·Article· **Advances in Polar Science**
doi: 10.12429/j.advps.2022.0054 June 2023 Vol. 34 No. 2: 91-104

Mesozooplankton distribution and diversity from the Bering Sea shelf to the Chukchi Sea

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Received 1 November 2022; accepted 20 June 2023; published online 30 June 2023

Abstract In recent decades, environmental changes in the Arctic have aroused widespread concern around the world. To better understand ecology issues such as ecosystem dynamics, the Arctic and the subarctic regions were integrated as the "pan-Arctic" region. In this study, mesozooplankton were sampled from the Bering Sea shelf to the northern Chukchi Sea during the 10th Chinese National Arctic Research Expedition in 2019. Based on the species composition and abundance, three geographical communities were identified: the Bering Sea shelf community (BSS), the Bering Strait transitional community (BST), and the Chukchi Sea shelf community (CSS). The BSS was characterized by Bering Sea oceanic species such as *Eucalanus bungii*; the BST was mainly composed of the pan-Arctic distributed *Calanus glacialis*, meroplankton of benthos, and neritic species such as *Centropages abdominalis*; copepods, especially the copepodite of *C. glacialis*, were predominant in the CSS community. The BSS community structure was strongly affected by the inflow of Bering Shelf Water, while those of BST and CSS were determined by the recruitment of local species. The zooplankton community structure is influenced by both advection and environmental changes such as warming and a prolonged productivity period. Here, it was difficult to distinguish the changes induced by climate change from the effects of the Bering Sea Water. The key to solving this problem is the accumulation of comparable data, which requires continuous monitoring of key species such as *C. glacialis* and *Calanus hyperboreus*.

Keywords **Mesozooplankton**, **Bering Sea shelf**, **Bering Strait**, **Chukchi Sea**, **geographical distribution**, **community structure**, **population recruitment**, **climate change**

Citation: Xu Z Q, Wang C F, Chao Y, et al. Mesozooplankton distribution and diversity from the Bering Sea shelf to the Chukchi Sea. Adv Polar Sci, 2023, 34(2): 91-104, doi: 10.12429/j.advps.2022.0054

1 Introduction

The Arctic Ocean is undergoing dramatic changes, especially the western Arctic Ocean (e.g., Arrigo and van Dijken, 2015). These changes include the rapid retreat of sea ice, rising temperature, and increasing input of freshwater (e.g., Johannessen and Miles, 2011; Stroeve et al., 2012; Chan et al., 2019). The Bering Strait is the only channel connecting the Pacific Ocean and the Arctic Ocean. In the northern Bering Strait, the Chukchi Sea is one of the marginal seas of the Arctic Ocean. It is considered the region most sensitive to climate change (e.g., Hassol, 2004;

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Grebmeier et al., 2006a). The water depth of the Bering Sea shelf is similar to that of the Chukchi Sea. As with other marginal seas of the Arctic Ocean, the north Bering Sea and the Chukchi Sea are experiencing the seasonal formation and retreat of sea ice (Pickart et al., 2010). Sea ice forms in late autumn and extends southward along the coast until it covers the entire northern Bering Sea in winter. Along with the increasing temperature and northward inflow of the Bering Sea Water, the sea ice begins to retreat and becomes ice-free in summer.

In the Arctic Ocean and subarctic ocean, the sea ice plays fundamental roles in marine ecosystems. The habitats of most marine organisms, including plankton, fish, birds, and mammals, are closely related to the seasonal formation and retreat of sea ice (Wassmann et al., 2011). Zooplankton are the link between primary producers and higher trophic-level organisms. Zooplankton with different body sizes feed on most of the phytoplankton cells. The materials and energy are gradually transferred to higher trophic levels along the food chain. The Bering Sea is a major fishing area in the world because of the high abundance and biomass of large copepods, such as *Calanus glacialis*, *Eucalanus bungii*, *Neocalanus cristatus,* and *Neocalanus flemingeri* (Hunt Jr et al., 2013). The opposite trends are observed in the Chukchi Sea and other shallow marginal seas of the Arctic Ocean. Only a small portion of the primary production in the Bering Sea shelf and the Chukchi Sea is utilized by zooplankton, so most of it settles to the bottom to support a large number of benthos (e.g., Carroll and Carroll, 2003; Feder et al., 2005; Grebmeier et al., 2006b). Therefore, the main catch in this area is primarily composed of snow crabs, flounders, and other benthos, and it is much more limited compared with that in the Barents Sea at the same latitude (Zeller et al., 2011).

The drifting characteristic of zooplankton means that they may be affected by the distribution of water masses. Thus, some species have been used as indicators of different water masses (Beaugrand et al., 2002; Hays et al., 2005). Previous studies have shown that the zooplankton assemblage is clearly related to the distribution of water masses in the north Bering Sea and Chukchi Sea (e.g., Hopcroft et al., 2010; Ershova et al., 2015a). The water in the Bering Strait can be divided into three different water masses: the Alaska Coastal Water, the Bering Shelf Water, and the Anadyr Water (Weingartner et al., 2005, 2013). At the same time, the cold Siberian Coastal Water originates from the Arctic deep basin and flows southward along the east Siberian coast. The Alaska Coastal Water and Bering Shelf Water flow through the northern shelf area of the Bering Sea, and the Anadyr Water originates from the Bering Sea Basin (Weingartner et al., 2005). Copepods, such as *E. bungii* and *N. cristatus*, can penetrate into the Canadian Basin when the inflow of Bering Shelf Water is strong (Lane et al., 2008).

With the intensification of climate change, the boundary between the Arctic and subarctic is disappearing. Consequently, the idea of a “pan-Arctic” region has been proposed in recent years. It is mainly intended to study and analyze the Arctic, subarctic, and adjacent regions as a whole (Carmack and Wassmann, 2006). However, the integrated study of the Bering Sea and the Chukchi Sea is difficult owing to the prolonged influence of geopolitics. Only in 1988 and 2004 did the United States and the Soviet Union/Russia (Kulikov, 1992; Hopcroft et al., 2010) carry out short-term collaborative projects. Although the species composition and spatial distribution of zooplankton in the Bering Sea shelf and the Chukchi Sea have been fully studied (e.g., Coyle et al., 1996; Hopcroft et al., 2010), investigation on a large spatial scale remains scarce. During the 10th Chinese National Arctic Research Expedition in 2019, the composition and geographical distribution of mesozooplankton were investigated in four areas: the BL transect located in the western part of the north Bering Sea, the BR transect in the eastern part of the north Bering Sea, the BS transect to the north of St. Lawrence Island, and the R transect in the central Chukchi Sea. The objectives of this study are to define the geographical distribution of the mesozooplankton community from the Bering Sea shelf to the Chukchi Sea, to compare the differences in community structure in different habitats, and to detect any ongoing changes and forecast future trends in mesozooplankton communities.

2 Method and materials

2.1 Study area and sample collection

Four transects were investigated from the Bering Sea shelf to the Chukchi Sea during the 10th Chinese National Arctic Research Expedition onboard the R/V *Xiangyanghong 01*, and mesozooplankton were collected at 17 stations between 27 August and 8 September 2019 (Figure 1, Table 1). The investigation started at the BL transect (four stations), followed by the BS (three stations) and R transects (six stations), and then the BR transect (four stations). Even though stations M11 and M14 were at a different longitude than the R transect, they were included in the R transect owing to the similar environmental conditions and species compositions.

At each station, mesozooplankton were collected via vertical hauls using a 500 μm Deep-Sea-I net (PLT-DW1, China) with a 0.5 m^2 mouth opening. The hauling speed was 1.5 $m \cdot s^{-1}$. The full water column (from 2 m above the bottom to the surface) was sampled at stations shallower than 200 m, and only the upper 200 m layer was sampled at stations BL07, M11, and M14. Immediately after collection, the mesozooplankton samples were preserved in a buffered 5% formalin solution for species identification. Temperature and salinity in the water column were measured with a Seabird CTD (SBE 911 Plus, USA). Chlorophyll-*a* (Chl-*a*) concentrations were determined by filtering 500 mL of seawater through a Whatman GF/F glass fiber filter.

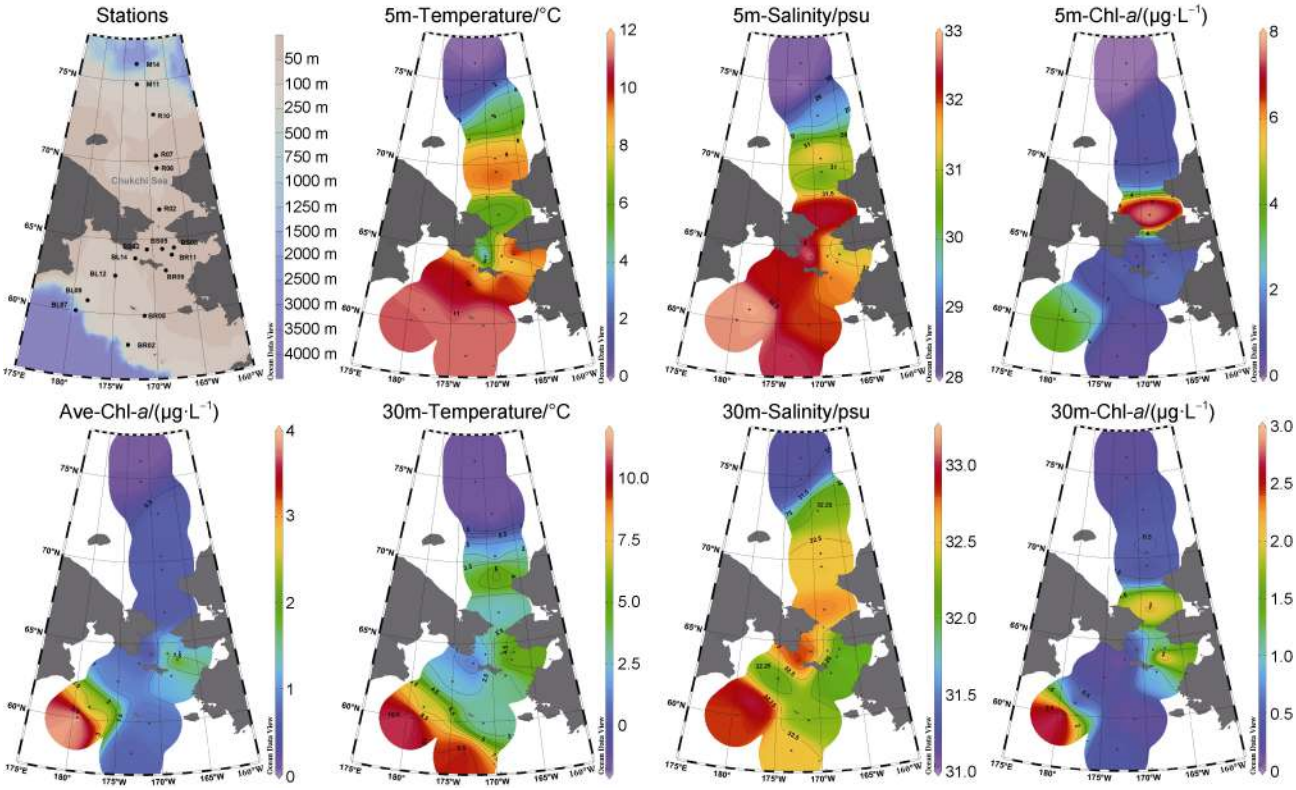

Figure 1 Sampling site during the 10th Chinese National Arctic Research Expedition and the geographical distribution of environmental factors (ave-Chl-*a* refers to average Chl-*a* concentration from 0 m to 30 m).

Table 1 Information of sampling stations, including sampling data, water depth and the depth of vertical towing (length)

Transect	Station	Longitude/(°W)	Latitude/(°N)	Date	Depth/m	Length/m
BL	BL07	179.5127	60.0359	2019-08-27	1521	200
	BL09	178.2111	60.7973	2019-08-27	157	145
	BL12	175.0103	62.5934	2019-08-28	76	70
	BL14	172.4077	63.7666	2019-08-28	44	35
BS	BS02	170.8207	64.3342	2019-08-29	41	35
	BS05	168.7089	64.3302	2019-08-29	40	35
	BS08	167.1212	64.3653	2019-08-29	31	25
R	R02	168.7482	66.8942	2019-08-30	43	35
	R06	168.7512	69.5333	2019-08-30	51	35
	R07	168.7503	70.3332	2019-08-31	41	35
	R10	168.7448	72.8982	2019-08-31	61	55
	M14	171.9799	76.0337	2019-09-02	2012	220
	M11	171.9950	74.803	2019-09-02	326	200
BR	BR11	167.4781	63.9011	2019-09-06	35	27
	BR09	168.4268	62.9067	2019-09-06	40	27
	BR05	171.3069	59.8991	2019-09-07	71	60
	BR02	173.2263	57.9018	2019-09-08	118	100

Immediately after extraction by acetone (volume percent, 90%), the fluorescence was measured according to the Joint Global Ocean Flux Study (JGOFS) protocol (Knap et al., 1996) using a Trilogy fluorometer (Turner 7200-002, USA)

2.2 Species identification

To avoid the effect of the movement of the ship, species identification was performed under a dissecting microscope (Olympus SZX16, Japan) at the laboratory on land. Copepods, chaetognaths, cnidarians, and tunicates were keyed to species. Juveniles in the genera *Pseudocalanus* were grouped together because they were morphologically indistinguishable. The species complex *Calanus glacialis/marshallae* was considered to be within our region and was recorded as *C. glacialis* (Nelson et al., 2009, Ershova et al., 2015a). Large copepods including *C. glacialis*, *C. hyperboreus,* and *Paraeuchaeta galacialis* were staged, and barnacle larvae were categorized as either cypris or nauplii owing to their high abundances (Xu et al., 2018a). All other species were identified to the taxon level. To determine and compare the community structures, all species were classified into several functional groups that we will refer to as "Copepoda", "Cnidaria", "Chaetognatha", "other Crustaceans", "meroplankton", "Tunicata", "Cladocera" and "others" (Table 1).

2.3 Data processing

The geographical communities were divided using cluster analysis based on species composition and abundance. Following log transformation, the Bray–Curtis similarity index was calculated for all stations. A Q-type cluster analysis was carried out using complete linkage. Because log transformation strongly increases the relative influences of rare groups of zooplankton, we choose those taxonomic categories that contributed at least 1% to any sample (e.g., Hopcroft et al., 2010). The SIMPER program (similarity percentage analysis) was used to determine the percent contribution of zooplankton taxa to the community clusters and the similarities between groups (Xu et al., 2018a). The BIO-EVN program was used to find the best combination of environmental factors that contributed the most to the species assemblage. All analyses were performed using the software PRIMER 6.0, and the geographical distribution map was prepared using Ocean Data View 5.2.

The dominant species of each group were determined according to their dominance (Y), which is defined as:

$$Y = (n_i / N) \times f_i$$

where n_i represents the total number of species i in one group, N represents the total number of all zooplankton species in this group, and f_i is the appearance frequency of species i, which is the ratio between the stations at which the species appeared and the total number of stations. Species for which $Y \geqslant 0.02$ were chosen as the dominant species.

3 Results

3.1 Hydrographic features

No sea ice was observed at any station during the survey period. Among all stations, water depths of more than 200 m were only observed at stations M14 and BL07. Similar water depths (< 50 m) were found at the stations near the Bering Strait, and the shallowest water depth (30 m) was recorded at BS08. The geographical distributions of temperature, salinity, and Chl-*a* concentration at depths of 5 m (surface) and 30 m are shown in Figure 1. Additionally, the average Chl-*a* concentration of the water column is an important environmental factor controlling zooplankton abundance (Søreide et al., 2010). Thus, its average value of 0–30 m was also shown here (e.g., Kosobokova and Hopcroft, 2010).

The geographical distribution of temperature tended to decrease from the Bering Sea shelf to the Chukchi Sea. All stations on the Bering Sea shelf had a similar surface temperature (5m-T), and ranged between 10.11 °C and 11.17 °C, with an average of 10.72 °C. However, 5m-T differed among the stations near the Bering Strait. It was only 2.37 °C at station BS02, while it was as high as 10.79 °C at station BS08. The lowest values of 5m-T were recorded at stations M14 and M11 and were 0.06 °C and 0.92 °C, respectively. The highest temperature values of the 30 m layer (30m-T) were recorded at stations BL07 and BR02 near the Bering Sea Basin, and they were 11.04 °C and 9.62 °C, respectively. The 30m-T showed little difference from the 5m-T. However, the temperature was much lower than that of 5m-T at other stations. The lowest values of 30m-T were recorded at stations R10, M11, and M14, with an average value of −1.47 °C.

The distribution patterns of salinity at the surface (5m-S) and the 30 m (30m-S) layers were similar to those of temperature. The highest values of 5m-S and 30m-S, which were 32.88 and 33.00, respectively, were recorded at station BL09. The lowest values (28.04 and 31.20) were recorded at station M11 in the northern Chukchi Sea. The salinity values at stations BS02 and BS08 were notable. Although both the temperatures at the 5 m and 30 m layers at station BS02 were the lowest, the salinity (32.85) was much higher than that of other stations. Meanwhile, the reverse trends were observed at station BS08. The temperature at station BS08 was higher than that at other stations. With the highest values of temperature, the salinities of the 5 m and 30 m layers of BS08 were the lowest (30.83 and 32.03).

The lowest concentrations of Chl-*a* were recorded in the northern Chukchi Sea. The values at the surface (5m-Chl-*a*), the 30 m layer (30m-Chl-*a*), and the average throughout the water column (Ave-Chl-*a*) were 0.04, 0.21, and 0.13 $\mu g \cdot L^{-1}$, respectively. In the Bering Sea shelf, the 5m-Chl-*a* of the BL transect was higher than that of the BR transect, with average values of 2.30 and 1.10 $\mu g \cdot L^{-1}$. The highest value of 5m-Chl-*a* was recorded at station R02 and was as high as 7.61 $\mu g \cdot L^{-1}$. The value of 5m-Chl-*a* was lower than that of 30m-Chl-*a* at each station. Stations BR11, BL07, and R02 were the three stations with the highest 30m-Chl-*a* values, at 2.91, 2.87, and 2.02 $\mu g \cdot L^{-1}$, respectively. The Ave-Chl-*a* was higher in the BR transect (average 2.01 μg·L^{-1}), followed by those of the stations near the Bering Strait (1.65 μg·L^{-1}). It was lower than 1.00 μg·L^{-1} at the other stations.

3.2 Species composition and geographical distribution

A total of 47 mesozooplankton species/taxa were identified in this study (Table 2). Copepods represented 22 species and were the most diverse group, followed by other Crustaceans with six species, Cnidaria with six species, meroplankton with four species, and Chaetognatha with three species. Only one species each of Tunica and Cladocera were recorded. The rare species, including *Clione limacina, Tomopteris* sp., fish larvae, and polychaetes were categorized under others.

Table 2 List of mesozooplankon collected during the 10th Chinese National Arctic Research Expedition in 2019, with their average abundance in three communities identified by cluster analysis

Species/taxon	Abundance/(ind.·m^{-3})			Species/taxon	Abundance/(ind.·m^{-3})		
	BSS	BST	CSS		BSS	BST	CSS
Copepoda				*Neocalanus plumchrus*	0.00	0.04	0.00
Calanus glacialis				*Pleuromamma robusta*	0.26	0.00	0.00
Adult	0.00	0.08	0.29	*Oithona smilis*	0.25	14.99	1.07
C5	0.00	5.87	10.85	Harpacticoida	0.10	0.00	0.04
C4	0.00	3.79	10.61	*Heterorhabdidae* sp.	0.00	0.00	0.00
C3	0.00	1.01	11.91	**Cnidaria**			
C2&C1	0.00	0.15	5.83	*Obelia longissina*	0.00	3.41	0.00
Calanus hyperboreus				*Dimophyes arctica*	0.06	0.00	0.00
Adult	0.00	0.00	0.01	*Muggiaea bargmannae*	0.00	0.00	0.12
C5	0.00	0.00	0.00	*Aglantha digitale*	53.76	41.03	5.50
C4	0.00	0.00	2.04	*Euphysa* sp.	0.02	0.00	0.00
C3	0.00	0.00	0.71	*Aeginopsis laurentii*	0.29	0.00	0.09
C2&C1	0.00	0.00	0.55	**Chaetognatha**			
Paraeuchaeta galacialis				*Pseudosagitta maxima*	0.00	0.00	0.03
Adult	0.00	0.00	0.00	*Parasagitta elegans*	13.26	9.69	5.90
C5	0.10	0.00	0.03	*Eukrohnia hamata*	2.69	0.43	0.28
C4	0.03	0.00	0.00	**Other Crustacean**			
C3	0.06	0.00	0.23	Euphausiacea	0.58	4.91	1.44
C2&C1	0.03	0.00	0.05	Euphausiacea larvae	0.06	0.00	0.00
Acartia longiremis	2.01	32.24	0.26	Brachyura larva	0.02	0.00	0.03
Aetideopsis rostrata	0.00	4.31	0.00	Macrura larva	0.09	0.35	0.02
Eucalanus bungii	14.17	13.38	4.06	Amphipoda	0.58	0.81	0.16
Centropages abdominalis	6.36	333.63	0.36	Ostracods	0.78	0.00	0.04
Pseudocalanus newmani	0.22	28.62	4.64	**Meroplankton**			
Pseudocalanus minutus	14.31	275.57	14.44	Barnacle nauplii	0.00	50.02	0.00
Pseudocalanus sp.	0.26	3.66	0.00	Barnacle cypris larva	0.00	0.64	0.05
Scolecithricella minor	0.22	0.00	0.01	Gastropods larva	0.50	34.05	0.26
Metridia longa				Ophiopluteus larva	0.00	0.66	0.00
Adult	0.00	0.00	1.41	**Tunicata**			
Copepodite	0.00	0.00	13.57	*Oikopleura vanhoffeni*	2.01	3.46	3.72
Metridia pacifica				**Cladocera**			
Adult	2.20	0.72	0.71	Cladocera	0.24	117.56	0.00
Copepodite	6.58	14.02	2.25	**Others**			
Chiridius pacificus	0.29	0.00	0.00	*Clione limacina*	0.02	0.00	0.00
Eurytemora pacifica	0.00	0.40	0.00	*Tomopteris* sp.	0.10	0.00	0.00
Neocalanus cristatus	0.14	0.11	0.00	Fish larvae	0.03	0.04	0.00
Neocalanus flemingeri	10.06	0.04	0.00	Polychaete	0.00	1.81	0.16

According to the geographical distribution for total abundance, the highest abundances were observed at stations along transects BS and BR, and they ranged from 770.12 to 2034.10 ind.·m^{-3} (Figure 2). The lowest total abundance values occurred at stations BL09 and R07 and were 68.85 and 82.07 ind.·m^{-3}, respectively. The geographical distribution of copepod abundance was consistent with that of total abundance, while the Cnidaria was mainly concentrated in the BR transect. Made up mostly of *Aglantha digitale*, the highest abundance of Cnidaria was 256.60 ind.·m^{-3} and recorded at station BR09. *Parasagitta elegans* was the most dominant species of Chaetognatha, while *Pseudosagitta maxima* was only recorded at station M11. Other Crustaceans were mainly distributed in the Bering Strait shelf and consisted of amphipods, ostracods, and Euphausiacea. The highest abundance of other Crustaceans was recorded at station BS05 and was mostly made up of Euphausiacea (80%). Meroplankton were concentrated at stations close to the coast. Barnacle nauplii and gastropods were the two main components of meroplankton, which contributed to more than 90% of the total abundance. Similar to meroplankton, Cladocera were also concentrated at stations BS05, BS08, and BR11, with the highest abundance at 547.80 ind.·m^{-3}. The abundance of others was the lowest among all the functional groups. Fish larvae and *C. limacina* were recorded occasionally, while polychaetes were mainly concentrated in shallow coastal stations.

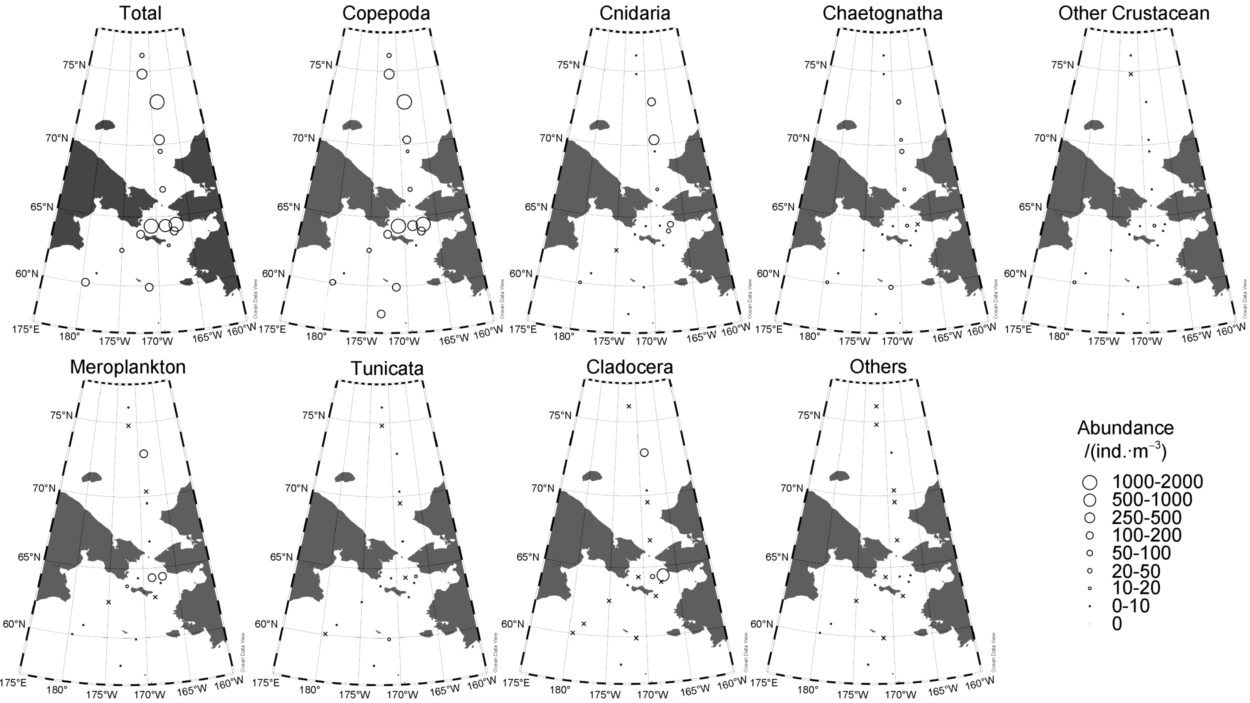

Figure 2 Geographical distribution of total abundance and the abundance of each functional group listed in Table 2.

3.3 Community classification and structure

Based on species composition and abundance, all stations were divided into three geographical communities: the north Bering Sea shelf community (BSS), the Bering Strait transitional community (BST) and the Chukchi Sea shelf community (CSS) (Figure 3). The ANOSIM (analysis of similarity) program showed that there were significant differences among the three communities (p=0.001). Notably, station BL12, located in the Bering Sea shelf, was divided into the CSS. These three communities were completely isolated from each other geographically after excluding station BL12 (Figure 4).

The community structures were also different (Figure 5). The total abundance of the BST was the highest (1000.94 ind.·m^{-3}) and was much higher than those of the other two communities. Copepods were the most abundant group in the BST, with an abundance of 732.62 ind.·m^{-3}, followed by meroplankton (117.56 ind.·m^{-3}) and other Crustaceans (85.36 ind.·m^{-3}). These three functional

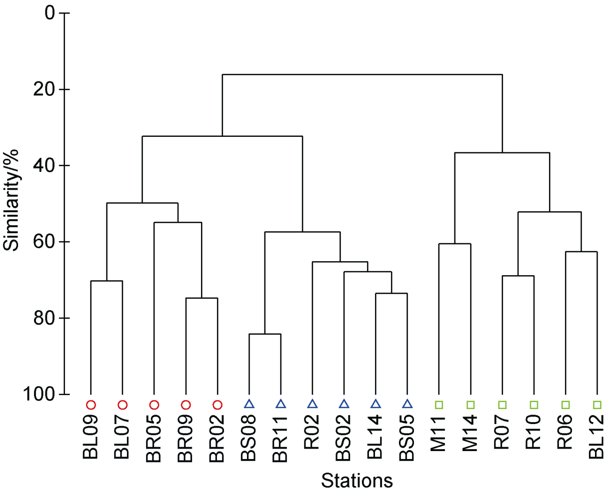

Figure 3 Three mesozooplankton groups were classified by cluster analysis based on the species composition and abundance (red circle: Bering Sea shelf community; blue triangle: Bering Strait transitional community; green square: Chukchi Sea shelf community) .

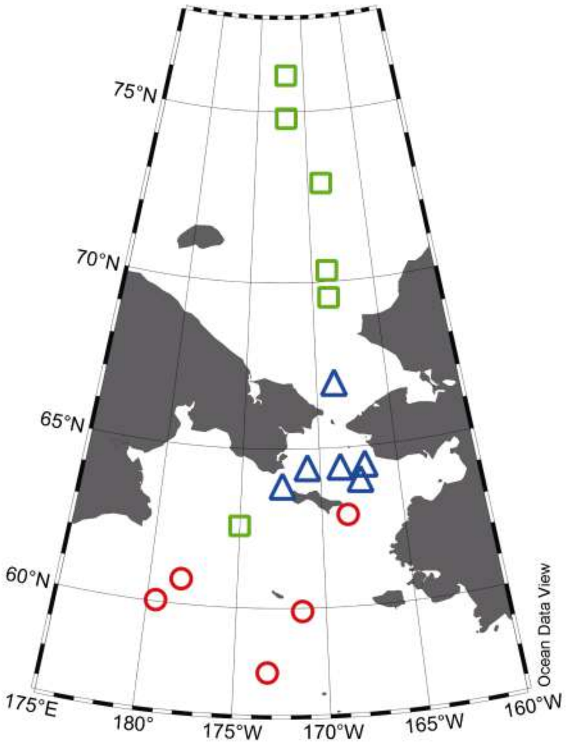

Figure 4 Geographical distribution of mesozooplankton identified by cluster analysis (color codes are the same as in Figure 3) .

groups contributed to 93.51% of the total abundance. The total abundance of the BSS was 132.94 ind.·m^{-3}. Copepods, Cnidaria, and Chaetognatha were the main components, with abundances of 57.65, 54.12, and 15.95 ind.·m^{-3}, respectively. The total abundance of the CSS was 104.53 ind.·m^{-3} and was dominated by copepods (82.19%). According to the SIMPER results, the most important species contributing to community division were endemic or abundant species (Table 3).

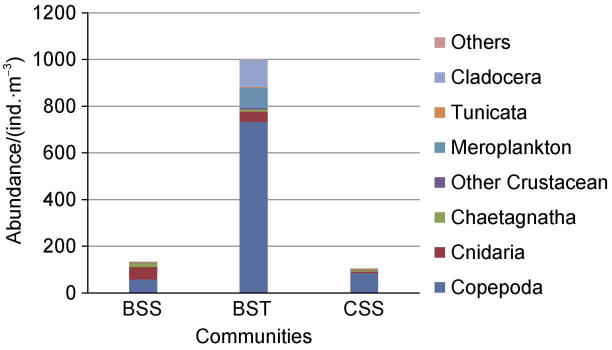

Figure 5 Stacked histogram of functional groups of each community (BSS: Bering Sea shelf community; BST: Bering Strait transitional community; CSS: Chukchi Sea shelf community).

Table 3 Species contribution in community classification (result of SIMPER program)

Community	Species	Contribution
BSS	*Neocalanus flemingeri*	14.43%
	Eucalanus bungii	12.96%
	Parasagitta elegans	12.93%
	Aglantha digitale	12.82%
	Pseudocalanus sp.	11.68%
	Metridia pacifica copepodite	9.82%
	Euphausiacea	4.15%
	Amphipoda	3.82%
BST	*Pseudocalanus* sp.	18.18%
	Centropages abdominalis	10.14%
	Metridia pacifica copepodite	8.18%
	C. glacialis C5	7.46%
	Acartia longiremis	6.20%
	Parasagitta elegans	5.96%
	Gastropods larva	5.62%
	Eucalanus bungii	4.66%
CSS	*Pseudocalanus* sp.	21.61%
	Pseudosagitta elegans	9.91%
	Oikopleura vanhoffeni	9.83%
	C. glacialis C4	8.75%
	C. glacialis C3	6.93%
	C. glacialis C5	2.82%
	C. glacialis C2&C1	5.80%
	Metridia pacifica copepodite	5.54%

The composition of dominant species also varied among communities (Table 4). *Parasagitta elegans* and *P. minutus* were the dominant species in all three communities, but their dominance was not consistent with each other. The dominant species of the BSS mainly comprised oceanic species. *Eucalanus bungii* was the most dominant species, followed by *A. digitale* and *Metridia pacifica* copepodites. Although *P. minutus* and *Eukrohnia hamata* were also dominant species in the BSS, they were the least dominant. The BST was dominated by neritic copepods and meroplankton. *Centropages abdominalis* and *P. minutus* had the highest dominance, followed by Cladocera, gastropod larva and barnacle nauplii. Except for *P. elegans,* all the dominant species of the CSS were copepods. All copepodite stages of the pan-Arctic distributed *C. glacialis* were dominant species in the CSS.

3.4 Correlations between mesozooplankton assemblage and environmental factors

According to the results of the BIO-EVN program, salinity was the most influential factor for mesozooplankton assemblage, followed by Ave-Chl-*a* (Table 5). The single most influential environmental factor for mesozooplankton composition and distribution was 30m-S. The most influential multi-factor was the combination of 5m-S and 30m-S.

Table 4 List of dominant species and their dominance (*Y*) in each community

Community	species	*Y*
BSS	*Eucalanus bungii*	0.22
	Aglantha digitale	0.19
	Metridia pacifica copepodite	0.12
	Parasagitta elegans	0.10
	Pseudocalanus minutus	0.06
	Eukrohnia hamata	0.02
BST	*Centropages abdominalis*	0.37
	Pseudocalanus minutus	0.26
	Cladocera	0.09
	Parasagitta elegans	0.04
	Gastropods larva	0.04
	Barnacle nauplii	0.03
	Pseudocalanus newmani	0.03
	Acartia longiremis	0.03
CSS	*C. glacialis* C4	0.14
	C. glacialis C3	0.12
	Pseudocalanus minutus	0.08
	C. glacialis C2＆C1	0.06
	C. glacialis C5	0.04
	Metridia longa copepodite	0.04
	Pseudocalanus newmani	0.03
	Parasagitta elegans	0.02

Table 5 Results of BIO-EVN

No. of variables	Correlation	Selections
1	0.503	5
2	0.486	2,5
4	0.451	1,2,5,7
3	0.451	1,5,7
3	0.448	2,5,7
2	0.446	4,5
3	0.446	1,2,5
2	0.443	5,7
1	0.441	2
3	0.44	2,4,5

Variables: 1: 5m-T; 2: 5m-S; 3: 5m-Chl-*a*; 4: 30m-T; 5: 30m-S; 6: 30m-Chl-*a*; 7: Ave-Chl-*a*

The correlation between different species abundance and environmental factors were also compared in this study (Table 6). There was no correlation between the abundance of any species and 5m-Chl-*a*. The species compositions that had significant ($p<0.05$) correlations with 5m-S and 30m-S were completely consistent, mainly composed of large-sized *C. glacialis*, *C. hyperboreus*, *Metridia longa*, *Paraeuchaeta glacialis*, and their copepodites. Compared with salinity, C4 and C3 stages of *C. glacialis* showed no significant correlation to 5m-T. The species compositions that were correlated with 30m-Chl-*a* and Ave-Chl-*a* were similar, being mainly composed of C5, the C4 stages of *P. glacialis*, and rare species such as *Aetideopsis rostrata* and *Dimophyes arctica*.

Table 6 Spearman's rank correlation between mesozoopalnkton species and environmental factors (only species with $p\leqslant0.05$ are showed here)

Factors	Species	Significance	Factors	Species	Significance
5m-T	*C. glacialis* Adult	0.000	5m-S	*C. hyperboreus* C4	0.000
	C. glacialis C1＆C2	0.002		*C. hyperboreus* C3	0.000
	C. hyperboreus C4	0.001		*C. hyperboreus* C1＆C2	0.000
	C. hyperboreus C3	0.001		*P. galacialis* C3	0.003
	C. hyperboreus C1＆C2	0.001		*M. longa* Adult	0.019
	P. galacialis C3	0.010		*M. longa* Copepodite	0.019
	M. longa Adult	0.050		*A. laurentii*	0.002
	M. longa Copepodite	0.050		*P. maxima*	0.019
	A. laurentii	0.010	5m-Chl-*a*	None	—
	P. maxima	0.050		*C. glacialis* Adult	0.025
5m-S	*C. glacialis* Adult	0.000		*C. glacialis* C4	0.016
	C. glacialis C4	0.000		*C. glacialis* C3	0.011
	C. glacialis C3	0.000		*C. glacialis* C1＆C2	0.006
	C. glacialis C1＆C2	0.000		*C. hyperboreus* Adult	0.034
	C. hyperboreus Adult	0.023		*C. hyperboreus* C3	0.036

continued

Factors	Species	Significance
30m-T	*C. hyperboreus* C1&C2	0.035
	P. galacialis C4	0.026
	E. bungii	0.001
	S. minor	0.047
	C. pacificus	0.026
	N. cristatus	0.033
	D. arctica	0.026
	E. hamata	0.023
	Euphausiacea larvae	0.026
	Amphipoda	0.000
	Ostracods	0.048
30m-S	*C. glacialis* Adult	0.018
	C. glacialis C4	0.004
	C. glacialis C3	0.019
	C. glacialis C1&C2	0.006
	C. hyperboreus Adult	0.024
	C. hyperboreus C4	0.000
	C. hyperboreus C3	0.000
	C. hyperboreus C1&C2	0.000
	P. galacialis C3	0.004
	M. longa Adult	0.024
	M. longa Copepodite	0.024
	A. laurentii	0.003
	P. maxima	0.024
30m-Chl-*a*	*P. galacialis* C5	0.035
	P. galacialis C4	0.013
30m-Chl-*a*	*Pseudocalanus* sp.	0.020
	S. minor	0.019
	C. pacificus	0.013
	E. pacifica	0.011
	P. robusta	0.013
	A. rostrata	0.023
	D. arctica	0.013
	E. hamata	0.019
	Tomopteris sp.	0.013
	Euphausiacea larvae	0.013
	Barnacle nauplii	0.030
	Ostracods	0.025
Ave-Chl-*a*	*P. galacialis* C5	0.003
	P. galacialis C4	0.000
	S. minor	0.001
	C. pacificus	0.000
	P. robusta	0.000
	D. arctica	0.000
	A. laurentii	0.020
	E. hamata	0.000
	Tomopteris sp.	0.000
	Euphausiacea larvae	0.000
	Amphipoda	0.008
	Ostracods	0.001
	Fish larvae	0.036

4 Discussion

4.1 Community patterns and geographical distribution

The community structure and geographical distribution of zooplankton can be affected by multiple factors. Varying results can be obtained owing to differences in the time of investigation, sampling method, station setting, and species identification accuracy (e.g., Ashjian et al., 2003; Lane et al., 2008; Hopcroft et al., 2010, Matsuno et al., 2011). In previous studies, large-scale surveys tended to result in geographical communities with obvious differences in species composition and abundance, while the communities identified in small-scale surveys tended to overlap with one another in geographical distribution (Xu et al., 2018a). For example, seven overlapping communities were identified in the survey of the eastern Chukchi Sea in 2007 and 2008 (Matsuno et al., 2011). Through our results, we identified three geographical communities, located in the Bering Sea shelf, Bering Strait, and the northern Chukchi Sea. The species composition of each community is consistent with single surveys conducted in the past (e.g., Coyle et al., 1996; Ershova et al., 2015a, 2015b). The CSS was dominated by copepods, and the pan-Arctic distributed *C. glacialis* and *Pseudocalanus* sp. were two of the most abundant species. The BSS was dominated by oceanic species originating in the Bering Sea. Besides neritic species, the BST had the characteristics of both BSS and CSS. Therefore, it was considered a transitional community. Generally, the community level better reflected the spatial differences of ecosystems than the species level in our study.

Zooplankton can be transported by ocean currents over a large scale. The inflow flux of Bering Sea Water is one of the key variables of hydrological monitoring in the Bering Strait (e.g., Woodgate et al., 2015; Woodgate, 2018). All previous studies near the Bering Strait tried to link the zooplankton community structures with water masses. For example, Hopcroft et al. (2010) divided the zooplankton in the Chukchi Sea into five communities that corresponded to five different water masses. According to the results of cluster analysis, the locations of geographical communities had significant differences in latitude direction. The CSS was dominated by copepodites of *C. glacialis*. The species *C. hyperboreus* and *M. longa* are typical Arctic oceanic species, which only survive in deep Arctic basins (Hirche and Mumm, 1992; Hirche and Niehoff, 1996). They were also recorded only at stations M11 and M14. Additionally, numerous *E. bungii* (24.20 ind.·m^{-3}) were recorded at station R06. As a representative species of the Bering Sea, the occurrence of *E. bungii* in the CSS indicates that the Bering Sea Water reached the middle area of the Chukchi Sea during our investigation. Affected by the Bering Shelf Water, the BSS was dominated by Bering Sea species. The most dominant species in the BSS, *E. bungii*, *A. digitale*, and *M. pacifica*, are all oceanic species of the Bering Sea. The BST was affected by Alaska Coastal Water, Bering Shelf Water, Anadyr Water, and Siberian Coastal Water (Pickart et al., 2010). This can also be distinguished from the BS transect in our study. Both the values of 5m-T and 30m-T at station BS02 were higher than that of station BS05, and they were the highest at station BS08. Meanwhile, the values of 5m-S and 30m-S were just the opposite. In addition, although Bering Sea species were also recorded in the BST, they were not dominant species. The BST was dominated by widely distributed *P. minuntes*, neritic *C. abdominalis* and larvae of benthos. This indicates that the inflow of Bering Sea Water did not play a decisive role in the composition of the community during our investigation.

In addition to physical transportation, the reproduction and development of local species also significantly influence zooplankton community structure. This is most obvious in the case of BST. There are many meroplankton in the BST. Barnacle nauplii and gastropods were two of the most abundant groups of the BST and they are both larvae of benthos. Barnacle nauplii were concentrated at stations BS08 (119 ind.·m^{-3}) and BR11 (168.3 ind.·m^{-3}), which is where benthic adults were also found (Schlüter and Rachor, 2001; Willis et al., 2006). In the growth period during summer, barnacle nauplii and cypris larvae often occur in high abundance and even exceed the total number of holozooplankton (Hopcroft et al., 2010; Xu et al., 2018a). The adults can also adsorb on the chitin shells of other organisms and migrate with them, spreading the larvae throughout the entire shelf areas. Barnacle feeding on phytoplankton is also considered a main competition factor in the reproduction and development of *C. glacialis* (Xu et al., 2018a). Gastropods were recorded only in shallow waters, with their highest abundance being 174.62 ind.·m^{-3} (BS05). Similar to barnacle nauplii, the geographic distribution of gastropod larvae overlapped with that of benthic adults. At the same time, there were also many Euphausiacea, with an average abundance of 4.91 ind.·m^{-3}. Barnacle larvae, gastropods, and Euphausiacea are typical filter-feeding species, and they are more adaptable to high phytoplankton concentrations (Clare and Walker, 1986). This confirms that the ecosystems of the Bering Sea shelf and Chukchi Sea are still dominated currently by the benthic food chain.

The abundance of small zooplankton (<2.0 mm) in our study was much lower than in previous studies (e.g., Hopcroft et al., 2010; Xu et al., 2018a). *Acartia longiremis* and *C. abdominalis* were not dominant in any community, and the abundance of barnacle larvae was much lower than reported in other surveys. This is mainly because of the size differences in dragging nets. The net mesh size in our study was 500 μm, whereas it was smaller (200 μm or 330 μm) in other studies. Moreover, many copepod nauplii (body length <200 μm) have been recorded in other studies (e.g., Hopcroft et al., 2010; Matsuno et al., 2011), which suggests that copepods in this region have an ability for rapid recruitment.

4.2 Effects of environmental factors on mesozooplankton assemblage

Although previous studies linked the zooplankton assemblage with water masses, they were descriptive in making geographical correlations and lacked statistical analyses (e.g., Matsuno et al., 2011; Ershova et al., 2015a). In this study, three geographical communities corresponding to three different habitats were identified (Table 7). The BSS was characterized by high temperature, high salinity, and high Chl-*a* concentrations. The BST was characterized by medium temperature, medium salinity, and low Chl-*a* concentrations. The CSS was characterized by low temperature, low salinity, and medium Chl-*a* concentrations. At the same time, there was no significant relationship between total mesozooplankton abundance and environmental factors (p>0.05). Meanwhile, the significant correlations (p<0.05) were found between some species and environmental factors (Table 6). Notably, these species included a lot of endemic or rare species within each community, such as *E. bungii* and *C. hyperboreus*. Statistically, endemic and rare species will strongly exaggerate their statistical significance when correlation analysis is performed. Thus, the assemblage of mesozooplankton can only be partly explained by environmental factors.

Studies in the eastern Canadian Archipelago showed that zooplankton tend to be concentrated in layers where the concentration of chlorophyll is the largest (Longhurst et al., 1984). In our results, no species showed a correlation with 5m-Chl-*a* (Table 6). The species that had significant correlations with Ave-Chl-*a* were all rare species, accounting for less than 3% of the total abundance. The results of the BIO-EVN program also showed that 5m-Chl-*a* had little effect on community structure. At shallow stations, the concentration of 5m-Chl-*a* was much higher than that of 30m-Chl-*a* and Ave-Chl-*a*. However, the concentration of 5m-Chl-*a* was extremely low at deep stations M11 and M14. The highest concentrations of these two stations were observed in the subsurface at 35 m. This

Table 7 Environmental conditions of each geographical community

Environmental factors	BSS		BST		CSS	
	Ave	Range	Ave	Range	Ave	Range
5m-T/°C	10.92	10.00–11.21	7.61	2.37–10.78	5.83	0.06–10.39
5m-S/psu	32.43	31.91–32.88	31.96	30.83–32.85	29.99	28.04–32.17
5m-Chl-*a*/(μg·L^{-1})	1.89	0.50–3.98	2.20	0.32–7.61	0.65	0.04–1.55
30m-T/°C	6.72	6.72–11.04	3.45	1.04–5.91	0.83	−1.50–5.85
30m-S/psu	32.54	32.04–33.00	32.49	31.89–32.85	31.99	31.21–32.55
30m-Chl-*a*/(μg·L^{-1})	0.91	0.18–2.87	1.20	0.09–2.91	0.33	0.21–0.55
Ave-Chl-*a*/(μg·L^{-1})	1.80	0.69–3.99	1.07	0.39–2.21	0.52	0.12–0.92

non-correlation between the dominant species and Chl-*a* concentration might be related to the investigation period. In late August and early September, the dominant species represented by *C. glacialis* have finished feeding and start to migrate to the deep water to overwinter (Thibault et al., 1999; Auel and Hagen, 2002), and the nauplii of benthos also start to enter the benthic attachment stage (Kędra et al., 2012). This suggests that food may not be the decisive factor for mesozooplankton distribution in late autumn.

Both the results of correlation analysis and the BIO-EVN program showed that salinity was the most influential factor for mesozooplankton assemblage, especially 30m-S (Tables 5, 6). Except for *A. laurentii*, all species that had significant correlations with salinity were endemic to the Arctic Ocean. The species that were significantly correlated with 5m-T were mostly consistent with those that were linked to salinity. This suggests that compared with the concentration of Chl-*a*, species with different ecological adaptability have stricter temperature and salinity requirements.

4.3 Possible response of mesozooplankton community to rapid ice retreat

Recent and projected changes in the extent and timing of the ice cover in the Arctic are expected to have a profound impact on Arctic marine ecosystems (Hassol, 2004). Our study areas will be completely covered by sea ice in the winter and ice-free in the summer. The seasonal formation and retreat of sea ice determine the time and intensity of ice-algae/phytoplankton blooms (Ardyna and Arrigo, 2020). The relatively short life histories and weak swimming abilities of zooplankton also suggest that they are more sensitive to environmental changes than other marine organisms (Smith and Schnack-Schiel, 1990; Deibel and Daly, 2007).

Presently, the trophic structures of Chukchi Sea and Bering Sea shelf are dominated by the benthic food chain. It is generally believed that only a small portion of primary production can be consumed by zooplankton and that most of it settles into the benthic food chain (Grebmeier et al., 2006b). With rising temperatures and the rapid decline of sea ice, many researchers have proposed that more primary production will be utilized by zooplankton, and that the pelagic food chain will eventually replace the benthic food chain as the dominant food chain (Feder et al., 2005; Grebmeier et al., 2006b). On the Bering Sea shelf, it has been observed that the species of benthos moved northward and that the number of higher trophic organisms such as seabirds and sea animals increased (Grebmeier et al., 2006a; Coyle et al., 2007).

For mesozooplankton, special hydrographic features determine whether the zooplankton communities on the Bering Sea shelf and in the Chukchi Sea will be affected by the inflow of Bering Sea Water (e.g., Hopcroft et al., 2010). In a long-term study on zooplankton in the Chukchi Sea, the abundances of *E. calanus*, *Neocalanus* sp., and *M. pacific* were directly related to the inflow flux of the Bering Sea (Ershova et al., 2015b). In the years with a high inflow flux, the abundance and proportion of species with Bering Sea origins increased significantly, and they even became the dominant species. To find the interannual changes in Bering Sea inflow flux, Woodgate (2018) conducted continuous monitoring year by year. They found that the inflow flux of the Bering Sea is fluctuating upward. According to the composition of dominant species, species with Bering Sea origins are dominant in the BSS, but the BST and CSS were dominated by endemic and pan-Arctic distributed species. This indicates that the Bering Sea Water did not play a significant role in community structures of the BST and CSS during our investigation.

The fluctuation in the inflow flux of Bering Sea Water also makes it difficult to identify the changes caused by local recruitment. For now, there are no acknowledged pioneer species of zooplankton responding to climate changes in the whole pan-Arctic. It is generally suggested that climate change is more beneficial to subarctic species than to Arctic species. Gregory et al. (2009) and Mueter et al. (2009) proposed that warming would promote the expansion of subarctic species (such as *Calanus finmarchicus*) into the Arctic Ocean, while the distribution of Arctic species (such as *C. glacialis*) would shrink. Using model simulations, Feng et al. (2018) predicted that the distribution of *C. glacialis* was moving toward the central area of the Arctic Ocean. According to the accumulated temperature development model, the life history cycle of copepods is related to water temperature. Falk-Petersen et al. (2007) and Kjellerup et al. (2012) pointed out that climate change is more beneficial to species with short life cycles but unfavorable to the traditional Arctic species with long life cycles. Also, given that the body size of zooplankton is related to temperature (Hop et al., 2006), species are expected to become smaller with climate warming (Hopcroft et al., 2010). Based on the relationship between zooplankton recruitment and ice-algae/phytoplankton blooms, Søreide et al. (2010) proposed the hypothesis of "Match-Mismatch." Its core idea is that the breeding cycle of *C. glacialis* is perfectly consistent with the continuous bloom of ice-algae and phytoplankton, so it may become the dominant zooplankton species in the pan-Arctic sea areas. The rapid retreat of sea ice will lead to the disappearance of this advantage, which may eventually lead to decreased population recruitment. However, the field survey conducted in the Chukchi Sea showed that the abundance of *C. glacialis* multiplied in 2012 (Ershova et al., 2015a; Xu et al., 2018a).

Station BL12 was categorized into the CSS in our results. According to the species composition, it is mainly because many *C. glacialis*, which commonly appeared in the CSS, were recorded at station BL12. The presence of two *C. glacialis* subspecies has been confirmed in the north of the Bering Sea and the Chukchi Sea (Nelson et al., 2009). Ershova et al. (2015a) believed that most of the *C. glacialis* migrated from the Bering Sea, while Xu et al. (2018a) suggested this was the result of local recruitment. According to the geographical distribution, *C. glacialis* is distributed unevenly in the Bering Sea shelf area, and only a few individuals were recorded at adjacent stations. The copepodite composition of *C. glacialis* at station BL12 was also different from that of other stations in the CSS. All *C. glacialis* individuals at station BL12 were C5 or C4 copepodites, and they were mainly composed of the early stages C1–C3 at stations in the CSS. This indicates that the *C. glacialis* individuals recorded at station BL12 had different origins from those recorded at other stations. Meanwhile, the inflow of Bering Sea Water had little effect on the composition of mesozooplankton in the CSS owing to the lack of species with Bering Sea origins. Additionally, it is difficult to distinguish the subarctic *Calanus marshallae* from *C. glacialis* via morphology (e.g., Frost, 1974). In many studies, the former was considered to be *C. glacialis* (e.g., Ershova, 2015a). However, regardless of which species they may be, they have similar niches and functions. Thus, identifying the origins of *C. glacialis* and its interannual changes are important to the studies of zooplankton responses to climate change.

Calanus hyperboreus is a typical dominant species of the Arctic Ocean and was recorded only at stations M11 and M14 in this study. It only lives in deep waters because it cannot overwinter in shallow waters. In its late stages it will migrate to deep waters to overwinter after accumulating a large amount of oil, and will migrate to the surface for feeding and breeding during the growing seasons. In our study, all *C. hyperboreus* individuals were C1–C3 copepodites. This supports the idea that the continental slope area is a potential hot spot for recruitment (Xu et al., 2018b). Similarly, Kristina et al. (2018) hold the same view after conducting model simulations. With climate warming and the rapid retreat of sea ice, primary production was thought to have increased in the shelf areas of the Arctic Ocean (Arrigo et al., 2008). Higher water temperatures and higher primary production may be more beneficial to the recruitment of *C. hyperboreus* and the development of its early stages. As *C. hyperboreus* is the main primary consumer in the central Arctic Ocean, there will be more primary production transferred into the pelagic food chain, and perhaps the pelagic food chain will thrive in the near future.

5 Conclusions

The mesozooplankton can be divided into three geographical communities from the Bering Sea shelf to the northern Chukchi Sea: the BSS, the BST and the CSS. In contrast to other studies, the dominant species in this study were mainly composed of large copepods (body length > 2 mm) rather than small copepods (body length <2 mm). This is because the mesh size of the net we used was larger (500 μm compared with 200 μm or 330 μm). Although the inflow of the Bering Sea Water can affect the community structure of mesozooplankton in the Bering Strait and the Chukchi Sea shelf, it did not play a major role during our investigation. The community structure of the BSS was strongly affected by the inflow of Bering Shelf Water, while that of the BST and CSS were determined by the recruitment of local species. It is difficult to distinguish the changes induced by climate change from the impact of Bering Sea Water. Accumulating comparable data is crucial for solving this problem. This requires continuous monitoring of key species such as *C. glacialis* and *C. hyperboreus*.

Acknowledgments This study was financially supported by the National Natural Science Foundation of China (Grant nos. 41706217, 42166228). We thank the crew of the R/V *Xiangyonghong 01* for their help in sampling during the 10th Chinese National Arctic Research Expedition. We also thank Dr. Zhensheng Liu and Dr. Chunsheng Wang as reviewers, another anonymous reviewer, and Associate Editor Dr. Ad H. L. Huiskes for reviewing this manuscript.

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