



Seasonal changes in the zooplankton community and population structure in the northern Bering Sea from June to September, 2017

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ABSTRACT

Zooplankton community structure in the northern Bering Sea may change significantly over relatively short periods due to the inflow of different water masses and the seasonal release of meroplankton, although details of these changes are still unclear. We studied the zooplankton community in the northern Bering Sea from June to September of 2017 and examined seasonal changes in the community structure and stage structure of the dominant species. Zooplankton abundance ranged from 41,000 to 928,000 ind. m⁻², with the greatest abundances near 174°W during July. Copepods were the dominant taxa, comprising 10–98% of zooplankton abundance, with benthic larvae such as bivalves dominant at some stations during July and August. Cluster analysis of abundances divided the station/zooplankton communities into seven groups. West of 172°W, clear seasonal changes were not observed, because the Bering Chukchi Winter Water persisted in the deep layer and sampling was only conducted in this region in July and August. In contrast, the community structures east of 172°W differed every month due to water masses changes, meroplankton release, and copepod production associated with the phytoplankton bloom. Despite the changes of water mass, development for the dominant large copepods (*Calanus glacialis/marshallae*, *Eucalanus bungii* and *Metridia pacifica*) was revealed from their population stage structures. Seasonal shifts in species within *Neocalanus* and appendicularians were driven by water mass exchanges. This study demonstrates that zooplankton community in the northern Bering Sea varies substantially on a monthly time scale. Therefore, to evaluate the impact of climate change on zooplankton, it is important to consider both the seasonal period and the dominant water masses present.

1. Introduction

The northern Bering Sea is a shallow shelf-sea with a depth of approximately 50 m connecting the Arctic Ocean to the remainder of the Bering Sea. It has high productivity that supports zooplankton, benthos, fish, marine mammals and seabirds due to its massive phytoplankton blooms and advection of plankton in the Anadyr Water (Springer et al., 1989, 1996; Springer and McRoy, 1993). In recent years, the magnitude and timing of the phytoplankton bloom has changed with the timing of the sea-ice retreat (Fujiwara et al., 2016). For instance, the timing of the sea-ice retreat was approximately two weeks earlier in 2018 than in previous years, influencing the marine ecosystem; the magnitude of the

bloom caused by ice algae was small and zooplankton abundance decreased (Cornwall, 2019; Fukai et al., 2019). Decreased sea ice also diminished the deep cold pool (<2 °C) south of St. Lawrence Island and fish shifted northward and their abundance decreased in the southeastern region (Cornwall, 2019; Duffy-Anderson et al., 2019). Thus, the marine ecosystem of the northern Bering Sea is facing rapid changes with sea-ice variations (Huntington et al., 2020).

The area has a complicated hydrographic environment due to the inflow of multiple currents with different hydrographic features. Three types of water masses enter this region from the south (Springer et al., 1989; Danielson et al., 2017) and are defined largely by salinity: Alaskan Coastal Water (ACW; S > 31.8), Bering Shelf Water (BSW; 31.8 < S <

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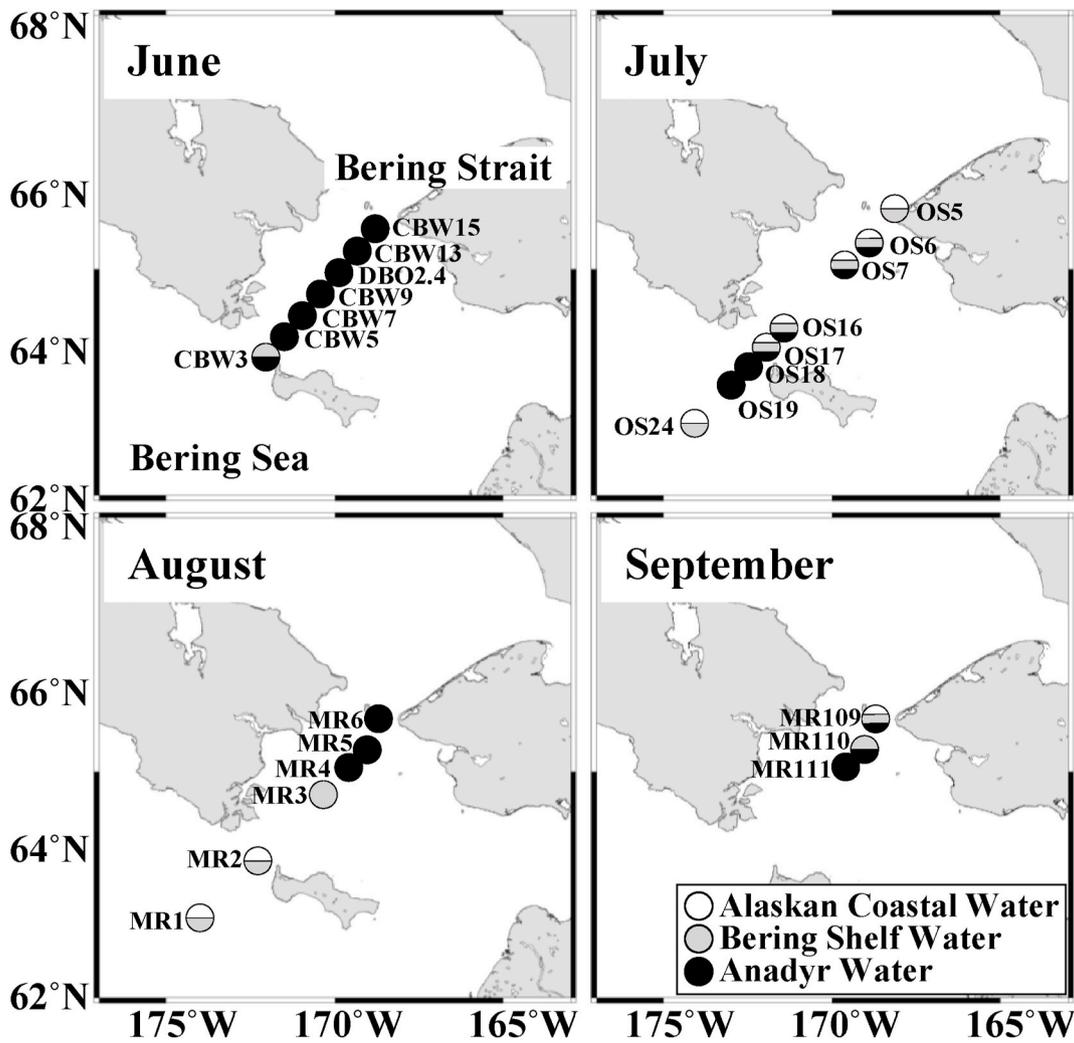


Fig. 1. Locations of the sampling stations in the Northern Bering Sea during June through September 2017. Color of the circles indicated spatial and vertical distribution of the water mass as defined by Coachman et al., (1975) (cf. Fig. 3).

Table 1

Zooplankton samples used in this study. All samples were collected with vertical hauls of 150- μ m mesh size nets but with slightly different net diameters on different vessels (60 cm for R/V *Sikuliaq*, 45 cm for T/S *Oshoro-Marui* and R/V *Mirai*).

Date	D/N	Station	Latitude (N)	Longitude (W)	Towed depth (m)	Vessel
June 23, 2017	Night	CBW15	65°30'	168°49'	53	Sikuliaq
June 24, 2017	Day	CBW13	65°14'	169°21'	45	Sikuliaq
June 24, 2017	Day	DBO2.4	64°58'	169°53'	43	Sikuliaq
June 24, 2017	Day	CBW9	64°41'	170°26'	45	Sikuliaq
June 25, 2017	Night	CBW7	64°25'	170°58'	40	Sikuliaq
June 25, 2017	Day	CBW5	64°09'	171°31'	41	Sikuliaq
June 25, 2017	Day	CBW3	63°53'	172°03'	43	Sikuliaq
July 11, 2017	Day	OS5	65°45'	168°09'	39	Oshoro-Marui
July 11, 2017	Day	OS6	65°20'	168°54'	50	Oshoro-Marui
July 12, 2017	Day	OS7	65°03'	169°38'	46	Oshoro-Marui
July 18, 2017	Day	OS16	64°15'	171°26'	42	Oshoro-Marui
July 18, 2017	Day	OS17	64°00'	171°57'	48	Oshoro-Marui
July 19, 2017	Night	OS18	63°45'	172°29'	43	Oshoro-Marui
July 19, 2017	Day	OS19	63°30'	173°00'	60	Oshoro-Marui
July 22, 2017	Night	OS24	63°00'	174°05'	71	Oshoro-Marui
August 26, 2017	Day	MR1	63°06'	174°01'	71	Mirai
August 26, 2017	Night	MR2	63°52'	172°18'	50	Mirai
August 27, 2017	Night	MR3	64°43'	170°21'	43	Mirai
August 27, 2017	Day	MR4	65°03'	169°36'	46	Mirai
August 27, 2017	Day	MR5	65°16'	169°03'	48	Mirai
August 27, 2017	Day	MR6	65°39'	168°42'	44	Mirai
September 20, 2017	Day	MR109	65°39'	168°43'	44	Mirai
September 20, 2017	Day	MR110	65°16'	169°03'	48	Mirai
September 20, 2017	Day	MR111	65°04'	169°36'	45	Mirai

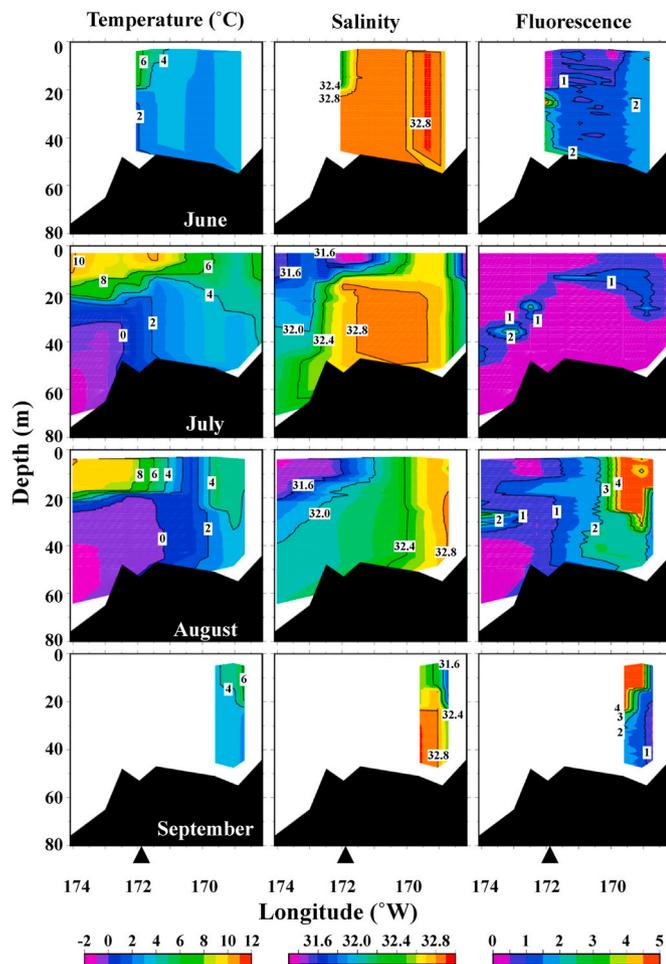


Fig. 2. Vertical sections of temperature, salinity and fluorescence across the transects of the Northern Bering Sea during June through September 2017. Solid triangles indicate the western end of the St. Lawrence Island.

32.5) and Anadyr Water (AW; $S < 32.5$) (Coachman et al., 1975). Since zooplankton communities differ in each water mass (Springer et al., 1989), community composition changes longitudinally in this region (Ozaki and Minoda, 1996). Focusing on particular species, the appendicularians *Oikopleura labradoriensis* and *O. vanhoeffeni* may be indicators of Anadyr Water and Bering Shelf Water, respectively, because their original distributions were different within the Bering Sea (Shiga, 1982, 1993a, 1993b). By contrast, Pacific copepods input to the northern Bering shelf are governed by the transport volume of Anadyr Water (Springer et al., 1989).

The species composition of the zooplankton communities can change significantly with water mass and the sudden appearance of meroplankton (Matsuno et al., 2011; Eisner et al., 2013). Barnacle larvae are often the dominant meroplankton on the Bering Sea Shelf where they may exceed 90% of zooplankton abundance (Matsuno et al., 2011). With a planktonic period of only 2–3 weeks (Herz, 1933), meroplankton can change the zooplankton community structure within a short period. During the phytoplankton bloom in the Chukchi Sea, sudden increases in meroplankton abundance can change the zooplankton community structure in a period of weeks (Questel et al., 2013). The large seasonal variations in the zooplankton community must be taken into account if accurate evaluation of interannual changes compared to sea-ice extent in the Chukchi Sea (Ershova et al., 2015a). In addition, despite reports that water masses change seasonally at Bering Strait (Woodgate et al., 2010), most studies of the zooplankton community in this region are based on snapshot observations. To overcome these problems, at least monthly sampling is needed. The use of inconsistent plankton net mesh

sizes by researchers has hampered prior attempts to examine seasonality, but the recent panArctic adoption of the 150- μ m mesh (Gill et al., 2011) by many researchers is resolving this limitation (e.g. Hopcroft et al., 2010; Ershova et al., 2015b).

In this study, we collected zooplankton samples using plankton nets with 150- μ m mesh in the northern Bering Sea during 2017 to examine seasonal changes in the structure of the zooplankton community. Hydrographic data and zooplankton samples were collected each month from June to September (a total of 4 times). Zooplankton community composition and its association with station location were analyzed. The development and reproduction of copepods, chaetognaths and appendicularians were evaluated based on seasonal changes in their population structure.

2. Materials and methods

A total of 24 zooplankton collections were taken by the T/S Oshoro-Marui, R/V Mirai, and R/V Sikuliaq in the northern Bering Sea (63° – $65^{\circ}75'N$, $168^{\circ}09'$ – $174^{\circ}05'W$) during June 23–25, July 11–22, August 26–27 and September 20, 2017 (Fig. 1, Table 1). Zooplankton samples were collected by vertical tows with a NORPAC net (mouth diameter: 45 cm; mesh size: 150 μ m) or twin ring nets (mouth diameter: 60 cm; mesh size: 150 μ m) from 5 m above the bottom to the surface during either day or night. The volume of water filtered through the net was estimated using a one-way flow meter mounted in the mouth of the net. Zooplankton samples were immediately preserved using 5% v/v borax buffered formalin. At all stations, temperature, salinity and fluorescence were measured using vertical casts of a CTD (Sea-Bird Electronics Inc., SBE 911 Plus) and a fluorometer package (Model FLRTD by Wetlabs Inc. or Fluorometer by Seapoint Sensors, Inc.). Water masses were classified by salinity according to Coachman et al. (1975).

Post cruise, zooplankton samples were split using a box splitter (Motoda, 1959). Zooplankton in the aliquots were identified and enumerated under a dissecting microscope. Calanoid copepods were identified to species and copepodid stage level. Identification of copepods followed Brodsky (1967), *Calanus glacialis* and *Calanus marshallae* were treated as *C. glacialis/marshallae* in this study because of the difficulty of species level identification (Frost, 1974). Gonad maturation for adult females of the dominant copepod species was evaluated as stage I (immature), stage II (small oocytes in the ovary or oviduct) and stage III (large eggs or distended opaque in oviduct) (Miller et al., 1984; Miller and Clemons, 1988; Niehoff, 1998). Mean Copepodid Stage (MCS) of the dominant large copepods (*C. glacialis/marshallae*, *Eucalanus bungii* and *Metridia pacifica*) was calculated using the following equation:

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

where i (1–6 indicate C1–C6) indicates the copepodid stage for a species, A_i (ind. m^{-2}) is the abundance of a copepodid stage (cf. Marin, 1987). Total lengths (TL, mm), from the top of the head to the end of the body without the caudal fin, of the dominant chaetognath, *Parasagitta elegans* was measured using calipers for large specimens (TL ≥ 10 mm) or an ocular micrometer for small specimens (TL < 10 mm) to a precision of 0.1 mm. Based on gonadal maturation, *P. elegans* was classified into five stages: juvenile, stages I, II, III, and IV (Terazaki and Miller, 1986). The identification of appendicularians followed Shiga (1993a) and Choe and Deibel (2008). The trunk length of *Oikopleura* spp. was measured with a precision of 0.1 mm using an ocular micrometer under a stereomicroscope.

The nonparametric Mann-Whitney U test was carried out to test whether there were significant difference in abundance (total abundance, copepod abundance and euphausiid abundance) between day and night sampling times. This analysis was carried out using Statview (SAS Institute Inc.). Abundance data (X : ind. m^{-2}) for each species were transformed to the fourth-root (X^{-4}) prior to cluster analysis in order to

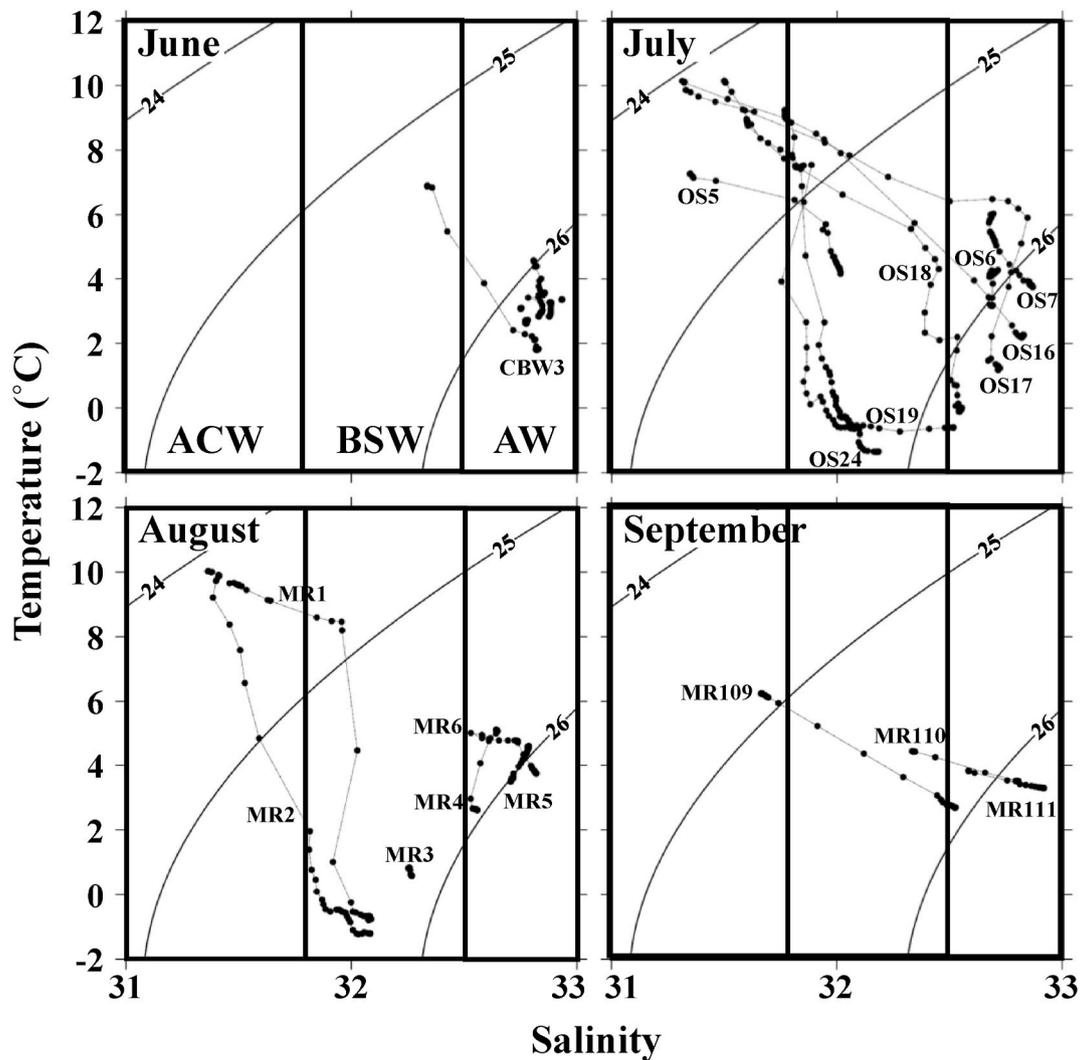


Fig. 3. T-S diagrams from the Northern Bering Sea during June through September 2017. Numbers and isolines indicate water density. Data from specific stations identified with labels. ACW: Alaskan coastal water, BSW: Bering Shelf water, AW: Anadyr water (cf. Coachman et al., 1975).

reduce the bias of abundant species. Similarities between samples were examined using the Bray-Curtis index according to differences in species composition. For grouping samples similarity indices were coupled with hierarchical agglomerative clustering and the complete linkage method (unweighted pair group method using arithmetic mean: UPGMA). Nonmetric multidimensional scaling (NMDS) ordination was carried out to delineate the sample groups on a two dimensional map. Multiple regression analysis was carried out for dependent hydrographic variables (latitude, longitude, depth, mean water column temperature, mean water column salinity and integrated water column fluorescence (the summation of the fluorescence values from the water column) and two dimensional NMDS as independent variables. PERMANOVA was carried out to determine the variables that significantly affected cluster grouping. These included sampling day, water mass and their interaction. The analyses were carried out using Primer7 software (PRIMER-E Ltd.). Intergroup differences in the abundance of each species and zooplankton taxon were tested with one-way ANOVA. If the ANOVA identified statistically significant differences ($p < 0.05$), a Tukey-Kramer post hoc test was carried out to clarify the interaction between groups. To clarify the factors that governed the MCS of the dominant large copepods (*C. glacialis*, *E. bungii* and *M. pacifica*), an analysis of covariance (ANCOVA) was performed using Statview (SAS Institute Inc.), with the day of the year and water mass as independent variables. A cohort analysis was made of *P. elegans* TL data with the aid of Microsoft Excel

Solver (Aizawa and Takiguchi, 1999). It is difficult to quantitatively capture euphausiids with nets due to net avoidance (Wiebe et al., 2004). Therefore, euphausiids were not included in population and lifecycle analyses.

3. Results

3.1. Hydrography

We identified three water masses in our study. Anadyr Water (AW, >32.5 salinity) was present every month, but dominated all layers during June and in the eastern region during July. Bering Shelf Water (BSW, 31.8–32.5 salinity) was observed every month, particularly at depth for the western stations during July and August. Alaskan Coastal Water (ACW, salinity <31.8) was seen at the surface in the Bering Strait (stn. OS5) and west of St. Lawrence Island during July (stn. 16–24), during August (stn. MR1 and MR2), and at the surface of stn. MR109 during September. Water temperature in the study ranged from -1.4 to 10.1 °C. A thermocline was present at approximately 20 m depth during July and August and was particularly strong to the west of 172° W. Salinity ranged from 31.3 to 32.9 and was freshest in the surface layer west of 172° W. Chlorophyll fluorescence ranged from 0.09 to 4.94, with a phytoplankton bloom (>4) in the upper half of the water column occurring to the east of 172° W during August and September (Figs. 2 and

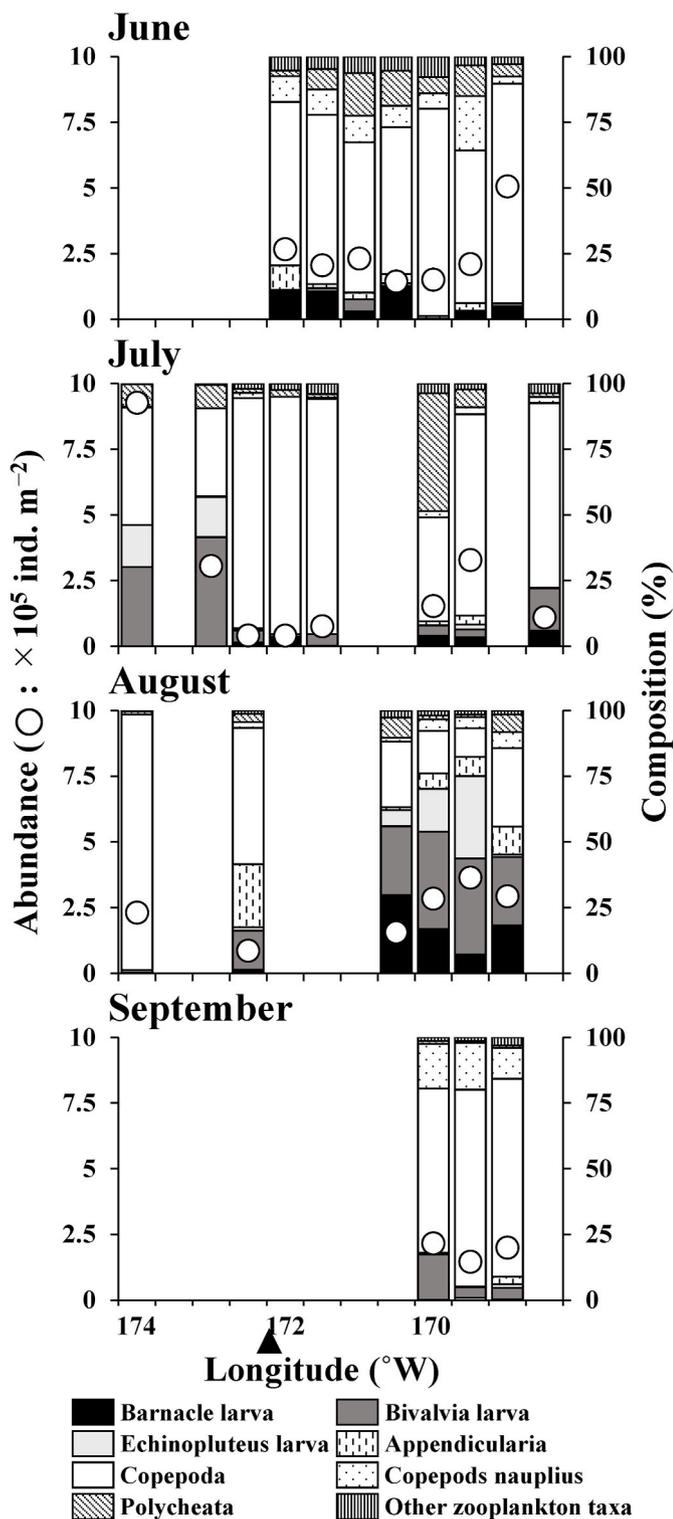


Fig. 4. Monthly changes in total zooplankton abundance and species composition in the northern Bering Sea during June through September 2017. Solid triangles indicate the western end of St. Lawrence Island.

3).

3.2. Zooplankton community

The zooplankton community composition changed every month with abundances ranging from 41,127 to 927,498 ind. m⁻². According to the Mann-Whitney *U* test, there were no significant differences in

abundance (total abundance, copepod and euphausiid abundance) between day and night. During June, abundances were similar between stations (144,436–268,357 ind. m⁻²) except stn. CBW15 that was dominated by Anadyr Water. The zooplankton community structure there was dominated by copepods, copepod nauplii and polychaeta (Fig. 4). During July, abundances varied greatly between stations, the greatest (927,498 ind. m⁻²) at 174°W and the lowest (41,127 ind. m⁻²) northwest of St. Lawrence Island near 172°W. Copepods still dominated, but bivalvia larva were the most dominant taxa at some of the stations. During August, copepods comprised 98% of zooplankton abundance at the most western station, but meroplankton (bivalvia larva, barnacle larva and echinopluteus larva) dominated at the other stations. During September, copepods and copepod nauplii dominated (Fig. 4). Twelve genera of copepods were identified (Table 2). Among these species, *E. bungii*, *M. pacifica*, *N. cristatus*, *N. flemingeri* and *N. plumchrus* were categorized as Pacific species.

Based on the cluster analysis of taxa abundance, stations were categorized based on zooplankton communities and separated into seven groups (A–G) at 64 and 70% similarity (Fig. 5a). The environmental variables significantly affecting cluster analysis were longitude, sampling depth, mean water column salinity and integrated water column fluorescence (Fig. 5b). Mean group abundance was the highest for group G and the lowest for group B. Groups A, B, C and F were characterized by the dominance of copepods *Pseudocalanus* spp. and Cyclopoida, while Groups D, E and G were characterized by the dominance of bivalvia and echinopluteus larvae (Fig. 5c). The distributions of each group changed greatly during the year but not west of 172°W during July and August (Fig. 6). To the east of 172°W, Group A occurred during June, Groups A, B and C occurred during July, Groups D and E occurred during August, and Group F occurred during September. On the other hand, to the west of 172°W, Groups C and G occurred during July and August. The hydrography (salinity and temperature) was similar within each group (Fig. 7). Note that there were no stations conducted to the west of 172°W in September. The groups observed east of 172°W were mainly distributed in AW. PERMANOVA indicated that sampling day, water mass and their interaction significantly affected the cluster grouping (Table 3).

The one-way ANOVA test for intergroup differences identified the characteristic taxa within each station group (Table 2). Euphausiids were important for Group A, *Oikopleura vanhoeffeni* for Group D, *Acartia* spp. and cladocerans for Group E, and *Calanus* nauplii for Group F. Some species were important in two groups including *Limacina helicina* in Groups B and D, barnacle nauplii in Groups D and E, and *Centropages* spp. in Groups E and F (Table 2).

3.3. Copepod population structure

The population structures of *C. glacialis/marshallae*, *E. bungii* and *M. pacifica* changed seasonally. For *C. glacialis/marshallae*, *E. bungii* and *M. pacifica*, copepodid stages I (CI) to IV (CIV) were abundant during June and decreased by August. In contrast, copepodid stage V (CV) was dominant during August. All copepodid stages of *Pseudocalanus* spp. appeared throughout the observation period but no clear change occurred in their population structure (Fig. 8).

Calanus spp. and *Pseudocalanus* spp. nauplii occurred in June, August and September, *Calanus* spp. nauplii were greater in abundance during September and *Pseudocalanus* spp. nauplii were greater during June in the eastern region (Fig. 9). *E. bungii* nauplii abundances were greater in June in the eastern region and near 172°W.

C. glacialis/marshallae adult females occurred in June, August and September (Fig. 8), and reproductively mature adult females were observed each month (Fig. 10). Adult females of *E. bungii* and *N. flemingeri* occurred only in July, approximately 40–50% of which were reproductively mature. Adult females of *M. pacifica* occurred during every month but reproductively mature females were seen only in September. Adult females of *Pseudocalanus* spp. with a high ratio of

Table 2

Comparisons of abundance in the northern Bering Sea during June through September of 2017. Values are mean abundance in each group of stations. Differences between groups were tested using one-way ANOVA and the Tukey-Kramer HSD post hoc test. Groups not connected by underlines are significant different ($p < 0.05$). *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Species/ Taxon	Groups							One-way Anova	Tukey-Kramer test
	A (9)	B (2)	C (3)	D (3)	E (1)	F (3)	G (3)		
<i>Acartia</i> spp.	174	0	632	0	2397	449	357	***	<u>A G F C E</u>
<i>Calanus glacialis/marshallae</i>	7333	1413	7553	451	599	87	15478	*	F D <u>E B A C G</u>
<i>Calanus</i> spp. nauplii	7460	178	1201	9218	0	23209	1002	***	<u>B G C A D F</u>
<i>Centropages</i> spp.	1766	0	405	6915	8788	22276	0	***	<u>C A D E F</u>
Cyclopoida	64625	31644	17101	8063	10385	64931	53930	NS	
<i>Eucalanus bungii</i>	1119	3813	22	294	749	818	0	*	<u>C D E F A B</u>
<i>Eucalanus bungii</i> nauplii	4872	0	0	0	0	0	0	NS	
<i>Metridia pacifica</i>	10636	800	307	5	50	2069	3375	*	Not detected
<i>Microcalanus</i> spp.	31134	622	69	1283	0	1550	511	NS	
<i>Microsetella</i> spp.	0	0	0	820	799	1387	0	**	Not detected
<i>Neocalanus cristatus</i>	42	44	0	0	0	0	0	NS	
<i>Neocalanus flemingeri</i>	3109	1902	709	41	50	0	279	NS	
<i>Neocalanus plumchrus</i>	0	0	0	0	0	37	0	*	Not detected
<i>Oncaea</i> spp.	0	0	0	5835	799	6578	462	***	<u>G E D F</u>
<i>Paraeuchaeta glacialis</i>	0	0	0	0	0	34	0	NS	
<i>Pseudocalanus</i> spp.	73751	12409	25915	33892	14092	31465	172589	NS	
<i>Pseudocalanus</i> spp. nauplii	5455	0	543	6086	2397	5604	0	NS	
Amphipoda	54	0	46	5	0	0	77	NS	
Barnacle cypris	3401	0	2001	13917	799	143	0	NS	
Barnacle nauplii	10620	836	774	28534	45535	577	0	***	<u>F C B A D E</u>
Bivalvia larvae	4163	1902	10810	104841	40742	17369	135696	*	<u>B A C F E D G</u>
Cladocerans	0	0	527	39	2996	0	0	***	<u>D C E</u>
<i>Clione limacina</i>	25	0	0	0	0	0	0	NS	
Decapod megalops	0	44	0	0	0	0	0	NS	
Decapod zoea	131	0	0	5	0	0	89	NS	
Echinoidea larvae	1780	0	0	0	0	0	0	NS	
Echinoidea pluteus	677	0	532	54466	9586	1076	65864	NS	
<i>Eukrohnia hamata</i>	22	36	6	0	0	0	0	**	Not detected
Euphausiacea	6295	560	256	397	0	0	251	***	<u>G C D B A</u>
Euphausiids nauplii	801	89	0	1102	0	2523	0	NS	
Fish larvae	0	53	0	0	0	0	0	NS	
<i>Fritillaria</i> spp.	5386	0	6960	12688	1598	1617	365	NS	
Hydrozoa	0	0	0	0	0	314	0	NS	
<i>Limacina helicina</i>	335	1058	722	2274	0	465	0	***	<u>A F C B D</u>
<i>Oikopleura labradoriensis</i>	1003	6	2	698	57	40	6	NS	
<i>Oikopleura vanhoeffeni</i>	260	0	2	9329	0	274	0	***	<u>C A F D</u>
<i>Oikopleura</i> spp.	74	0	5	2049	0	294	0	NS	
<i>Parasagitta elegans</i>	646	181	436	1437	387	363	1025	NS	
Polychaeta	25246	1067	1627	9023	11983	1721	36529	NS	
Unidentified nauplii	145	0	0	0	799	0	0	NS	
Total copepods	183478	52826	54457	72903	41104	160494	247982	NS	
Total zooplankton	244543	58658	79163	313708	155586	187271	487885	NS	

reproductively mature females occurred during every month. For *C. glacialis/marshallae*, *E. bungii* and *M. pacifica*, the association of the mean copepodite stage (MCS) with day of the year and water mass type (ACW, BSW, AW) was evaluated using ANCOVA; none were associated with water mass, but all had a positive correlation with day of the year (Table 4, Fig. 11). MCS indicated no significant difference within water mass, but large divisions might be affected by the difference in water mass. Notably, development of *C. glacialis/marshallae* was faster from June to July and slower after August when most individuals had reached CV.

Seasonal occurrence of the three species of *Neocalanus* spp. differed among species: *N. cristatus* occurred during June through July,

N. flemingeri occurred from June to August, and *N. plumchrus* occurred during September (Fig. 12). For these three species, CI–CIII were not observed (Fig. 12). *N. cristatus* was composed of CIV–CV, *N. flemingeri* of CIV, CV, adult male and adult females, and *N. plumchrus* of CIV–CV.

3.4. Chaetognatha

Parasagitta elegans was the predominant chaetognath species with only trace occurrences of *Eukrohnia hamata* at several stations and abundance for the two species ranging from 90 to 2486 ind. m⁻² and 0–45 ind. m⁻², respectively. *P. elegans* TL separated into one or two cohorts (Fig. 13). The mean TL of each cohort ranged from 2.7 cm (small

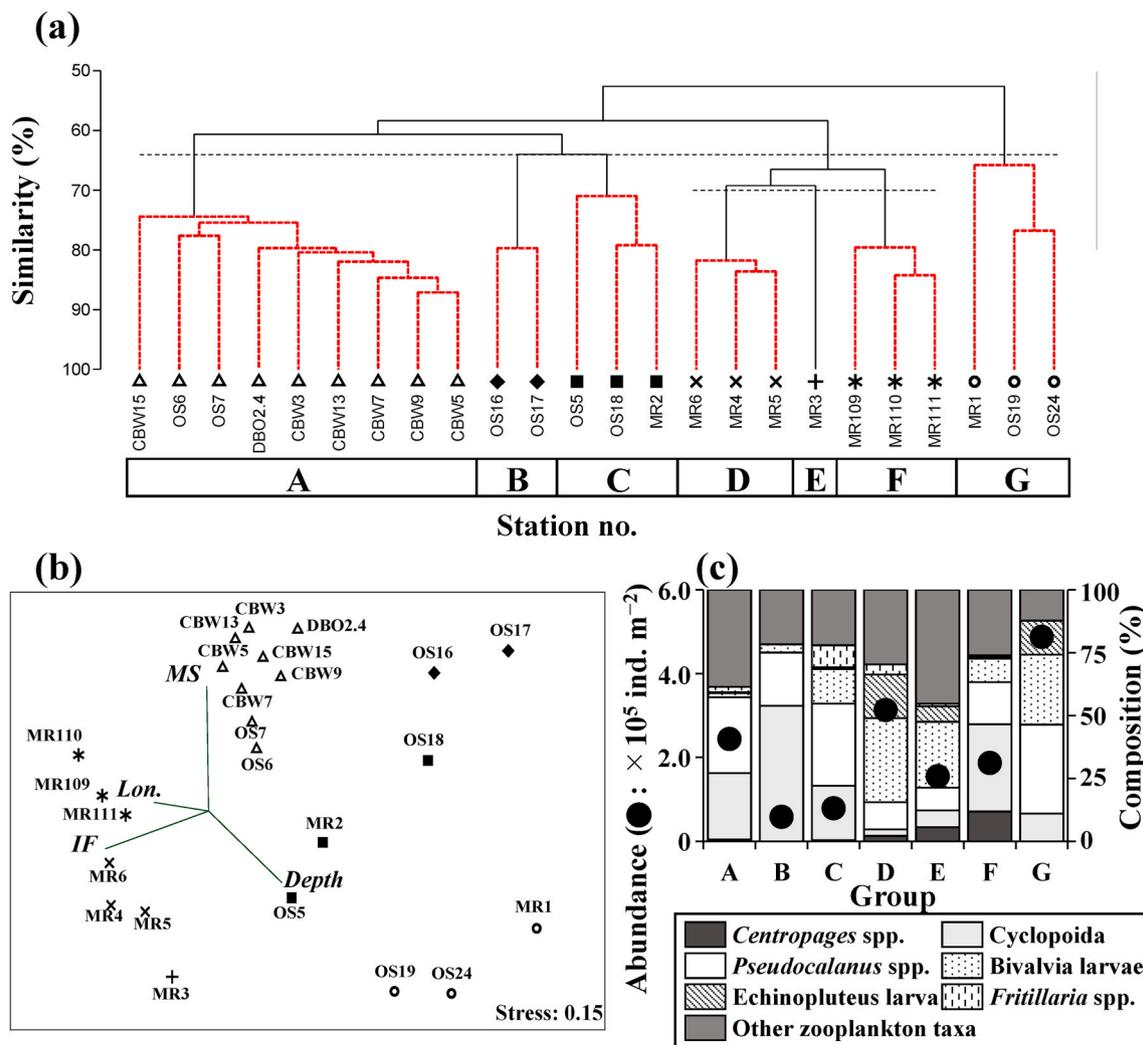


Fig. 5. (a) Dendrogram showing Bray-Curtis similarity results for zooplankton abundance. Eight groups (A–G) were identified at 64 and 70% similarity. (b) Nonmetric multidimensional scaling plots of the seven groups, with arrows indicating directions of environmental parameters. (c) The mean abundance and taxonomic composition of each group; only groups with a high % composition are separated. *Depth*: sampling depth (5 m off of the sea floor), *IF*: integrated water column fluorescence, *MS*: mean water column salinity, *Lon.*: longitude.

cohort in August) to 16.1 cm (large cohort in August). The abundance of smaller individuals was greater in June than in other months. Mature individuals were typically over 22 mm length and occurred during August and September.

3.5. Appendicularia

The appendicularians *Fritillaria* spp., *O. labradoriensis* and *O. vanhoeffeni* occurred in abundances ranging from 0 to 23,615, 0–4415 and 0–16,345 ind. m^{-2} , respectively. *Fritillaria* spp. was usually the dominant taxon. Species composition and trunk length of *Oikopleura* showed that smaller individuals (less than 1 mm trunk length) pre-dominated (Fig. 14). A clear seasonal change in species composition was observed: *O. labradoriensis* dominated in June and July while *O. vanhoeffeni* dominated in August and September (Fig. 14).

4. Discussion

4.1. Seasonal changes in community structure

Most of the previous studies of zooplankton community in the northern Bering Sea were based on snapshot observations, and because of this, it has been difficult to examine short term impacts of changes in

water mass on the zooplankton community. In this study, by same sampling for four straight months, we found that the zooplankton community and population structure for dominant species vary substantially on a monthly time scale in the northern Bering Sea.

Separate summer (Springer et al., 1989) and autumn (Pinchuk and Eisner, 2017) communities have been reported previously in the northern Bering Sea, but seasonal changes in zooplankton during each month have not been studied previously. In the southern Chukchi Sea, the zooplankton community showed interannual changes with sea-ice reduction and water mass changes (Ershova et al., 2015a). However, the sampling periods were different among years, creating unclear long-term trends due to large yearly variation. The biomass of Pacific zooplankton carried onto the northern Bering shelf is governed by the volume transport of Anadyr Water (Springer et al., 1989). According to Matsuno et al. (2011), the zooplankton community was changed by increased Pacific Water inflow; however, monthly changes were not explicitly evaluated in that paper. Resolving seasonal variability is critical for evaluation of long-term trends for zooplankton influenced by sea-ice variation and climate change in the northern Bering Sea, as well as in the Chukchi Sea.

In the northern Bering Sea, seasonal change patterns for water masses were different east and west of 172°W. West of 172°W a two-layer structure was observed with dominance of ACW in the surface

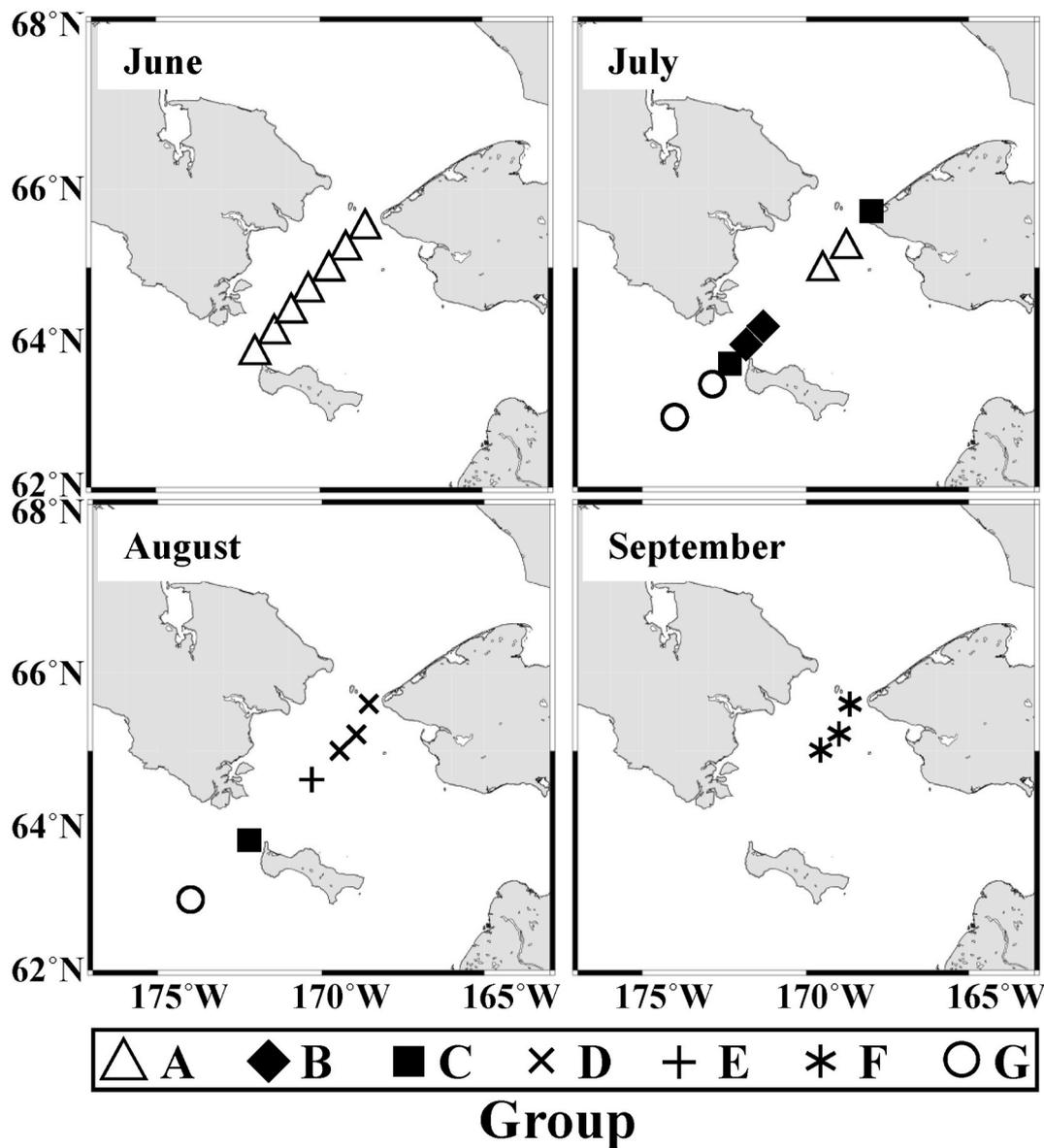


Fig. 6. Horizontal distributions of the seven station groups identified using Bray-Curtis similarity cluster analysis based on zooplankton abundance (cf. Fig. 5a) in the northern Bering Sea during June through September 2017.

layer and BSW in lower layers during July and August. It is unusual for ACW to appear west of St. Lawrence Island. East of 172°W, AW was dominant at lower depths during all seasons but the water masses in the surface layer changed seasonally.

West of 172°W, only two zooplankton communities (Groups C and G) occurred during July and August. Group G occurred most westerly and showed the highest abundance through the sampling period. In the previous studies, it was reported that zooplankton community structure was strongly related to bottom water mass because large-sized zooplankton were concentrated in the bottom layer (Coyle et al., 1996; Eisner et al., 2013; Questel et al., 2013; Ershova et al., 2015a, 2015b). Therefore, the zooplankton community of the western region may be affected by cold water masses that occur in the bottom layer in this region. Although not significant, more *C. glacialis/marshallae* occurred in Groups C and G than in other groups suggesting that these species are mainly distributed in cold water masses in the bottom layer. In the Bering and Chukchi seas, the biomass of *C. glacialis* is strongly correlated with Bering Chukchi Winter Water, with temperatures less than 0 °C (Pinchuk and Eisner, 2017). The population migrates down into the lower layer by winter convection (Coyle et al., 1996).

Additionally, the towing depth of plankton nets at stations in Group G were deeper than for the other groups (average 67 vs 45 m). Thus, the occurrence of Group G could be associated with a deeper water mass with high zooplankton density and the greater towing depth of the net. In this study, since cold water masses occurred in the bottom layer of the western region during July and August, the community structures of Groups G and C may have been greatly affected by these cold water masses. Therefore, seasonal change in the community was not observed in the western region, presumably because a colder water mass with abundant large copepods (i.e. *C. glacialis/marshallae*) was always present in the bottom layer during July and August.

On the other hand, seasonal change in the community structure was clearly observed east of 172°W. During June through July, Groups A and B contained many Pacific copepods and euphausiids. This is induced by inflow of Anadyr Water, with high salinity and a greater abundance of Pacific copepods and euphausiids (Springer et al., 1989). In August, Group E contained many cladocerans, *Acartia* spp. and *Centropages* spp., characteristic species of ACW (Hopcroft et al., 2010). However, hydrography of the station where Group E occurred had moderate salinity (32.2–32.3) and lower temperatures (0.5–0.9 °C), suggesting that it was

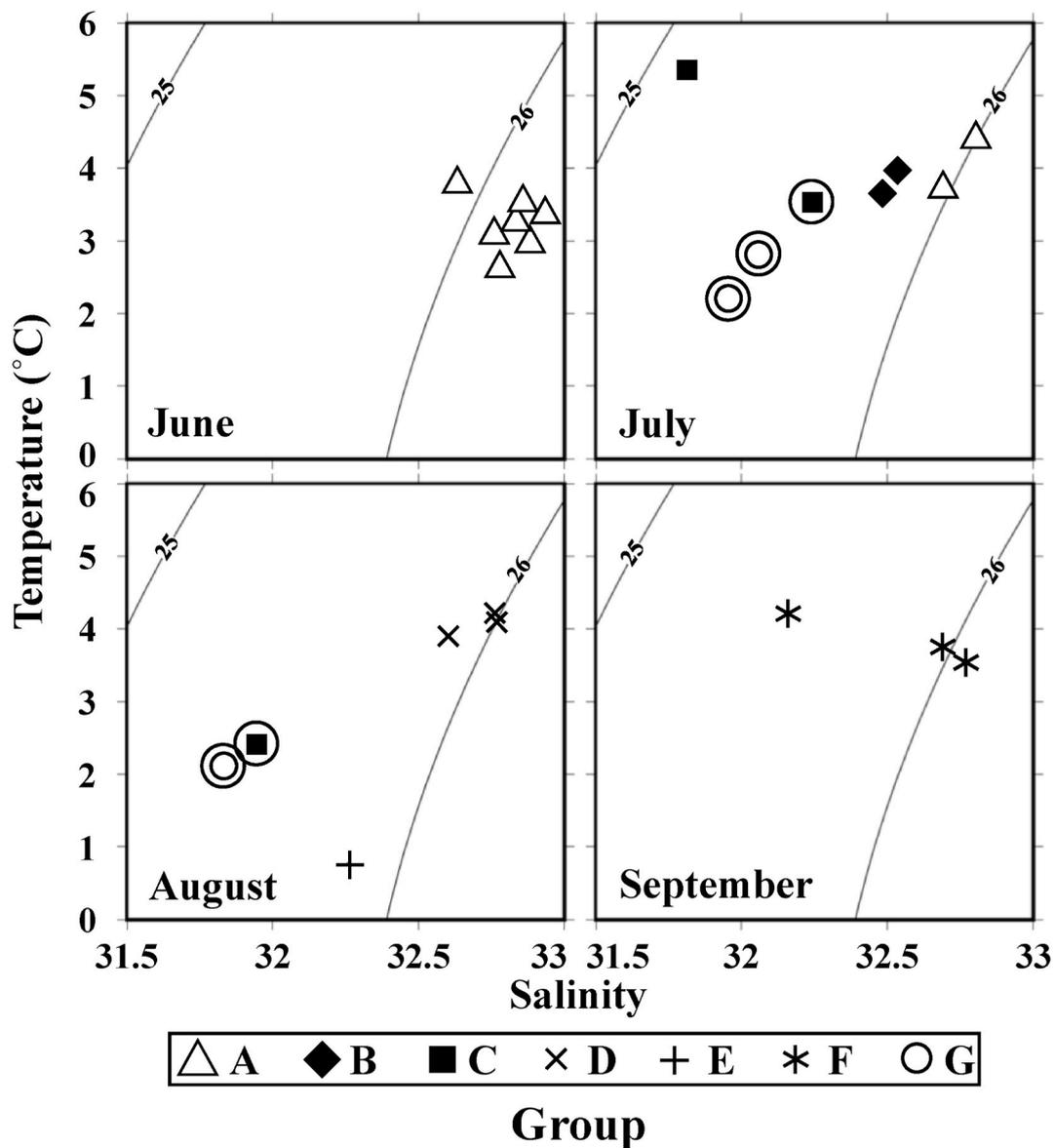


Fig. 7. T-S diagram with the seven groups identified from Bray-Curtis similarity based on zooplankton abundances (cf. Fig. 5a) in the northern Bering Sea during June through September of 2017. The plot position is mean values in the water column. Circles indicate that the stations were located west of 172°W.

Table 3
Results of PERMANOVA on zooplankton community with day and water mass in the northern Bering Sea during June through September of 2017.

Source	d.f.	SS	F-value	p-value
Day	10	13,720	3.9401	***
Water mass	1	2839.7	4.0547	***
Day × water mass	2	1550.9	3.2373	**

d.f., degrees of freedom; SS, sum of squares.
***: $p < 0.001$; **: $p < 0.01$.

not ACW. Furthermore, because of the vertically similar water mass structure, it is possible that strong vertical mixing was stimulated by wind and small eddies that resulted in a different zooplankton community structure compared to adjacent stations. In addition, there were many appendicularian *O. vanhoeffeni* in Group D, barnacle nauplii in Groups D and E, and the phytoplankton bloom was observed at the same time in these groups. Because *O. vanhoeffeni* occurs mainly in Bering Shelf Water (Shiga, 1993a, 1993b), Group D is believed to have

originated from Bering Sea Water. The onset of phytoplankton bloom is a key factor in the timing of barnacle larvae release from benthic adults (Crisp, 1962), consistent with presence of barnacle nauplii concurrent with elevated August phytoplankton concentrations.

In September, Group F occurred with many *Centropages* spp. and *Calanus* nauplii. As mentioned above, *Centropages* spp. is abundant within the ACW, suggesting that a similar water mass inflow occurred during September and August. The reproduction of *C. glacialis* uses mainly energy from feeding (Søreide et al., 2010) with the maximum reproduction rate coincident with the phytoplankton bloom (Niehoff et al., 2002). While the water mass did not change from August to September, the influx of a large number of *C. glacialis* nauplii following the phytoplankton bloom, resulted in a change in the community composition.

The difference between taxa (barnacles vs copepods) in the timing of abundance increases triggered by the phytoplankton bloom is thought to reflect differences in their reproductive timing and growth rates. Thus, barnacles rapidly reproduce releasing nauplii in associated with the phytoplankton bloom (Costlow and Bookhout, 1957; Crisp, 1962), but copepods need time to grow large enough to be collected by nets after

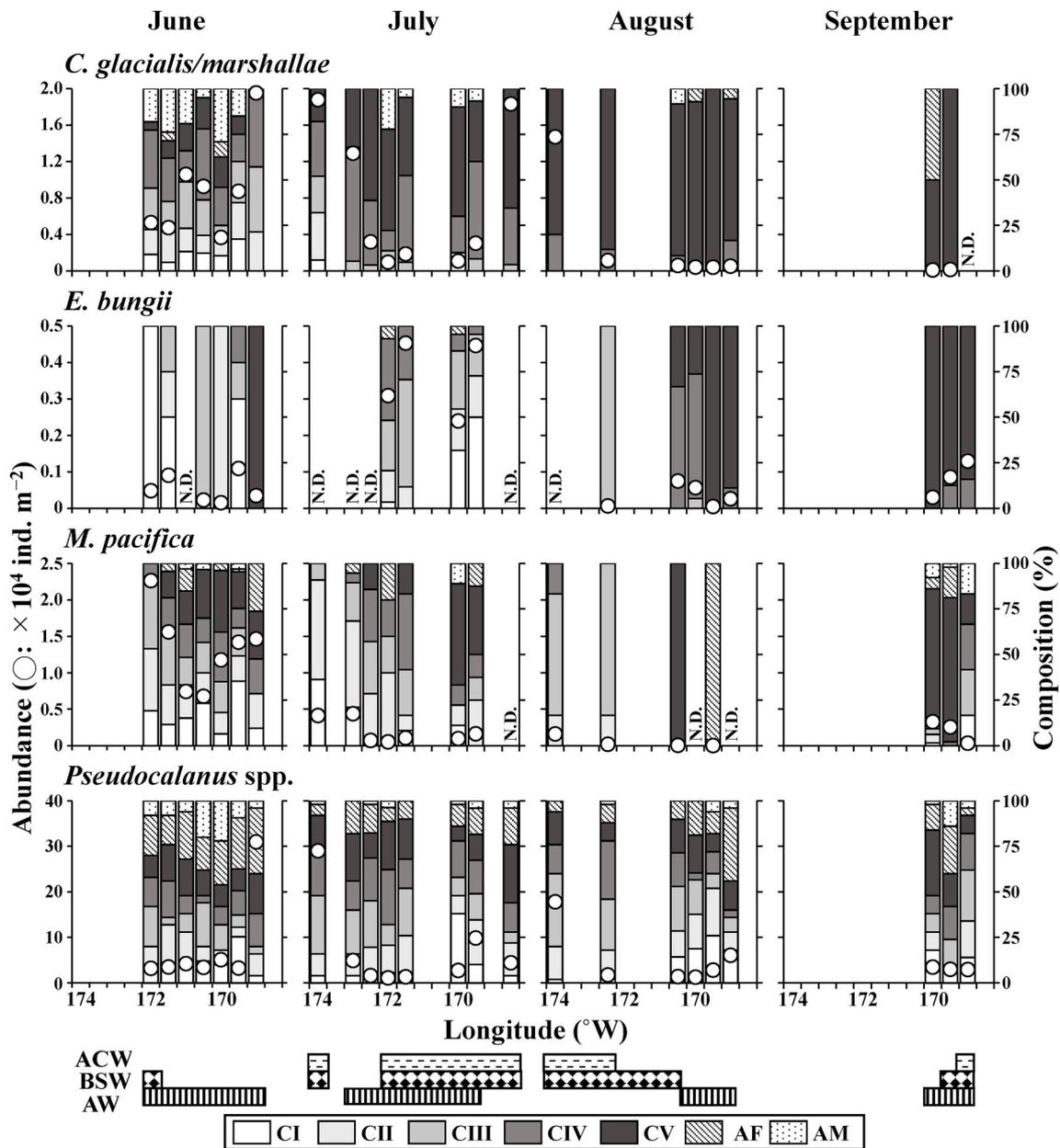


Fig. 8. Monthly changes in abundance and population structure for the dominant copepods in the northern Bering Sea during June through September 2017. Horizontal bars below the plots indicate the water masses (ACW, BSW and AW) were present for each station.

reproduction (Peterson, 1986). In summary, for seasonal changes in the eastern northern Bering Sea, the zooplankton community structure changed every month due to differing advection of water masses and different reproductive attributes of copepods and benthos in response to the phytoplankton bloom.

4.2. Reproduction and development of dominant copepods

Based on population structure and nauplii occurrence, most of the dominant copepods in this ecosystem developed and reproduced during the sampling period. In terms of their reproductive timing, *C. marshallae* reproduces during early spring (April) in the southeastern Bering Sea (Vidal and Smith, 1986), and *C. glacialis* reproduces during March to June in the Chukchi Sea (Ashjian et al., 2003). It is suggested that *C. glacialis/marshallae* reproduces during a prolonged period in our study area because nauplius and reproductively mature adult females occurred from June to September in this study. Their early copepodite

stages were most abundant in June then matured throughout the summer so that the CV stage was most abundant in August, suggesting a one-year life cycle in the northern Bering Sea. *Calanus* spp. has a diapause phase in their life cycle, with CV being the diapause stage for *Calanus glacialis/marshallae* in the Bering Sea. Accordingly, delayed development at CV was observed. While the relationship between developmental stage and day of the year is not a general method for evaluating the development of copepods, it has the advantage of using field data directly without incubation experiments. A relational expression in this study (June to August: $MCS = 0.0183D \pm 0.6215$, August to September: $MCS = 0.0132D \pm 1.786$) showed a steeper slope and faster development than previously observed in the Chukchi Sea ($MCS = 0.012D \pm 0.881$, Matsuno et al., 2016). They sampled from July to October in the Chukchi Sea so the difference in rate between these two studies may be due to environmental conditions (temperature, sea-ice coverage) of the sampling region (Chukchi Sea vs northern Bering Sea) or to observational periods.

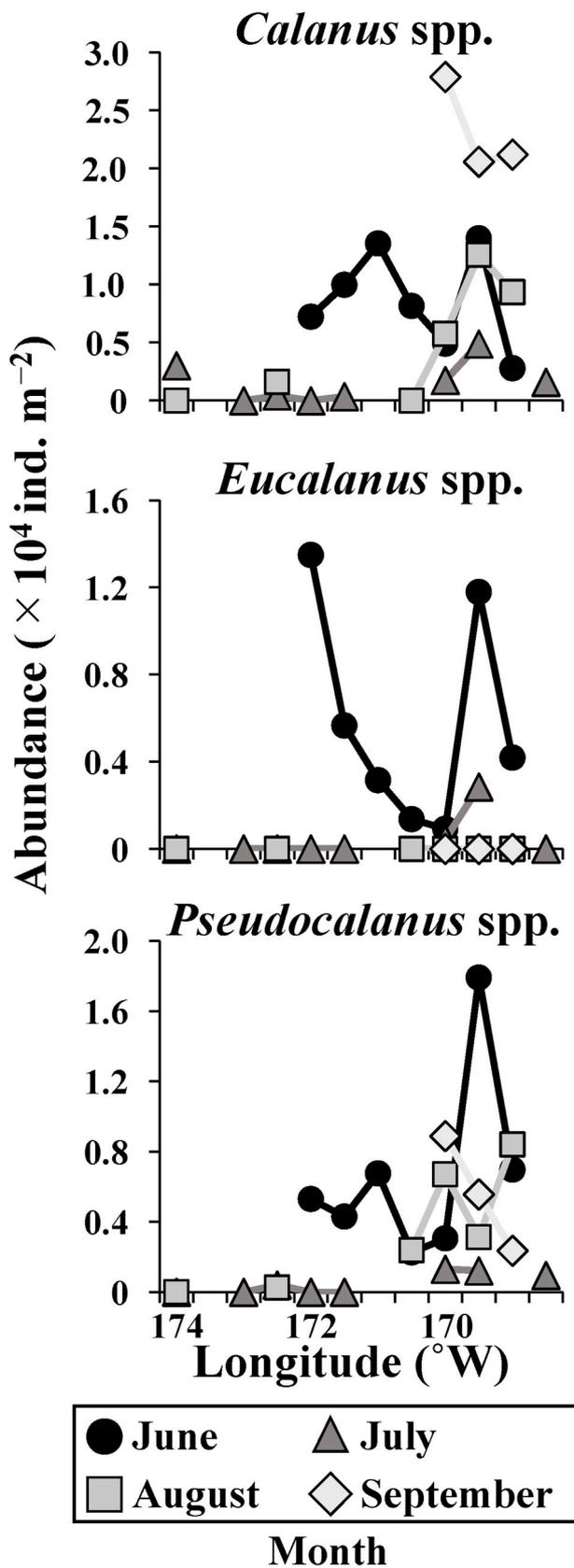


Fig. 9. Monthly changes in abundance of nauplii of the dominant copepods species in the northern Bering Sea during June through September 2017.

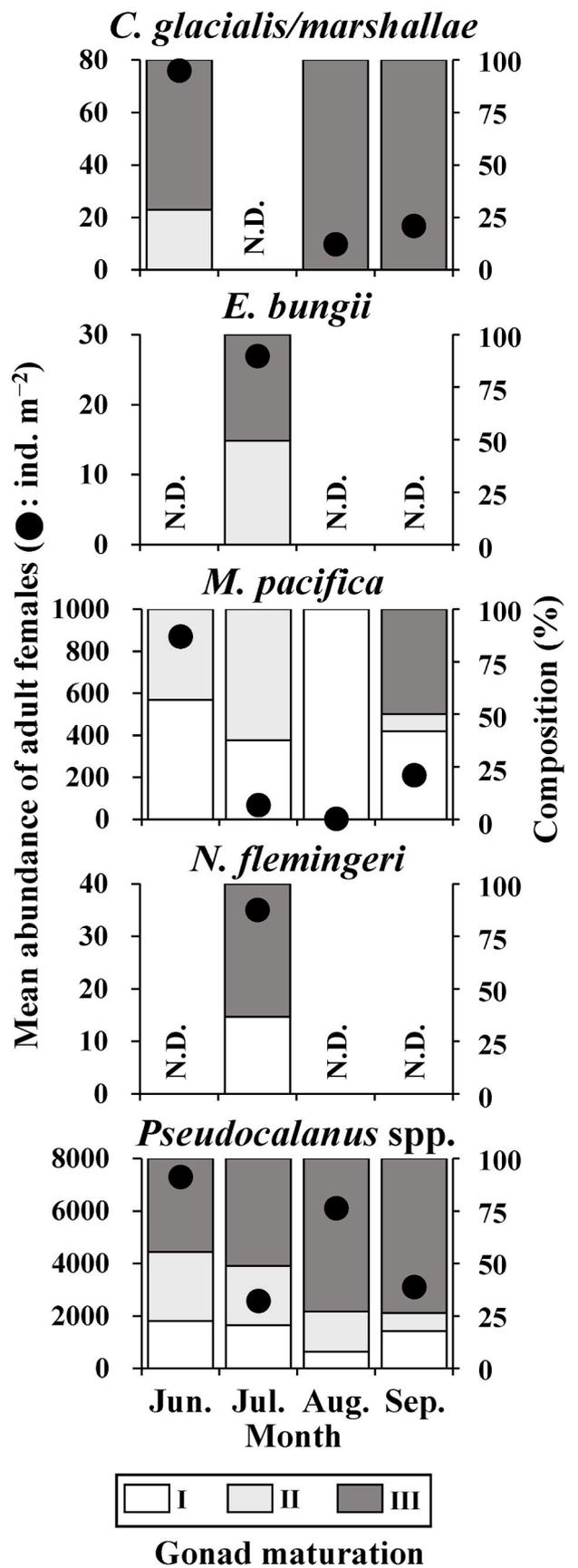


Fig. 10. Monthly changes in abundance and gonad maturation for adult females of the dominant copepods in the northern Bering Sea during June through September 2017.

Table 4
Result of the ANCOVA for MCS of the dominant large copepods with Julian day and water mass (cf. Fig. 7) applied as independent variables.

Species	Parameters	d.f.	SS	F-value	p-value
<i>C. glacialis/marshallae</i>	Water	2	0.205	0.553	N.S.
	Day	1	2.652	14.328	***
	Water × day	2	0.207	0.560	N.S.
	Error	31	5.738		
<i>E. bungii</i>	Water	2	0.546	0.351	N.S.
	Day	1	13.312	17.139	***
	Water × day	2	0.535	0.344	N.S.
	Error	21	16.311		
<i>M. pacifica</i>	Water	2	0.602	0.493	N.S.
	Day	1	6.376	10.446	**
	Water × day	2	0.594	0.486	N.S.
	Error	30	18.312		

d.f., degrees of freedom; SS, sum of squares.
N.S., not significant.
***: $p < 0.001$; **: $p < 0.01$.

E. bungii is mainly distributed in the subarctic North Pacific Ocean, with individuals occurring in the northern Bering Sea thought to be transported there in Anadyr Water (Springer et al., 1989). This species has a one-year or two-year life cycle in the western and eastern North Pacific Ocean, respectively (Miller et al., 1984; Shoden et al., 2005). Reproduction is performed at the surface during the phytoplankton bloom (Miller et al., 1984). The reproductive period of this species varies according to the region, in the Oyashio region in April to May (Tsuda et al., 2004) and in the central Gulf of Alaska from June to July (Miller et al., 1984). In the southeastern Bering Sea, reproduction is during April to May and the early copepodite stages occur in early June (Vidal and Smith, 1986). In this study, nauplii occurred in June, suggesting that reproduction occurred before June in this region. For this species, the development time from egg to C5 is 3–4 months at 5 °C based on incubation experiments in the laboratory (Takahashi and Ide, 2011). On the other hand, *Calanus finmarchicus*, distributed in the subarctic Atlantic Ocean, develops from egg to CV in 50 days at 5 °C (Corkett, 1986). Therefore, the development rate of *E. bungii* would not be faster than that of *Calanus* spp. at the same temperature based on previous laboratory experiments. However, in this study, development of *E. bungii* was the fastest among the dominant three large-bodied copepods. This might be caused by reproduction before our observation period or input of nauplii and early copepodite stages since many early copepodite stages occurred during June through July. Unfortunately, population development could not be accurately evaluated due to seasonal changes in water masses and low abundances with high variation for this species compared to the other two species.

M. pacifica is distributed throughout the subarctic North Pacific Ocean and does not have a diapause phase (Padmavati et al., 2004). This species is believed to be transported to the study area in Anadyr Water because it occurs mainly in Gulf of Anadyr and to the west of St. Lawrence Island (Springer et al., 1989; Ozaki and Minoda, 1996). *M. pacifica* reproduces from March through October, peaking with the spring bloom in the Gulf of Alaska (Hopcroft et al., 2005), develops during summer to autumn, then develops to adult during December to January (Nau- menko, 1979). In the northern Bering Sea, we hypothesize that they reproduce though the observed period because early copepodite stages and adult female occurred during June through September. This species develops during June through August because the population composition of early copepodite stages was highest in June, while later copepodite stages dominated during August to September. The development of this species was the slowest among the dominant copepods. This may be due to the continuous occurrence of adult females and reproduction.

Neocalanus spp. are known to be mainly transported in Anadyr Water (Springer et al., 1989). This genus diapauses at depth, with timing of

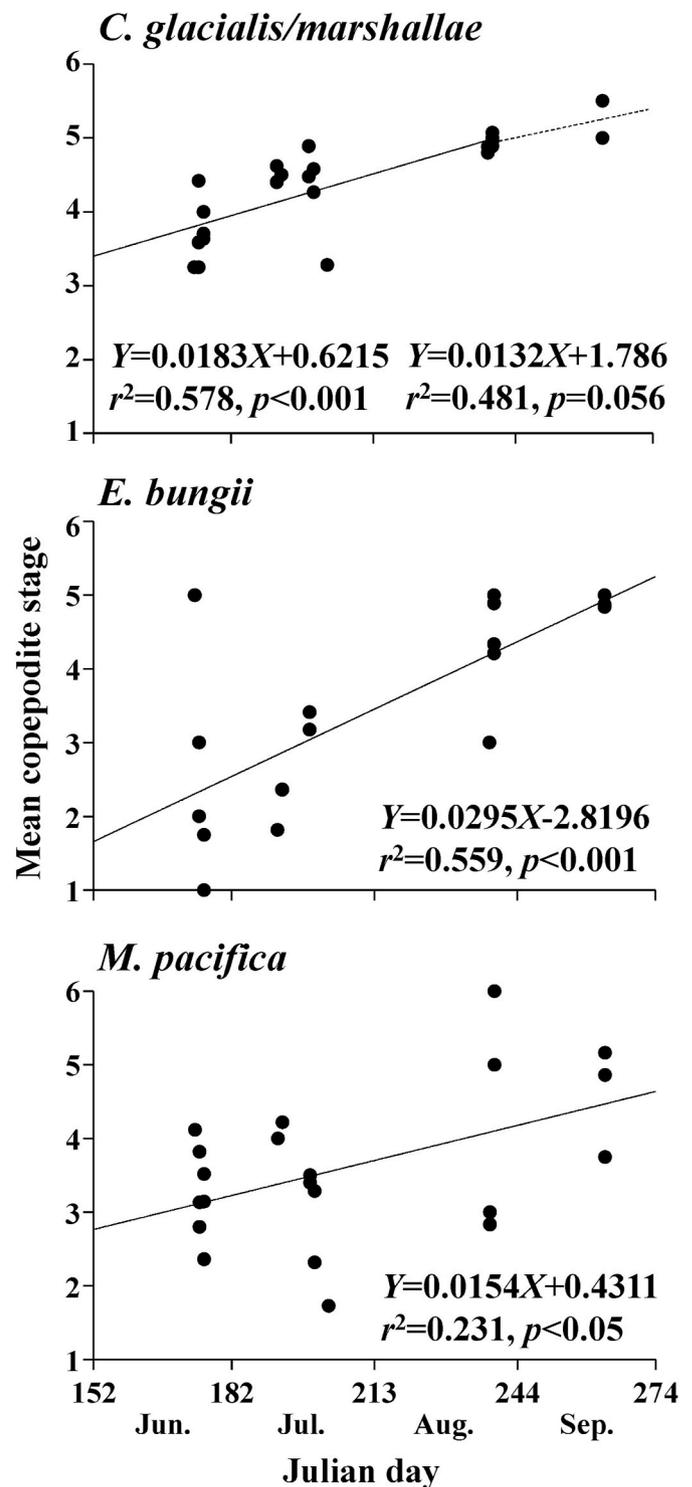


Fig. 11. Relationships between mean copepodite stage and Julian day for the dominant copepods in the northern Bering Sea during June through September 2017.

diapause cessation and CV migration to the surface layer differing between the species: *N. cristatus* in May–July, *N. flemingeri* in April, *N. plumchrus* in July (Tsuda et al., 1999, 2004). In this study, the timing of the occurrence of *N. plumchrus* was later than for the other two species, with both CV and CIV observed.

Four species of *Pseudocalanus* genus are known to occur in the study region (Ershova et al., 2016). *Pseudocalanus acuspes*, dominant in this region (Ershova et al., 2016), spawns throughout all seasons in the Baltic

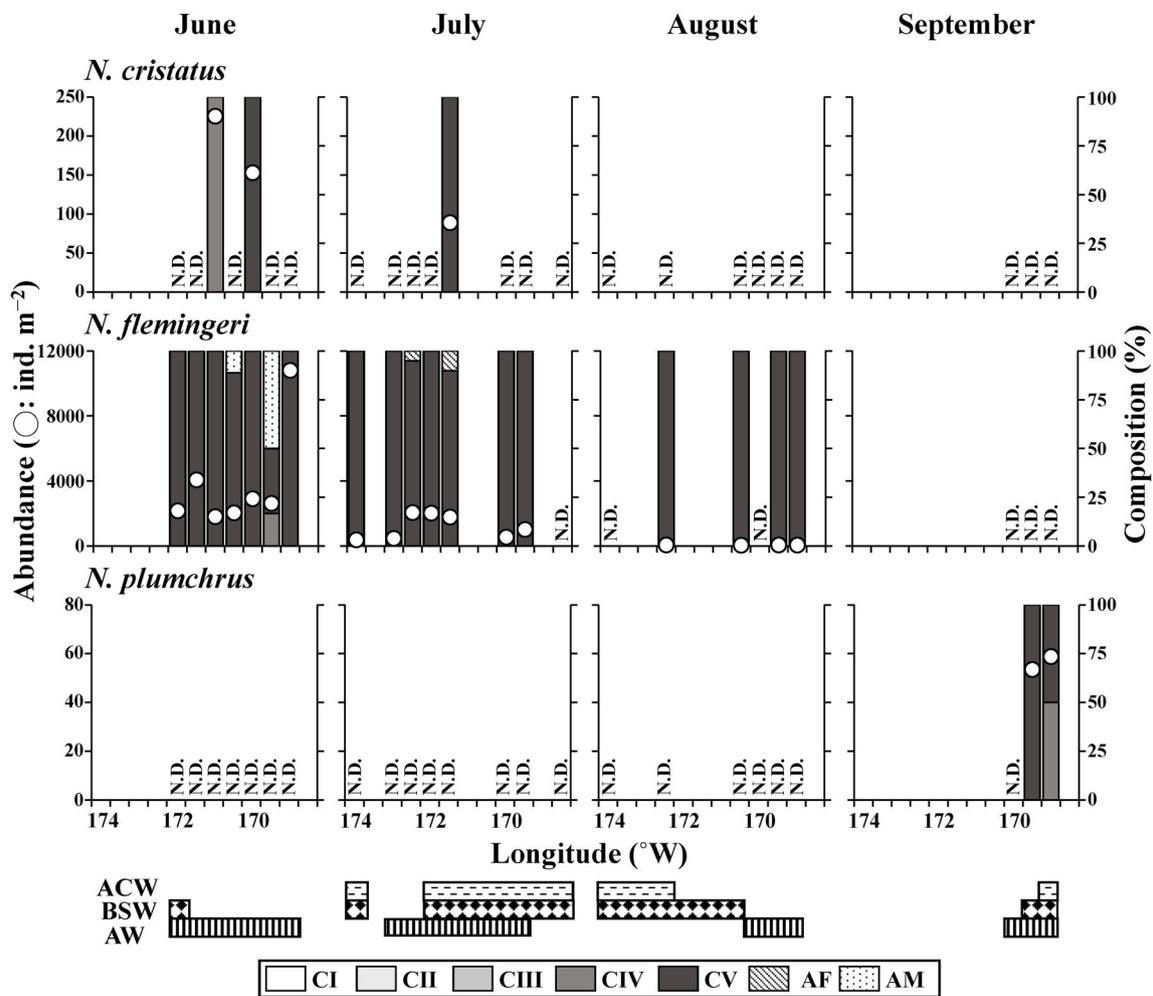


Fig. 12. Monthly changes in abundance and population structure for the *Neocalanus* species in the northern Bering Sea during June through September 2017. Horizontal bars below the plots indicate the water masses (ACW, BSW and AW) present for each station.

Sea (Renz et al., 2007). In this study, reproduction occurred over the entire observation period with *Pseudocalanus* nauplii occurred during in June through September in the east region. We cannot comment on population dynamics because we did not distinguish species.

4.3. Seasonal changes in chaetognatha

Two species of chaetognaths, *P. elegans* and *E. hamata*, were observed between 0 and 150 m, especially *P. elegans*, with a widespread distribution (Kotori, 1976). Formerly, the species present were used as an index for water mass type, but in our study, these two species had similar distributions with regard to water mass type. Growth rates of chaetognaths differ regionally from 3 to 6 mm month⁻¹ in the Celtic Sea (Conway and Williams, 1986; Terazaki and Miller, 1986), and with temperature (Sameoto, 1971). Unfortunately, it was impossible to estimate growth rate in this study, possibly due to water mass exchanges accompanying different temperatures.

The timing of *P. elegans* reproduction varies with region. Reproduction is observed during three times (early summer, autumn and winter) in the eastern North Pacific (Terazaki and Miller, 1986), or two times (from spring to autumn) in the Bedford Basin, Celtic Sea and Canadian Arctic Ocean (Zo, 1973; Conway and Williams, 1986; Grigor et al., 2014, 2017). In this study, because smaller individuals occurred in every month while mature individuals occurred only during August and September, this species reproduced at least in August/September.

4.4. Seasonal changes in Appendicularia

It is known that appendicularians rapidly reproduce by utilizing phytoplankton blooms and that they have a short generation time (Deibel and Lowen, 2012). In this study, while *O. labradoriensis* was abundant in June and July, *O. vanhoeffeni* occurred in August and September. In Conception Bay, Newfoundland, it has been reported that the occurrence of *F. borealis*, *O. labradoriensis* and *O. vanhoeffeni* correspond to variations in prey size arising from changes in the phytoplankton assemblage (Choe and Deibel, 2008). In our study region, seasonal succession of the phytoplankton community and cell-size may be a factor, but these were not consistently measured on most cruises. The two species of *Oikopleura* are distributed in different regions: *O. labradoriensis* occurs in the Bering Basin at depths greater than 200 m (Shiga, 1982), *O. vanhoeffeni* is distributed in the Bering Shelf Water (Shiga, 1993a, 1993b) and throughout the Arctic Ocean. We presume high abundance of *O. labradoriensis* in June and July was driven by inflow of Anadyr Water, and *O. vanhoeffeni* in August and September by inflow of Bering Shelf water (Shiga, 1993a, 1993b). Although BSW was not dominant during August and September, *O. vanhoeffeni* was increased by their active reproduction accompanying the phytoplankton bloom (Deibel and Lowen, 2012). These results are consistent with the seasonal exchange of water masses as revealed by changes in zooplankton community structure. In other words, it is suggested that appendicularian species composition may change seasonally because of inflows of different water masses and active reproduction associated

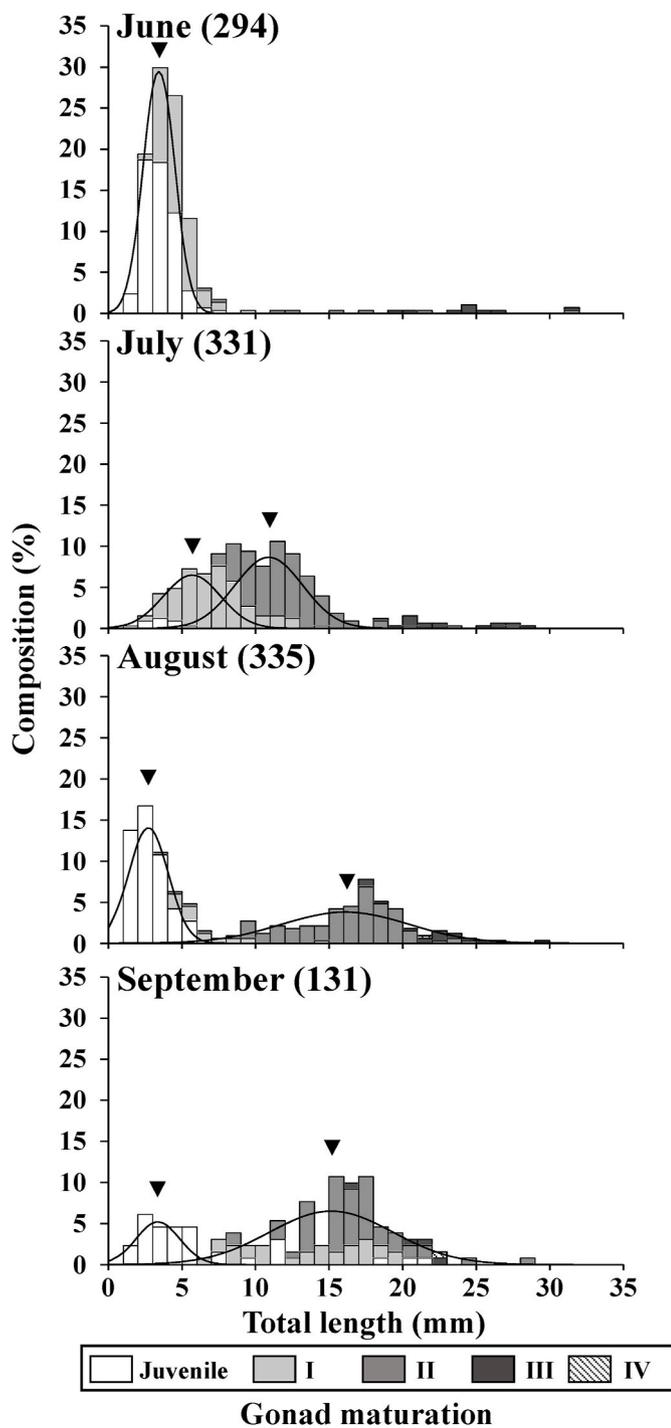


Fig. 13. Monthly changes in the total length of *Parasagitta elegans* in the northern Bering Sea during June through September 2017. Numbers in parentheses show total individual measurements. Smooth curves indicate the results of a cohort analysis.

with rich food conditions in the northern Bering Sea.

5. Conclusions

This study examined seasonal changes in the zooplankton community and population structure for dominant species in the northern Bering Sea from June to September of 2017. Community composition differed regionally and seasonally in association with changes in water mass distribution. In the western region seasonal changes were not

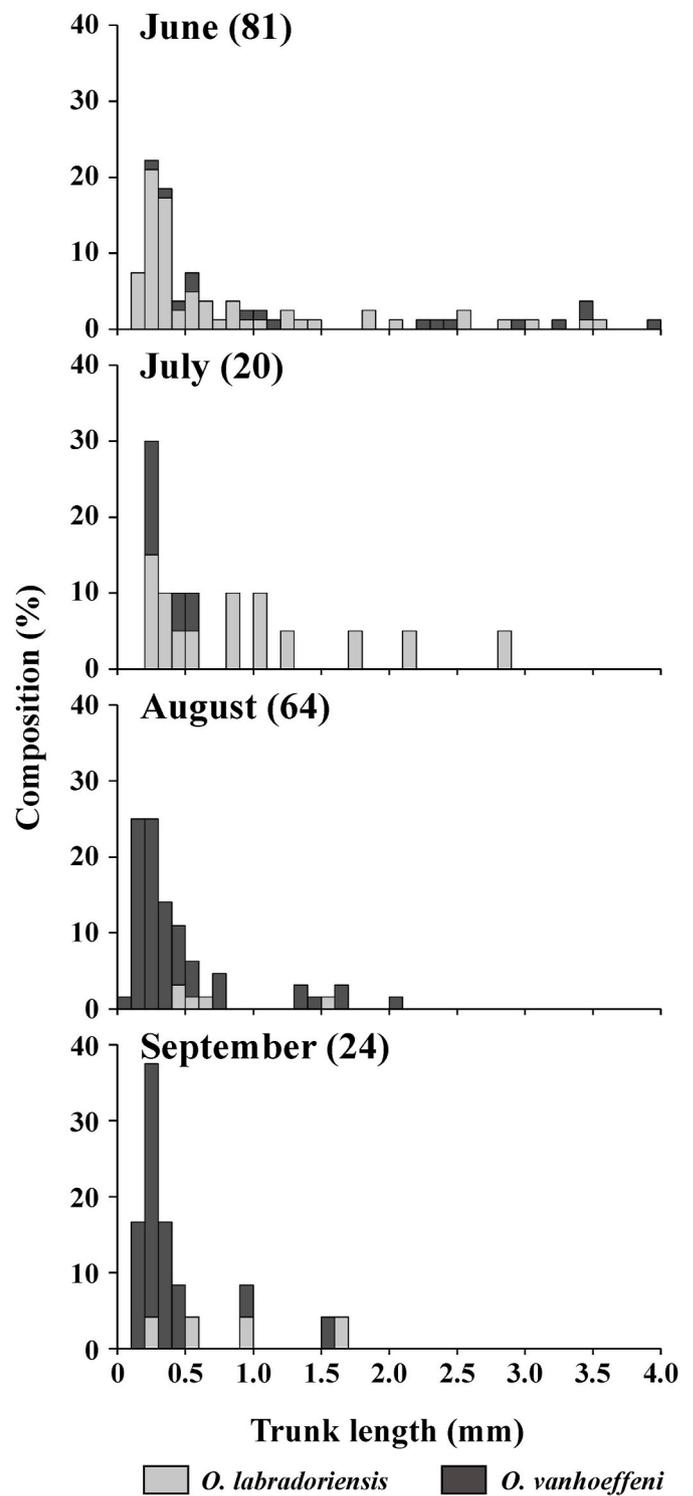


Fig. 14. Monthly changes in the trunk length of *Oikopleura* spp. in the northern Bering Sea during June through September 2017. Numbers in parentheses show total individual measurements.

observed due to the dominance of BCWW in the bottom layer during July and August. In the eastern region, community structure differed every month due to inflow of different water masses, meroplankton release, and copepod reproduction associated with the phytoplankton bloom. For copepod population structures, *C. glacialis/marshallae*, *E. bungii* and *M. pacifica* showed stage progression during the observation period, differing between species according to their life cycle. These results illustrate that the zooplankton community and the population

structure of dominant species changed seasonally due to changes in hydrography (water mass) and primary productivity in the northern Bering Sea. These large seasonal changes in zooplankton between months are important to the evaluation of long-term changes in the region. Evaluating long-term changes including seasonal changes will allow us to more accurately predict changes in marine ecosystems under rapid changes such as changes in the extent of sea ice.

Author statement

Fumihiko Kimura: Formal analysis, Investigation, Writing - Original Draft, Visualization, Yoshiyuki Abe: Investigation, Kohei Matsuno: Conceptualization, Writing - Review & Editing, Supervision, Project administration, Russell R. Hopcroft: Investigation, Writing - Review & Editing, Atsushi Yamaguchi: Conceptualization, Investigation, Project administration

Declaration of competing interest

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

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