly influenced the distribution and interannual variations in zooplankton communities in the Pacific Arctic Ocean, as evidenced by the correlation analysis (Fig. 6). Among the various hydrographic variables examined, temperature was the most significant driver of the zooplankton community structure. Although the fundamental spatial distribution of zooplankton was primarily determined by geographical characteristics, seasonal environmental changes, particularly during the summer months, played a crucial role in modifying the community composition.

The results indicate that temperature variations influence the spatial distribution and abundance of different zooplankton communities. Pacific-influenced communities, such as Communities E and F, were primarily found in warm waters, particularly the Bering Strait and Chukchi Sea, where the inflow of Pacific Summer Water was most pronounced (Fig. 4; Table 4). In contrast, Community D was primarily found in relatively cooler waters in the Chukchi Sea and the southern East Siberian Sea (Fig. 4; Table 4). These temperature-driven shifts were particularly evident in the Chukchi Sea, where the influence of Pacific water varied annually, altering the boundaries between different zooplankton assemblages.

In addition to temperature, seasonal environmental factors played a role in reshaping the zooplankton distribution. Communities C and F exhibited relatively high Iflu values, which can be interpreted as a response to sea ice retreat during summer. This resulted in enhanced stratification and fluctuations in primary productivity, ultimately influencing zooplankton abundance and distribution (Table 4). Correlation analysis revealed that although communities initially followed their typical geographical distribution patterns, they became more dynamic in response to seasonal temperature increases and oceanographic changes (Fig. 4). The expansion of Pacific-influenced communities in warm years and the contraction of Arctic communities indicate that ongoing climate-driven temperature increases may cause long-term shifts in zooplankton community composition.

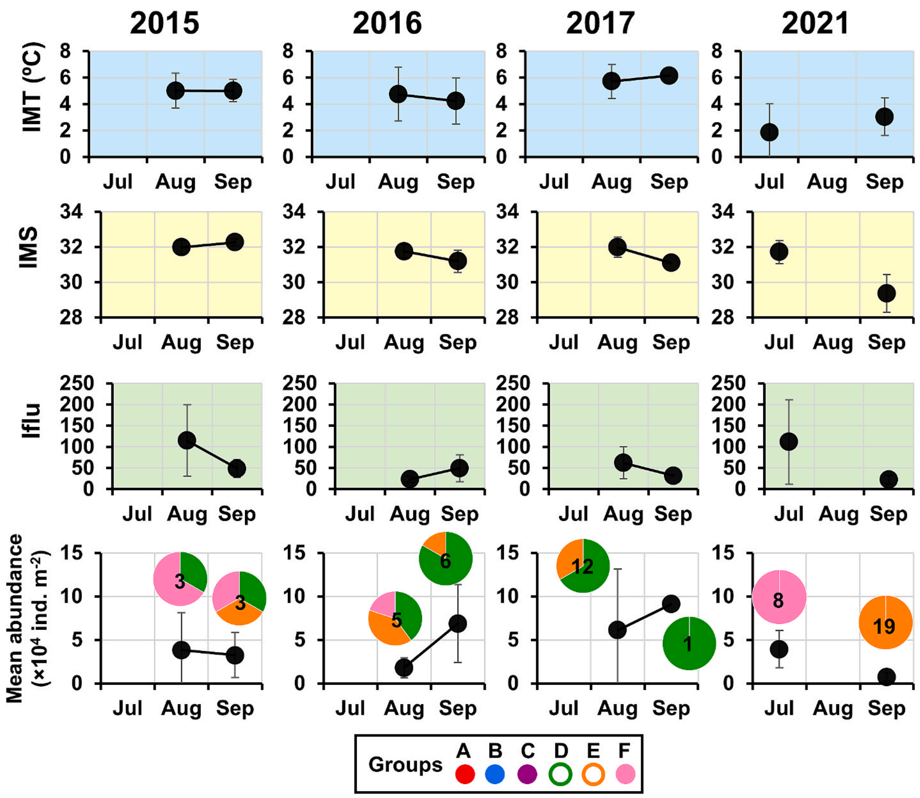

Fig. 7. Temporal changes in hydrography, zooplankton abundance, and community composition from the Bering Strait to 71° N in the southern Chukchi Sea. Circles and bars represent the mean and standard deviation for each parameter. Pie chart for the abundance panel shows the composition of the zooplankton group identified by cluster analysis (cf. Fig. 3). The values on the pie chart represent the number of stations.

4. Discussion

4.1. Hydrographic variability and drivers of zooplankton community dynamics

During the comprehensive study period from 2008 to 2021, the hydrographic conditions in the Pacific Arctic Ocean exhibited significant spatial, seasonal, and interannual variability. These patterns are consistent with the broader, well-documented transformations in Arctic marine ecosystems driven by global climate change, which include rising seawater temperatures, altered circulation patterns, and the loss of sea ice. The IMT consistently demonstrated a clear latitudinal gradient, with the highest temperatures near the Bering Strait, decreasing progressively northward and exhibiting a distinct seasonal cooling trend from August to September. On an interannual scale, pronounced temperature anomalies were observed in specific years (e.g., 2017, 2019, and 2021), which were consistently linked to enhanced Pacific Summer Water inflow, highlighting temperature as a major environmental driver of the zooplankton community structure. IMS generally reflected this hydrographic variability, with higher salinity in Pacific-influenced regions and lower salinity in coastal zones or areas where warm water inflow accelerated sea ice melt. These patterns also showed clear seasonal differences, particularly in 2021. Moreover, Integrated Fluorescence (Iflu) data revealed spatial heterogeneity in biological activity, with generally higher values in the Pacific-influenced regions during August compared with the ice-dominated northern areas, and a marked seasonal decline into autumn, as observed in 2021.

The distribution of the zooplankton community in the Pacific Arctic Ocean is primarily shaped by environmental factors, with temperature and salinity emerging as key drivers (Abe et al., 2020; Ashjian et al., 2021; Ershova et al., 2015; Kim et al., 2022; Kimmel et al., 2024; Matsuno et al., 2016a; Matsuno et al., 2016b; Mueter et al., 2021; Spear et al., 2019; Xu et al., 2018). Our results indicate that Pacific-influenced communities, such as Communities E and F, are closely associated with warm water, whereas Arctic-associated communities, such as Communities A and B, are more prevalent in colder regions (Fig. 4). When warm water was introduced into the Chukchi Sea, the zooplankton communities were differentiated based on salinity. Community E was observed in relatively lower salinity waters, whereas Community F was prevalent in higher-salinity conditions (Table 4). When both salinity and temperature were high, the Pacific-origin species were more dominant (Tables 2, 4). In addition, barnacle larvae, which serve as an indicator of shelf water intrusion into the basin, were also associated with salinity (Matsuno et al., 2016c). This pattern is consistent with that of previous studies, indicating that hydrographic variability, particularly Pacific water inflow, has a major role in structuring Pacific Arctic zooplankton assemblages during the summer (Ershova et al., 2015; Hibino et al., 2025; Kim et al., 2020).

During the summer, Pacific-origin Alaskan Coastal Water and Bering Shelf Water (or Bering Summer Water) enter the Chukchi Sea (Corlett and Pickart, 2017; Gong and Pickart, 2015), flowing through Barrow Canyon and the Chukchi Slope Current before reaching the Chukchi Borderland (Boury et al., 2020). This seasonal inflow of Pacific water not only introduces warmer temperatures and more variable salinity conditions depending on the water mass (Corlett and Pickart, 2017; Pickart et al., 2019), but also changes nutrient availability (Danielson et al., 2017; Whitney et al., 2005), upwelling processes (Lin et al., 2019), and stratification (Zhuang et al., 2016), which affects the zooplankton community structure. Community C, characterized by a high abundance of barnacle larvae, was closely associated with strong Pacific water inflow, particularly in the Chukchi Borderland. Community F was distinguished from other communities by the increased presence of the Pacific species *M. pacifica* and was associated with warm waters entering through the Bering Strait (Fig. 4; Table 4). Its absence in the East Siberian Sea further supports the influence of Pacific water. In contrast, Community D, which was prevalent in relatively cooler waters, was less abundant in years experiencing a stronger Pacific influence. This supports the idea that temperature and salinity changes drive shifts in community composition. These results suggest that ongoing climate-driven hydrographic changes may result in long-term shifts in zooplankton distribution, favoring Pacific-influenced communities, while altering Arctic zooplankton assemblages (Ershova et al., 2015).

From an ecological perspective, the shift in zooplankton communities in response to hydrographic variability may have a cascading effect on the Arctic marine food web (Choi et al., 2021; Lane et al., 2008; McMeans et al., 2013). Changes in the relative abundance of Arctic versus Pacific zooplankton species may affect energy transfer efficiency, particularly for predators that rely on lipid-rich Arctic copepods as a primary food source (Juma et al., 2025; Pecuchet et al., 2025). The observed shift in the zooplankton community composition in the study area suggests that resource availability for predators may fluctuate significantly over short time scales and may potentially influence the energy transfer dynamics within the Arctic marine food web.

4.2. Seasonal transition of zooplankton communities and its ecological implications

The seasonal transition from summer (August) to early autumn (September) represents an important period of ecological change in the Pacific Arctic Ocean (Feng et al., 2018; Wood et al., 2015). The integration of the August (IBRV Araon) and September (RV Mirai) datasets enabled us to capture distinct seasonal shifts in the zooplankton community structure, which reflected variations in the hydrographic conditions and ecosystem interactions (Fig. 4). Although August surveys showed a dominance of Pacific-influenced communities, particularly in the Chukchi Sea and along the Bering Strait, September surveys revealed a shift toward Arctic-associated communities (Fig. 4). This seasonal transition, coinciding with cooling sea temperatures in autumn, is a natural phenomenon; however, the CTD data in this study did not exhibit a clear corresponding trend (Fig. 7). This finding underscores the high variability and reinforces the notion that our CTD-based measurements represent instantaneous snapshots, whereas the zooplankton community integrates the cumulative effects of environmental conditions over several days. It also highlights that summer zooplankton communities, despite strong interannual variability in environmental conditions, consistently exhibit a distinct seasonal signal (Fig. 7).

Variations in underwater light conditions and algal food availability primarily drive changes in the zooplankton community structure and vertical distribution, with season being the most significant factor associated with this variability (Søreide et al., 2022). As sea ice retreats in summer, increased light availability stimulates phytoplankton blooms, which support zooplankton productivity (Huntington et al., 2020). Alternatively, phytoplankton blooms can also occur beneath the ice (Arrigo et al., 2014; Assmy et al., 2017). Our findings for Iflu are consistent with this pattern, showing elevated values in the Pacific-influenced regions during summer (August), which are indicative of robust primary productivity. However, these values markedly decreased by September and were particularly evident in the 2021 data (Fig. 2). This seasonal decline in algal food availability, as reflected by Iflu, correlates directly with the observed shifts in zooplankton community composition and abundance. For example, Communities C and F, which had relatively high Iflu values and were predominant in August (Table 4), were replaced by communities with lower total abundance as autumn progressed (Figs. 4, 5). However, as autumn progresses and primary production declines, zooplankton communities must adapt by adjusting their feeding strategies or relying on stored lipid reserves (Søreide et al., 2010; Stige et al., 2019). Previous studies have suggested that zooplankton species such as *C. glacialis* exhibit vertical migration in response to decreasing phytoplankton availability (Daase et al., 2008), which can explain some of the observed seasonal changes in the community structure.

Given the ongoing warming of the Arctic, the timing and extent of seasonal transitions in zooplankton communities may continue to shift (Ershova et al., 2015; Grebmeier, 2012; Kim et al., 2022). If the Pacific water inflow strengthens and persists later into the year, the seasonal shift from Pacific- to Arctic-dominated communities could be delayed, potentially disrupting the established predator–prey relationships. This delay could trigger cascading effects on higher trophic levels and alter energy transfer to Arctic fish, seabirds, and marine mammals (Pecuchet et al., 2025). A more comprehensive understanding of seasonal zooplankton dynamics requires the integration of spatially extensive and multi-season datasets. This enables a comprehensive assessment of the long-term effects of Pacific water inflow on Arctic ecosystems.

4.3. *Methodological considerations and broader implications*

This study provides a comprehensive assessment of the spatiotemporal variability in zooplankton communities in the western Arctic Ocean (2008–2021), and provides insight into the ecosystem shifts during climate change; however, several methodological limitations warrant consideration. First, zooplankton sampling was restricted to the epipelagic layer (0–200 m). RV *Mirai* and IBRV *Araon* collected samples from maximum depths of 150 m and 200 m, respectively. This likely undersampled deep-water and interzonal taxa, which limits insight into the full vertical structure and biodiversity of zooplankton communities (Skjoldal et al., 2013; Weydmann-Zwolicka et al., 2021). Second, the use of coarse mesh nets (330, 335 μm) may have underestimated small taxa, such as *Pseudocalanus* spp. and meroplankton larvae, despite their ecological importance and adaptability to changing conditions (Turner, 2004; Boissonnot et al., 2016).

Our results corroborate previous findings indicating that temperature and salinity shape zooplankton distribution (Abe et al., 2020; Ershova et al., 2015; Kim et al., 2022), with Pacific-origin communities expanding northward and competing with Arctic species (Matsuno et al., 2016a,b; Mueter et al., 2021). Notably, the dominance of small copepods (*Pseudocalanus* spp.) and barnacle larvae in Pacific-influenced communities demonstrates the ongoing shifts toward smaller-bodied assemblages, consistent with their shorter life cycles and higher adaptability (Boissonnot et al., 2016; Turner, 2004); however, the present study provides a more nuanced understanding of these shifts. Although the habitat of Pseudocalanus spp. expanded, no increasing trend in its overall abundance was evident in the Chukchi Sea. Furthermore, the occurrence of Pacific-influenced communities, such as Community F, was associated with a decrease in total zooplankton abundance (Fig. 7). These results raise important questions for future research on the balance between species replacement and net productivity in the rapidly changing Arctic, which is a complexity often overlooked in previous studies constrained by limited spatial and temporal coverage.

Although this study emphasizes hydrographic drivers, particularly temperature and salinity, as the primary determinants of zooplankton community structure, several biological factors, including predation, interspecific competition, vertical migration, and species-specific life histories, also affect zooplankton dynamics in the western Arctic Ocean. Predation pressure affects not only zooplankton abundance and distribution, but also energy transfer efficiency to higher trophic levels that are reliant upon lipid-rich Arctic copepods, potentially triggering cascading effects throughout the food web (Juma et al., 2025; Pecuchet et al., 2025). Concurrently, the northward expansion of Pacific-origin copepods intensifies interspecific competition with native Arctic species and potentially disrupts established ecological balances (Mueter et al., 2017; Ershova et al., 2015). Native Arctic copepods have distinct depth preferences and reproductive timing to mitigate competition and maintain community stability (Søreide et al., 2022); however, these strategies may be challenged by ongoing warming and increased stratification.

Vertical migration and species-specific life cycles are important for zooplankton survival and distribution, particularly during seasonal transitions. Zooplankton communities adapt by adjusting feeding strategies or relying on stored lipid reserves as primary production decreases (Søreide et al., 2010; Stige et al., 2019). For example, *C. glacialis* exhibits vertical migration in response to decreasing phytoplankton availability (Daase et al., 2008). The shorter life cycles and higher adaptability of small-sized copepod species, such as *Pseudocalanus* spp. (Boissonnot et al., 2016; Turner, 2004), enables them to be more resilient toward environmental fluctuations; however, their lower lipid reserves compared with larger Arctic copepods may affect energy transfer within the food web (Boissonnot et al., 2016).

4.4. *Potential long-term effects of Arctic warming on zooplankton communities*

Given that temperature emerged as the primary driver of zooplankton community shifts, continued Arctic warming is expected to favor the expansion of Pacific species, leading to fundamental changes in community composition. However, the adaptability of certain Pacific species to these changes remains unclear. Still, a gradual increase in communities influenced by Pacific water during the summer can be predicted (Ershova et al., 2015; Kim et al., 2020; Pinchuk and Eisner, 2017).

This study confirmed that Communities D, E, and F are primarily distributed in the Chukchi Sea and are strongly associated with warmer water conditions. These three communities are commonly dominated by the small-sized copepod *Pseudocalanus* spp., indicating that zooplankton assemblages may shift toward a structure dominated by smaller species, particularly during the warming summer months (Fig. 5). Small-sized copepod species typically have shorter life cycles and higher adaptability to environmental changes, making them more resilient to fluctuations (Boissonnot et al., 2016; Turner, 2004). However, they contain relatively lower lipid reserves compared to larger Arctic copepods, which could have implications for energy transfer within the Arctic food web (Boissonnot et al., 2016). Arctic species exhibit distinct life histories, depth preferences, and reproductive timing, which minimize interspecific competition and help maintain a stable zooplankton abundance (Søreide et al., 2022). However, the continued range expansion of Pacific copepods and small-sized copepods may disrupt this ecological balance.

Although *Pseudocalanus* spp.–dominated communities were prevalent in summer, the introduction of Community F—characterized by Pacific species— was not accompanied by an increase in total zooplankton abundance (Figs. 4, 5**)**. The observed lack of increase in total zooplankton abundance, despite the introduction of Pacific-influenced communities, raises critical questions about the balance between species replacement and net productivity in a changing Arctic. Future studies should integrate high-resolution time-series observations with ecosystem and species distribution models to disentangle the interactive effects of warming, stratification, and species competition on zooplankton population dynamics.

5. Conclusions

This study highlights the influence of temperature and seasonal hydrographic changes on zooplankton community structure in the Pacific Arctic Ocean. By integrating long-term summer (IBRV Araon) and autumn (RV Mirai) datasets, we captured seasonal shifts in zooplankton composition, demonstrating how Pacific- and Arctic-associated communities fluctuate in response to environmental variability. In August, the inflow of Pacific water introduced warm, high-salinity conditions to the Chukchi Sea, facilitating the expansion of Community F, which was characterized by an introduction of Pacific species such as *M. pacifica* without a corresponding increase in total zooplankton abundance. By September, the rapid decline in Pacific water influence was promptly reflected in zooplankton community shifts, with small copepods remaining dominant but total zooplankton abundance showing no sustained increase. This suggests that while the summer inflow of Pacific water may temporarily favor Pacific and small copepod species, these effects do not persist into September, indicating that such communities remain highly volatile, environmentally dependent, and not yet fully established.

CRediT authorship contribution statement

Jee-Hoon Kim: Writing – original draft, Methodology, Data curation, Conceptualization. **Yuya Hibino:** Methodology, Data curation. **Eun Jin Yang:** Supervision, Funding acquisition. **Kyoung-Ho Cho:** Data curation. **Hyoung Sul La:** Data curation. **Sung-Ho Kang:** Supervision, Funding acquisition. **Jeong-Hyun Kim:** Data curation. **Hyeju Yoo:** Data curation. **Jong-Kuk Moon:** Data curation. **Yoshiyuki Abe:** Data curation. **Nanami Hosoda:** Data curation. **Atsushi Yamaguchi:** Supervision, Funding acquisition. **Kohei Matsuno:** Visualization, Software, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2025.103634.

Data availability

Data will be made available on request.

References

Abe, Y., Matsuno, K., Fujiwara, A., Yamaguchi, A., 2020. Review of spatial and interannual changes in the zooplankton community structure in the western Arctic Ocean during summers of 2008–2017. Prog. Oceanogr. 186, 102391. https://doi.org/10.1016/j.pocean.2020.102391.

Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., Van Dijken, G.L., Lowry, K.E., Mills, M.M., Palmer, M.A., Balch, W.M., Bates, N.R., 2014. Phytoplankton blooms beneath the sea ice in the Chukchi Sea. Deep Sea Res. II. 105, 1–16. https://doi.org/10.1016/j.dsr2.2014.03.018.

Ashjian, C.J., Pickart, R.S., Campbell, R.G., Feng, Z., Gelfman, C., Alatalo, P., Zhang, J., 2021. Springtime renewal of zooplankton populations in the Chukchi Sea. Prog. Oceanogr. 197, 102635. https://doi.org/10.1016/j.pocean.2021.102635.

Assmy, P., Fernández-Méndez, M., Duarte, P., Meyer, A., Randelhoff, A., Mundy, C.J., Olsen, L.M., Kauko, H.M., Bailey, A., Chierici, M., 2017. Leads in Arctic pack ice enable early phytoplankton blooms below snow-covered sea ice. Sci. Rep. 7, 40850. https://doi.org/10.1038/srep40850.

Boissonnot, L., Niehoff, B., Hagen, W., Søreide, J.E., Graeve, M., 2016. Lipid turnover reflects life-cycle strategies of small-sized Arctic copepods. J. Plankton Res. 38, 1420–1432. https://doi.org/10.1093/plankt/fbw076.

Boury, S., Pickart, R.S., Odier, P., Lin, P., Li, M., Fine, E.C., Simmons, H.L., MacKinnon, J. A., Peacock, T., 2020. Whither the Chukchi slope current? J. Phys. Oceanogr. 50, 1717–1732. https://doi.org/10.1175/JPO-D-19-0273.1.

Brodskii, K.A., 1950. Calanoida of the far-eastern seas and polar basin of the USSR. Key. to. Fauna. USSR. 35, 1–440.

Brugler, E.T., Pickart, R.S., Moore, G., Roberts, S., Weingartner, T.J., Statscewich, H., 2014. Seasonal to interannual variability of the Pacific water boundary current in the Beaufort Sea. Prog. Oceanogr. 127, 1–20. https://doi.org/10.1016/j.pocean.2014.05.002.

Carstensen, J., Olszewska, A., Kwasniewski, S., 2019. Summer mesozooplankton biomass distribution in the West Spitsbergen current (2001-2014). Front. Mar. Sci. 6, 202. https://doi.org/10.3389/fmars.2019.00202.

Choi, H., Won, H., Kim, J.H., Yang, E.J., Cho, K.H., Lee, Y., Kang, S.H., Shin, K.H., 2021. Trophic dynamics of *Calanus hyperboreus* in the Pacific Arctic Ocean. J. Geophys. Res. Oceans 126, e2020JC017063. https://doi.org/10.1029/2020JC017063.

Christiansen, J.S., Mecklenburg, C.W., Karamushko, O.V., 2014. Arctic marine fishes and their fisheries in light of global change. Glob. Chang. Biol. 20, 352–359. https://doi.org/10.1111/gcb.12395.

Corlett, W.B., Pickart, R.S., 2017. The Chukchi slope current. Prog. Oceanogr. 153, 50–65. https://doi.org/10.1016/j.pocean.2017.04.005.

Daase, M., Eiane, K., Aksnes, D.L., Vogedes, D., 2008. Vertical distribution of *Calanus* spp. and *Metridia longa* at four Arctic locations. Mar. Biol. Res. 4, 193–207. https://doi.org/10.1080/17451000801907948.

Danielson, S.L., Eisner, L., Ladd, C., Mordy, C., Sousa, L., Weingartner, T.J., 2017. A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas. Deep Sea Res. II. 135, 7–26. https://doi.org/10.1016/j.dsr2.2016.05.024.

Dezutter, T., Lalande, C., Dufresne, C., Darnis, G., Fortier, L., 2019. Mismatch between microalgae and herbivorous copepods due to the record sea ice minimum extent of 2012 and the late sea ice break-up of 2013 in the Beaufort Sea. Prog. Oceanogr. 173, 66–77. https://doi.org/10.1016/j.pocean.2019.02.008.

Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., Matsuno, K., Nelson, R.J., Yamaguchi, A., Eisner, L.B., 2015. Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945–2012. Oceanography 28, 100–115. https://www.jstor.org/stable/24861904.

Ershova, E.A., Kosobokova, K.N., Banas, N.S., Ellingsen, I., Niehoff, B., Hildebrandt, N., Hirche, H.J., 2021. Sea ice decline drives biogeographical shifts of key *Calanus* species in the central Arctic Ocean. Glob. Chang. Biol. 27, 2128–2143. https://doi.org/10.1111/gcb.15562.

Feng, Z., Ji, R., Ashjian, C., Campbell, R., Zhang, J., 2018. Biogeographic responses of the copepod *Calanus glacialis* to a changing Arctic marine environment. Glob. Chang. Biol. 24, e159–e170. https://doi.org/10.1111/gcb.13890.

Frost, B., 1974. *Calanus marshallae*, a new species of calanoid copepod closely allied to the sibling species *C. finmarchicus* and *C. glacialis*. Mar. Biol. 26, 77–99. https://doi.org/10.1007/BF00389089.

Gong, D., Pickart, R.S., 2015. Summertime circulation in the eastern Chukchi Sea. Deep Sea Res. II. 118, 18–31. https://doi.org/10.1016/j.dsr2.2015.02.006.

Grebmeier, J.M., 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Annu. Rev. Mar. Sci. 4, 63–78. https://doi.org/10.1146/annurev-marine-120710-100926.

Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E.H., Høines, Å.S., Hoel, A. H., Ingvaldsen, R.B., Jørgensen, L.L., Knutsen, T., 2017. Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. Fish. Res. 188, 38–57. https://doi.org/10.1016/j.fishres.2016.12.002.

Hibino, Y., Matsuno, K., Fujiwara, A., Abe, Y., Hosoda, N., Itoh, M., Yamaguchi, A., 2025. Effect of delayed sea ice retreat on zooplankton communities in the Pacific Arctic Ocean: a generalized dissimilarity modeling approach. Front. Mar. Sci. 12, 1484609. https://doi.org/10.3389/fmars.2025.1484609.

Huntington, H.P., Danielson, S.L., Wiese, F.K., Baker, M., Boveng, P., Citta, J.J., De Robertis, A., Dickson, D.M., Farley, E., George, J.C., 2020. Evidence suggests potential transformation of the Pacific Arctic ecosystem is underway. Nat. Clim. Chang. 10, 342–348. https://doi.org/10.1038/s41558-020-0695-2.

Juma, G.A., Meunier, C.L., Herstoff, E.M., Irrgang, A.M., Fritz, M., Weber, C., Lantuit, H., Kirstein, I.V., Boersma, M., 2025. Future Arctic: how will increasing coastal erosion shape nearshore planktonic food webs? Limnol. Oceanogr. Lett. 10, 5–17. https://doi.org/10.1002/lol2.10446.

Kim, J.-H., Cho, K.-H., La, H.S., Choy, E.J., Matsuno, K., Kang, S.-H., Kim, W., Yang, E.J., 2020. Mass occurrence of Pacific copepods in the Southern Chukchi Sea during summer: Implications of the high-temperature Bering summer water. Front. Mar. Sci. 7, 612. https://doi.org/10.3389/fmars.2020.00612.

Kim, J.H., La, H.S., Cho, K.H., Jung, J., Kang, S.H., Lee, K., Yang, E.J., 2022. Spatial and interannual patterns of epipelagic summer mesozooplankton community structures in the western Arctic Ocean in 2016–2020. J. Geophys. Res. Oceans 127, e2021JC018074. https://doi.org/10.1029/2021JC018074.

Kimmel, D.G., Crouser, D.C., Harpold, C.E., Lamb, J.F., Spear, A.H., 2024. Rapid Zooplankton Assessment: evaluating a Tool for Ecosystem-Based Fisheries Management in the Large Marine Ecosystems of Alaska. Fish. Oceanogr. e12707. https://doi.org/10.1111/fog.12707.

Kimura, F., Abe, Y., Matsuno, K., Hopcroft, R.R., Yamaguchi, A., 2020. Seasonal changes in the zooplankton community and population structure in the northern Bering Sea from June to September, 2017. Deep Sea Res. II. 181, 104901. https://doi.org/10.1016/j.dsr2.2020.104901.

Lane, P.V., Llinás, L., Smith, S.L., Pilz, D., 2008. Zooplankton distribution in the western Arctic during summer 2002: hydrographic habitats and implications for food chain dynamics. J. Mar. Syst. 70, 97–133. https://doi.org/10.1016/j.jmarsys.2007.04.001.

Lin, P., Pickart, R.S., McRaven, L.T., Arrigo, K.R., Bahr, F., Lowry, K.E., Stockwell, D.A., Mordy, C.W., 2019. Water mass evolution and circulation of the northeastern Chukchi Sea in summer: Implications for nutrient distributions. J. Geophys. Res. Oceans 124, 4416–4432. https://doi.org/10.1029/2019JC015185.

Lynch, A.H., Norchi, C.H., Li, X., 2022. The interaction of ice and law in Arctic marine accessibility. Proc. Natl. Acad. Sci. 119, e2202720119. https://doi.org/10.1073/pnas.2202720119.

Matsuno, K., Abe, Y., Yamaguchi, A., Kikuchi, T., 2016a. Regional patterns and controlling factors on summer population structure of *Calanus glacialis* in the western Arctic Ocean. Polar Sci. 10, 503–510. https://doi.org/10.1016/j.polar.2016.09.001.

Matsuno, K., Sanchez, J.M.L., Yamaguchi, A., Hirawake, T., Kikuchi, T., 2016b. Spatial and geographical changes in the mesozooplankton community in the Bering and Chukchi Seas during the summers of 2007 and 2008. Polar Sci. 10, 335–345. https://doi.org/10.1016/j.polar.2016.04.006.

Matsuno, K., Yamaguchi, A., Fujiwara, A., Onodera, J., Watanabe, E., Harada, N., Kikuchi, T., 2016c. Seasonal changes in mesozooplankton swimmer community and fecal pellets collected by sediment trap moored at the Northwind Abyssal Plain in the western Arctic Ocean. Bull. Fish. Sci. Hokkaido Univ 66, 77–85. https://doi.org/10.14943/bull.fish.66.2.77.

Matsuno, K., Yamaguchi, A., Hirawake, T., Imai, I., 2011. Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008. Polar Biol. 34, 1349–1360. https://doi.org/10.1007/s00300-011-0988-z.

Matsuno, K., Yamaguchi, A., Shimada, K., Imai, I., 2012. Horizontal distribution of calanoid copepods in the western Arctic Ocean during the summer of 2008. Polar Sci. 6, 105–119. https://doi.org/10.1016/j.polar.2012.01.002.

McMeans, B.C., Rooney, N., Arts, M.T., Fisk, A.T., 2013. Food web structure of a coastal Arctic marine ecosystem and implications for stability. Mar. Ecol. Prog. Ser. 482, 17–28. https://doi.org/10.3354/meps10278.

Mueter, F.J., Iken, K., Cooper, L.W., Grebmeier, J.M., Kuletz, K.J., Hopcroft, R.R., Danielson, S.L., Collins, R.E., Cushing, D.A., 2021. Changes in diversity and species composition across multiple assemblages in the eastern Chukchi Sea during two contrasting years are consistent with borealization. Oceanography 34, 38–51. https://www.jstor.org/stable/27085037.

Mueter, F.J., Weems, J., Farley, E.V., Sigler, M.F., 2017. Arctic ecosystem integrated survey (Arctic Eis): marine ecosystem dynamics in the rapidly changing Pacific Arctic Gateway. Deep Sea Res. II. 135, 1–6. https://doi.org/10.1016/j.dsr2.2016.11.005.

Pecuchet, L., Mohamed, B.A., Hayward, A., Alvera Azcarate, A., Dörr, J., Filbee-Dexter, K., Kuletz, K.J., Luis, K., Manizza, M., Miller, C.E., 2025. Arctic and Subarctic marine heatwaves and their ecological impacts. Front. Environ. Sci. 13. https://doi.org/10.3389/fenvs.2025.1473890.

Pickart, R.S., Lin, P., Bahr, F., McRaven, L.T., Huang, J., Pacini, A., Arrigo, K.R., Ashjian, C.J., Berchok, C., Baumgartner, M.F., 2023. The Pacific water flow branches in the eastern Chukchi Sea. Prog. Oceanogr. 219, 103169. https://doi.org/10.1016/j.pocean.2023.103169.

Pickart, R.S., Nobre, C., Lin, P., Arrigo, K.R., Ashjian, C.J., Berchok, C., Cooper, L.W., Grebmeier, J.M., Hartwell, I., He, J., 2019. Seasonal to mesoscale variability of water masses and atmospheric conditions in Barrow Canyon. Chukchi Sea. Deep Sea Res. II. 162, 32–49. https://doi.org/10.1016/j.dsr2.2019.02.003.

Pinchuk, A.I., Eisner, L.B., 2017. Spatial heterogeneity in zooplankton summer distribution in the eastern Chukchi Sea in 2012–2013 as a result of large-scale interactions of water masses. Deep Sea Res. II. 135, 27–39. https://doi.org/10.1016/j.dsr2.2016.11.003.

Skjoldal, H.R., Wiebe, P.H., Postel, L., Knutsen, T., Kaartvedt, S., Sameoto, D.D., 2013. Intercomparison of zooplankton (net) sampling systems: results from the ICES/GLOBEC sea-going workshop. Prog. Oceanogr. 108, 1–42. https://doi.org/10.1016/j.pocean.2012.10.006.

Søreide, J.E., Dmoch, K., Blachowiak-Samolyk, K., Trudnowska, E., Daase, M., 2022. Seasonal mesozooplankton patterns and timing of life history events in high-arctic fjord environments. Front. Mar. Sci. 9, 933461. https://doi.org/10.3389/fmars.2022.933461.

Søreide, J.E., Leu, E.V., Berge, J., Graeve, M., Falk-Petersen, S., 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Glob. Chang. Biol. 16, 3154–3163. https://doi.org/10.1111/j.1365-2486.2010.02175.x.

Spear, A., Duffy-Anderson, J., Kimmel, D., Napp, J., Randall, J., Stabeno, P., 2019. Physical and biological drivers of zooplankton communities in the Chukchi Sea. Polar Biol. 1–18. https://doi.org/10.1007/s00300-019-02498-0.

Stige, L.C., Eriksen, E., Dalpadado, P., Ono, K., 2019. Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea. ICES J. Mar. Sci. 76, i24–i36. https://doi.org/10.1093/icesjms/fsz063.

Turner, J.T., 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool. Stud. 43, 255–266.

Weydmann-Zwolicka, A., Balazy, P., Kuklinski, P., Søreide, J.E., Patuła, W., Ronowicz, M., 2021. Meroplankton seasonal dynamics in the high Arctic fjord: comparison of different sampling methods. Prog. Oceanogr. 190, 102484. https://doi.org/10.1016/j.pocean.2020.102484.

Whitney, F., Crawford, W., Harrison, P., 2005. Physical processes that enhance nutrient transport and primary productivity in the coastal and open ocean of the subarctic NE Pacific. Deep Sea Res. II. 52, 681–706. https://doi.org/10.1016/j.dsr2.2004.12.023.

Wood, K.R., Bond, N.A., Danielson, S.L., Overland, J.E., Salo, S.A., Stabeno, P.J., Whitefield, J., 2015. A decade of environmental change in the Pacific Arctic region. Prog. Oceanogr. 136, 12–31. https://doi.org/10.1016/j.pocean.2015.05.005.

Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2006. Interannual changes in the Bering Strait fluxes of volume, heat and freshwater between 1991 and 2004. Geophys. Res. Lett. 33. https://doi.org/10.1029/2006GL026931.

Xu, Z., Zhang, G., Sun, S., 2018. Inter-annual variation of the summer zooplankton community in the Chukchi Sea: spatial heterogeneity during a decade of rapid ice decline. Polar Biol. 41, 1827–1843. https://doi.org/10.1007/s00300-018-2324-3.

Zhuang, Y., Jin, H., Li, H., Chen, J., Lin, L., Bai, Y., Ji, Z., Zhang, Y., Gu, F., 2016. Pacific inflow control on phytoplankton community in the Eastern Chukchi Shelf during summer. Cont. Shelf Res. 129, 23–32. https://doi.org/10.1016/j.csr.2016.09.010.