



ELSEVIER

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Review of spatial and inter-annual changes in the zooplankton community structure in the western Arctic Ocean during summers of 2008–2017

Yoshiyuki Abe^{a,b,*}, Kohei Matsuno^{c,d}, Amane Fujiwara^e, Atsushi Yamaguchi^{c,d}

^a Research Development Section, Office for Enhancing Institutional Capacity, Hokkaido University, Kita 21, Nishi 10, Kita-ku, Sapporo, Hokkaido 001-0021, Japan

^b Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan

^c Graduate School of Fisheries Science, Hokkaido University, 3-1-1 Minatomachi, Hakodate, Hokkaido 041-8611, Japan

^d Arctic Research Center, Hokkaido University, Kita-21 Nishi-11 Kita-ku, Sapporo, Hokkaido, 001-0021, Japan

^e Japan Agency for Marine-Earth Science and Technology, 2–15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan

ARTICLE INFO

Keywords:

Western Arctic Ocean
Mesozooplankton
Copepods
Spatial distribution
Community structure
Pelagic ecosystem

ABSTRACT

Reduction in summer sea ice coverage has recently been observed in the western Arctic Ocean. Changes in the coverage and timing of sea ice retreat are expected to have a great impact on the marine ecosystem. In this study, we evaluated inter-annual changes in the spatial distribution of zooplankton communities in the western Arctic Ocean, during the summers of 2008, 2010, 2012–2017. A total of 339 casts were conducted to collect zooplankton by vertical hauls at 22–63 stations per year in the western Arctic Ocean, between August 26 and October 13, 2008, 2010, 2012–2017. Based on cluster analysis, four zooplankton communities (basin, slope, shelf, and new-shelf) were identified. Horizontal distribution of the zooplankton communities corresponded with the depth of the sea floor. No significant interannual variability in zooplankton and copepod abundance was observed in the Canada basin; however, a decline in the abundance of dominant copepods associated with an enhanced freshening of seawater was suggested by a General Linear Model analysis. The shelf assemblage was characterized by a high abundance of Pacific species that was predicted by the length of the open water period. The new-shelf assemblage, located between the shelf and the slope, showed low species diversity and abundance and was observed only in 2012, 2015, 2016 and 2017 when the melting day of sea ice was significantly earlier than in the other years. Our study indicates that different changes in each region can be expected in response to the possible environmental changes in the Pacific Arctic.

1. Introduction

Recently, atmospheric warming in the Arctic has been progressing at twice or thrice the rate in other parts of the globe (Trenberth et al., 2007). A reduction in sea ice coverage during summer has also been reported for the Arctic Ocean (Duarte et al., 2012). The Pacific Arctic (western Arctic Ocean, Fig. 1), consisting of a shallow continental shelf extending from northern Bering Sea to the Chukchi Sea and the Canada Basin, is one of the areas showing the highest sea ice reduction (Comiso et al., 2008; Markus et al., 2009; Shimada et al., 2001, 2006; Stroeve et al., 2007). In reality, because of an earlier sea ice melt timing and a later autumn freeze-up, it has been reported that the melt season in the Chukchi Sea has increased at a rate of 13.2 days decade⁻¹, from 1979 to 2013 (Stroeve et al., 2014). Although there are numerous processes that can accelerate the reduction of sea ice in summer (Kashiwase et al., 2017; Stroeve et al., 2012), the Western Arctic reduction in sea ice is related to an increased inflow of warm Pacific waters (Shimada et al.,

2006; Woodgate et al., 2010). It has been reported that the increased Pacific summer water (PSW) inflow not only affects the reduction of sea ice, but also causes changes in the marine environment, such as the occurrence of a large warm-core eddy within the shelf break area of the Chukchi Sea and the enhancement of the Beaufort Gyre (Kwok et al., 2013; Nishino et al., 2011a). These changes in the coverage and retreat timing of sea ice are expected to have a great impact on the marine environment (Grebmeier et al., 2006; Hunt and Drinkwater, 2007) making it increasingly important to study the lower trophic levels in the western Arctic Ocean, in order to evaluate the effects of sea ice reduction on marine ecosystems.

Environmental changes caused by sea ice reduction in the Pacific Arctic are thought to have a relatively early impact on the plankton communities that have a shorter life cycle than organisms at higher trophic levels. Accurate evaluations and predictions of the plankton community structures are becoming increasingly important to understanding marine ecosystem dynamics in the western Arctic Ocean.

* Corresponding author.

E-mail address: y.abe@aori.u-tokyo.ac.jp (Y. Abe).

<https://doi.org/10.1016/j.pocean.2020.102391>

Received 1 November 2019; Received in revised form 4 March 2020; Accepted 7 June 2020

Available online 20 June 2020

0079-6611/ © 2020 Elsevier Ltd. All rights reserved.

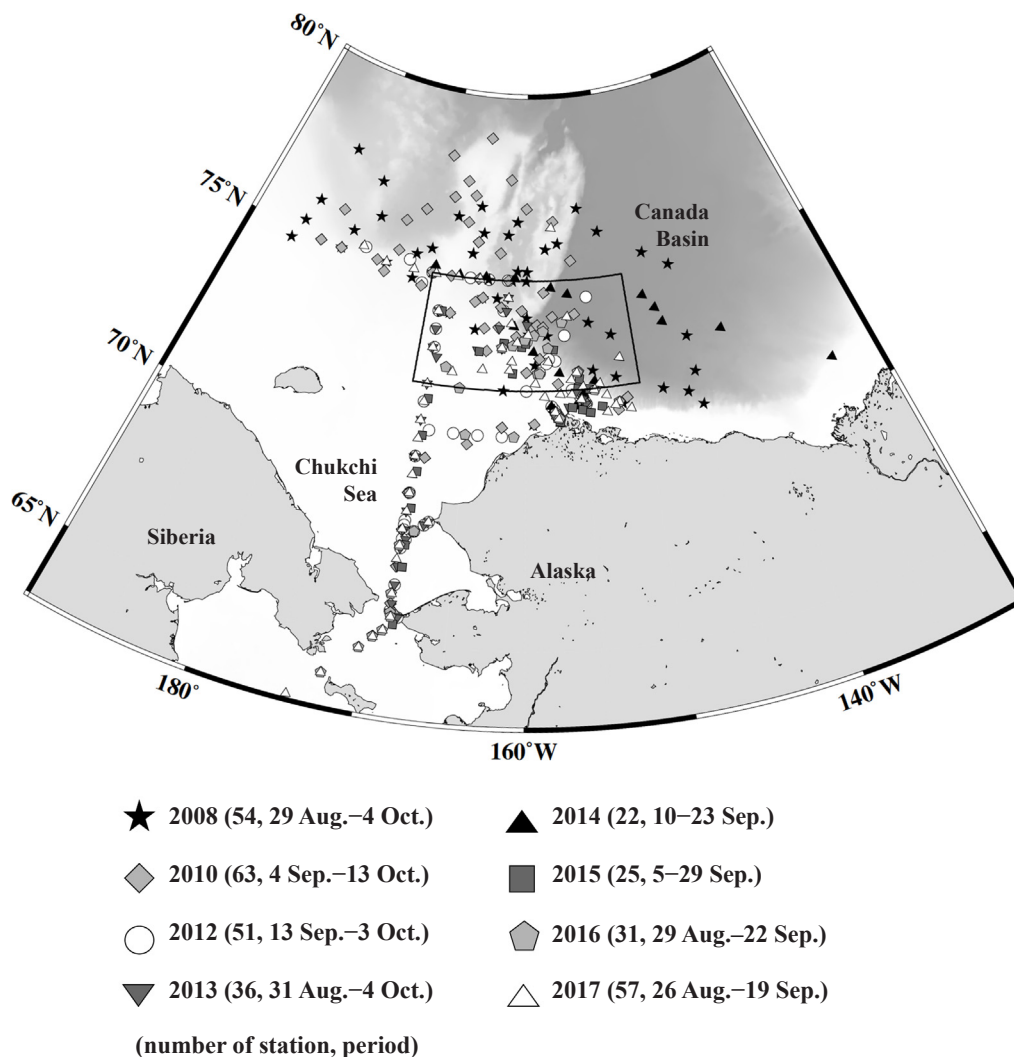


Fig. 1. Location of the sampling stations in the western Arctic Ocean during August–October 2008 and 2017. For the generalized linear model (GLM) analysis, we extracted the abundance data from a gridded area (72°N–75°N, 150°W–170°W), where net sampling was conducted every study year.

Phytoplankton communities exhibit major seasonal and spatial variations (Codispoti et al., 2005; Springer and McRoy, 1993), and Matsuno et al. (2014) reported that the distribution of microplankton communities, including organisms from phytoplankton to ciliates, varies with the latitude. Furthermore, environmental changes, such as earlier sea ice retreat, can influence the phytoplankton community structure, e.g., haptophytes dominate the surface layer in the northern Chukchi Sea with earlier melt year (Fujiwara et al., 2014; Lee et al., 2019).

Zooplankton, the secondary producers in the marine ecosystem, connect the lower and upper trophic levels and are an important food source for pelagic fishes, seabirds, and whales (Ashjian et al., 2010; Lowry et al., 2004; Wassmann et al., 2006). Zooplankton communities show great spatial variations, corresponding to the water masses of the northern Bering Sea and the southern Chukchi Sea (Ershova et al., 2015a; Hopcroft et al., 2010; Sasaki et al., 2016; Xu et al., 2018), the eastern Chukchi Sea (Ashjian et al., 2017; Pinchuk and Eisner, 2017; Spear et al., 2019), and the Beaufort Sea (Smoot and Hopcroft, 2017). It also has been shown that the yearly strength of PSW advection influences zooplankton community structure, resulting in differences in their interannual horizontal distribution during summer in the Chukchi Sea (Matsuno et al., 2011; Pinchuk and Eisner, 2017; Spear et al., 2019). Despite numerous studies of zooplankton community structure in the western Arctic Ocean, the majority of past studies have focused on limited regions and years, with only a few long-term studies since

2000, when sea ice reduction became rapid, covering broader areas.

In this study, we first evaluated inter-annual changes in the horizontal distribution of zooplankton assemblages, derived from zooplankton abundance, biomass, and species diversity data collected from the northern Bering Sea and the southern Chukchi Sea to the Canada Basin in the western Arctic Ocean, during the summers of 2008, 2010, and 2012–2017. We then explored the characteristics of each group by cluster analysis to reveal further the inter-annual changes in the zooplankton assemblages of each group. In the shelf break and slope area, where sampling was possible every year, we evaluated the parameters governing the standing stock of the Arctic copepod *Calanus glacialis*, a key species in the western Arctic Ocean, in addition to predicting their future abundance using a statistical model.

2. Materials and methods

2.1. Field sampling

A total of 339 vertical hauls of a NORPAC net (mouth diameter 45 cm, mesh size 335 μ m) from 150 m (for stations with > 150 m depth) or 5 m above the sea bottom (for stations with < 150 m depth) up to the sea surface were conducted to collect zooplankton (Table S1; Fig. 1). Sampling was conducted from the R/GC Amundsen in 2014 and from the R/V Mirai in other years. The volume of water filtered through

the net was estimated using a flow-meter (Rigosha Co. Ltd.) mounted on the mouth of the net. Once onboard, zooplankton samples were immediately preserved in 5% v/v borax buffered formalin. At each station, the temperature and salinity were measured with a rosette mounted CTD sampler (Sea-Bird Electronics Inc., SBE 911 Plus). Seawater samples were collected from 4 to 9 discrete depths as well as at 5 m and at 150 m (for stations in > 150 m bottom depth) or 10 m above the sea bottom (for stations with < 150 m depth), using Niskin bottles mounted on a rosette. Nutrient concentrations (NO_2 , NO_3 , NH_4 , PO_4 and $\text{Si}(\text{OH})_4$) in the water samples were analyzed onboard using an auto-analyzer. Chlorophyll *a* (Chl. *a*) concentrations were also determined fluorometrically by the non-acidification technique (Welschmeyer, 1994), using a 10-AU fluorometer (Turner Designs Inc., San Jose, CA, USA). All hydrographic datasets were provided by Japan Agency for Marine-Earth Science and Technology (JAMSTEC).

2.2. Samples and data analyses

In the laboratory, zooplankton samples were split using a Motoda box splitter (Motoda, 1959). An aliquot from each sample was weighed for wet mass (WM), with a precision of 0.01 g, using an electronic balance (Mettler PM4400). The sample remaining was used for the identification and enumeration of zooplankton under a dissecting microscope. Calanoid copepods were identified to the species level, following mainly Brodskii (1967) and Frost (1989) for *Pseudocalanus* spp. (*P. acuspes*, *P. mimus*, *P. minutus* and *P. newmani*), and Miller (1988) for *Neocalanus* spp. Because *Calanus glacialis* and *C. marshallae* are morphologically very similar, the two species were not differentiated and were pooled as *C. glacialis*. For the early copepodid stages of *Calanus* spp. (*C. glacialis* and *C. hyperboreus*), we used the prosome length for species identification (Hirche et al., 1994; Kosobokova and Hirche, 2016). For *Pseudocalanus* spp., species identification was done for late copepodid stages (C5F/M and C6F/M), and the early copepodid stages were integrated as *Pseudocalanus* spp. For *C. glacialis*, the Mean Copepodid Stage (MCS) was calculated using the following equation:

$$MCS = \frac{\sum_{i=1}^6 i \times A_i}{\sum_{i=1}^6 A_i} \quad (1)$$

where *i* is the copepodid stage (1–6 indicates C1–C6), and A_i (ind.m⁻²) is the abundance of the *i*th copepodid stage (cf. Marin, 1987). A species diversity index (*H'*) was calculated using the following equation:

$$H' = - \sum (ni/N) \times \ln(ni/N) \quad (2)$$

where *ni* is the abundance (ind.m⁻²) of the *i*th species, and *N* is the abundance of total calanoid copepods in the group (Shannon and Weaver, 1949). The abundance datasets (*X*, ind.m⁻²) for each species were log-transformed ($\log_{10}[X + 1]$). The community analysis performed for log-transformed abundance using the all of the station data across all years. Similarity between samples were calculated using the Bray-Curtis similarity index (Bray and Curtis, 1957). For grouping the samples, similarity indices were coupled with hierarchical agglomerative clustering, using a complete linkage method (UPGMA: Unweighted Pair Group Method using Arithmetic mean) (Field et al., 1982). A similarity percentage analysis (SIMPER) was conducted to determine the percent contribution of each species/taxa to the observed similarity between groups. Nonmetric Multi-Dimensional Scaling (NMDS) ordination was employed to delineate the sample groups on a two-dimensional map. The NMDS plots and the hydrographic data (latitude, longitude, depth, integrated mean temperature, integrated mean salinity, integrated mean Chl. *a*) were subjected to multiple-regression analyses. All these analyses were performed in the PRIMER v7 software (PRIMER-E Ltd., Plymouth, UK). Differences in zooplankton and copepod abundance and environmental parameters, between years and sampling days were compared using two-way ANOVA, performed using the Stat View v5 software (SAS Institute Inc.).

To evaluate the relationship between the abundance of dominant species/taxa and environmental parameters, Generalized Linear Models (GLM) were constructed in R version 3.4.3, using the glm2 package (Marschner, 2011; R Development Core Team, 2017). Abundances were used as response data for each group separated by the cluster analyses. Five explanatory variables obtained from CTD data, integrated mean water column temperature (IMT), integrated mean water column salinity (IMS), integrated mean water column chlorophyll *a* concentration (IMC), sea surface temperature (SST), and sea surface Chl. *a* (SSC), and four explanatory variables obtained from the satellite datasets (collected daily, 72 km resolution; Fujiwara et al., 2014, 2016, 2018), including annual median Chl. *a* (AMchl), annual median temperature (AMtemp), annual primary production (APP) and open period of sea ice (OpenPeriod) were included in the GLM. Backward stepwise model selection using the “MASS” package was done to fit the models. The most appropriate models were selected using the Akaike Information Criterion (AIC) (Yamaoka et al., 1978).

3. Results

3.1. Hydrography

Integrated mean temperature ranged between -1.4 and 7.8 °C during the study period, and was high in the shelf but low in the basin, particularly in the western part of the basin (Fig. 2). Integrated mean salinity during the study period ranged from 29.4 to 33.2 and was low in the eastern basin and on the shelf only in 2012. Chlorophyll *a* ranged from 8 to 290 mg m⁻², and was high on the shelf particularly off of the coast of Utqiagvik in 2008 and around the Bering Strait in 2015 and 2016.

3.2. Zooplankton abundance and biomass

Zooplankton abundance during the study period ranged between 2889 and 274,021 ind.m⁻², and was greater on the shelf than in the basin (Fig. 3). Zooplankton biomass ranged from 1 to 263 g WM m⁻², and showed a spatial pattern similar to that of the abundance distribution.

3.3. Community structure

Sixty-nine species/taxa of zooplankton and 36 species belonging to 25 genera of calanoid copepods were identified (Table 1). Based on cluster analysis of zooplankton community composition, four groups of stations: basin (*n* = 47 stations), slope (*n* = 166 stations), shelf (*n* = 80 stations) and new-shelf (*n* = 36 stations) were identified at 57% and 62% similarity levels (Fig. 4A).

Zooplankton abundance varied greatly depending on the station group. The basin stations had the second-lowest mean abundances and low species diversity, with averages of 14,029 ind.m⁻² and 1.80, respectively (Fig. 4C). For the species/taxa composition in abundance, the percentage of other copepods in the basin assemblage (13.1%) was higher than that of other groups (6.6–8.1%). The slope assemblage had intermediate abundance and species diversity, with averages of 48,329 ind.m⁻² and 1.95, respectively. In the slope assemblage, the average abundance of *C. glacialis* (14,703 ind.m⁻²) was the highest within the four groups. The shelf assemblage had the highest abundance and species diversity, with averages of 73,022 ind.m⁻² and 2.19, respectively. The shelf assemblage was characterized by a high abundance of Pacific species, especially the copepod *Metridia pacifica* (9%) that had presumably been transported from the Bering Sea. In the new-shelf assemblage, the species composition was similar to that of the slope assemblage, but it had the lowest abundance and species diversity of the groups, with averages of 13,815 ind.m⁻² and 1.75, respectively. According to the results of SIMPER analysis, the top four species that contributed most to the dissimilarity in the community structure of the

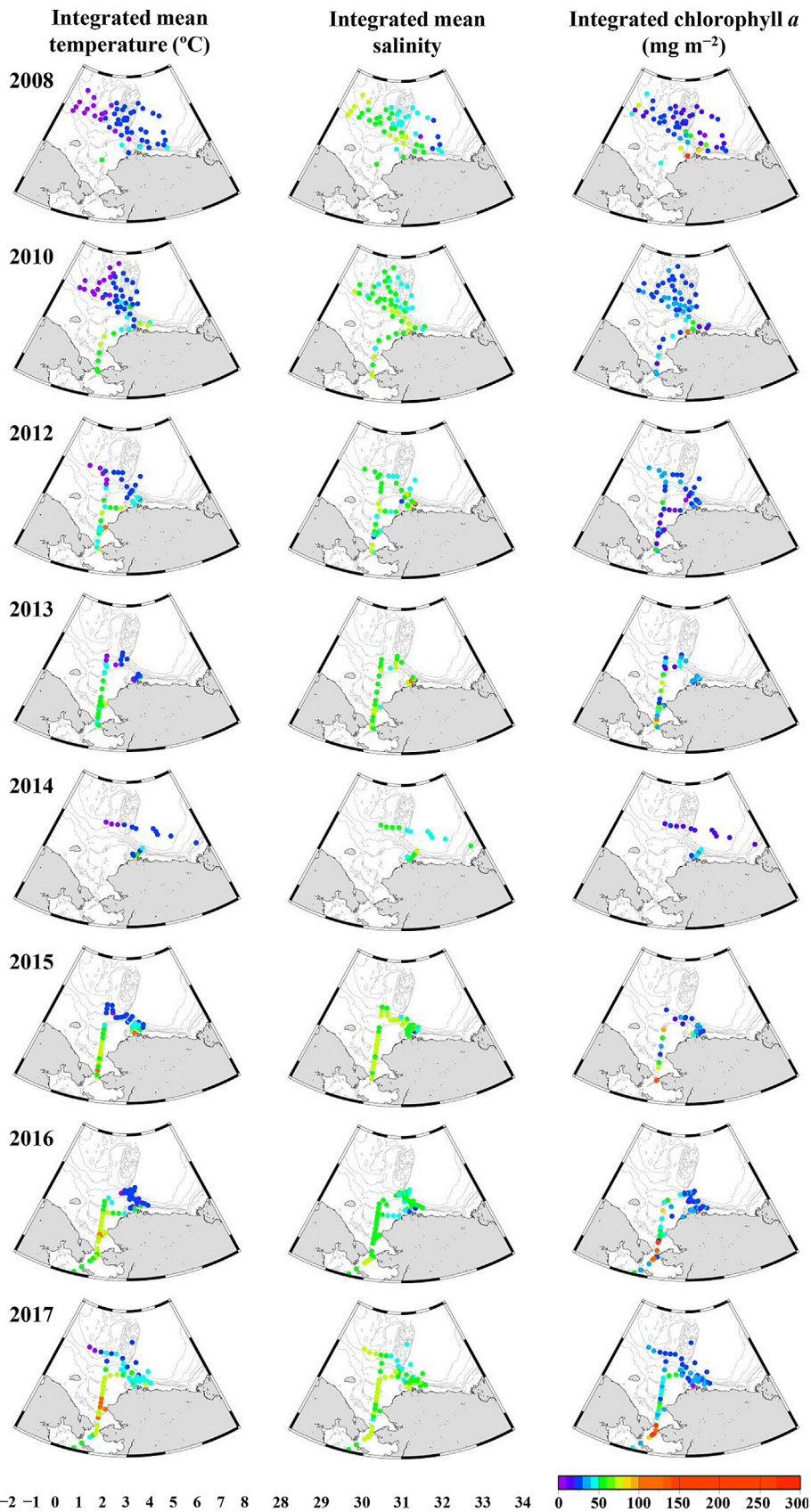


Fig. 2. Spatial changes in the integrated mean temperature, integrated mean salinity, and integrated chlorophyll a in the western Arctic Ocean during August–October 2008 and 2017.

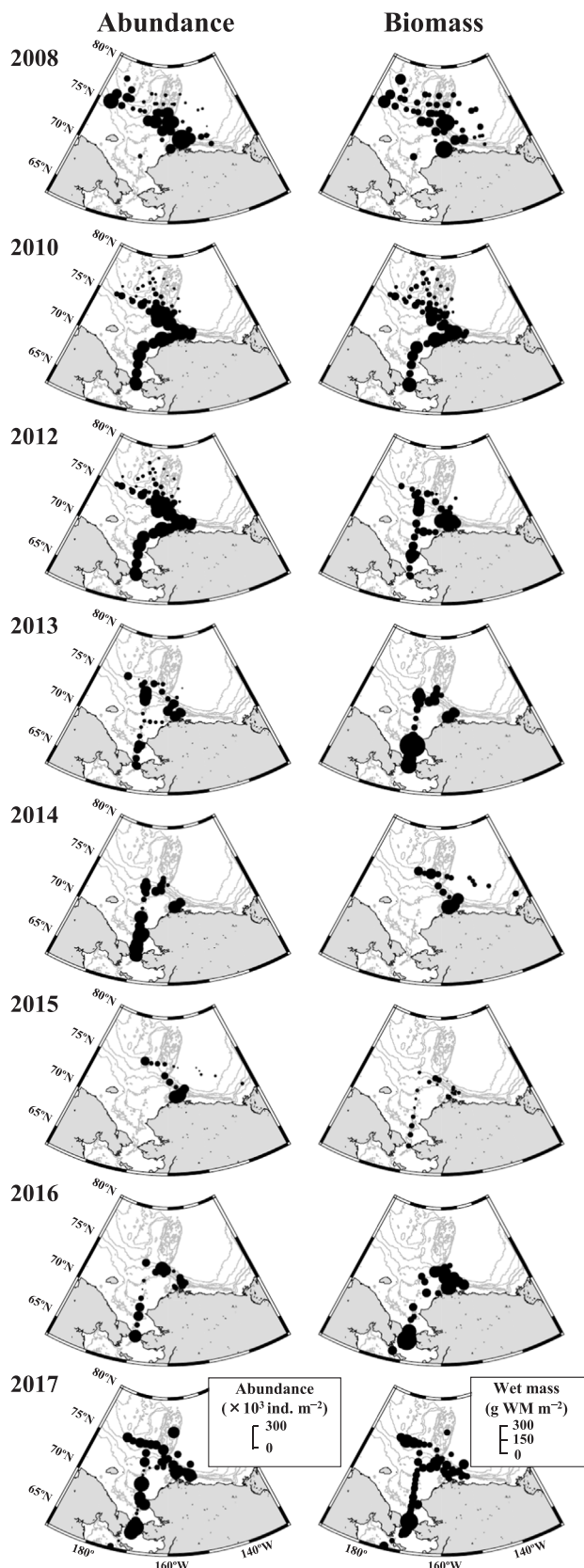


Fig. 3. Horizontal distribution of zooplankton abundance and biomass in the western Arctic Ocean during August–October of 2008–2017.

Table 1

List of mesozooplankton species identified in the western Arctic Ocean during 2008–2017.

Species/taxa	Grand mean (ind.m ⁻²)
Calanoid copepods	
<i>Calanus glacialis</i>	10,309
<i>Pseudocalanus newmani</i>	4921
<i>Pseudocalanus</i> spp. (C1–C4)	4603
<i>Pseudocalanus acuspes</i>	4373
<i>Pseudocalanus minutus</i>	2785
<i>Metridia pacifica</i> *	1370
<i>Pseudocalanus mimus</i>	988
<i>Acartia longiremis</i>	897
<i>Metridia longa</i>	847
<i>Centropages abdominalis</i>	549
<i>Microcalanus pygmaeus</i>	362
<i>Eucalanus bungii</i> *	268
<i>Calanus hyperboreus</i>	96
<i>Eurytemora herdmani</i>	73
<i>Paraeuchaeta glacialis</i>	62
<i>Calanus marshallae</i>	37
<i>Acartia hadsonica</i>	33
<i>Neocalanus flemingeri</i> *	30
<i>Scolecithricela minor</i>	22
<i>Neocalanus plumchrus</i> *	18
<i>Chiridius obtusifrons</i>	16
<i>Spinocalanus lomgicornis</i>	13
<i>Heterorhabdus norvegicus</i>	13
<i>Temotites brevis</i>	10
<i>Neocalanus cristatus</i> *	8
<i>Aetideopsis multiserrata</i>	6
<i>Gaetanus tenuispinus</i>	5
<i>Gaidius brevispinus</i>	4
<i>Epilabidocera amphitrites</i>	3
<i>Scaphocalanus magnus</i>	2
<i>Tortanus discaudatus</i>	1
<i>Aetideopsis rostrata</i>	1
<i>Heterorhabdus compactus</i>	0.5
<i>Rincalanus nasutus</i>	0.4
<i>Undinella oblonga</i>	0.3
<i>Racovitzanus antarcticus</i>	0.2
<i>Lucicutia anomala</i>	0.1
Other taxa	
Barnacle larvae	2895
Echinodermata larvae	2626
Appendicularians	2395
Cyclopoid copepods	2194
Hydrozoans	1193
Polychaetes	1026
Chaetognaths	934
Bivalvia larvae	399
Pteropods (<i>Limacina helicina</i>)	264
Cladocerans (<i>Podon</i> spp.)	138
Euphausiids	121
Ostracods	52
Cladocerans (<i>Evadne</i> spp.)	37
Amphipods	32
Pteropods (<i>Clione limacina</i>)	19
Eubrachyura zoea	8
Isopods	8
Poecilostomatoid copepods	5
Harpacticoid copepods	0.7

* Pacific species.

slope and the new-shelf were *M. pacifica*, barnacle larvae, *Centropages abdominalis*, and polychaetes, with a cumulative contribution rate of 22.7% (Table S2). Each assemblage was also clearly separated in the NMDS plot (Fig. 4B). For the ordination of NMDS plots, several environmental parameters (temperature, salinity, Chl. *a*, latitude, and depth) were significant ($r^2 = 0.14$ – 0.62).

The horizontal distributions of the zooplankton communities were separated and corresponded with the depth (Fig. 5). Interannual variation in horizontal distribution was observed every year, except 2015, for the slope assemblage, and in the basin assemblage, variation was

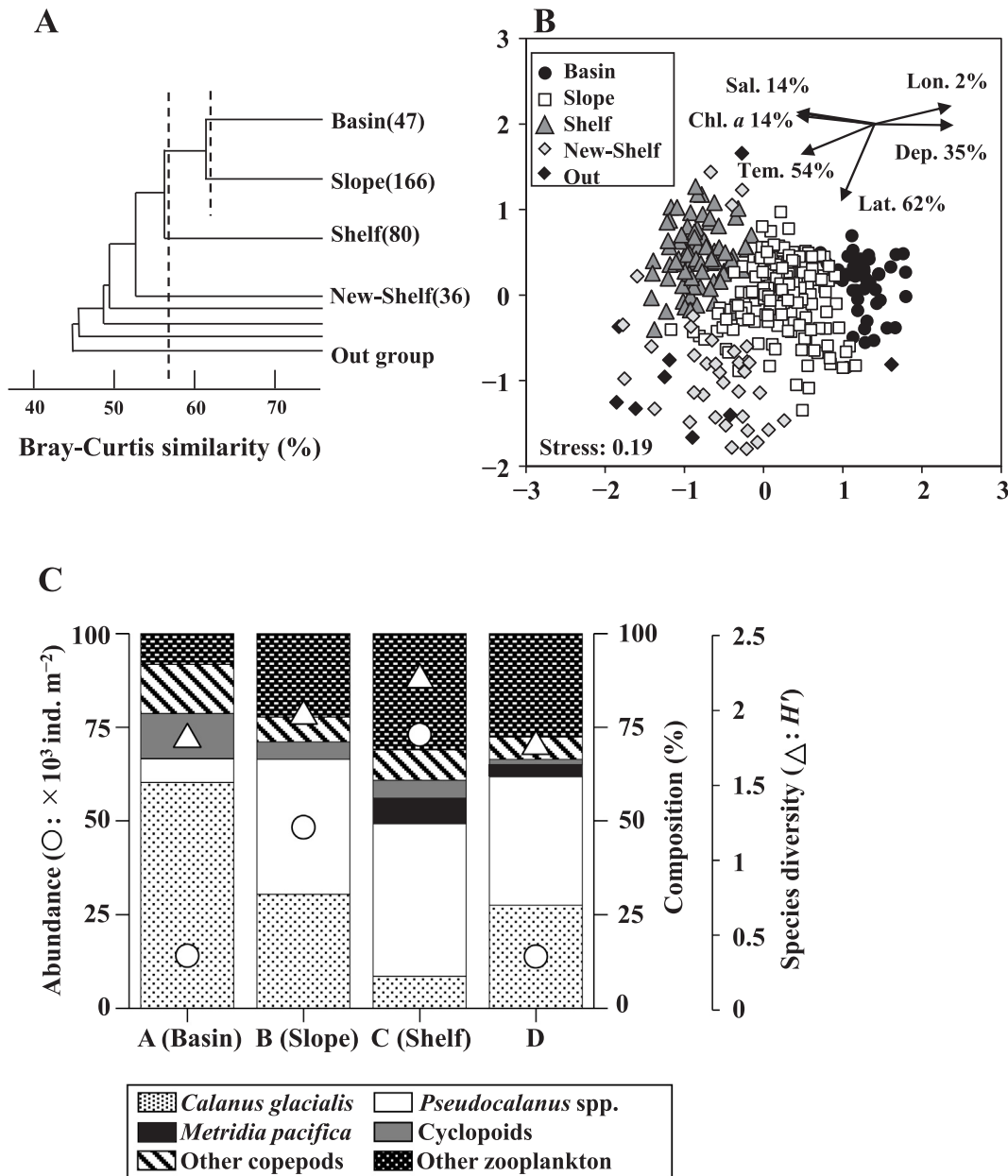


Fig. 4. Results of cluster analysis based on zooplankton abundance by Bray-Curtis similarity connected UPGMA. Four assemblages were identified with the similarity at 57% and 62%, respectively (*dashed lines*) (A). Non-metric multidimensional scaling plots of each group (B). For various environmental parameters, their directions and coefficients of determination (%) are shown. Sal.: salinity, Chl. *a*: chlorophyll *a*, Tem.: temperature, Lon.: longitude, Lat.: latitude, Dep.: sampling depth. The mean abundance, species diversity and taxonomic composition of each group (C).

observed in all years when observation in this area was possible. The new-shelf assemblage, located between the shelf and slope, occurred for the first time in 2012 and was then observed mainly in 2015, 2016 and 2017.

We performed two-way ANOVA analyses to determine if there were significant annual variability or seasonal changes in environmental variables, and copepod and zooplankton abundance within each assemblage (Table 2). The new-shelf assemblage was not included due to the insufficient number of samples. In the basin assemblage, significant inter-annual variability was observed for salinity and Chl. *a*, however, no significant difference in seasonal changes was observed. No significant differences were observed in inter-annual and seasonal changes for zooplankton and copepod abundance in the basin assemblage. In the slope assemblage, located mainly in the shelf break and slope areas, significant inter-annual variability and seasonal changes were observed for all environmental parameters (IMT, IMC, OpenPeriod, AMtemp, and

AMchl), however, no significant inter-annual differences were observed for zooplankton and copepod abundance. There was a significant difference in the inter-annual variability and seasonal changes in the integrated mean Chl. *a*, and zooplankton and copepod abundance of the shelf assemblage.

3.4. GLM analyses

The results of the relationship between environmental variables and the abundance of species/taxa, which showed a high contribution in the SIMPER analysis, in each group, determined using the GLM analysis, are shown in Table 3. In the basin assemblage, every three species and the total copepod abundance had a significant positive or negative relationship with the variation of IMS. The slope assemblage showed a more distinct relationship with the sea surface satellite data than the basin assemblage. In the basin assemblage, *C. glacialis* showed a

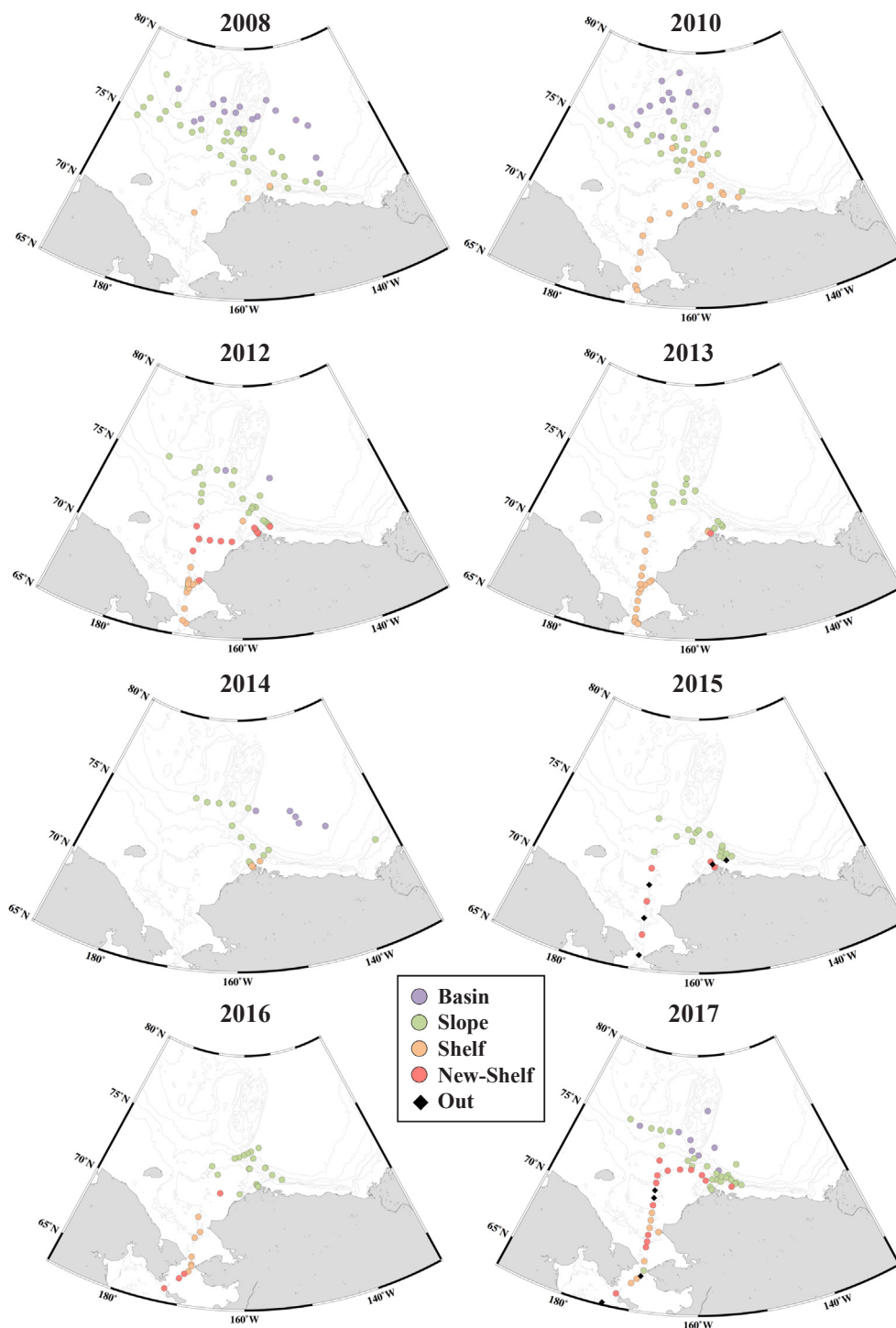


Fig. 5. Horizontal distribution of the four groups (Basin, Slope, Shelf, New-Shelf) identified from the Bray-Curtis similarity index based on abundances data in the western Arctic Ocean during summers of 2008–2017.

significant positive relationship with OpenPeriod and IMS, and a significant negative relationship with AMtemp. *Pseudocalanus* spp. had a significant positive relationship with AMtemp, and a negative relationship with APP.

The abundance of *C. glacialis*, the most abundant species, in the slope assemblage had a significant relationship with the satellite data based on the GLM analysis (cf. Table 3). If the annual variability in the predicted abundance close to the annual changes in the observed abundance data, the prediction model based on the satellite data would become available as a good model. To evaluate the relationship

between the predicted data and the observed data, at first, we extracted *C. glacialis* abundance data from a gridded area (72°N–75°N, 150°W–170°W) where net sampling was conducted every study year (Fig. 1). The GLM analysis was performed using the extracted abundance data of *C. glacialis* as the response variable and the environmental parameters (72 km grid resolution including sampling station) derived from the satellite data (OpenPeriod, AMtemp, AMchl, APP) as explanatory variables (Table S3). Since models including OpenPeriod and AMtemp showed the best fit based on AIC, we used the GLM analysis including these two parameters. We simulated the entire time series of

Table 2

SIMPER analyses showing differences in species/taxa assemblage between the groups, species/taxa (with % contribution) contributing to the dissimilarities between pair of groups.

Group	A (Basin)	B (Slope)	C (shelf)
B (Slope)	<i>Centropages abdominalis</i> (5.0%) <i>M. longa</i> (4.6%) <i>Pseudocalanus</i> spp. (4.6%) <i>M. pacifica</i> (4.5%)		
C (shelf)	<i>Pseudocalanus</i> spp. (11.5%) <i>Acartia longiremis</i> (5.6%) Barnacles nauplii (5.5%) Polychaetes (4.9%)	<i>M. longa</i> (6.0%) <i>M. pacifica</i> (5.9%) <i>Centropages abdominalis</i> (5.8%) <i>Eucalanus bungii</i> (4.7%)	
D	<i>M. longa</i> (6.9%) <i>M. pygmaeus</i> (6.4%) <i>P. glacialis</i> (5.8%) <i>C. hyperboreus</i> (5.6%)	<i>M. longa</i> (7.7%) Barnacles nauplii (5.7%) <i>M. pygmaeus</i> (5.4%) <i>Pseudocalanus</i> spp. (5.2%)	<i>M. pacifica</i> (5.9%) Barnacles nauplii (5.6%) <i>Centropages abdominalis</i> (5.6%) Polychaetes (5.6%)

Table 3

Variance analyses (two-way ANOVA) on year to year and day to day differences in environmental parameter and abundance of zooplankton and copepod of group A (Basin), group B (Slope) and group C (Shelf) during summers of 2008–2017. IMT: integrated mean temperature (0–150 m or 0–bottom–5 m), IMS: integrated mean salinity (0–150 m or 0–bottom–5 m), IMC: Integrated mean chl. a (0–150 m or 0–bottom–5 m), OpenPeriod: Open period of sea ice, AMtemp: Annual median temperature, AMchl: Annual median chl. a, APP: Annual Primary Production, Zooplankton: zooplankton abundance, Copepods: copepod abundance.

Group	Parameter	F-value		
		Year	Day	Year × Day
A (Basin)	IMT	0.495 ^{ns}	0.011 ^{ns}	2.466 ^{ns}
	IMS	4.318 ^{**}	0.448 ^{ns}	4.308 ^{**}
	IMC	4.901 ^{**}	0.918 ^{ns}	4.713 ^{**}
	OpenPeriod	0.832 ^{ns}	0.337 ^{ns}	0.800 ^{ns}
	AMtemp	0.476 ^{ns}	0.345 ^{ns}	0.556 ^{ns}
	AMchl	0.579 ^{ns}	0.188 ^{ns}	0.620 ^{ns}
	APP	–	–	–
	Zooplankton	0.419 ^{ns}	0.060 ^{ns}	0.436 ^{ns}
	Copepods	0.329 ^{ns}	0.051 ^{ns}	0.391 ^{ns}
	B (Slope)	IMT	5.572 ^{***}	10.766 ^{***}
IMS		2.746 [*]	1.016 ^{ns}	2.395 [*]
IMC		2.154 [*]	6.230 [*]	2.159 [*]
OpenPeriod		9.910 ^{**}	7.581 ^{**}	9.740 ^{**}
AMtemp		10.085 ^{***}	9.027 ^{**}	9.954 ^{***}
AMchl		14.092 ^{***}	62.684 ^{***}	13.629 ^{***}
APP		7.939 ^{**}	0.006 ^{ns}	7.737 ^{**}
Zooplankton		1.332 ^{ns}	4.088 [*]	1.327 ^{ns}
Copepods		1.823 ^{ns}	2.552 ^{ns}	1.815 ^{ns}
C (Shelf)		IMT	1.208 ^{ns}	3.704 ^{ns}
	IMS	1.205 ^{ns}	0.226 ^{ns}	1.138 ^{ns}
	IMC	6.400 ^{***}	20.246 ^{***}	6.310 ^{***}
	OpenPeriod	0.457 ^{ns}	0.104 ^{ns}	0.459 ^{ns}
	AMtemp	0.538 ^{ns}	0.343 ^{ns}	0.574 ^{ns}
	AMchl	1.555 ^{ns}	0.852 ^{ns}	1.573 ^{ns}
	APP	1.538 ^{ns}	0.115 ^{ns}	1.457 ^{ns}
	Zooplankton	2.795 [*]	9.639 ^{**}	2.789 ^{ns}
	Copepods	4.381 ^{**}	14.877 ^{**}	4.400 ^{**}

^{ns} Not significant.

^{*} $p < 0.05$.

^{**} $p < 0.01$.

^{***} $p < 0.001$.

C. glacialis abundance from the satellite data (OpenPeriod and AMtemp) in the grid area (72°N–75°N, 150°W–170°W), and compared the

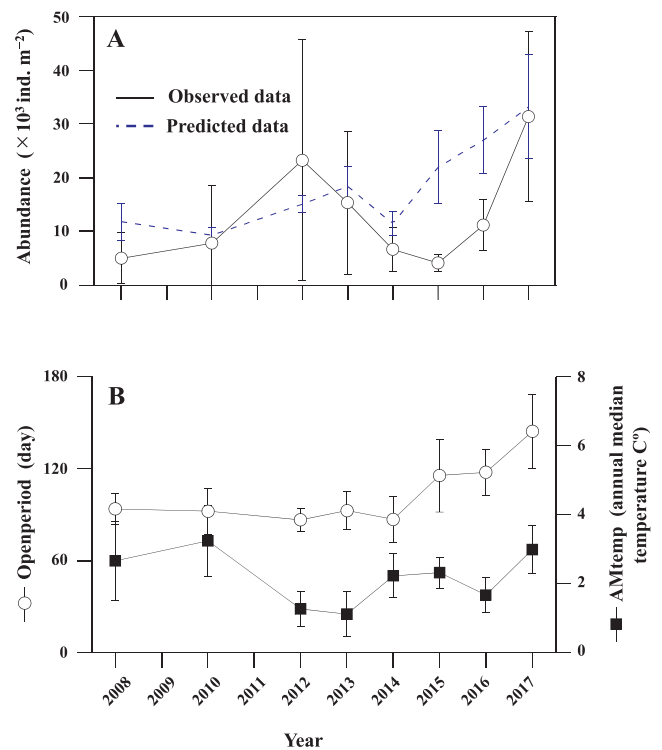


Fig. 6. Inter-annual variability of the observed data and GLM predicted data of *C. glacialis* abundance in the gridded area (cf. Fig. 1) (A). Inter-annual variability of the selected explanatory variables in the GLM. OpenPeriod: a period of open water, AMtemp.: annual median temperature from the satellite data.

observed abundance data with the predicted data (Fig. 6A). Inter-annual changes in the two parameters are shown in Fig. 6B. A similar variation was observed in both observed and predicted data; however, the observed data showed lower variation than the predicted data in 2015 and 2016.

4. Discussion

4.1. Horizontal distribution

Four major groups of stations were identified based on faunal assemblages. In previous studies, it had been suggested that such a distribution is related to biogeographic variations and the presence of several water masses in the western Arctic Ocean (Ershova et al.,

2015a; Hopcroft et al., 2010; Matsuno et al., 2011; Smoot and Hopcroft, 2017; Spear et al., 2019; Xu et al., 2018). Owing to the large coverage of the western Arctic Ocean region, in the present study, the coverage of each assemblage was larger than that of any previous study. Hence, we did not observe small community variations in response to fine water mass variability as observed in previous studies.

The basin assemblage had the lowest abundance of *Pseudocalanus* spp., and a lower abundance of *C. glacialis* compared to the slope assemblage. Furthermore, this group exhibited the second-lowest zooplankton abundance (Fig. 5). A low zooplankton abundance has previously been documented in this area (Ashjian et al., 2003; Lane et al., 2008; Rutzen and Hopcroft, 2018). The low abundance of zooplankton observed in the basin in the present study is consistent with the previous studies showing low abundances in the Canada Basin, inside of the Beaufort Gyre. The basin assemblage was also characterized by the presence of mesopelagic copepod species (*Heterorhabdus norvegicus*, *Paraeuchaeta glacialis*, *Spinocalanus longicornis*, *Temorites brevis*), consistent with the basin location. Previous studies, with an approach similar to the present study, have reported the occurrence of mesopelagic copepods and a reduction in the zooplankton abundance around the deep pelagic stations in the western Arctic Ocean (Smoot and Hopcroft, 2017; Xu et al., 2018).

The slope assemblage was widely distributed across the slope and shelf-break regions and included the highest number of stations. The slope assemblage was characterized by *C. glacialis*, which was most abundant, *Pseudocalanus* spp. and appendicularians. The mean copepodid stage (MCS) of *C. glacialis* (3.57) in the slope assemblage was lower compared to other groups (basin: 4.20, shelf: 4.28, new-shelf: 4.51); in other words, the abundance of early copepodid stages was high in this group. The mtCOI gene analysis revealed that the Bering haplotype of *C. glacialis* dominated the shelf region of the Chukchi Sea while the Arctic haplotype was dominant in the slope area (Ashjian et al., 2017; Nelson et al., 2009). *C. glacialis* undergoes a diapause period in the mesopelagic layer, requiring depths greater than that of the shelves to complete their life cycle (Ashjian et al., 2003; Hirche, 1991). As a result, low abundances of *C. glacialis*, especially early copepodid stages, are observed on the shallow (< 50 m) Chukchi Shelf (Matsuno et al., 2012b, 2016). The characteristic high abundance and low MCS of *C. glacialis* in the slope assemblage suggest that it is a habitat of the Arctic haplotype population. Also, the presence of the Bering haplotype indicates to its transport from the Bering Strait.

The shelf assemblage, with many stations in the northern Bering Sea and the shelf region of the southern Chukchi Sea, was characterized by a high zooplankton abundance, and the occurrence of Pacific and coastal species, with a high species diversity in the slope region (Table S2, Fig. 5). The SIMPER analysis revealed that *M. pacifica* was the most frequent Pacific copepod in this assemblage with a higher contribution to the total abundance (9%) compared to that in other assemblages. Johnson (1963) has reported the occurrence of the Pacific copepods *Neocalanus cristatus* and *Eucalanus bungii* on the Chukchi Abyssal Plain (85°06'N, 168°40'W) in 1953. The major distribution of Pacific copepods in the western Arctic Ocean has been described in Nelson et al. (2014). The Pacific zooplankton species seem to have arrived with the advection of Pacific water (Ershova et al., 2015a; Hopcroft et al., 2010; Matsuno et al., 2011), which is warm and enriched with nutrients, passing through the Bering Strait with several other water masses (Anadyr Water, Bering Sea Water and Alaskan Coastal Water) (Coachman et al., 1975; Danielson et al., 2017). The shelf assemblage had the highest zooplankton abundance composed primarily of *Pseudocalanus* spp., Pacific copepods, and benthic larvae. Based on morphological and molecular approaches, four species of the genus *Pseudocalanus* (*P. minutus*, *P. acuspes*, *P. mimus*, *P. newmani*) have been documented in the western Arctic Ocean (Ershova et al., 2017); the presence of these four species was confirmed in this study. It was evident from the GLM that annual mean temperature and annual mean primary production were significant predictors of the abundance of

Pseudocalanus spp. so that high abundances are expected when these two parameters increase. It has been established that there is a direct relation between the number of larvae ejected by barnacles, bivalves, and polychaetes and the phytoplankton density (Ambrose and Renaud, 1997; Clare and Walker, 1986; Graf et al., 1982). Hence, the high abundance of *Pseudocalanus* spp., the Pacific copepods and the benthic larvae in the shelf assemblage might have been caused by the high integrated mean temperature, integrated mean salinity, and annual primary production from the inflow of the warm Pacific water.

4.2. Inter-annual changes

Inter-annual changes in the zooplankton community structure during summer in the western Arctic Ocean were different for each assemblage. Notwithstanding with some differences in the annual distribution of sea-ice during the sampling years, it was evident that the melt day of sea ice in the study region was significantly different (one-way ANOVA, $p < 0.05$). The melt day was clearly earlier than day 200 in 2012, 2015, 2016 and 2017, which corresponded with the appearance of the new-shelf assemblage with low average abundance and low species diversity. Okkonen et al. (2019) found interdependent relationships between changes in seasonally regional winds and the timing of sea ice retreat and water mass in the northwestern Chukchi Sea. Changes in the phytoplankton community structure and a decrease in the abundance and distribution of phytoplankton has been reported in summer, when the sea surface temperature increase and nutrient depletion occurs in response to early sea ice retreat in the western Arctic Ocean (Li et al., 2009; Fujiwara et al., 2014). The occurrence of the new-shelf assemblage, with low abundances and species diversity in the northern Bering Sea and southern Chukchi Sea, might be due to changing phytoplankton community structure due to early sea ice retreat correlated with seasonally-averaged regional winds.

Inter-annual variability or seasonal changes in the environmental factors and zooplankton abundance were small in the basin assemblage during our study period (Table 2). The low variability in the zooplankton community was expected due to the small changes in the environmental factors in the Canada Basin, which included almost all stations of the basin group. However, low primary production is expected in the central Canada Basin, due to the intensification of the anticyclonic circulation, enhanced stratification by the accumulation of less saline meltwater at the surface, and deepening of the nutricline (Nishino et al., 2011b; Zhang et al., 2020). The effects of changing environmental conditions on lower trophic levels in the western Arctic Ocean have also been reported, including a change in the size of the dominant phytoplanktons from nano to pico (Li et al. 2009), and a dominance of haptophytes during the early sea ice retreat years (Fujiwara et al., 2014). The results of GLM analysis indicated that in the basin, the abundance of dominant copepods is declining with decreasing salinity, except for the *Microcalanus* abundance. Although variability has not been observed in the abundance of all zooplanktons, *Metridia longa* abundance decreased significantly from 2008 to 2014, with the low salinity period (one-way ANOVA, $p < 0.001$). The freshening of seawater has also been documented in the Canada Basin (Yamamoto-Kawai et al., 2009). Our results suggest that a decline in the standing stock of zooplankton and changes in their community structure are expected as freshening of seawater increases, along with a recent increase in river discharge (Peterson et al., 2002) and changes in the phytoplankton community structure in the western Arctic Ocean basin.

Significant variability was observed for Chl. *a*, and zooplankton and copepod abundance in the shelf region (Table 2). An inter-annual variability in the sea ice retreat rate and the sea ice melt season, which depends on various factors (e.g., ice-albedo feedback, the inflow of PSW and winds) (Serreze and Stroeve, 2015; Steele et al., 2015; Stroeve et al., 2014), has also been observed. Such variability has a crucial effect on the community structure and size of phytoplankton that

sustains the zooplankton in the lower trophic level (Fujiwara et al., 2016, 2014; Lee et al., 2019; Selz et al., 2018). Based on the long-term observations, there is a trend of an increase in the zooplankton abundance in the shelf region (Ershova et al., 2015b; Matsuno et al., 2011), and the increased inflow of the warm Pacific water (Woodgate et al., 2010) can potentially lead to an increase in the zooplankton biomass (Matsuno et al., 2011, Matsuno et al., 2012a,b). Moreover, Sasaki et al. (2016) tested the relationship between environmental variables and the zooplankton standing stock using statistical models and found that zooplankton abundance increased with early sea ice melt in the northern Bering Sea and the southern Chukchi Sea. In the present study, as OpenPeriod and AMtemp were selected as the explanatory variables in the GLM, an increase in zooplankton and Pacific copepod abundance might result from an increase in these variables. Hence, the zooplankton standing stock might vary depending on the variation in the rate of sea ice reduction and the extent of open areas formed due to various factors, such as an increase in the inflow of Pacific water.

In the slope assemblage nestled between the basin and the shelf, a significant variation in the environmental factors was detected (Table S2, Fig. 5). In this region of the western Arctic Ocean, the environment changes considerably due to the variation in inflow of Pacific water in the subsurface layer (Pickart et al., 2019), inter-annual changes in the sea ice cover in summer (Kwok et al., 2009; Tivy et al., 2011; Wang et al., 2019), the occurrence of upwelling (Hufford, 1974; Lin et al., 2019; Schulze and Pickart, 2012), and the formation of a large warm-core eddy due to the inflow of Pacific water and sea ice reduction (Nishino et al., 2011a). The high abundance of *C. glacialis* has previously been reported in the slope region of the Chukchi Sea (Matsuno et al., 2016), as was observed in the present study. Since *C. glacialis* is a highly dominant zooplankton species and has an important role in connecting the lower and higher trophic levels, it is considered as a key species in the shelf region (Hopcroft et al., 2010; Matsuno et al., 2012b). To determine the environmental factors affecting the abundance of *C. glacialis* in the slope region, we performed a GLM analysis. The best-fit models included AMtemp and OpenPeriod as the explanatory variables (Table S3). The GLM showed that the abundance of *C. glacialis* increased with increasing OpenPeriod and AMtemp in the gridded slope region. The OpenPeriod, in particular, was an important predictor of *C. glacialis* abundance, and the observed abundance data also showed a similar increasing trend. Based on modeling studies, Wassmann et al. (2015) have predicted that the main geographical distribution of *C. glacialis* will have shifted from the Atlantic to the Pacific Arctic by 2099. Taking this into account, it becomes very important to predict the abundance of *C. glacialis* in the slope region, where they showed a high abundance during the present study. The OpenPeriod has increased in the gridded area (Fig. 6B), and the summer melt season in the western Arctic Ocean has lengthened at a rate of 13.2 days decade⁻¹ (Stroeve et al., 2014). We predict that the abundance of *C. glacialis* might increase when the earlier sea ice reduction increases the period of open water, increasing the temperature in the slope region. Such a change can potentially affect the lower trophic levels in the western Arctic Ocean.

5. Conclusion

In the present study, four major faunal groups (basin, slope, shelf, and new-shelf) were identified by cluster analysis. The community structure and inter-annual variations were different for each assemblage. In the basin, though no significant interannual variations in zooplankton and copepod abundance were observed, the possibility of a decline in the abundance of dominant copepods with an increased freshening of seawater was suggested by the GLM. A high abundance of *C. glacialis*, a key species, was observed in the slope region, and the environmental factors in this region exhibited significant inter-annual variation. Inter-annual changes in *C. glacialis* abundance were found to be strongly related to the period of open water and the annual median

temperature, and the prediction models showed that their abundance would increase with an increase in the aforementioned environmental factors. In the shelf group, the period of open water was a significant predictor of the abundance of Pacific copepods, with longer periods, caused by an increase in the annual median temperature, increasing the copepod abundance. These results suggest that earlier sea ice reduction and enhanced inflow of the warm Pacific Water resulted in a higher diversity of Pacific species in the shelf region. This change can possibly lead to an increase in the area of new-shelf, which showed a low species diversity and zooplankton abundance. Our study suggests that environmental changes in the Pacific Arctic will have varied effects on the zooplankton communities in each region.

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.

Acknowledgements

The authors are indebted to the captain, officers, and crews of the R/V Mirai and CCGS Amundsen. This research was funded by the Japan Society for the Promotion of Science (JSPS) (Grant-in-Aid for JSPS Fellows), the GRENE Arctic Climate Change Research Project, and the Arctic Challenge for Sustainability (ArCS) Project.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2020.102391>.

References

- Ambrose, W.G.J., Renaud, P.E., 1997. Does a pulsed food supply to the benthos affect polychaete recruitment patterns in the northeast water Polynya? *J. Mar. Syst.* 10, 483–495.
- Ashjian, C.J., Braund, S.R., Campbell, R.G., George, J.C., Kruse, J., Maslowski, W., Moore, S.E., Nicolson, C.R., Okkonen, S.R., Sherr, B.F., Sherr, E.B., Spitz, Y.H., 2010. Climate variability, oceanography, bowhead whale distribution, and Inupiat subsistence whaling near Barrow, Alaska. *Arctic* 63, 179–194. <https://doi.org/10.14430/arctic973>.
- Ashjian, C.J., Campbell, R.G., Gelfman, C., Alatalo, P., Elliott, S.M., 2017. Mesozooplankton abundance and distribution in association with hydrography on Hanna Shoal, NE Chukchi Sea, during August 2012 and 2013. *Deep Res. Part II Top. Stud. Oceanogr.* 144, 21–36. <https://doi.org/10.1016/j.dsr2.2017.08.012>.
- Ashjian, C.J., Campbell, R.G., Welch, H.E., Butler, M., Van Keuren, D., 2003. Annual cycle in abundance, distribution, and size in relation to hydrography of important copepod species in the western Arctic Ocean. *Deep Res. Part I Oceanogr. Res. Pap.* 50, 1235–1261. [https://doi.org/10.1016/S0967-0637\(03\)00129-8](https://doi.org/10.1016/S0967-0637(03)00129-8).
- Bray, J.B., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27, 325–349.
- Brodskii, K.A., 1967. Calanoida of the Far Eastern Seas and Polar Basin of the USSR. [Translated from the Russian. Originally published 1950]. Israel Program for Scientific Translations, Jerusalem.
- Clare, A.S., Walker, G., 1986. Further studies on the control of the hatching process in *Balanus balanoides* (L.). *J. Exp. Mar. Biol. Ecol.* 97, 295–304. [https://doi.org/10.1016/0022-0981\(86\)90247-9](https://doi.org/10.1016/0022-0981(86)90247-9).
- Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The Regional Physical Oceanography. University of Washington Press, Seattle.
- Codispoti, L.A., Flagg, C., Kelly, V., Swift, J.H., 2005. Hydrographic conditions during the 2002 SBI process experiments. *Deep Res. Part II Top. Stud. Oceanogr.* 52, 3199–3226. <https://doi.org/10.1016/j.dsr2.2005.10.007>.
- Comiso, J.C., Parkinson, C.L., Gersten, R., Stock, L., 2008. Accelerated decline in the Arctic sea ice cover. *Geophys. Res. Lett.* 35, 1–6. <https://doi.org/10.1029/2007GL031972>.
- Danielson, S.L., Eisner, L., Ladd, C., Mordy, C., Sousa, L., Weingartner, T.J., 2017. Deep-Sea Research II Regular article A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas. *Deep Res. Part II* 135, 7–26. <https://doi.org/10.1016/j.dsr2.2016.05.024>.
- Duarte, C.M., Lenton, T.M., Wadhams, P., Wassmann, P., 2012. Climate change in the Arctic. *Nat. Clim. Chang.* 2, 60–63. <https://doi.org/10.1163/9789004303188-004>.
- Ershova, E.A., Hopcroft, R., Kosobokova, K., Matsuno, K., Nelson, R.J., Yamaguchi, A., Eisner, L., 2015a. Long-term changes in summer zooplankton communities of the

- Western Chukchi Sea, 1945–2012. *Oceanography* 28, 100–115. <https://doi.org/10.5670/oceanog.2015.60>.
- Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., 2015b. Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004–2012. *Polar Biol.* 38, 1461–1481. <https://doi.org/10.1007/s00300-015-1709-9>.
- Ershova, E.A., Questel, J.M., Kosobokova, K., Hopcroft, R.R., 2017. Population structure and production of four sibling species of *Pseudocalanus* spp. in the Chukchi Sea. *J. Plankton Res.* 39, 48–64. <https://doi.org/10.1093/plankt/fbw078>.
- Field, J., Clarke, K., Warwick, R., 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8, 37–52. <https://doi.org/10.3354/meps008037>.
- Frost, B.W., 1989. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can. J. Zool.* 67, 525–551.
- Fujiwara, A., Hirawake, T., Suzuki, K., Eisner, L., Imai, I., Nishino, S., Kikuchi, T., Saitoh, S.I., 2016. Influence of timing of sea ice retreat on phytoplankton size during marginal ice zone bloom period on the Chukchi and Bering shelves. *Biogeosciences* 13, 115–131. <https://doi.org/10.5194/bg-13-115-2016>.
- Fujiwara, A., Hirawake, T., Suzuki, K., Imai, I., Saitoh, S.I., 2014. Timing of sea ice retreat can alter phytoplankton community structure in the western Arctic Ocean. *Biogeosciences* 11, 1705–1716. <https://doi.org/10.5194/bg-11-1705-2014>.
- Fujiwara, A., Nishino, S., Matsuno, K., Onodera, J., Kawaguchi, Y., Hirawake, T., Suzuki, K., Inoue, J., Kikuchi, T., 2018. Changes in phytoplankton community structure during wind-induced fall bloom on the central Chukchi shelf. *Polar Biol.* 41, 1279–1295. <https://doi.org/10.1007/s00300-018-2284-7>.
- Graf, G., Bengtsson, W., Diesner, U., Schulz, R., Theede, H., 1982. Benthic response to sedimentation of a spring phytoplankton bloom: Process and budget. *Mar. Biol.* 67, 201–208. <https://doi.org/10.1007/BF00401286>.
- Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Prog. Oceanogr.* 71, 331–361. <https://doi.org/10.1016/j.pocean.2006.10.001>.
- Hirche, H.J., 1991. Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. *Polar Biol.* 11, 351–362. <https://doi.org/10.1007/BF00239687>.
- Hirche, H.-J., Hagen, W., Mumm, N., Richter, C., 1994. The Northeast Water polynya, Greenland Sea: III. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. *Polar Biol* 14 (7). <https://doi.org/10.1007/BF00239054>.
- Hopcroft, R.R., Kosobokova, K.N., Pinchuk, A.I., 2010. Zooplankton community patterns in the Chukchi Sea during summer 2004. *Deep Res. Part II Stud. Oceanogr.* 57, 27–39. <https://doi.org/10.1016/j.dsr2.2009.08.003>.
- Hufford, G.L., 1974. On apparent upwelling in the southern Beaufort sea. *J. Geophys. Res.* 79, 1305–1306.
- Hunt Jr., George L., Drinkwater, Ken, 2007. Introduction to the proceedings of the GLOBEC symposium on effects of climate variability on sub-arctic marine ecosystems. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 54 (23–26), 2453–2455. <https://doi.org/10.1016/j.dsr2.2007.07.029>.
- Johnson, M.W., 1963. Zooplankton collections from the high polar basin with special reference to the Copepoda. *Limnol. Oceanogr.* 8, 89–102. <https://doi.org/10.4319/lo.1963.8.1.0089>.
- Kashiwase, H., Ohshima, K.I., Nihashi, S., Eicken, H., 2017. Evidence for ice-ocean albedo feedback in the Arctic Ocean shifting to a seasonal ice zone. *Sci. Rep.* 7, 1–10. <https://doi.org/10.1038/s41598-017-08467-z>.
- Kosobokova, K.N., Hirche, H.J., 2016. A seasonal comparison of zooplankton communities in the Kara Sea. With special emphasis on overwintering traits. *Estuar. Coast. Shelf Sci.* 175, 146–156. <https://doi.org/10.1016/j.ecss.2016.03.030>.
- Kwok, R., Cunningham, G.F., Wensnahan, M., Rigor, I., Zwally, H.J., Yi, D., 2009. Thinning and volume loss of the Arctic Ocean sea ice cover: 2003–2008. *J. Geophys. Res.* 114, 2003–2008. <https://doi.org/10.1029/2009JC005312>.
- Kwok, R., Spreen, G., Pang, S., 2013. Arctic sea ice circulation and drift speed: Decadal trends and ocean currents. *J. Geophys. Res.* 118, 2408–2425. <https://doi.org/10.1002/jgrc.20191>.
- Lane, P.V.Z., 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.* <https://doi.org/10.1016/j.jmarsys.2007.04.001>.
- Lee, Y., Min, J.O., Yang, E.J., Cho, K.H., Jung, J., Park, J., Moon, J.K., Kang, S.H., 2019. Influence of sea ice concentration on phytoplankton community structure in the Chukchi and East Siberian Seas, Pacific Arctic Ocean. *Deep Res. Part I Oceanogr. Res. Pap.* 147, 54–64. <https://doi.org/10.1016/j.dsr.2019.04.001>.
- Li, W.K.W., McLaughlin, F.A., Lovejoy, C., Carmack, E.C., 2009. Smallest algae thrive as the arctic. *Science* (80-) 326, 539. <https://doi.org/10.1126/science.1179798>.
- Lin, P., Pickart, R.S., Moore, G.W.K., Spall, M.A., Hu, J., 2019. Characteristics and dynamics of wind-driven upwelling in the Alaskan Beaufort Sea based on six years of mooring data. *Deep Res. Part II Top. Stud. Oceanogr.* 162, 79–92. <https://doi.org/10.1016/j.dsr2.2018.01.002>.
- Lowry, L.F., Sheffield, G., George, J.C., 2004. Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. *J. Cetacean Res. Manag.* 6, 215–223.
- Marin, V., 1987. The oceanographic structure of the eastern Scotia sea-IV. Distribution of copepod species in relation to hydrography in 1981. *Deep Sea Res. Part A Oceanogr. Res. Pap.* 34, 105–121. [https://doi.org/10.1016/0198-0149\(87\)90125-7](https://doi.org/10.1016/0198-0149(87)90125-7).
- Markus, T., Stroeve, J.C., Miller, J., 2009. Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. *J. Geophys. Res.* 114, 1–14. <https://doi.org/10.1029/2009JC005436>.
- Marschner, I.C., 2011. *Glm2: Fitting generalized linear models with convergence problems.* *R J.* 3, 12–15.
- Matsuno, K., Abe, Y., Yamaguchi, A., Kikuchi, T., 2016. 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., Ichinomiya, M., Yamaguchi, A., Imai, I., Kikuchi, T., 2014. Horizontal distribution of microprotist community structure in the western Arctic Ocean during late summer and early fall of 2010. *Polar Biol.* 37, 1185–1195. <https://doi.org/10.1007/s00300-014-1512-z>.
- 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., Imai, I., 2012a. Biomass size spectra of mesozooplankton in the Chukchi Sea during the summers of 1991/1992 and 2007/2008: an analysis using optical plankton counter data. *ICES J. Mar. Sci.* 69, 1205–1217. <https://doi.org/10.1038/278097a0>.
- Matsuno, K., Yamaguchi, A., Shimada, K., Imai, I., 2012b. 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>.
- Miller, C.B., 1988. *Neocalanus flemingeri*, a new species of Calanidae (Copepoda: Calanoida) from the subarctic Pacific Ocean, with a comparative redescription of *Neocalanus plumchrus* (Marukawa) 1921. *Prog. Oceanogr.* 20, 223–273. [https://doi.org/10.1016/0079-6611\(88\)90042-0](https://doi.org/10.1016/0079-6611(88)90042-0).
- Motoda, S., 1959. *Devices of Simple Plankton Apparatus* 7, 73–94.
- Nelson, R.J., Ashjian, C.J., Bluhm, B.A., Conlan, K.E., Gradinger, R.R., Grebmeier, Jacqueline M., Hill, V.J., Hopcroft, R.R., Hunt, B.P.V., Joo, H.M., Kirchner, D.L., Kosobokova, K.N., Lee, S.H., Li, W.K.W., Lovejoy, C., Poulin, M., Sherr, E., Young, K.V., 2014. Biodiversity and biogeography of the lower trophic taxa of the Pacific Arctic Region: sensitivities to climate change. In: Grebmeier, J.M., Maslowski, W. (Eds.), *The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment*. Springer, pp. 269–336. <https://doi.org/10.1007/978-94-017-8863-2>.
- Nelson, R.J., Carmack, E.C., McLaughlin, F.A., Cooper, G.A., 2009. Penetration of pacific zooplankton into the western arctic ocean tracked with molecular population genetics. *Mar. Ecol. Prog. Ser.* 381, 129–138. <https://doi.org/10.3354/meps07940>.
- Nishino, S., Itoh, M., Kawaguchi, Y., Kikuchi, T., Aoyama, M., 2011a. Impact of an unusually large warm-core eddy on distributions of nutrients and phytoplankton in the southwestern Canada Basin during late summer/early fall 2010. *Geophys. Res. Lett.* 38, 1–6. <https://doi.org/10.1029/2011GL047885>.
- Nishino, S., Kikuchi, T., Yamamoto-Kawai, M., Kawaguchi, Y., Hirawake, T., Itoh, M., 2011b. Enhancement/reduction of biological pump depends on ocean circulation in the sea-ice reduction regions of the Arctic Ocean. *J. Oceanogr.* 67, 305–314. <https://doi.org/10.1007/s10872-011-0030-7>.
- Okkonen, S., Ashjian, C., Campbell, R.G., Alatalo, P., 2019. The encoding of wind forcing into the Pacific-Arctic pressure head, Chukchi Sea ice retreat and late-summer Barrow Canyon water masses. *Deep Sea Res. Part II* 162, 22–31. <https://doi.org/10.1016/j.dsr2.2018.05.009>.
- Peterson, B.J., Holmes, R.M., McClelland, J.W., Vo, C.J., Lammers, R.B., Shiklomanov, A.I., Shiklomanov, I.A., Rahmstorf, S., 2002. Increasing river discharge to the Arctic Ocean. *Science* (80-) 298, 2171–2174.
- 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., Itoh, M., Kikuchi, T., Nishino, S., Vagle, S., 2019. Seasonal to mesoscale variability of water masses and atmospheric conditions in Barrow Canyon, Chukchi Sea. *Deep Res. Part II Top. Stud. Oceanogr.* 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 Res. Part II Top. Stud. Oceanogr.* 135, 27–39. <https://doi.org/10.1016/j.dsr2.2016.11.003>.
- R Development Core Team, 2017. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria3-900051-07-0. <http://www.R-project.org>.
- Rutzen, I., Hopcroft, R.R., 2018. Abundance, biomass and community structure of epipelagic zooplankton in the Canada Basin. *J. Plankton Res.* 40, 486–499. <https://doi.org/10.1093/plankt/fby028>.
- Sasaki, H., Matsuno, K., Fujiwara, A., Onuka, M., Yamaguchi, A., Ueno, H., Watanuki, Y., Kikuchi, T., 2016. Distribution of Arctic and Pacific copepods and their habitat in the northern Bering and Chukchi seas. *Biogeosciences* 13, 4555–4567. <https://doi.org/10.5194/bg-13-4555-2016>.
- Schulze, L.M., Pickart, R.S., 2012. Seasonal variation of upwelling in the Alaskan Beaufort Sea: Impact of sea ice cover. *J. Geophys. Res.* 117, 1–19. <https://doi.org/10.1029/2012JC007985>.
- Selz, V., Laney, S., Arnsten, A.E., Lewis, K.M., Lowry, K.E., Joy-Warren, H.L., Mills, M.M., van Dijken, G.L., Arrigo, K.R., 2018. Ice algal communities in the Chukchi and Beaufort Seas in spring and early summer: Composition, distribution, and coupling with phytoplankton assemblages. *Limnol. Oceanogr.* 63, 1109–1133. <https://doi.org/10.1002/lno.10757>.
- Serreze, M.C., Stroeve, J., 2015. Arctic sea ice trends, variability and implications for seasonal ice forecasting. *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.* 373. <https://doi.org/10.1098/rsta.2014.0159>.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication.* The University of Illinois Press 10.1145/584091.584093.
- Shimada, K., Carmack, E.C., Hatakeyama, K., Takizawa, T., 2001. Varieties of shallow temperature maximum waters in the Western Canadian Basin of the Arctic Ocean. *Geophys. Res. Lett.* 28, 3441–3444. <https://doi.org/10.1029/2001GL013168>.
- Shimada, K., Kamoshida, T., Itoh, M., Nishino, S., Carmack, E., McLaughlin, F., Zimmermann, S., Proshutinsky, A., 2006. Pacific Ocean inflow: Influence on catastrophic reduction of sea ice cover in the Arctic Ocean. *Geophys. Res. Lett.* 33, 3–6. <https://doi.org/10.1029/2005GL025624>.
- Smoot, C.A., Hopcroft, R.R., 2017. Cross-shelf gradients of epipelagic zooplankton

- communities of the Beaufort Sea and the influence of localized hydrographic features. *J. Plankton Res.* 39, 65–75. <https://doi.org/10.1093/plankt/fbw080>.
- 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.* 42, 1107–1124. <https://doi.org/10.1007/s00300-019-02498-0>.
- Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea-III. Patterns of primary production. *Cont. Shelf Res.* 13, 575–599. [https://doi.org/10.1016/0278-4343\(93\)90095-F](https://doi.org/10.1016/0278-4343(93)90095-F).
- Steele, M., Dickinson, S., Zhang, J., Lindsay, W.R., 2015. Seasonal ice loss in the Beaufort Sea: Toward synchrony and prediction. *J. Geophys. Res. Ocean.* 120, 1118–1132. <https://doi.org/10.1002/2014JC010247>.
- Stroeve, J., Holland, M.M., Meier, W., Scambos, T., Serreze, M., 2007. Arctic sea ice decline: Faster than forecast. *Geophys. Res. Lett.* 34, 1–5. <https://doi.org/10.1029/2007GL029703>.
- Stroeve, J.C., Markus, T., Boisvert, L., Miller, J., Barrett, A., 2014. Changes in Arctic melt season and implications for sea ice loss. *Geophys. Res. Lett.* 41, 1216–1225. <https://doi.org/10.1002/2013GL058951>. Received.
- Stroeve, J.C., Serreze, M.C., Holland, M.M., Kay, J.E., Malanik, J., Barrett, A.P., 2012. The Arctic's rapidly shrinking sea ice cover: A research synthesis. *Clim. Change* 110, 1005–1027. <https://doi.org/10.1007/s10584-011-0101-1>.
- Tivy, A., Howell, S.E.L., Alt, B., McCourt, S., Chagnon, R., Crocker, G., Carrieres, T., Yackel, J.J., 2011. Trends and variability in summer sea ice cover in the Canadian Arctic based on the Canadian Ice Service Digital Archive, 1960–2008 and 1968–2008. *J. Geophys. Res. Ocean.* 116. <https://doi.org/10.1029/2009JC005855>.
- Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein-Tank, A., Parker, D., Rahimzadeh, F., Renwick, J., Rusticucci, M., Soden, B., Zhai, P., 2007. Observations: Surface and atmospheric climate change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B. (Eds.), *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, Cambridge, pp. 235–336.
- Wang, Y., Bi, H., Huang, H., Liu, Yanxia, Liu, Yilin, Liang, X., Fu, M., Zhang, Z., 2019. Satellite-observed trends in the Arctic sea ice concentration for the period 1979–2016. *J. Oceanol. Limnol.* 37, 18–37. <https://doi.org/10.1007/s00343-019-7284-0>.
- Wassmann, P., Kosobokova, K.N., Slagstad, D., Drinkwater, K.F., Hopcroft, R.R., Moore, S.E., Ellingsen, I., Nelson, R.J., Carmack, E., Popova, E., Berge, J., 2015. The contiguous domains of Arctic Ocean advection: Trails of life and death. *Prog. Oceanogr.* 139, 42–65. <https://doi.org/10.1016/j.pocean.2015.06.011>.
- Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M.L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D., Pavlova, O., 2006. Food webs and carbon flux in the Barents Sea. *Prog. Oceanogr.* 71, 232–287. <https://doi.org/10.1016/j.pocean.2006.10.003>.
- Welschmeyer, N.A., 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnol. Oceanogr.* 39, 1985–1992. <https://doi.org/10.1111/j.1540-5931.2009.00571.x>.
- Woodgate, R.A., Weingartner, T., Lindsay, R., 2010. The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. *Geophys. Res. Lett.* 37, 1–5. <https://doi.org/10.1029/2009GL041621>.
- 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>.
- Yamamoto-Kawai, M., McLaughlin, F.A., Carmack, E.C., Nishino, S., Shimada, K., Kurita, N., 2009. Surface freshening of the Canada Basin, 2003–2007: River runoff versus sea ice meltwater. *J. Geophys. Res. Ocean.* 114, 2003–2007. <https://doi.org/10.1029/2008JC005000>.
- Yamaoka, K., Nakagawa, T., Uno, T., 1978. Application of Akaike's information criterion (AIC) in the evaluation of linear pharmacokinetic equations. *J. Pharmacokinetic. Biopharm.* 6, 165–175. <https://doi.org/10.1007/BF01117450>.
- Zhang, J., Spitz, Y.H., Steele, M., 2020. Biophysical consequences of a relaxing beaufort gyre geophysical research letters. *Geophys. Res. Lett.* 47 <https://doi.org/10.1029/2019GL085990>. e2019GL085990.