

Spatial and geographical changes in the mesozooplankton community in the Bering and Chukchi Seas during the summers of 2007 and 2008



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ABSTRACT

From July to August 2007 and June to July 2008, the horizontal/geographical changes in the zooplankton community in the Bering and Chukchi Seas were studied. The geographical patterns, which were common for these two years, were observed for salinity, chlorophyll *a* (Chl. *a*), zooplankton chaetognaths, hydrozoans and the whole zooplankton community. Among them, the patterns of salinity and Chl. *a* were related with the horizontal distribution of the water masses. The distributions of the two carnivorous taxa were correlated with their prey (copepods or barnacle larvae). The analysis of the structural equation model (SEM) revealed that the horizontal distribution of the zooplankton abundance and biomass were governed by the different taxa. Thus, the zooplankton abundance was governed by the numerically dominant but smaller-bodied taxa, such as the barnacle larvae and copepod *Pseudocalanus* spp., while the zooplankton biomass was determined by the large-bodied copepods, such as *Calanus glacialis/marshallae* and *Eucalanus bungii*.

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1. Introduction

In the Chukchi Sea, located in the Pacific sector of the Arctic Ocean, under the recent climate changes, the sea ice is melting faster (Markus et al., 2009) and the primary production is increasing (Arrigo et al., 2014). Concerning the zooplankton, extensions of the distribution range of the sub-Arctic (Bering Sea) fauna to the Arctic Chukchi Sea were reported under the effect of the inflow of Pacific Water (Matsuno et al., 2011; Nelson et al., 2014). Because the climate-induced changes in the zooplankton community in this region occurred in conjunction with the oscillation of the horizontal distribution of the community, information regarding the horizontal/geographical distribution of the zooplankton community in the Bering and Chukchi Seas is of primary importance.

Previously, the zooplankton communities in the Bering Sea and

Chukchi Sea were studied independently. For instance, in the Bering Sea, various projects, such as the Bering Ecosystem Study (BEST) and Bering Sea Integrated Ecosystem Research Program (BSIERP), were performed (Stabeno et al., 2012; Eisner et al., 2014). For the Chukchi Sea, the zooplankton studies were conducted with comparable programs, such as the Russian-American Long-term Census of the Arctic (RUSALCA) and the Chukchi Acoustic, Oceanographic and Zooplankton (CHAOZ) study (Hopcroft et al., 2010; Questel et al., 2013). Because these projects were conducted independently in the Bering Sea and Chukchi Sea, little information is available for the horizontal distribution of the zooplankton community more broadly throughout the two regions (cf. Pomerleau et al., 2014).

In the present study, we evaluated the horizontal/geographical distribution of the zooplankton community in the Bering and Chukchi Seas from July to August in 2007 and June to July in 2008 based on the samples collected using the same methods in each location. To identify the governing factors of zooplankton abundance and biomass in this region, we conducted a structural

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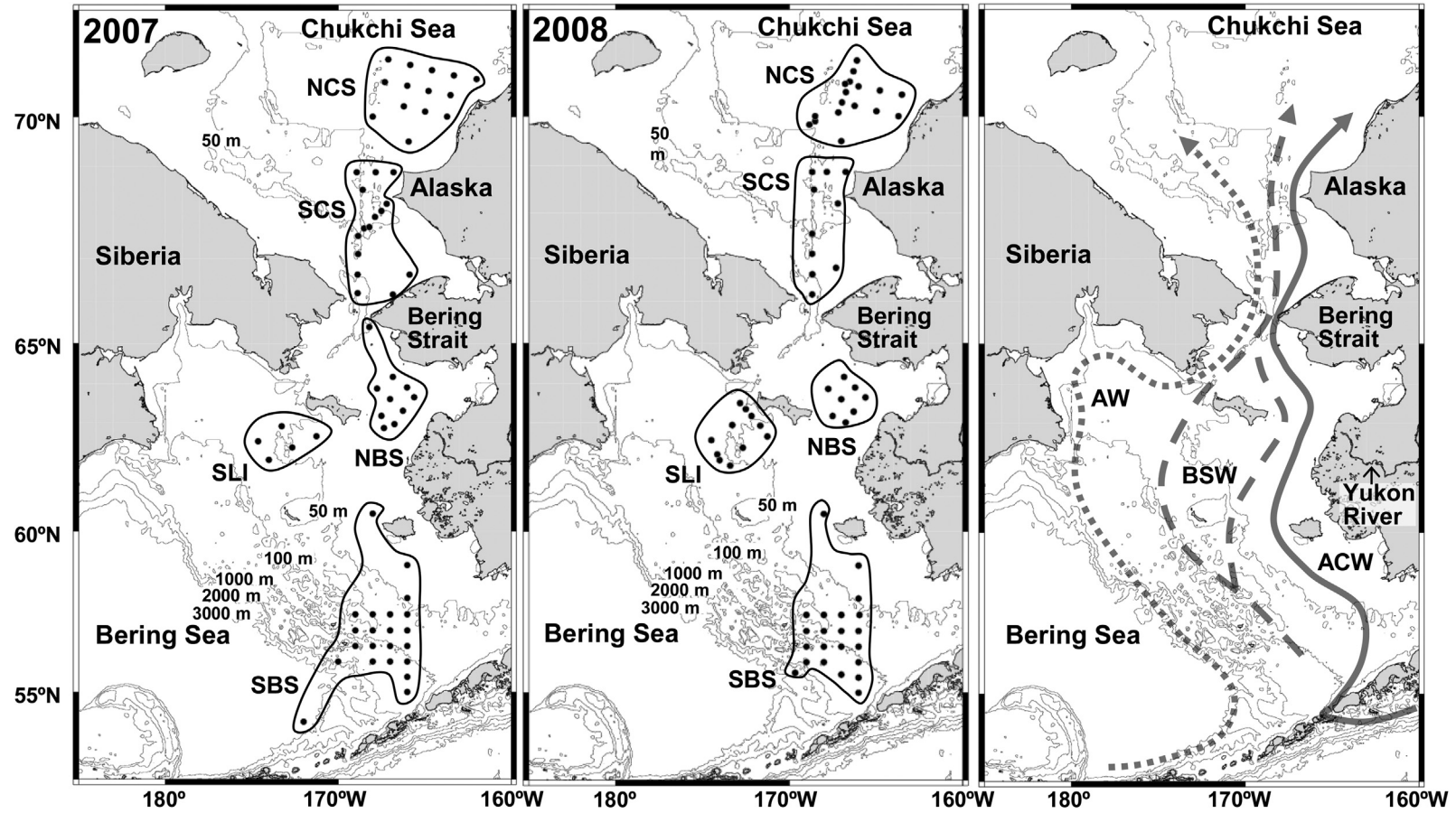


Fig. 1. Location of the sampling stations in the Bering and Chukchi Seas from June to August of 2007 and 2008. Symbols denote stations where the samplings were conducted. Depth contours (50, 100, 1000, 2000 and 3000 m) are superimposed. Based on geographical distribution, the stations are grouped into five regions: southern Bering Sea (SBS), around St. Lawrence Island (SLI), northern Bering Sea (NBS), southern Chukchi Sea (SCS) and northern Chukchi Sea (NCS). For the right panel, arrows indicate the approximate current flows. ACW: Alaskan Coastal Water, BSW: Bering Shelf Water, AW: Anadyr Water.

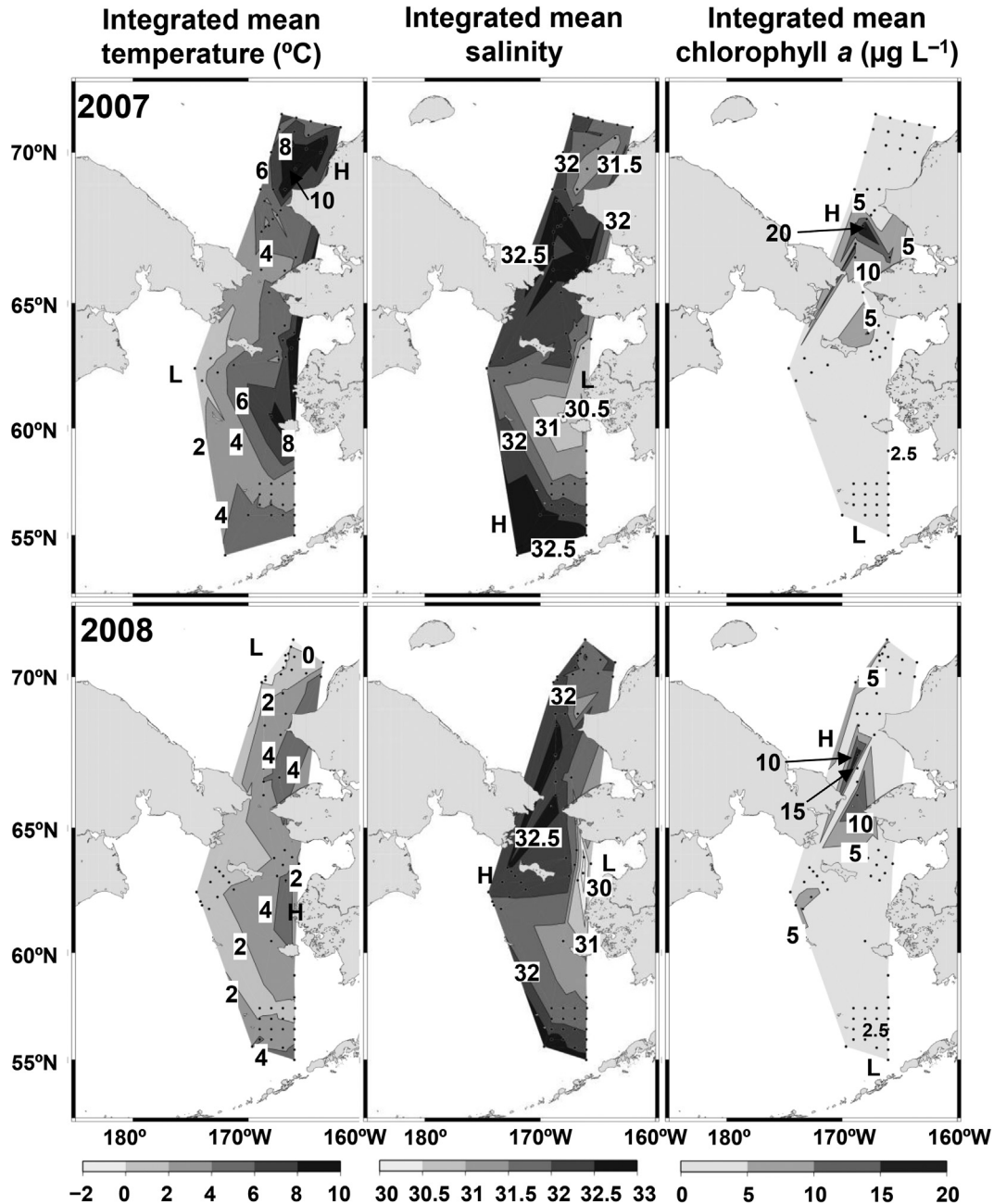


Fig. 2. Integrated mean temperature ($^{\circ}\text{C}$), salinity and chlorophyll a ($\mu\text{g L}^{-1}$) in the water column of stations in the Bering and Chukchi Seas from June to August of 2007 and 2008.

equation model (SEM) analysis (Stomp et al., 2011). Using the results of these analyses, we will discuss the special characteristics of the zooplankton community in this region during the summer.

2. Materials and methods

2.1. Field sampling

The zooplankton samplings were conducted throughout the Bering and Chukchi Seas from 20 July to 13 August 2007 (68 stations) and 24 June to 13 July 2008 (70 stations) (Fig. 1). The stations were categorized into five sub-regions: the southern Bering Sea (SBS), around St. Lawrence Island (SLI), the northern Bering Sea (NBS), the southern Chukchi Sea (SCS) and the northern Chukchi Sea (NCS) (Fig. 1). The zooplankton samples were collected by

vertical hauls of a NORPAC net (mouth diameter 45 cm, mesh size 0.335 mm) from a 150 m depth (bottom depth is deeper than 150 m) or the sea bottom, -5 m (the bottom depth is shallower than 150 m). The volume of water filtered through the net was calculated using a flowmeter mounted at the mouth ring of the net. The zooplankton samples were immediately preserved with 5% v/v borax-buffered formalin. At each sampling station, the temperature and salinity were measured by a CTD sensor (Sea-Bird Electronics Inc., SBE 911 Plus). The water samples for the chlorophyll a (Chl. a) were collected from a maximum of 9 depths (0, 5, 10, 20, 30, 50, 75, 100 and 125 m, which varied depending on the bottom depth) by a bucket and rosette multi-sampler mounted on the CTD. The water samples were filtered through GF/F filters and Chl. a was extracted with N,N -dimethylformamide and measured by a fluorometer (Turner Designs, Inc., 10-AU-005).

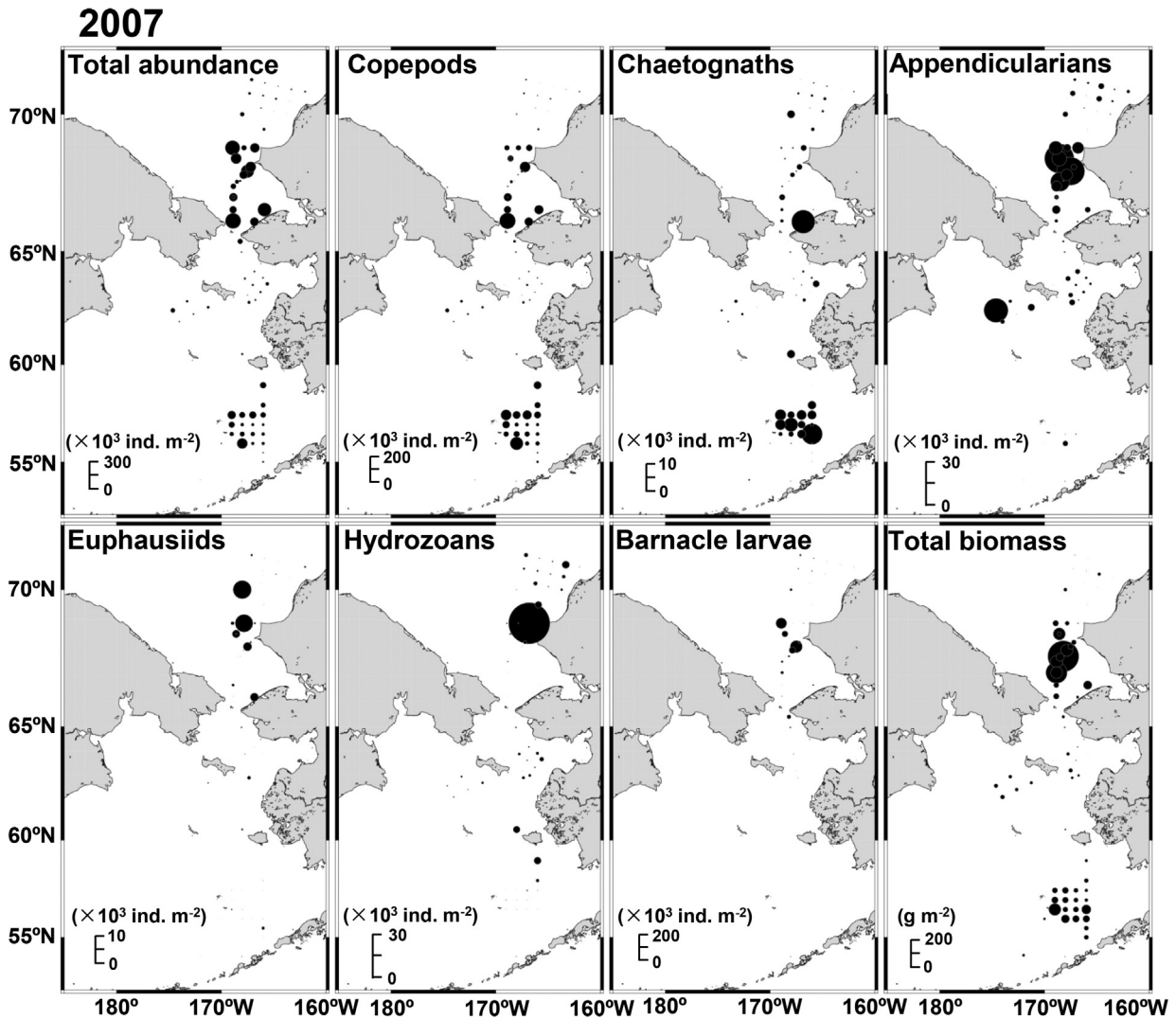


Fig. 3. Horizontal distribution of zooplankton abundance (total and each taxon) and biomass (total) in the Bering and Chukchi Seas from July to August of 2007.

2.2. Samples and data analysis

In the land laboratory, the zooplankton samples were divided using a Motoda box splitter (Motoda, 1959), and half of the aliquots were weighed for wet weight (WW) with a precision of 0.01 g using an electronic balance (Mettler PM4000). The zooplankton in the remaining aliquots were used for the identification and enumeration of the zooplankton community under a stereomicroscope. For species identification of the calanoid copepods, we referred mainly to Brodsky (1967). Because of the difficulty in species identification, we treated *Pseudocalanus* without species identification (i.e., *Pseudocalanus* spp.). We also treated the sympatric congeners *Calanus glacialis* and *Calanus marshallae* (Frost, 1974) as *Calanus glacialis/marshallae* for the same reason.

The zooplankton abundance data (X : ind. m^{-2}) for each species were transformed to $\log_{10}(X + 1)$ prior to the cluster analysis to reduce the bias of the abundant species. The similarities between the samples were examined using the Bray-Curtis index according to the differences in the species composition. For grouping the samples, the similarity indices were coupled with hierarchical agglomerative clustering with a complete linkage method (Unweighted Pair Group Method using Arithmetic mean: UPGMA) (Field et al., 1982). The inter-group differences in the zooplankton abundance were tested

with one-way ANOVA. If the ANOVA identified statistically significant differences ($p < 0.05$), an ex post facto Tukey-Kramer test was conducted to clarify the interaction between the groups. Cluster analysis was performed by PRIMER v6 and one-way ANOVA, and the Tukey-Kramer test was performed by StatView v5.

To evaluate the factors governing the changes in the zooplankton abundance and biomass, we applied SEM analysis (e.g., Stomp et al., 2011). For the SEM analysis, the hydrographic parameters (latitude, Julian day, integrated mean temperature, salinity and Chl. *a*) and the zooplankton abundance and biomass were transformed to normalized values (average = 0, standard deviations = 1), and regressions between all of the parameters were calculated. For the path analysis, we set the parameters with three category levels (1: latitude and Julian day, 2: temperature, salinity and Chl. *a*, 3: zooplankton). Subsequently, the insignificant relations between the parameters were removed from the final model. The overall fit of the final model was evaluated by the goodness-of-fit index (GFI) and the adjunct goodness-of-fit index (AGFI). The standardized path coefficients are independent variables, which indicate the relative contributions of the different paths within the SEM (Stomp et al., 2011). The SEM analysis was performed using add-in software for MS-Excel (<http://www.ohmsha.co.jp/data/link/978-4-274-06925-3/>).

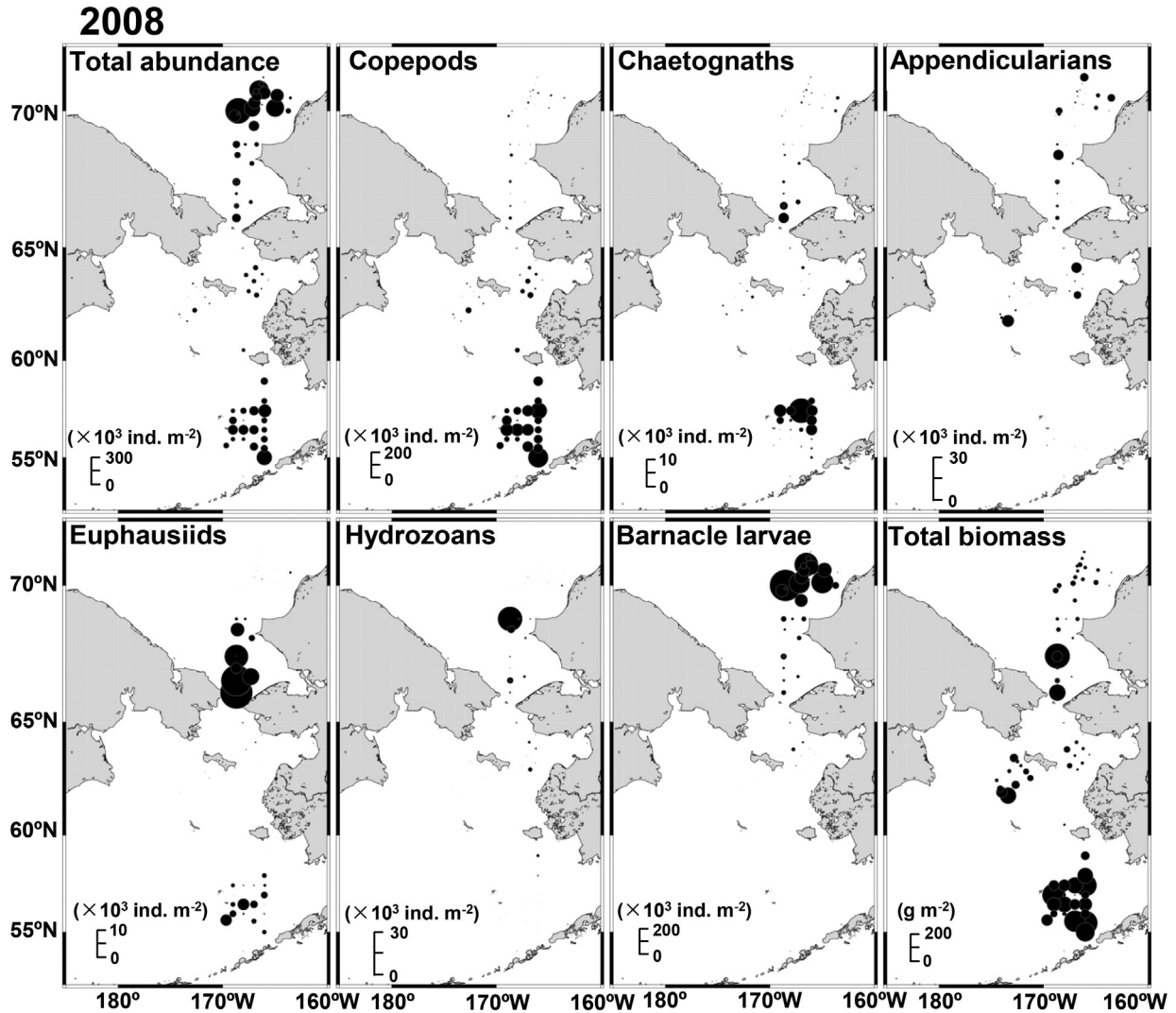


Fig. 4. Horizontal distribution of zooplankton abundance (total and each taxon) and biomass (total) in the Bering and Chukchi Seas from June to July of 2008.

3. Results

3.1. Hydrography

Regarding the horizontal/geographical changes, we considered them when similar results were observed for both 2007 and 2008. During both years, the salinity and Chl. *a* showed similar geographical patterns. The integrated mean salinity ranged from 29.7 to 33.0 and was high in the western side of the Bering Sea within the investigating area of this study, while it was low around the mouth of the Yukon River (Fig. 2). The integrated mean Chl. *a* ranged from 0.03 to 21.4 $\mu\text{g L}^{-1}$ and showed high values at the SCS in both years.

Differences in hydrography between 2007 and 2008 were mainly observed for the temperature. The integrated mean temperature ranged between -1.5 and 10.5 °C, and the horizontal distribution varied with the year (Fig. 2). Thus, temperatures in July–August 2007 were high (10 °C) at the NCS and low (<2 °C) at SLI, while those in June–July 2008 were high (>4 °C) around the Alaskan coastal area, especially at the Yukon River mouth, and low (<0 °C) at the ice edge area of the NCS.

3.2. Zooplankton taxa

The total zooplankton abundance ranged from 1103 to 316,409 ind. m^{-2} and was dominated by copepods (60%), followed by barnacle larvae (24%). Common horizontal distributions through the two years were observed for the chaetognaths and hydrozoans. Chaetognaths were abundant at the SBS and the SCS, while hydrozoans were abundant around the coastal areas of the NCS (Figs. 3 and 4).

Concerning the differences in zooplankton between 2007 and 2008, the total abundance was high at the SCS from July to August 2007 (Fig. 3). This was caused by the dominance of copepods and appendicularians in this region. The zooplankton biomass in 2007 showed a similar horizontal distribution of abundance. While in June–July 2008, the zooplankton abundance was high at the SBS and the NCS, and the dominant taxa varied between the SBS and the NCS; thus, copepods and chaetognaths were dominant at the SBS, while barnacle larvae dominated at the NCS (Fig. 4). Because of the smaller body size, the individual mass of barnacle larvae (dominant taxa at NCS in 2008) was small and the zooplankton biomass at the NCS in 2008 was small (Fig. 4). The zooplankton biomass in 2008 was high at the SCS and the SBS and showed a

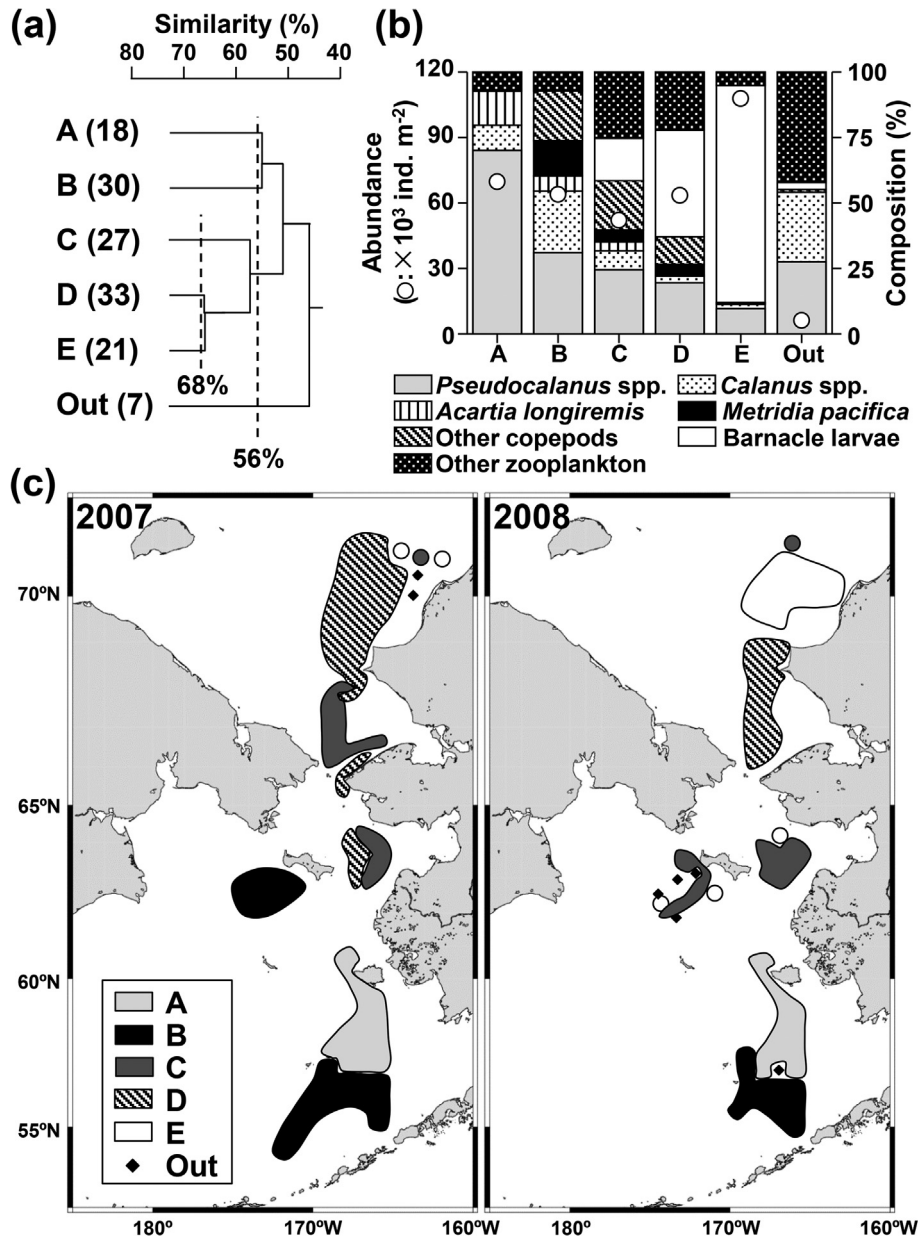


Fig. 5. Dendrogram showing the Bray–Curtis similarity results based on zooplankton abundance (a). Five groups (A–E) and an out group (Out) were identified at 56 and 68% similarity. Numbers in parentheses indicate the number of stations included in each group. The mean abundance and taxonomic composition of each group (b). Horizontal distributions of the five groups in the Bering and Chukchi Seas from June to August of 2007 and 2008 (c).

similar horizontal distribution with the biomasses in 2007 (Figs. 3 and 4).

3.3. Zooplankton community

Based on the zooplankton abundance, the zooplankton community was classified into five groups (A–E) by cluster analysis, with clusters having 56% and 68% similarity (Fig. 5a). The dominant groups varied by region. For both years of the study, groups A and B observed at the inshore (57–60.5°N, 166–169°W) and offshore (54–57.5°N, 166–172°W) areas of the SBS, respectively (Fig. 5c). Characteristic species of group A was *Acartia longiremis*, *Pseudocalanus* spp. and chaetognaths (Fig. 5b, Table 1). While group B had a high abundance of *C. glacialis/marshallae*, oceanic copepods (*Metridia pacifica*, *Neocalanus* spp. and *Scolecithricella minor*) and amphipods.

Differences in zooplankton community between 2007 and 2008 were seen in the northern areas from SLI to the NCS (Fig. 5c). Groups B, C, D and E, which were observed in this region, showed clear gradients of abundance of the barnacle larvae, which were most abundant in E, followed by D and C, with no occurrence in B (Fig. 5b, Table 1). In June–July 2008, groups E, D and C distributed with a north-to-south order through the NCS and SLI, which corresponded with the order of the numerical abundance of the barnacle larvae mentioned above (Fig. 5c); however, in July–August 2007, the barnacle larvae predominating in group E were not seen, group D distributed in the NCS, and groups C and B were seen in the SCS and SLI, respectively (Fig. 5c). Thus, this north-to-south order also corresponded with that of the barnacle larvae (abundance was greater in the north and lowest in the south).

Table 1

Comparison of zooplankton abundances between five groups in the Bering Sea and Chukchi Seas during July–August 2007 and June–July 2008. The five groups were identified from a cluster analysis of copepod abundance using a Bray–Curtis similarity connected with UPGMA (cf. Fig. 5a). Values represent the mean abundance (ind. m⁻²) in each group. The differences between regions were tested by one-way ANOVA and a post-hoc test using Tukey–Kramer test. Any groups not connected by the underlines are significantly different ($p < 0.05$). Numbers in the parentheses indicate the number of stations included in each group. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$, NS: not significant.

Species/taxa	Mean abundance (ind. m ⁻²)					One-way ANOVA	Tukey–Kramer test
	A (18)	B (30)	C (27)	D (33)	E (21)		
Calanoid copepods							
<i>Acartia hudsonica</i>	0	0	3	64	31	*	Not detected
<i>Acartia longiremis</i>	9154	3744	1782	277	447	****	D E C B A
<i>Acartia tumida</i>	0	43	18	14	0	NS	
<i>Calanus glacialis/marshallae</i>	6769	15,203	3806	1596	1780	****	D E C A B
<i>Centropages abdominalis</i>	90	27	6503	1776	55	**	B E A D C
<i>Eucalanus bungii</i>	0	7783	2055	3377	25	NS	
<i>Eurytemora herdmani</i>	0	0	137	5	18	*	D E C
<i>Epilabidocera amphitrites</i>	26	0	4	4	0	*	Not detected
<i>Metridia pacifica</i>	27	8728	2409	2622	6	***	E A C D B
<i>Microcalanus pygmaeus</i>	11	244	235	212	6	NS	
<i>Neocalanus</i> spp.	23	3939	87	409	43	****	A E C D B
<i>Pseudocalanus</i> spp.	49,460	20,053	12,970	12,578	10,514	****	E D C B A
<i>Racovitzanus antarcticus</i>	0	4	0	0	0	NS	
<i>Scolecithricela minor</i>	0	177	54	52	0	**	D C B
<i>Scolecithricella ovata</i>	0	18	0	0	0	NS	
<i>Tortanus discaudatus</i>	88	0	0	0	23	NS	
<i>Undinopsis pacificus</i>	0	5	0	0	0	NS	
Cyclopoid copepods	0	0	857	875	106	****	E C D
Amphipods	21	218	72	10	0	****	D A C B
Appendicularians	0	1243	3052	3995	2179	***	B E C D
Barnacle larvae	56	0	8552	26,088	89,952	****	A C D E
Bivalvia larvae	14	344	172	371	29	NS	
Chaetognaths	2951	1399	658	1142	541	****	E C D B A
Cladocerans	0	0	1700	0	3	*	Not detected
<i>Clione limacina</i>	0	10	25	82	51	*	B C E D
Echinoidea larvae	145	120	1293	472	0	**	B A D C
Eubrachyura zoea	90	73	16	102	62	NS	
Euphausiids	451	877	108	2648	197	****	C E A B D

(continued on next page)

Table 1 (continued)

Species/taxa	Mean abundance (ind. m ⁻²)					One-way ANOVA	Tukey-Kramer test
	A (18)	B (30)	C (27)	D (33)	E (21)		
Hydrozoans	1067	324	852	2852	407	**	B E C A D
Isopods	0	0	9	27	147	**	C D E
<i>Limacina helicina</i>	0	0	0	89	0	****	Not detected
Polychaetes	77	77	5432	2493	1978	**	A B E D C
Total copepods	65,649	59,968	30,920	23,861	13,055	****	E D C B A
Total zooplankton	70,519	64,654	52,862	64,233	108,601	**	C D B A E

3.4. SEM analysis

Through SEM analysis, within the five hydrographic parameters (Julian day, latitude, temperature, salinity and Chl. *a*), a high correlation (path coefficients: $pc = 0.70$) was observed between the Julian day and temperature; thus, the temperature increased with the Julian day (Fig. 6). The interactions between the environmental parameters and the zooplankton abundance, biomass and the two dominant taxa (copepods and barnacle larvae) varied greatly with each other. For example, the zooplankton biomass had negative correlations with the Julian day and latitude ($pc = -0.39$ and -0.27) and a positive correlation with Chl. *a* ($pc = 0.48$), and the determination coefficient (r^2) was 47% (Fig. 6). For the two dominant taxa,

copepods had a negative correlation ($pc = -0.52$) with the latitude, while the barnacle larvae had positive and negative correlations with the latitude ($pc = 0.49$) and the temperature ($pc = -0.38$), respectively ($r^2 = 27-38\%$). The zooplankton abundance showed a negative correlation ($pc = -0.28$) with temperature, while the determination coefficient was extremely low ($r^2 = 8\%$).

4. Discussion

4.1. Spatial/geographical change

The following five spatial/geographical results were seen: the salinity was high in the western Bering Sea and low around the

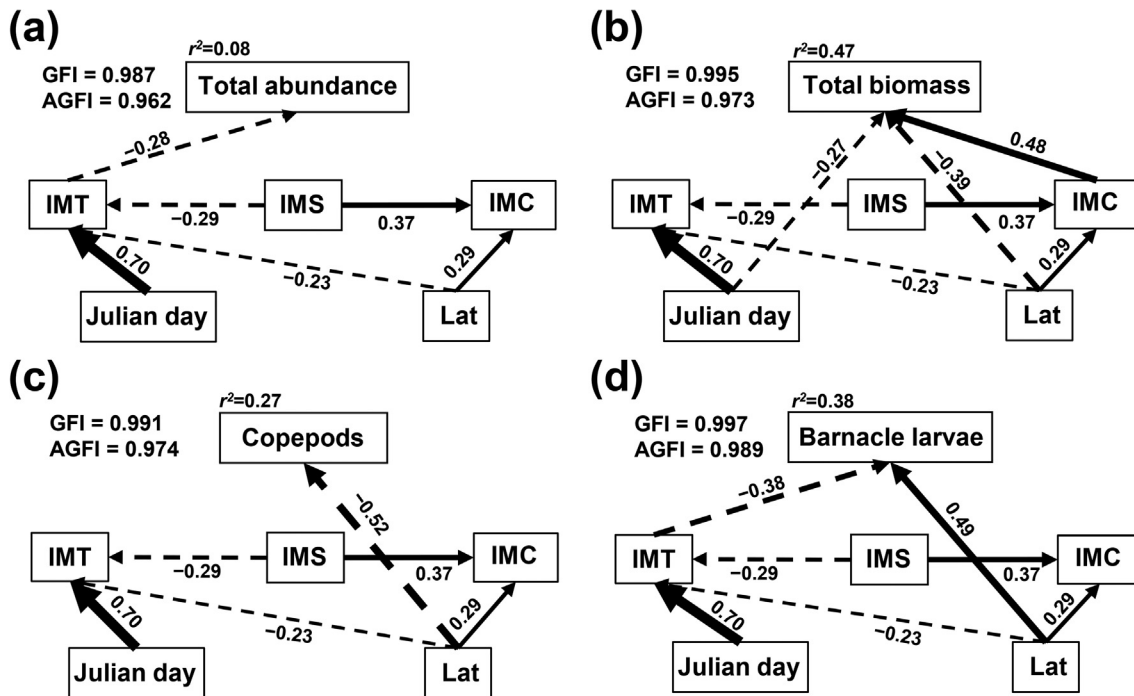


Fig. 6. Results of the structural equation model (SEM) for total zooplankton abundance (a) and biomass (b) and abundance of copepods (c) and barnacle larvae (d) with environmental factors. The values along the pathways represent standardized path coefficients. Arrows with solid or dashed lines indicate positive or negative effects. The thickness of the arrows varies with the path coefficient values. The overall fit of the model was evaluated using the goodness-of-fit index (GFI) and the adjunct goodness-of-fit index (AGFI). IMT: integrated mean temperature, IMS: integrated mean salinity, IMC: integrated mean chlorophyll, Lat: latitude.

Table 2

Comparison of taxonomic composition (%) in abundance (ind. m⁻²) and biomass (g VVV m⁻²) throughout the Bering and Chukchi Seas during July–August 2007 and June–July 2008.

Species/taxa	Composition (%)	
	Abundance	Biomass
Barnacle larvae	32.9	1.4
<i>Pseudocalanus</i> spp.	27.3	3.3
<i>Calanus glacialis/marshallae</i>	8.5	34.5
<i>Metridia pacifica</i>	4.6	1.9
<i>Eucalanus bungii</i>	4.4	19.7
<i>Acartia longiremis</i>	3.7	0.2
<i>Centropages abdominalis</i>	2.6	0.6
<i>Neocalanus</i> spp.	1.5	2.3
Other zooplankton	14.4	36.1

Yukon River, Chl. *a* was high in the SCS (Fig. 2), the chaetognaths presented high abundance in the SBS and the SCS, the hydrozoans presented high abundance in the NCS (Figs. 3 and 4), and the zooplankton community was latitudinally separated within the SBS (Fig. 5). These results would be related with the ocean currents and water masses in this region.

The ocean currents in this region are dominated by the northward flow from the Gulf of Alaska to the Chukchi Sea through the Bering Sea, and three currents were identified (Coachman and Charnell, 1979; Coachman, 1986). Thus, the Alaskan Coastal Water (ACW) flows at the easternmost (inshore) route, the Anadyr Water (AW) flows at the westernmost (offshore) route and the Bering Shelf Water (BSW) flows between them and is centred on St. Lawrence Island (Fig. 1). The salinity is high for the waters originating in the Gulf of Alaska and low for the ice-melt water or river runoff; thus, the salinity, from highest to lowest, can be represented as AW > BSW > ACW (Fig. 2) (Coachman and Charnell, 1979; Coachman, 1986). In the shallow Bering Strait (maximum 54 m depth), deep Bering Sea water was upwelling and provided plentiful nutrients through the Anadyr Water to the Chukchi Sea, which resulted in a constant phytoplankton bloom at the SCS (Springer and McRoy, 1993). This information on the horizontal distribution

of the salinity and phytoplankton (Chl. *a*) corresponds well with the findings of the present study (Fig. 2).

The chaetognaths and hydrozoans, which had horizontal distribution patterns, were carnivores and were mainly composed of mono-species; the chaetognaths are *Parasagitta elegans* (Ohashi et al., 2013), and the hydrozoans are *Aglantha digitale* (Shiota et al., 2012). Shiota et al. (2012) reported that the mature body size of *A. digitale* decreased with increasing latitudes, which suggests that the small-bodied hydrozoans utilized the acquired energy for gonad maturation and rapid reproduction in the Bering and Chukchi Seas. From a smaller body size (Shiota et al., 2012), the main prey of *A. digitale* is assumed to be the barnacle larvae that were abundant at the NCS, both in 2007 and 2008 (Figs. 3 and 4). Cnidarians feeding on barnacle larvae is well documented for coastal waters (Sullivan et al., 1994). For *P. elegans*, their abundance is known to be highly correlated with that of their prey (copepods) through long-term observation at the SBS over 16 years (Ohashi et al., 2013). In addition, in the present study, the horizontal abundance of the chaetognaths was highly correlated with that of the copepods ($r = 0.37, p < 0.0001$) (Figs. 3 and 4). Thus, the horizontal distributions of the two carnivorous taxa would be governed by the bottom-up control of their prey (barnacle larvae or copepods).

Hydrographically, the SBS is divided into three regions: Inner (<50 m bottom depth), Middle (50–100 m) and Outer domains (100–150 m) (Coachman and Charnell, 1979; Coachman, 1986). The zooplankton community at the SBS is also reported to vary with the region (Cooney and Coyle, 1982). Groups A and B, observed at the SBS in this study, may correspond with the Inner-Middle and Outer groups of Cooney and Coyle (1982), respectively. The neritic Inner group is dominated by *A. longiremis* and *Pseudocalanus* spp., while the Outer group is abundant with the oceanic copepods, *Neocalanus cristatus*, *Neocalanus plumchrus*, *Eucalanus bungii* and *M. pacifica* (Cooney and Coyle, 1982). These dominant species correspond with those of groups A and B in this study (Table 1). At the SBS, the inter-annual changes in the zooplankton community are also reported between the warm and cold years (Napp et al., 2002; Ohashi et al., 2013; Eisner et al., 2014). Because the years 2007 and 2008 in this

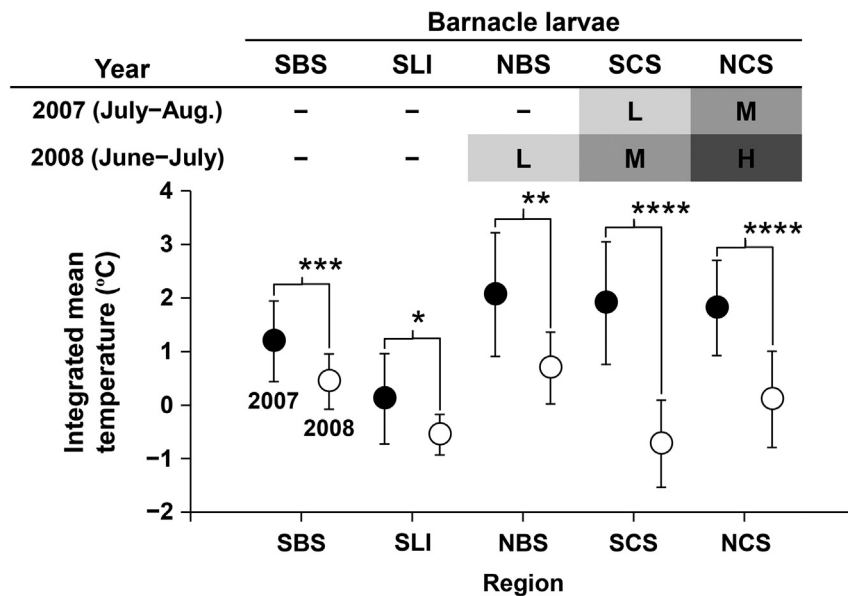


Fig. 7. Regional and temporal differences in the barnacle larvae abundance and the temperature in the Bering and Chukchi Seas from June to August of 2007 and 2008. SBS: southern Bering Sea, SLI: around St. Lawrence Island, NBS: northern Bering Sea, SCS: southern Chukchi Sea, NCS: northern Chukchi Sea. L: low, M: medium, H: high abundance. Circle and bars indicate mean and standard deviation, respectively. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, ****: $p < 0.0001$.

study are both categorized as cold years (Stabeno et al., 2012), the inter-annual changes in the zooplankton community may not be observed at the SBS in this study.

4.2. SEM analysis

To identify the controlling environmental factors on the plankton community, SEM analysis is considered to be an adequate statistical method (Stomp et al., 2011; Miyamoto et al., 2014). In this study, the abundances of the two dominant taxa (copepods and barnacle larvae) had different correlations with the latitude; the copepods showed a strong negative correlation with the latitude, while the barnacle larvae had a strong positive correlation (Fig. 6). As a consequence, the latitudinal patterns were offset for the total zooplankton abundance. The weak negative correlation of the temperature observed for the total zooplankton abundance may be a reflection of what was seen for the barnacle larvae (Fig. 6).

On the other hand, the zooplankton biomass showed negative correlations with the Julian day and latitude and a positive correlation with Chl. *a* (Fig. 6). These interactions with the environmental parameters are similar to those of the copepod abundance (negative correlation with latitude) (Fig. 6). However, two additional factors of the zooplankton biomass (negative correlation with the Julian day and positive correlation with the Chl. *a*) suggest that other factors may affect the zooplankton biomass.

To evaluate the relative importance of each species in the total zooplankton abundance and biomass, Table 2 shows the species/taxa composition of the whole zooplankton abundance (grand mean: 66,766 ind. m⁻²) and biomass (45.6 g wet weight m⁻²), which were calculated by multiplying the individual biomass (WW) of each copepod species which were published elsewhere (Mauchline, 1998; Ozaki et al., 2001; Matsuno et al., 2012) and the directly measured values for the barnacle larvae. The remaining fraction of the biomass (total WW – (copepod WW and barnacle WW)) was treated as other zooplankton. In abundance, the barnacle larvae and *Pseudocalanus* spp. were dominant and composed 33% and 27% of the total abundance, respectively, while measured in biomass, their compositions were extremely low (1% for the former and 3% for the latter) (Table 2). This discrepancy in species composition between abundance and biomass is caused by the smaller individual biomass of the two numerically dominant taxa. Within the biomass, the large-bodied *Calanus glacialis/marshallae* (35%), the oceanic copepod *E. bungii* (20%) and the other large-bodied taxa (e.g., euphausiids) (36%) were dominant. These taxa/species were abundant at the SCS (Figs. 3–5), where the constant phytoplankton bloom occurred, which was enhanced by the inflow of upwelling nutrients from the Bering Sea basin (Fig. 2) (Springer and McRoy, 1993). This is why the zooplankton biomass had a positive correlation with the Chl. *a* (Fig. 6). Because biomass-dominant copepods (*Calanus* spp. and *E. bungii*) descend to deep layers from summer to autumn (Miller et al., 1984; Conover, 1988), this seasonal vertical migration may cause the negative correlation of the Julian day with the zooplankton biomass (Fig. 6).

Thus, from the SEM analysis, it was revealed that different taxa/species govern the changes in zooplankton abundance and biomass in the Bering and Chukchi Seas during the summer. The zooplankton abundance was determined by the barnacle larvae and small-bodied copepods (*Pseudocalanus* spp.), while their biomass was governed by the large-bodied copepods (*C. glacialis/marshallae* and *E. bungii*).

4.3. Difference between 2007 and 2008

Through this study, the following three differences were detected between 2007 and 2008: the temperature, especially at

the NCS—the lowest temperature (<0 °C) from June to July 2008, while the highest temperature (10 °C) was from July to August 2007 (Fig. 2); the zooplankton abundance was extremely high at the NCS from June to July 2008 with a dominance of barnacle larvae (Figs. 3 and 4); differences were detected for the zooplankton community in the northern regions (SLI to NCS) (Fig. 5). The differences in the temperature and the barnacle larvae abundance at each of the five sub-regions are summarized in Fig. 7. The temperature showed significant differences for all of the regions and was higher for July–August 2007 than June–July 2008. The differences in the temperature were the greatest at the SCS and the NCS ($p < 0.0001$) (Fig. 7). These temperature differences may be related with the one-month differences in the observation period between 2007 (July–August) and 2008 (June–July). The heating on the upper surface water caused by the increasing solar radiation from June to August may be a primary factor that governs the differences in temperature (Mizobata et al., 2010; Vanin, 2010). It also should be noted that the 2007 summer is the second minimum of the sea ice extent in the observational record (Comiso et al., 2008).

For barnacle larvae, their abundance was higher from June to July (2008) than from July to August (2007) in all of the regions (Fig. 7). The mean abundance at the NCS was 2194 ind. m⁻³ from June to July 2008, while it was 149 ind. m⁻³ from July to August 2007. The barnacle larvae abundance at the NCS was also reported to be 34–253 ind. m⁻³ (=1714–12,632 ind. m⁻²/50 m depth) during September 2007 (Eisner et al., 2013). Thus, the barnacle larvae abundance is high in June and, while is low during autumn. The one-month differences in the sampling period between 2007 and 2008 are considered to be a possible cause of the differences in the meroplanktonic barnacle larvae abundance in this region.

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References

- Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., Lowry, K.E., Mills, M.M., Palmer, M.A., Balch, W.M., Bates, N.R., Benitez-Nelson, C.R., Brownlee, E., Frey, K.E., Laney, S.R., Mathis, J., Matsuoka, A., Mitchell, B.G., Moore, G.W.K., Reynolds, R.A., Sosik, H.M., Swift, J.H., 2014. Phytoplankton blooms beneath the sea ice in the Chukchi Sea. *Deep Sea Res. II* 105, 1–16.
- Brodsky, K.A., 1967. Calanoida of the Far-eastern Seas and Polar Basin of the USSR. Israel Program Scientific Translation, Jerusalem.
- Coachman, L.K., Charnell, R.L., 1979. On lateral water mass interaction – a case study, Bristol Bay, Alaska. *J. Phys. Oceanogr.* 9, 278–297.
- Coachman, L.K., 1986. Circulation water masses, and fluxes on the southeastern Bering Sea shelf. *Cont. Shelf Res.* 5, 23–108.
- Comiso, J.C., Parkinson, C.L., Gersten, R., Stock, L., 2008. Accelerated decline in the Arctic sea ice cover. *Geophys. Res. Lett.* 35, L01703. <http://dx.doi.org/10.1029/2007GL031972>.
- Conover, R.J., 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167/168, 127–142.
- Cooney, R.T., Coyle, K.O., 1982. Trophic implications of cross-shelf copepod distributions in the southeastern Bering Sea. *Mar. Biol.* 70, 187–196.
- Eisner, L., Hillgruber, N., Martinson, E., Maselko, J., 2013. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi Seas. *Polar Biol.* 36, 87–113.
- Eisner, L.B., Napp, J.M., Mier, K.L., Pinchuk, A.I., Andrews, A.G., 2014. Climate-mediated changes in zooplankton community structure for the eastern Bering

- Sea. Deep Sea Res. II 109, 157–171.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analyzing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37–52.
- Frost, B.W., 1974. *Calanus marshallae*, a new species of calanoid copepod closely allied to the sibling species *C. finmarchicus* and *C. glacialis*. Mar. Biol. 26, 77–99.
- Hopcroft, R.R., Kosobokova, K.N., Pinchuk, A.I., 2010. Zooplankton community patterns in the Chukchi Sea during summer 2004. Deep Sea Res. II 57, 27–39.
- 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, C12024. <http://dx.doi.org/10.1029/2009JC005436>.
- 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.
- Matsuno, K., Yamaguchi, A., Shimada, K., Imai, I., 2012. Horizontal distribution of calanoid copepods in the western Arctic Ocean during the summer of 2008. Polar Sci. 6, 105–119.
- Mauchline, J., 1998. The biology of calanoid copepods. Adv. Mar. Biol. 33, 1–660.
- Miller, C.B., Frost, B.W., Batchelder, H.P., Clemons, M.J., Conway, R.E., 1984. Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. Prog. Oceanogr. 13, 201–243.
- Miyamoto, H., Kotori, M., Itoh, H., Nishida, S., 2014. Species diversity of pelagic chaetognaths in the Indo-Pacific region. J. Plankton Res. 36, 816–830.
- Mizobata, K., Shimada, K., Woodgate, R., Saitoh, S.-I., Wang, J., 2010. Estimation of heat flux through the eastern Bering Strait. J. Oceanogr. 66, 405–424.
- Motoda, S., 1959. Devices of simple plankton apparatus. Mem. Fac. Fish. Hokkaido Univ. 7, 73–94.
- Napp, J.M., Baier, C.T., Brodeur, R.D., Coyle, K.O., Shiga, N., Mier, K., 2002. Interannual and decadal variability in zooplankton communities of the southeast Bering Sea shelf. Deep Sea Res. II 49, 5991–6008.
- Nelson, R.J., Ashjian, C.J., Bluhm, B.A., Conlan, K.E., Gradinger, R.R., Grebmeier, J.M., Hill, V.J., Hopcroft, R.R., Hunt, B.P.V., Joo, H.M., Kirchman, 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, Dordrecht, pp. 269–336.
- Ohashi, R., Yamaguchi, A., Matsuno, K., Saito, R., Yamada, N., Iijima, A., Shiga, N., Imai, I., 2013. Interannual changes in the zooplankton community structure on the southeastern Bering Sea shelf during summers of 1994–2009. Deep Sea Res. II 94, 44–56.
- Ozaki, K., Takeuchi, T., Shiga, N., Mito, K., 2001. Winter zooplankton biomass and population structure of calanoid copepods in the Bering Sea basin. Plankton Biol. Ecol. 48, 46–51.
- Pomerleau, C., Nelson, R.J., Hunt, B.P.V., Sastri, A.R., Williams, W.J., 2014. Spatial patterns in zooplankton communities and stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in relation to oceanographic conditions in the sub-Arctic Pacific and western Arctic regions during the summer of 2008. J. Plankton Res. 36, 757–775.
- Questel, J.M., Clarke, C., Hopcroft, R.R., 2013. Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. Cont. Shelf Res. 67, 23–41.
- Shiota, T., Yamaguchi, A., Saito, R., Imai, I., 2012. Geographical variations in abundance and body size of the hydromedusa *Aglantha digitale* in the northern North Pacific and its adjacent seas. Bull. Fish. Sci. Hokkaido Univ. 62, 63–69.
- 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.
- Stabeno, P.J., Kachel, N.B., Moore, S.E., Napp, J.M., Sigler, M., Yamaguchi, A., Zerbini, A.N., 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Res. II 65–70, 31–45.
- Stomp, M., Huisman, J., Mittelbach, G.G., Litchman, E., Klausmeier, C.A., 2011. Large-scale biodiversity patterns in freshwater phytoplankton. Ecology 92, 2096–2107.
- Sullivan, B.K., Garcia, J.R., Klein-MacPhee, G., 1994. Prey selection by the scyphomedusan predator *Aurelia aurita*. Mar. Biol. 121, 335–341.
- Vanin, N.S., 2010. Thermohaline water structure on the southwestern Chukchi Sea shelf under conditions of opposite regimes of atmospheric circulation in summer periods of 2003 and 2007. Russ. Meteorol. Hydrol. 35, 468–475.