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Year-to-year changes of the mesozooplankton community in the Chukchi Sea during summers of 1991, 1992 and 2007, 2008

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Abstract

A recent drastic decrease in sea ice cover area was observed in the western Arctic Ocean during summer, yet little information is available for its effect on zooplankton community. To evaluate the effect of sea ice reduction on zooplankton, we studied year-to-year changes of zooplankton community structure in the Chukchi Sea during summers of 1991, 1992 (when sea ice extended), 2007 and 2008 (when sea ice reduced). Zooplankton abundance ranged from 4,000 to 316,000 ind. m^{-2} (mean: 70,000), and was greater north of Lisburne Peninsula in 2008. Zooplankton biomass ranged from 0.07 to 286 g wet mass m^{-2} (mean: 36), and was greater south of Lisburne Peninsula in 2007. Cluster analysis based on zooplankton abundance showed a division of the zooplankton community into four groups. Occurrence of each group was separated geographically and interannually, and geographic distributions of each group in 1991 and 1992 were similar but those in 2007 and 2008 were shifted northward. Abundance and biomass in 2007/08 were higher than in 1991/92, indicating that further sea ice reduction would have a positive effect on zooplankton production (e.g. invasion of large Pacific species and temperature effects on their growth rate). The northern shift in geographic distribution of the zooplankton community in 2007/08 indicates that sea ice reduction would have a negative effect on the zooplankton community (loss of characteristic Arctic species) in part of the Chukchi Sea. These apparently contradictory effects of sea ice reduction on zooplankton community emphasize the critical need for continued monitoring in this area.

Keywords Barnacle larvae · Chukchi Sea · Copepods · Interannual variability · Zooplankton community

Introduction

Remarkable reduction of sea ice coverage in the Arctic Ocean was detected by satellite observation during 1991 to 2007. The major factor affecting this large reduction of ice coverage is considered to be increased inflow of warm Pacific Summer Water (PSW) passed through the Bering Strait into the Chukchi Sea, a marginal sea of the western Arctic Ocean (Shimada et al. 2006; Woodgate et al. 2010). The western Arctic Ocean is composed of shallow (Chukchi Sea and East Siberia Sea) and deep (Canada Basin and Mendeleyev Ridge) areas, and the sea ice reduction in these areas is the largest in the Arctic Ocean (Shimada et al. 2001, 2006). According to Woodgate et al. (2010), in 2007, sea ice coverage was the lowest, and inflow quantity of PSW and water temperature in the Bering Strait were the highest observed during the 1991–2007 satellite observation period. The effect of these drastic sea ice reductions on marine ecosystem in Arctic Ocean is of concern (Grebmeier et al. 2006; Hunt and Drinkwater 2007). To evaluate the effect of ice reduction on marine ecosystem, year-to-year comparative study in the western Arctic Ocean is essential.

Zooplankton are secondary producers of the marine ecosystem and comprise a vital link between primary production and fishes or marine mammals in the western Arctic Ocean (Lowry et al. 2004; Wassmann et al. 2006). In the southern Chukchi Sea, since Pacific water flows into the sea through the Bering Strait, not only Arctic copepods (*Calanus glacialis* Jaschnov) but also large-sized Pacific copepods (*Calanus marshallae* Frost, *Neocalanus cristatus* (Kröyer), *Neocalanus flemingeri* Miller, *Neocalanus plumchrus* (Marukawa), *Eucalanus bungii* Giestbrecht and *Metridia pacifica* Brodsky) are dominant taxa (Springer et al. 1989). Zooplankton community structure in the southern Chukchi Sea varies geographically and is governed by water masses (Springer et al. 1989; Lane et al. 2008; Hopcroft et al. 2010). While most of the studies of zooplankton in the western Arctic Ocean treated a large geographic area, such as the Beaufort Sea (e.g. Thibault et al. 1999; Ashjian et al. 2005; Darnis et al. 2008), few studies were made in the Chukchi Sea, especially in the vicinity of Lisburne Peninsula.

The zooplankton community in the western Arctic Ocean is expected to be changed after 2007 when the drastic decrease of sea ice area was observed, but no study has contrasted zooplankton community structure between 1990s (extended sea ice coverage) and recent years (reduced sea ice coverage). In the present study, we examined year-to-year changes of the zooplankton community in the western Arctic Ocean in 1991 and 1992 (extended sea ice area) and in 2007 and 2008 (reduced sea ice area). Based on the whole-year zooplankton abundance data, zooplankton community clustering and year-to-year changes in abundance, biomass and community structure are evaluated. Year-to-year changes in stage composition of large copepods are also revealed. Through these results, we discuss the effects of sea ice reduction on the zooplankton community in the western Arctic Ocean.

Materials and Methods

A total of 120 zooplankton samplings were conducted by T.S. *Oshoro-Maru* in the Chukchi Sea (66°00′−71°11′N, 162°02′−168°58′W) during 24−31 July 1991 (n = 27), 24−31 July 1992 (n = 34), 5−13 August 2007 (n = 31) and 7−13 July 2008 (n = 28) (Fig. 1). Zooplankton samples were collected at day or night by vertical tows with a NORPAC net (mouth diameter 45 cm, mesh size 335 μm) from 5 m above the bottom to the surface (depths of most stations were about 50 m). The volume of water filtered through the net was estimated using a flow-meter mounted in the mouth of the net. Zooplankton samples were immediately preserved with 5% v/v borax buffered formalin. At zooplankton sampling stations, temperature and salinity were measured by CTD (Neil Brown, Mark 3B [1991 and 1992] or Sea-Bird Electronics Inc., SBE 911 Plus [2007 and 2008]) casts. These hydrographic data are published elsewhere (Hokkaido University 1992, 1993, 2008 and 2009).

In the land laboratory, zooplankton samples were split using a Motoda box splitter (Motoda 1959), and half aliquots were weighed for wet mass (WM) with a precision of 0.01 g using an electronic balance (Mettler PM4000). Zooplankton in the remaining aliquots were identified and enumerated under a dissecting microscope. Calanoid copepods were identified to species and copepodid stage level. Identification of copepods mainly followed Brodsky (1967), but identification of *C. marshallae* and *Pseudocalanus* spp. (*P. acuspes*, *P. major*, *P. mimus*, *P. minutus* and *P. newmani*) followed Frost (1974, 1989). Identification of *Pseudocalanus* species late copepodid stages (C5F/M and C6F/M) was at species level, but early copepodid stages (C1−C4) were treated as *Pseudocalanus* spp. because of the difficulty in species-level identification. Since the coarseness of mesh size (335 μm), there may be some underestimations of smaller zooplankton forms (*Pseudocalanus* spp. C1−C4 and Cyclopoida). While the early copepodid stages of large-sized copepods were sampled quantitatively (e.g. *C. glacialis*, *E. bungii* and *M. pacifica*), and their Mean Copepodid Stage (*MCS*) was calculated using the following equation:

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

where i (1−6 indicate C1−C6) is the copepodid stage for a species, Ai (ind. m^{-2}) is the abundance of a copepodid stage (cf. Marin 1987).

Zooplankton samplings were conducted during July and August (Arctic summer), and daytime sampling accounted for 91% of total sampling stations (Fig. 1). Because of this reason, we made no day-night conversion on abundance and biomass data. Abundance data (X: ind. m^{-2}) for each species were transformed to $\log_{10}(X+1)$ prior to cluster analysis in order to reduce the bias of abundant species. Similarities between samples were examined by Bray-Curtis index (Bray and Curtis 1957) according to the differences in 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). Nonmetric Multi-Dimensional Scaling (NMDS) ordination was carried out to delineate the sample groups on a two-dimensional map. All of these analyses were carried out using BIOSTAT II software (Sigma Soft). Multiple-regression analysis was carried out for dependent hydrographic variables (latitude, longitude, depth, integrated mean temperature and salinity) and two-dimensional NMDS as independent variables. A species diversity index (H') in each group was calculated using the equation:

$$H' = -\sum n/Ni \times \ln n/Ni$$

where n is the abundance (ind. m^{-2}) of ith species and Ni is the total zooplankton abundance (ind. m^{-2}) in the group (Shannon and Weaver 1949). This calculation was made over all zooplankton taxa (not limited to copepods) because zooplankton taxa other than copepods (e.g. barnacle larvae) dominated at some stations. Inter-group differences in abundance of each copepod and zooplankton taxon, and *MCS* of large copepods, were tested with one-way ANOVA. If the ANOVA identified statistically significant differences ($p < 0.05$), an ex post facto test by Fisher's Protected Least Significant Difference test (PLSD) was carried out to clarify the interaction between groups.

Results

Hydrography

Throughout the study area, sea surface and bottom temperatures ranged from −0.9 to 14.0°C and −1.7 to 8.0°C, respectively (Fig. 2A). In 1991, 1992 and 2008, sea surface temperatures ranged from −0.9 to 9.6°C, but those in 2007 were 3.9 to 14.0°C, substantially higher than the other years. Sea surface and bottom salinities ranged from 25.3 to 32.9 and 30.7 to 33.5, respectively (Fig. 2B). Sea surface salinities in 1991, 1992 and 2008 ranged from 25.3 to 32.8, but those in 2007 ranged from 30.0 to 32.9 and were significantly higher than the other years (one-way ANOVA, $p < 0.0001$), although bottom salinity did not show interannual variability (Fig. 2B).

Water masses in the Chukchi Sea during summer were separated mainly by salinity: Surface Mixed Layer Water (SMLW, salinity < 30), Eastern Chukchi Summer Water (ECSW, 31−32 salinity) and Western Chukchi Summer Water (WCSW, salinity > 32) (Shimada et al. 2001). Based on sea surface temperature and salinity, all stations in 2007 belonged to ECSW, but those in the other years belonged to SMLW (Fig. 3). The surface salinities in 1991 and 1992 were significantly lower than in 2007 and 2008 (one-way ANOVA, $p < 0.0001$).

Zooplankton

Zooplankton abundance ranged from 4,000 to 316,000 ind. m^{-2} (mean: 70,000) (Fig. 4A). Abundance in 1991, 1992 and 2008 was greater north of Lisburne Peninsula, while in 2007 abundance was greater south of Lisburne Peninsula (Fig. 4A). Zooplankton biomass ranged from 0.07 to 286 g WM m^{-2} (mean: 36). The geographic distribution of biomass was not parallel with abundance except for the south of Lisburne Peninsula in 2007 (Fig. 4B).

Copepods composed 2−86% (mean: 31) of zooplankton abundance, and barnacle nauplii and cypris larvae (*Balanus crenatus* Brugiere) were also dominant and composed 2−95% (mean: 47) of abundance in the northern area (Fig. 5). Within the copepods, proportions of *C. glacialis* and *Pseudocalanus* spp. were relatively high, especially in 1991 and 1992. In 2007, proportions of Pacific copepods (*E. bungii* and *M. pacifica*) were high, while the proportion of barnacle larvae was low (Fig. 5). Barnacle larvae predominated in 2008. Through the four years of analysis, 22 species of calanoid copepods belonging to 13 genera were identified (Table 1). Within these species, 6 species belonging to 4 genera: *C. marshallae*, *E. bungii*, *M. pacifica*, *N. cristatus*, *N. flemingeri* and *N. plumchrus* were Pacific copepods (Springer et al. 1989).

Statistical analyses on year-to-year changes in zooplankton abundance showed significant differences for 21 taxa/species (Table 2). Abundance of total copepods was the highest in 2007, while that of total zooplankton was the highest in 2008. Significantly abundant taxa/species in each year were Appendicularia in 1991, the Arctic copepod *C. glacialis* in 1992, and various copepods (*Acartia tumida* Willey, *Centropages abdominalis* Sato, Cyclopoida, *E. bungii*, *M. pacifica*, *Microcalanus pygmaeus* (Sars), *N. cristatus*, *P. minutus* and *Scolecithricella minor* (Brady)), Echinodermata larvae and Polychaeta in 2007, and several copepods (*Eurytemora* *herdmani* Thompson and Scott, *N. plumchrus* and *Tortanus discaudatus* (Thompson and Scott)), barnacle larva (*B. crenatus*), Eubrachyura zoea and *Limacina helicina* (Phipps) in 2008. Since Pacific copepods were dominant in 2007, total copepod abundance was the greatest in 2007. When barnacle larvae were dominant in 2008, total zooplankton abundance was the highest in 2008 (Table 1).

Year-to-year changes in the *MCS* of large copepods: *C. glacialis*, *E. bungii* and *M. pacifica* were tested by one-way ANOVA. The *MCS* of *C. glacialis* and *M. pacifica* in 2007 was significantly higher (= dominated by late copepodid stage and faster growth) than in other years (Table 2).

Based on the taxon abundance, zooplankton communities were classified into six groups (A−F) by cluster analysis with 28% and 34% dissimilarities (Fig. 6A). The quantity of stations in each group varied between 3 and 60, and groups C and F were considered to be outlier groups because few stations (3−4 stations) belonged to each group (Fig. 6A). Environmental parameters significantly affecting cluster analysis were latitude, longitude, sea surface temperature, sea surface salinity and bottom salinity, with 24–37% coefficient of determinations (r^2) (Fig. 6B). Mean abundances of groups A, B and D ranged from 76,800 to 101,030 ind. m^{-2}, but those of groups C, E and F were lower, and ranged from 5,744 to 30,283 ind. m^{-2} (Fig. 6C). For groups B, C and E, barnacle larvae dominated and species diversities were low. Groups A, D and F were characterized by few barnacle larvae and dominance of Pacific copepods (groups A, D) or Arctic copepods (group F) (Fig. 6C). Species diversity of groups A and D was high because of the occurrence of both Pacific and Arctic copepods.

Distribution of each group was well separated both geographically and interannually (Fig. 7). Group B was observed offshore north of Lisburne Peninsula, and group E was observed inshore of the same region (Fig. 7). Group A was observed south of Lisburne Peninsula in 1991 and 1992, and north of Lisburne Peninsula in 2007 and 2008. Group D, characterized by the high abundance and dominance of Pacific copepods, was observed only south of Lisburne Peninsula in 2007.

Concerning interannual variability in the zooplankton community, geographic distribution was similar for 1991 and 1992 (Fig. 7). In 2007, the whole distribution area was shifted northward compared to 1991 and 1992, and group D, characterized by dominance of Pacific copepods, was observed south of Lisburne Peninsula. In 2008, geographic distribution of groups was similar to 1991 and 1992, but distribution of group A, which was observed south of Lisburne Peninsula in 1991 and 1992, also penetrated to the north of Lisburne Peninsula (Fig. 7). Year-to-year characteristics in hydrographic environment, zooplankton biomass, community structure, species diversity and growth of large copepods in 1991, 1992, 2007 and 2008 are summarized in Table 3.

Discussion

Environmental and zooplankton characteristics in each year

The years 1991 and 1992 showed similar characteristics: i.e. presence of fresh and cold ice melt water in the surface, low zooplankton biomass and low species diversity due to the dominance of small-sized Arctic copepods and their slower development under the low temperature condition. The zooplankton community in 1991 was characterized by dominance of Appendicularia (mainly *Oikopleura vanhoeffeni*), which is known to occur around the ice edge area of the Arctic Ocean (Acuña et al. 1999). Dominance of Appendicularia in 1991 may be related to the strong presence of ice melt water in this year.

Water mass formation in 2007 was extremely different from the other years. During 2007, warm and saline ECSW, which originated from Pacific, predominated throughout the stations. In 2007, zooplankton biomass was high south of Lisburne Peninsula, which was caused by the dominance of large-sized Pacific copepods transported by ECSW. Zooplankton species diversity was also high in 2007, when the zooplankton community was characterized by a mixture of the Arctic and Pacific species. Warm temperature is the primary cause of faster development of copepods (cf. Corkett and McLaren 1978). Development of large copepods (*C. glacialis* and *M. longa*) in 2007 was significantly faster than the other years. Since the population structure of *E. bungii* in 2007 was characterized by the dominance of nauplii and early copepodid stages which may reflect of reproduction, this species had no significant year-to-year differences in *MCS*.

Zooplankton characteristics in 2008 were similar to those in 1991/92, while the hydrography in 2008 was characterized by high saline water in the surface layer in contrast to the ice melt water in 1991/92. In detail, zooplankton biomass in 2008 was low but its abundance was the highest within the four years, which was caused by the dominance of the small-sized barnacle larvae (*B. crenatus*) in 2008 (Table 1, Fig. 5). Because of the predominance of barnacle larvae in 2008, species diversity was low. The moderate temperature condition in 2008 may have induced ordinary developmental rates of large copepods in that year.

Throughout the four years studied, 2007 was the most distinctive year. According to Woodgate et al. (2010), volume and temperature of inflow PSW in 2007 was the greatest and warmest of the 1991–2007 period. High volume of PSW in 2007 may have induced high advection of large-sized Pacific copepods and led to the high zooplankton biomass and high species diversity observed in that year. Higher temperature may have led to faster development of large copepods in that year, which this study observed for both the Pacific copepod (*M. pacifica*) and the Arctic copepod (*C. glacialis*). Hence, the increase of inflow of the warm PSW is considered to have a positive effect on zooplankton community in terms of biomass and development of large copepods.

Comparison between 1991/92 and 2007/08

Comparison between 1991/92 (sea ice extent) and 2007/08 (sea ice reduced) showed a remarkable northward shift in geographic distribution of zooplankton communities (Fig. 7). This northward shift in zooplankton community in 2007/08 may be related to the differences in formation of water masses. The greatest differences in the hydrographic environment between 1991/92 and 2007/08 was in the presence (1991/92) or absence (2007/08) of sea ice melt water and was also evident in the salinity of the surface layer, which was low for 1991/92 and high for 2007/08 (Fig. 3).

Concerning the zooplankton community, the Arctic copepod *C. glacialis* was relatively abundant in 1991/92, and less so in 2007/08. The zooplankton community in 2007 was characterized by the dominance of Pacific copepods, and in 2008 was dominated by barnacle larvae (Table 1, Fig. 5). The dominance of barnacle larvae in 2008 suggests an earlier release of the larvae from their benthic adult form than in 1991/92.

Concerning the release timing of barnacle larvae from benthic adults, laboratory rearing studies show that the amount of food concentration (phytoplankton) is a key factor for release timing (Clare et al. 1984; Clare and Walker 1986). Field studies also indicate that onset of the phytoplankton bloom is a key factor stimulating the release of barnacle larvae (Barnes 1957; Crisp 1962). Because the sea surface salinity was higher in 2007/08 than in 1991/92 (Fig. 3), the timing of sea ice reduction was considered to be earlier in 2007/08 (Markus et al. 2009). This earlier sea ice reduction in 2007/08 may induce that earlier phytoplankton bloom for these years because of the earlier release from the light limitation on the photosynthesis. The earlier onset of the phytoplankton bloom in 2008 is considered to be a cause of the dominance of the barnacle larvae in that year. The earlier sea ice reduction and onset of phytoplankton bloom was also the case of 2007. However, the greater inflow of PSW in 2007 forced the barnacle distribution area north (Fig. 7), leading to a lower abundance of barnacle larvae in 2007 than 2008.

The future prospect

Year-to-year comparisons in this study revealed significant differences in zooplankton abundance, biomass and community structure (Table 3). Under the global warming condition, a highly relevant issue in recent years, a large reduction of ice cover area and increased inflow of the PSW are expected. Since PSW contains higher nutrient levels than Arctic water (Springer and McRoy 1993; Cota et al. 1996), increase of the inflow of the PSW is expected to induce the expansion of the high primary production area in the Chukchi Sea. Thus in terms of primary production, global warming may have a positive function in this area.

From the viewpoint of zooplankton production, increased inflow of PSW induced the dominance of the large-sized Pacific copepods, and thus may have positively affected productivity. However, increased inflow of PSW caused changes in the marine ecosystem structure in the Chukchi Sea (loss of characteristic Arctic species in part of the region), which is considered as a negative effect of global warming.

The zooplankton fauna is completely different between the Pacific and Arctic Oceans. The PSW contains various Pacific copepods: i.e. *E. bungii*, *M. pacifica*, *N. cristatus*, *N. flemingeri* and *N. plumchrus* (Springer et al. 1989). *Eucalanus bungii*, the most dominant copepod in the PSW, has a diapause phase during autumn and winter and a flexible generation length of one to three years (Miller et al. 1984; Tsuda et al. 2004; Shoden et al. 2005). Because the family Eucalanidae is a minor component of the North Atlantic and Arctic Oceans, the ecological niche that *E. bungii* occupies in the PSW is considered to be underutilized in these oceans. If this assumption is correct, and the Pacific copepods colonize the Arctic Ocean, they may increase their population by utilizing this vacant ecological niche. In the future Chukchi Sea, reduction of ice cover area may accelerate changes in marine ecosystem structure. Therefore, a critical and continuous monitoring of zooplankton community structure in this area is needed for future study.

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Figure legends

Fig. 1 Location of the sampling stations in the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008. Open and solid symbols denote stations where the samplings were conducted in day and night, respectively. Three digits of station names are shown in the panels; the official station names combine these numbers with a cruise identifier, i.e. OS91, OS92, OS07 or OS08. Details of sampling stations are published elsewhere (Hokkaido University 1992, 1993, 2008 and 2009)

Fig. 2 Temperature (A) and salinity (B) of the sea surface (left) and bottom (right) of the stations in the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008

Fig. 3 T-S diagrams in the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008. Hydrographic data were collected from 0, 10, 20, 30, 40 and 50 m. Numbers in the panels indicate water densities (sigma-T). SMLW: Surface Mixed Layer Water (salinity < 30), ECSW: Eastern Chukchi Summer Water (salinity = 31−32), WCSW: Western Chukchi Summer Water (salinity > 32) (cf. Shimada et al. 2001)

Fig. 4 Geographic distribution of the zooplankton abundance (A) and biomass (B) in the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008. Values in the parentheses indicate mean values of each year

Fig. 5 Taxonomic composition in total zooplankton abundance of the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008

Fig. 6 Results of cluster analysis based on zooplankton abundance by Bray-Curtis similarity connected with UPGMA. Six groups (A−F) were identified with the dissimilarity at 28 and 34%, respectively (dashed lines) (A). Numbers in the parentheses (A) indicate quantity of stations included in each group. Nonmetric multi-dimensional scaling plots of the six groups, with arrows and percentages indicating directions of environmental parameters and coefficient of determination (r^2), respectively (B). BS: bottom salinity, Lat: latitude, Lon: longitude, SSS: sea surface salinity, SST: sea surface temperature. Abundance, species diversity and taxonomic composition of each group (C). Vertical bars in abundance indicate standard deviations

Fig. 7 Geographic distributions of the six groups (A−F) identified from Bray-Curtis similarity based on zooplankton abundances (cf. Fig. 6) in the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008

Table 1. Year-to-year comparison of zooplankton abundances in the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008. Values are mean abundances in each year. Differences between years were tested by one-way ANOVA and post-hoc test by Fisher's PLSD. Any years not connected by the underlines are significantly different ($p < 0.05$). Numbers in the parentheses indicate number of stations in each year. *: $p < 0.05$, **: $p < 0.01$, NS: not significant.

Species	Abundance (ind. m^{-2})				one-way ANOVA	Fisher's PLSD			
	91 (27)	92 (34)	07 (31)	08 (28)					
Acartia hudsonica	13	31	64	37	NS				
Acartia longiremis	181	255	247	277	NS				
Acartia tumida	0	0	31	0	*				07
Calanus marshallae	11	50	40	11	NS				
Calanus glacialis	2,019	5,565	1,038	1,266	**	07	08	91	92
Centropages abdominalis	403	5	6,665	199	**	92	08	91	07
Cyclopoida	358	1,144	1,210	202	*	08	91	92	07
Eucalanus bungii	540	560	5,305	159	**	08	91	92	07
Eurytemora herdmani	0	2	3	15	*		92	07	08
Epilabidocera amphitrites	0	0	5	0	NS				
Gaidius brevispinus	0	1	0	0	NS				
Metridia pacifica	33	972	4,906	96	**	91	08	92	07
Microcalanus pygmaeus	7	18	412	41	*	91	92	08	07
Neocalanus cristatus	6	5	44	34	**	92	91	08	07
Neocalanus flemingeri	49	72	34	42	NS				
Neocalanus plumchrus	51	83	163	271	**	91	92	07	08
Pseudocalanus spp. (C1−C4)	2,562	3,068	2,877	4,186	NS				
Pseudocalanus acuspes	1,488	1,279	2,363	1,987	NS				
Pseudocalanus major	1,222	306	449	502	NS				
Pseudocalanus mimus	662	311	474	614	NS				
Pseudocalanus minutus	1,182	2,239	3,481	2,011	*	91	08	92	07
Pseudocalanus newmani	2,091	3,498	3,853	1,671	NS				
Scolecithricella minor	0	6	80	23	*		92	08	07
Tortanus discaudatus	0	0	0	17	*				08
Amphipoda	3	5	36	1	NS				
Appendicularia	9,461	2,808	5,129	2,107	**	08	92	07	91
Balanus crenatus (nauplius and cypris larva)	39,625	19,114	20,029	79,899	**	92	07	91	08
Bivalvia larva	0	0	495	48	NS				
Chaetognatha	958	581	1,060	721	NS				
Clione limacina	12	170	50	110	NS				
Echinoidea larva	0	0	1,420	14	**			08	07
Eubrachyura zoea	49	96	29	221	**	07	91	92	08
Euphausiacea	1,475	1,237	967	1,958	NS				
Evadne spp.	56	2	190	2	NS				
Hydrozoa	500	922	2,171	1,422	NS				
Isopoda	14	76	27	123	NS				
Limacina helicina	24	29	9	84	*	07	91	92	08
Polychaeta	1,161	1,930	5,763	2,703	*	91	92	08	07
Total copepods	12,878	19,470	33,744	13,661	**	91	08	92	07
Total zooplankton	66,216	46,439	71,117	103,075	**	92	91	07	08

Table 2. Year-to-year comparison on mean copepodid stage of *C. glacialis*, *E. bungii* and *M. pacifica* in the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008. Differences between years were tested by one-way ANOVA and post-hoc test by Fisher's PLSD. Any years not connected by the underlines are significantly different ($p < 0.05$). Values are mean copepodid stage±sd. Numbers in the parentheses indicate number of stations in each year. *: $p < 0.05$, **: $p < 0.01$.

Species	Mean copepodid stage				one-way ANOVA	Fisher's PLSD			
	91 (27)	92 (34)	07 (31)	08 (28)					
C. glacialis	3.32±0.63	3.61±0.81	4.34±0.52	2.92±0.69	**	08	91	92	07
E. bungii	3.44±2.32	3.85±1.39	2.91±0.90	3.85±1.22	NS				
M. pacifica	1.94±0.81	3.14±0.93	4.42±0.51	3.25±1.43	**	91	92	08	07

Table 3. Summary of the year-to-year comparisons in hydrography, zooplankton (biomass, community and diversity) and development of large copepods in the Chukchi Sea during July−August of 1991, 1992, 2007 and 2008. Values in the parentheses indicate mean±sd for sea surface salinity (SSS), temperature (SST) and biomass, and mean for H'. ECSW: Eastern Chukchi Summer Water.

Year	Hydrography	Zooplankton			Development of large copepods
		Biomass	Community	Diversity	
	(SSS, SST)	(g WM m^{-2})		(H')	(cf. Table 2)
1991	Ice melt water (30.0±1.3, 5.2±1.7)	Low (38±26)	Arctic	Low (1.61)	Slow
1992	Ice melt water (29.4±1.9, 5.2±2.1)	Low (27±18)	Arctic	Low (2.18)	Slow
2007	ECSW (31.9±0.7, 9.7±2.6)	High (43±60)	Pacific+Arctic	High (2.56)	Fast
2008	High saline water (30.9±1.1, 4.3±1.9)	Low (38±27)	Arctic (*Balanus* larvae dominant)	Low (1.13)	Slow

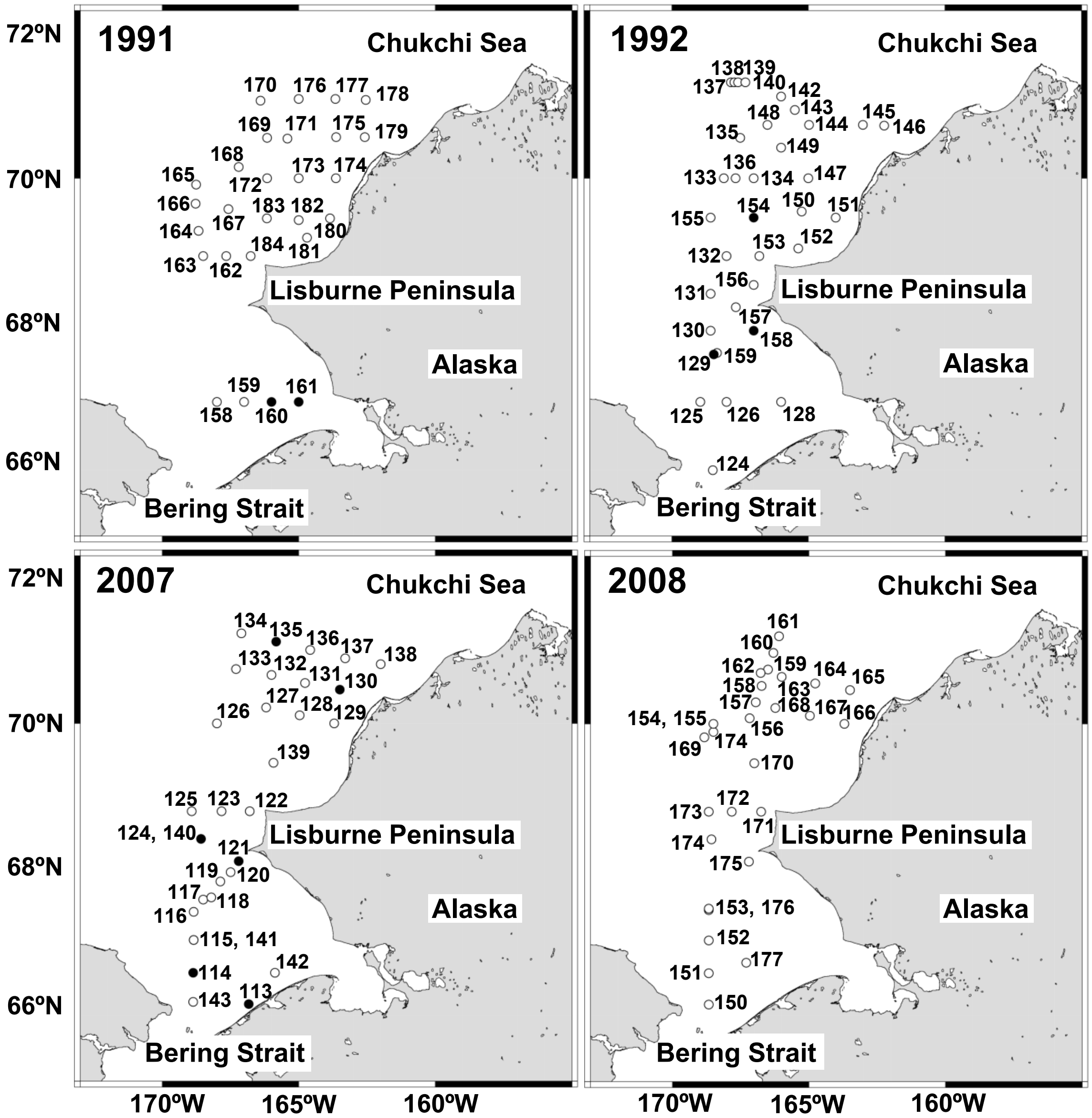
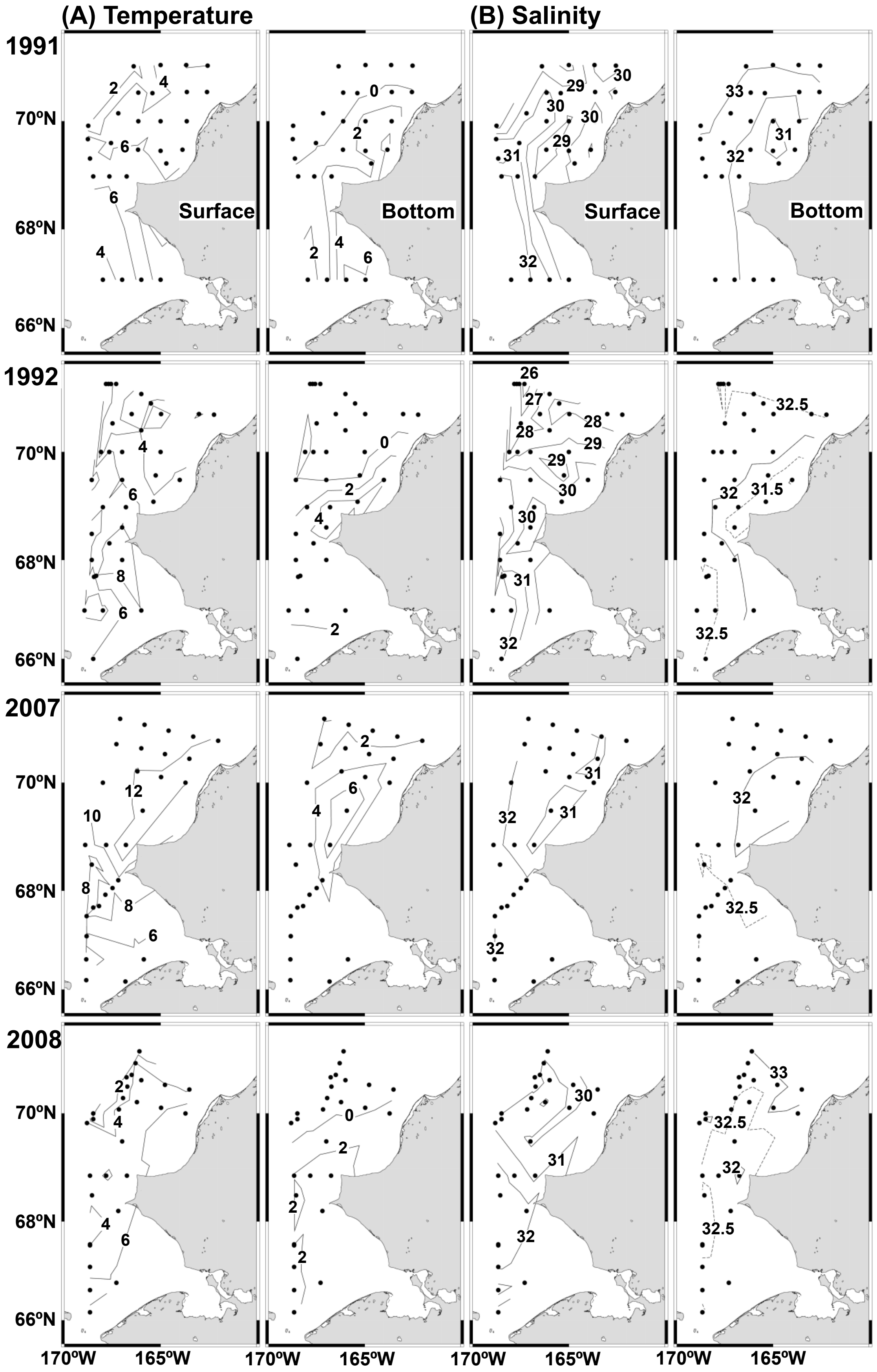


Fig. 1 (Matsuno et al.)



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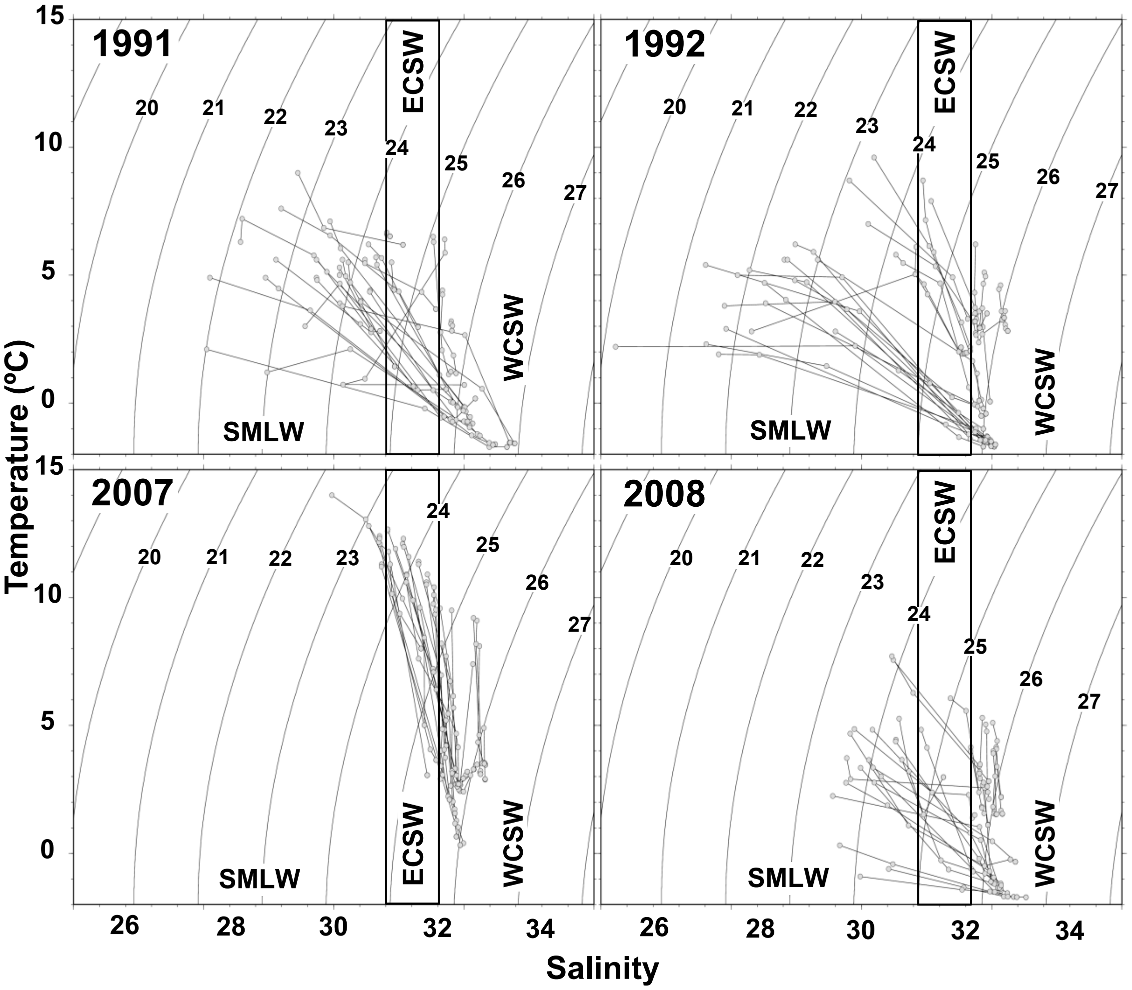

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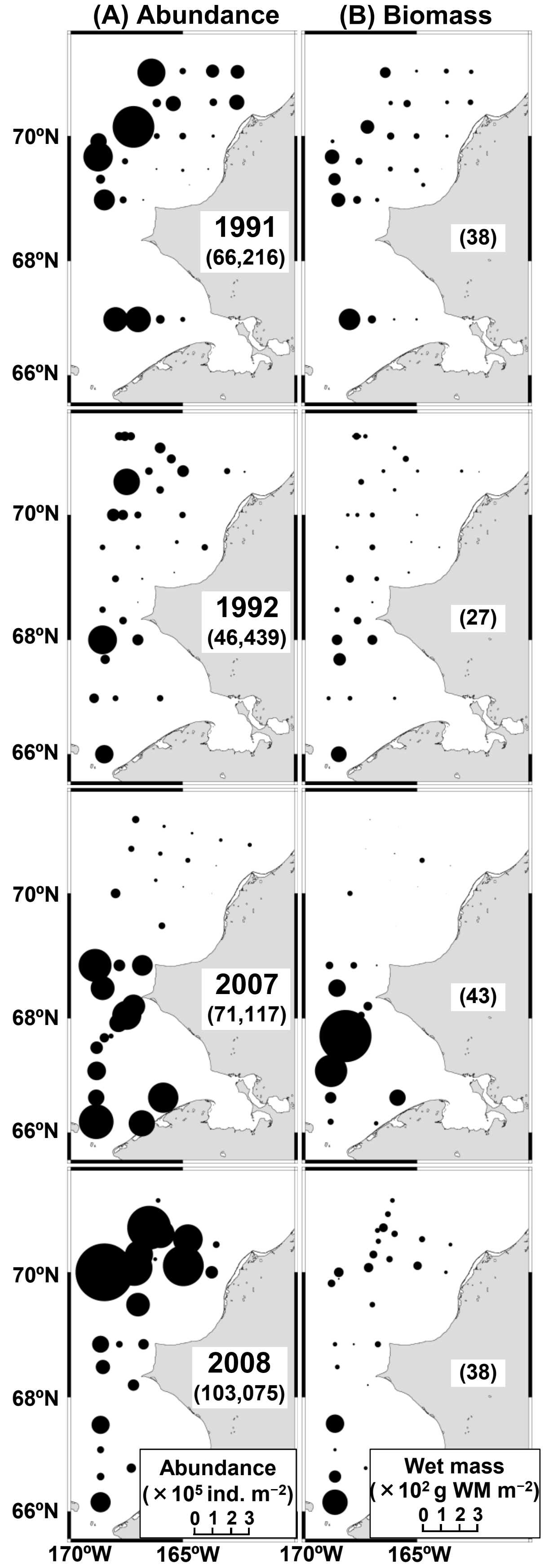

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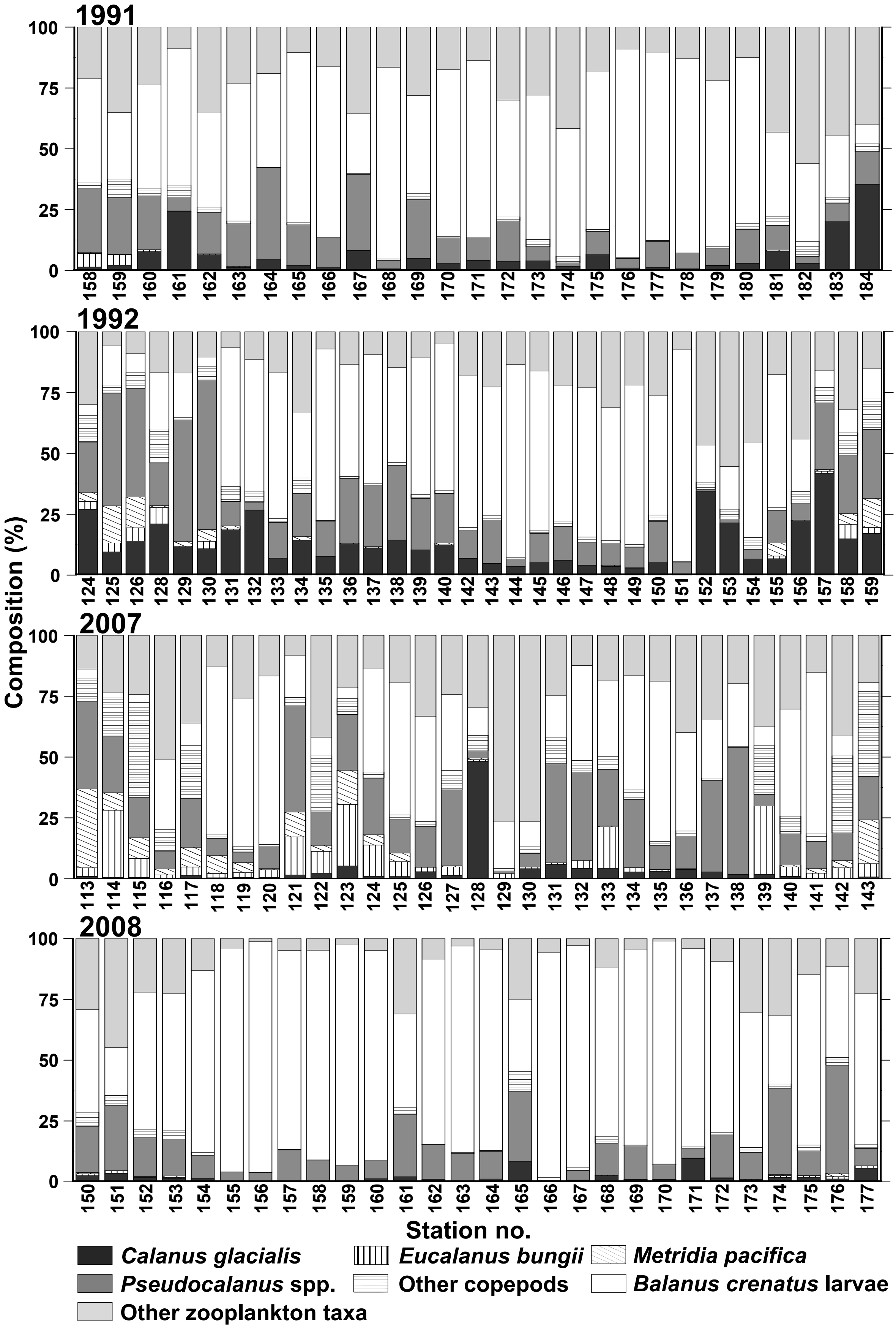

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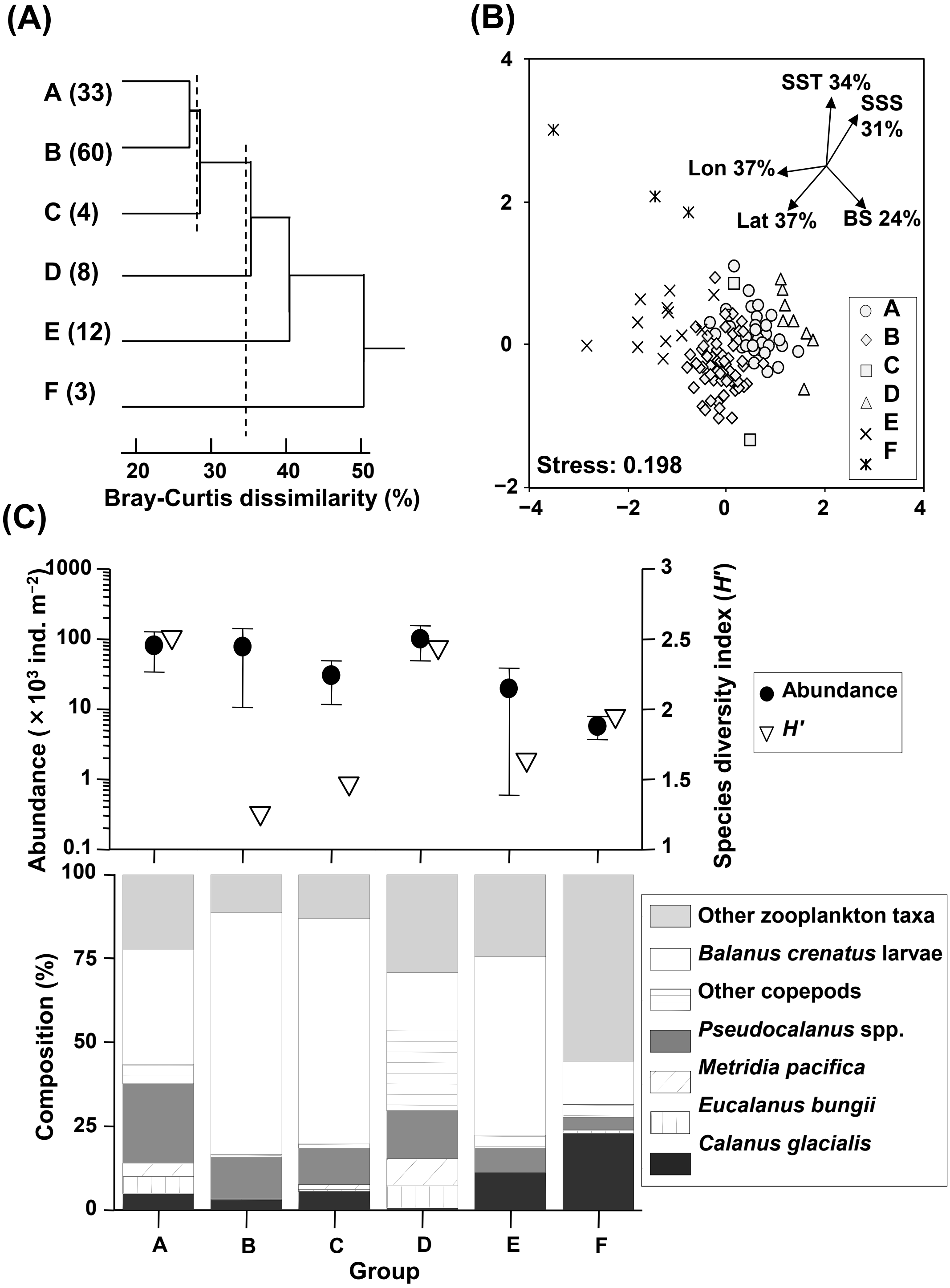

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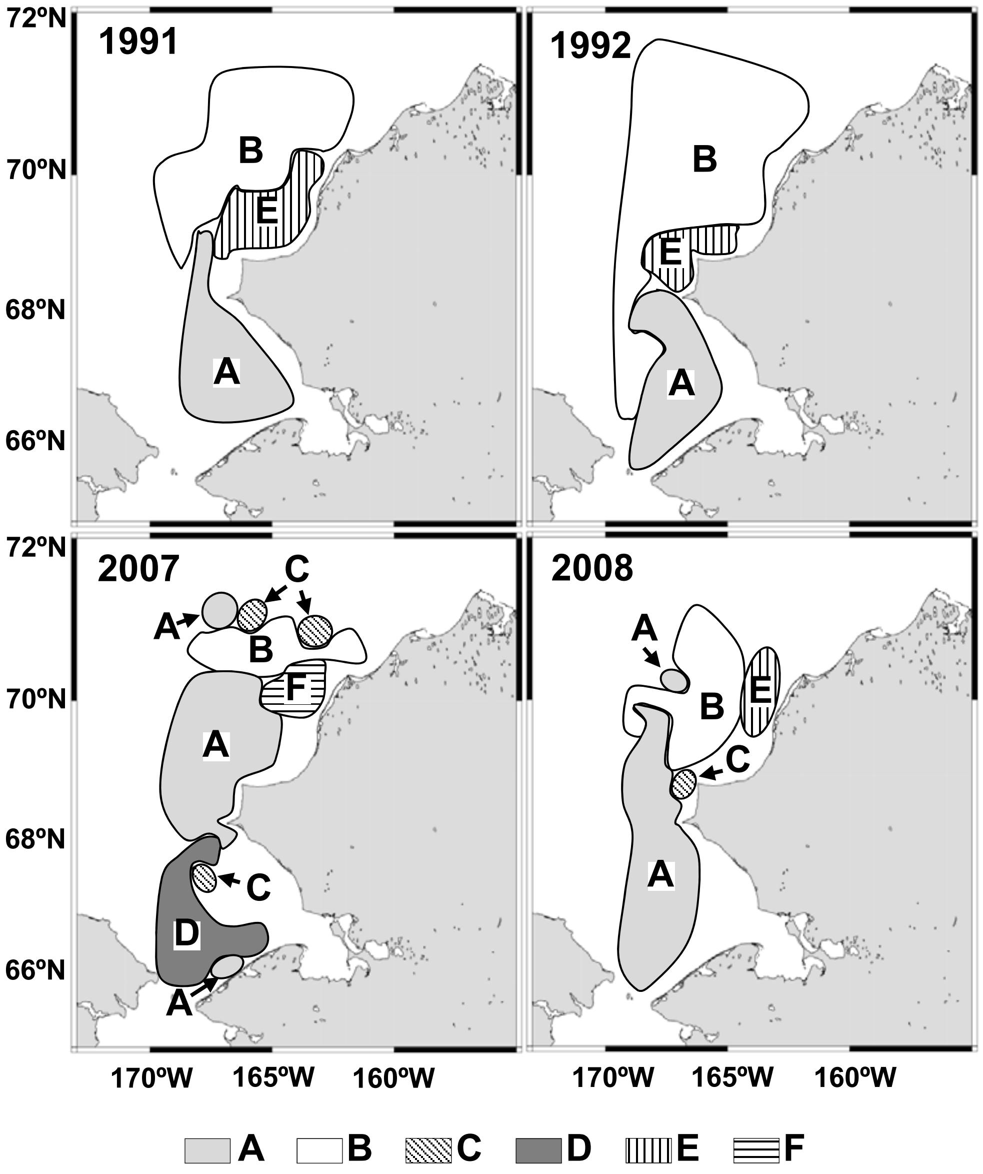

Fig. 7 (Matsuno et al.)