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Biomass size spectra of mesozooplankton in the Chukchi Sea during summers of  
1991/1992 and 2007/2008: an analysis by optical plankton counter

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## **Abstract**

To evaluate regional characteristics, zooplankton communities were analyzed by an Optical Plankton Counter (OPC) in the Chukchi Sea during summers of 1991, 1992, 2007 and 2008. Zooplankton abundance and biomass ranged from 5000 to 1 170 000 ind.  $m^{-2}$  and 0.2 to 10.9 g dry-mass  $m^{-2}$ , respectively. Based on the zooplankton biovolume at 48 bins every 0.1 mm between 0.25–5.0 mm equivalent spherical diameters (ESD), Bray-Curtis cluster analysis classified zooplankton communities into four groups (A–D). There was no observed change in zooplankton communities in the south of Lisburne Peninsula (group A) throughout the four years, while there observed change in zooplankton communities north of Lisburne Peninsula: group B (normal) in 1991/1992, group D (low biomass) in 2007, and group C (predominance of barnacle larvae) in 2008. Analysis of Normalized Biomass Size Spectra (NBSS) with groups revealed that the groups A and C were highly productive. Thus, the zooplankton community in the south of Lisburne Peninsula was constantly highly productive, which may be caused by the continuous inflow of Pacific Water containing high nutrients. The zooplankton community in the north of Lisburne Peninsula varied greatly by year, which may be related to the inter-annual changes in sea ice extension.

**Keywords:** Chukchi Sea, mesozooplankton community, normalized biomass size

spectra (NBSS), optical plankton counter (OPC), Pacific Water.

## **Introduction**

The Chukchi Sea is located in the Pacific sector of the Arctic Ocean. It is mainly composed by a shallow shelf (depth < 50 m), and recent observations show the most drastic sea ice reduction within the Arctic Ocean (Shimada *et al.*, 2001, 2006) occurs here. It is believed that the large sea ice reduction in the Chukchi Sea is due to increased inflow of the warm Pacific Water passing through the Bering Strait (Shimada *et al.*, 2006). Based on satellite observations during 1991–2007, both the volume and temperature of the Pacific Water that passed through the Bering Strait was highest in 2007 when the sea ice extent was the least (Woodgate *et al.*, 2010). The sea surface temperature in the Chukchi Sea is normally 4–6°C, yet rose up to 12°C in 2007 (Vanin, 2010). This anomalously high temperature in 2007 is considered to be caused by the early sea ice reduction (Markus *et al.*, 2009), and also the intensive solar heating by a stationary presence of anticyclonic circulation over the Chukchi Sea in that year (Mizobata *et al.*, 2010; Vanin, 2010). Such drastic changes in recent hydrography in this region are considered to have a great effect on the marine ecosystem, especially on plankton community (Grebmeier *et al.*, 2006; Hunt and Drinkwater, 2007).

In the Chukchi Sea, zooplankton is an important secondary producer in the marine ecosystem, which is a vital link between phytoplankton and fish or marine

mammal (Lowry *et al.*, 2004; Wassmann *et al.*, 2006). The southern Chukchi Sea is reported to have high primary production enhanced by inflow of the Pacific Water containing high nutrients (Sambrotto *et al.*, 1984; Springer and McRoy, 1993). Since the Pacific Water also transports zooplankton inhabiting the Bering Sea, inflow of the Pacific Water has a great effect on the spatial distribution of zooplankton biomass and species composition (Springer *et al.*, 1989; Hopcroft *et al.*, 2010; Matsuno *et al.*, 2011). The zooplankton community in the Chukchi Sea is dominated by both Arctic (*Calanus glacialis*) and Pacific (*Eucalanus bungii* and *Metridia pacifica*) copepods (Springer *et al.*, 1989; Matsuno *et al.*, 2011), while an occasional predominance of small barnacle larvae (*Balanus crenatus*) after a phytoplankton bloom is also reported (Barnes, 1957; Crisp, 1962).

Zooplankton size spectrum is an important factor to evaluate marine ecosystem structure (Sheldon *et al.*, 1972; Kerr, 1974), and also for growth rate and metabolic activity of zooplankton (Platt and Denman, 1977, 1978). While their importance, size measurements on zooplankton by microscopic observation is time consuming and difficult to make accurate measurement. To overcome these problems, an Optical Plankton Counter (OPC) instrument (Herman, 1988), which can measure zooplankton size and number quickly and accurately, has been applied for various marine ecosystems

(Herman, 1992; Huntley *et al.*, 1995; Nogueira *et al.*, 2004; Baird *et al.*, 2008). Specifically, Normalized Biomass Size Spectra (NBSS) analysis (Platt and Denman, 1978) on zooplankton size spectrum data by OPC measurement is used to evaluate the marine ecosystem structure from world-wide oceans (Nogueira *et al.*, 2004; Herman and Harvey, 2006; Basedow *et al.*, 2010). NBSS analysis can evaluate whether bottom-up or top-down controls are dominant in each marine ecosystem (Suthers *et al.*, 2006; Moore and Suthers, 2006; Finlay *et al.*, 2007). Thus, the combination of OPC and NBSS analyses may allow us to evaluate the zooplankton characteristics in the Chukchi Sea. However, few studies have been made on zooplankton size spectra in this region.

In the present study, we performed OPC analysis on preserved zooplankton samples collected in the Chukchi Sea during summers of 1991/1992 (when the sea ice extended) and 2007/2008 (when the sea ice reduced). Spatial and temporal changes in zooplankton size spectra were evaluated by cluster analysis based on biovolume data binned into 48 size classes between 0.25 and 5.0 mm ESD. The NBSS analysis was performed on each clustered group. Based on NBSS data, we evaluate zooplankton productivity of summer Chukchi Sea and clarify the ecosystem characteristics of Chukchi Sea through comparison with other oceans.

## **Materials and Methods**

### **Field sampling**

A total of 119 zooplankton samplings were conducted by TS “Oshoro-Marū” 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 ( $n = 33$ ), 5–13 August 2007 ( $n = 31$ ) and 7–13 July 2008 ( $n = 28$ ) (Figure 1). Samples were collected at day or night by vertical tows with a NORPAC net (mouth diameter 45 cm, mesh size 0.335 mm) from 5 m above the bottom (depths of most stations were about 50 m). The volume of water filtered through the net was estimated from reading of a flow-meter (Rigosha Co. Ltd.) mounted on the net ring. The volume of water filtered through net ranged between 2.1 and 10.1 m<sup>3</sup> (mean±sd: 5.5±1.6 m<sup>3</sup>). This large range of filtered volume was caused by the large differences in net towing depth (25–63 m, mean 45 m) which determined by water depth at each station. Once on board, samples were immediately preserved with 5% v/v borax buffered formalin. At each sampling station, 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 have already been published elsewhere (Hokkaido University, 1992, 1993, 2008, 2009).

## **OPC analysis**

In the land laboratory, 1/2–1/8 aliquot of zooplankton samples, made by Motoda box splitter (Motoda, 1959), was used for OPC measurement (OPC-1L: Focal Technologies Corp.). The OPC can measure the number of particles with 4096 size categories between 0.250–20 mm ESD with a precision of 0.001–0.021 mm. Since we collected samples by vertical hauls of NORPAC net, large plankton such as giant jellyfish (Brodeur *et al.*, 2008) or euphausiids (Ashjian *et al.*, 2010) were not quantitatively collected. Because of this, data by OPC analysis treated only on mesozooplankton size range: 0.25–5.0 mm ESD which is sufficient for NORPAC net collection. To evaluate accurate size and number, the measurements were made using adequate flow rate (10 L min<sup>-1</sup>) and particle density (< 10 counts sec<sup>-1</sup>) according to the procedures of Mullin *et al.* (2000) and Yokoi *et al.* (2008). In addition to whole sample measurements, OPC measurements on individuals; i.e. each copepodid stage of the dominant copepods (*Calanus glacialis* and *Pseudocalanus* spp.) and barnacle larvae (*Balanus crenatus*) sorted from the samples, were also made.

## **Abundance**

Abundance per square meter ( $N$ , ind.  $\text{m}^{-2}$ ) at each ESD size category was calculated from the following equation:

$$N = \frac{n \times D}{s \times F}$$

where  $n$  is the number of particles (= zooplankton individual),  $s$  is the split factor of each sample,  $F$  is the filtered volume of the net ( $\text{m}^3$ ) and  $D$  is the net-towed depth (m).

## **Biomass**

Zooplankton wet mass (WM) at 4096 size categories was calculated from ESD data by assuming the relative density of zooplankton to be equal to seawater (=  $1 \text{ mg mm}^{-3}$ ).

WM was converted to dry mass (DM) assuming that the water content of zooplankton was 90% ( $\text{DM} = 0.1 \times \text{WM}$ ), which is the mean water content of zooplankton in the Chukchi Sea (Matsuno *et al.*, 2009).

For comparison with OPC derived biomass, direct WM measurements were made for 1/2 aliquot of all samples. Samples were filtered on pre-weighed  $100 \mu\text{m}$  mesh, and weighed a precision of 10 mg. During this WM measurement, samples dominated by phytoplankton were marked (19 of total 119 samples).

Since zooplankton samplings were conducted during July–August (Arctic summer), daytime sampling accounted for 91% of total sampling stations (Figure 1).

Day-night comparison on zooplankton abundance and biomass also showed no significant differences (*U-test*,  $p = 0.15\text{--}0.39$ ). Because of this, we made no day-night conversion with abundance and biomass data.

### **Cluster analysis**

To evaluate spatial and temporal changes in zooplankton biovolume size spectra, we applied a cluster analysis. Prior to analysis, biovolume data at 1761 categories between 0.25–5.0 mm ESD were binned into 48 size classes at every 0.1 mm ESD (e.g., 0.25–0.30, 0.30–0.40..., 4.90–5.00 mm). Based on the biovolume data in 48 size classes, similarities between the samples were evaluated by Bray-Curtis methods (Bray and Curtis, 1957). 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).

To clarify what environmental parameters (latitude, longitude, depth, sea surface temperature, salinity, bottom temperature and salinity) have significant

relationships with zooplankton grouping, multiple regressions ( $Y=aX_1+bX_2+c$ , where  $Y$  is environmental variable,  $X_1$  and  $X_2$  are Axis1 and 2 of NMDS, respectively) were made by aid of StatView (SAS Institute Inc.).

### **Normalized biomass size spectra (NBSS)**

Based on the OPC data, NBSS was calculated following the procedure of Suthers *et al.* (2006). Zooplankton biovolume ( $B$ :  $\text{mm}^3 \text{ m}^{-3}$ ) was calculated in each of the 48 size classes. To calculate  $X$  axis of NBSS ( $\log_{10}$  zooplankton biovolume [ $\text{mm}^3 \text{ ind.}^{-1}$ ]),  $B$  was divided with abundance of each size class ( $\text{ind. m}^{-3}$ ) and converted to  $\log_{10}$ . To calculate  $Y$  axis of NBSS ( $\log_{10}$  normalized biovolume [ $\text{mm}^3 \text{ m}^{-3}$ ] /  $\Delta$ biovolume [ $\text{mm}^3$ ]),  $B$  was divided by interval of biovolume between a consecutive size class ( $\Delta$ biovolume [ $\text{mm}^3$ ]), and converted to  $\log_{10}$ . Based on these data, NBSS liner model was calculated (Platt and Denman, 1978):  $Y = aX + b$ , where  $a$  and  $b$  are slope and intercept of NBSS, respectively.

### **Statistical analysis**

Based on the zooplankton groups clustered by their size spectra, inter-group differences in hydrography (sea surface temperature, salinity, bottom temperature and salinity) and

zooplankton data (abundance, biomass and slope of NBSS) were tested using one-way ANOVA and Fisher's PLSD. For evaluation of abundant zooplankton species in each group, taxonomic account data on the same samples (Matsuno *et al.*, 2011) were also used for analyses using one-way ANOVA and Fisher's PLSD. To clarify what factors govern the slope of NBSS, ANCOVA with independent variables with intercept of NBSS and zooplankton group was made with aid of StatView.

## **Results**

### **Hydrography**

Sea surface and bottom temperatures ranged from  $-0.9$  to  $14.0^{\circ}\text{C}$  and  $-1.7$  to  $8.0^{\circ}\text{C}$ , respectively (Figure 2a). Sea surface temperatures in 2007 were  $3.9$ – $14.0^{\circ}\text{C}$  (mean:  $9.7^{\circ}\text{C}$ ), and were significantly higher than those in the other three years ( $-0.9$  to  $9.6^{\circ}\text{C}$ , mean:  $4.8^{\circ}\text{C}$ ) (one-way ANOVA,  $p < 0.0001$ ). In 2007, differences in temperature between the sea surface and bottom (surface–bottom values) were significantly higher, especially to the north of Lisburne Peninsula ( $4.4$ – $11.0^{\circ}\text{C}$ , mean  $8.7^{\circ}\text{C}$ ) than those in the other years ( $0.1$ – $8.6^{\circ}\text{C}$ , mean:  $4.1^{\circ}\text{C}$ ) (one-way ANOVA,  $p < 0.0001$ ). Sea surface and bottom salinities ranged from  $25.3$  to  $32.9$  and  $30.7$  to  $33.5$ , respectively (Figure 2b). Sea surface salinities in 2007 ranged from  $30.0$  to  $32.9$  and were significantly higher

than the other three years (one-way ANOVA,  $p < 0.0001$ ). No interannual variability in bottom salinity was observed (Figure 2b).

### **Characteristics of OPC measurement**

Comparisons on abundance (ind.  $m^{-2}$ ) and wet mass (g WM  $m^{-2}$ ) between OPC derived data and direct measurements were made (Figure 3). Based on whole samples ( $n = 119$ ), OPC measurements overestimated zooplankton abundance (Figure 3a), yet underestimated zooplankton biomass (Figure 3b). Since 19 samples were dominated by phytoplankton, elimination of these data ( $n = 100$ , normal sample) provided substantial matches between OPC derived and directly measured data by a factor of 0.974–1.047 (Figure 3).

### **Zooplankton abundance and biomass**

Zooplankton abundance ranged from 5000 to 1 171 000 ind.  $m^{-2}$  (mean: 111 002).

There was little regional change in abundance between 1991, 1992 and 2008, with less observed change in the area north of Lisburne Peninsula in 2007 (Figure 4a).

Zooplankton biomass ranged from 0.2 to 10.9 g DM  $m^{-2}$  (mean: 3.1) (Figure 4b).

Similar to abundance, biomass had little regional change in 1991, 1992 and 2008, with

less observed change in the area north of the Peninsula in 2007 (Figure 4b).

### **Zooplankton community**

Based on the biovolume in 48 size classes, zooplankton communities were classified into four groups (A–D) by cluster analysis at 55 and 73% dissimilarities (Figure 5a). Each group contained 16–45 stations. Hydrographic parameters showing significant relationships on NMDS ordination were latitude, longitude, depth, sea surface temperature, bottom temperature and salinity (Figure 5b). Mean abundances were higher for groups A and C (152 000–194 000 ind. m<sup>-2</sup>) than those of groups B and D (22 000–54 000 ind. m<sup>-2</sup>) (Table 1). Mean biomasses also had a similar pattern, and were higher for group A (4.96 g DM m<sup>-2</sup>), and lower for group D (0.55 g DM m<sup>-2</sup>) (Table 1). In terms of size composition, the predominance of the smallest size class (0.25–1 mm) in group C was marked (Figure 5c).

Distribution and occurrence of each zooplankton group had clear spatial and interannual patterns (Figure 6). In the area south of Lisburne Peninsula, group A dominated throughout the study period. To the north of Lisburne Peninsula, dominant groups varied with year: group B in 1991 and 1992, group D in 2007, and group C in 2008 (Figure 6).

The dominant taxonomic accounts varied by group. Various copepods (*C. glacialis*, *Centropages abdominalis*, Cyclopoida, *Eucalanus bungii*, *Metridia pacifica*, *Pseudocalanus acuspes*, *P. newmani*), Appendicularia, Echinoidea larvae and Polychaeta were abundant in group A (Table 2). There was no species showing greater abundance in group B. Group C was characterized by few large-sized copepods with the predominance of barnacle larvae (*B. crenatus*). Group D was characterized by the least abundant of the juvenile stages (C1–C4) of *Pseudocalanus* spp. (Table 2).

## **NBSS**

ANCOVA on slope of NBSS showed that there were two significant relationships: between slope and intercept ( $p < 0.01$ ) and between slope and group ( $p < 0.05$ ), while the interaction of group and intercept had no significant relationship on slope (Table 3). Slope of NBSS for each group ranged from  $-0.78$  to  $-1.11$  (Table 1). Results on mean NBSS for each group are shown in Figure 7. There observed significant inter-group difference in slope of NBSS (Table 1). The slope of NBSS was steeper in order of  $C > A > B > D$  (Table 1).

## **Discussion**

### **Abundance, biomass and NBSS**

As characteristics of the OPC measurement method, overestimation in abundance was the case for the samples dominated by phytoplankton (Figure 3a). This overestimation in abundance is most likely caused by the OPC detection on large-sized chain-forming diatoms. Because of the phytoplankton counting, the zooplankton abundance obtained using the OPC method may be larger than zooplankton abundance obtained by microscopic observation (Herman, 1992; Herman and Harvey, 2006).

Interestingly, the reverse pattern (underestimation) was the case in biomass values for the same phytoplankton dominant samples (Figure 3b). Biomass values calculated by direct measurement inevitably include phytoplankton debris in the phytoplankton dominant samples. Since OPC detects particles from much larger sizes (> 250  $\mu\text{m}$ ), this method's biomass values may be lower than the values obtained by direct measurement (Matsuno *et al.*, 2009).

While such overestimation (abundance) or underestimation (biomass) was observed for the phytoplankton dominated samples, OPC and directly measured values were nearly equal for most of the samples (normal,  $n = 100$ ) both in abundance and biomass (Figure 3). These facts suggest that the OPC analysis is an adequate method for estimation of zooplankton abundance and biomass in this region.

NBSS analysis based on the zooplankton biovolume size spectra is applied for evaluation of the marine ecosystem structure from world-wide oceans (Herman and Harvey, 2006; Baird *et al.*, 2008; Basedow *et al.*, 2010). The slope of NBSS is an important index to assess marine ecosystem structure and its productivity (Rodriguez and Mullin, 1986; Splures and Munawar, 1986). Sheldon *et al.* (1972) reported that the slope of NBSS at stable marine ecosystem is  $-1$ , and the higher and lower slopes than  $-1$  indicate that the ecosystems are high and low productivity, respectively (cf. Rodriguez and Mullin, 1986; Splures and Munawar, 1986). Slopes of NBSS in each group were in the order of  $D < B < A < C$ , and the slopes of groups A and C were higher than  $-1$ , while these of groups B and D were lower than  $-1$  (Table 1). The high NBSS slopes, observed for groups A and C, indicate that those groups were high productivity. While the low NBSS slopes of groups B and D suggest that those groups were low productivity. The high slope of group A was composed by *Pseudocalanus* spp. and *C. glacialis* and that of group C derived by barnacle larvae (Figure 7).

Comparisons with slopes of NBSS between the present study and previous studies from world-wide oceans are shown in Table 4. Slope of group C ( $-1.11$ ) was close to the values from North Pacific Ocean ( $-1.13$ ) and Atlantic Ocean ( $-1.14$ ), but that of group A ( $-1.01$ ) was similar to those of the coral seas ( $-0.97$  to  $-1.00$ ). Since

the area south of the Lisburne Peninsula was occupied by group A throughout the four years (Figure 6), zooplankton community in this area is considered to have highly productive ecosystem, which caused by the continuous inflow of the Pacific Water. While in the north of Lisburne Peninsula, groups B and D with gradual slope ( $-0.78$  to  $-0.86$ ) were distributed in 1991/1992 and 2007, and group C with steep slope ( $-1.11$ ) was observed in 2008 (Figure 6). As mentioned below, mass recruitment of meroplankton (barnacle larvae) was the case of highly productive group C. Thus, zooplankton community to the north of Lisburne Peninsula is highly variable by year.

### **Zooplankton community**

Distribution and occurrence of each zooplankton community grouped by cluster analysis based on biovolume size spectra varied spatially and interannually (Figure 6). Vertical profiles of temperature, salinity, dissolved inorganic nitrogen and chlorophyll *a* at each group are shown in Figure 8. Group A commonly occurred to the south of Lisburne Peninsula, which was characterized by higher sea surface temperature, nutrients and chlorophyll *a*. To the north of Lisburne Peninsula, dominant groups varied with year: i.e. group B in 1991/1992, C in 2008 and D in 2007 (Figure 6). Temperature profiles in each group varied greatly in the order of  $C < B < D$  (Figure 8).

Within the three groups, group D was characterized by high surface temperature and salinity, and had a strong thermocline around 15 m depth (Figure 8).

The zooplankton community in group A was dominated by both small and large-sized zooplankton (Table 2). The continuous inflow of Pacific Water containing high nutrients implies high primary production in the south of Lisburne Peninsula (Sambrotto *et al.*, 1984; Springer and McRoy, 1993). While primary production in the north of Lisburne Peninsula was lower than the south of Lisburne Peninsula (Hill and Cota, 2005). Concerning the zooplankton community, a drastic increase of large-sized Pacific copepods to the south of Lisburne Peninsula during 2007 was reported (Matsuno *et al.*, 2011). In the present study, the abundance of the Pacific copepods (*E. bungii* and *M. pacifica*) of group A was significantly higher than the other groups (Table 2). In addition to the Pacific copepods, both Arctic copepods (*C. glacialis*) and small-sized copepods (*C. abdominalis*, Cyclopoida, *P. acuspes* and *P. newmani*) also exhibited significantly greater abundance in group A than the other groups (Table 2). Thus, the greater abundance of copepods in group A may be caused by the invasion of Pacific copepods through inflow of Pacific Water, and also by the high abundance of Arctic copepods and small-sized neritic copepods, whose nutrition may be supported by high primary production in the south of Lisburne Peninsula.

Group B was observed to the north of Lisburne Peninsula during 1991/1992 (Figure 6). The temperature condition of group B was between those of group D (2007) and C (2008) in the same region (Figure 8). Concerning zooplankton community, the abundance of most of the species/taxa in group B was moderate, and had no specific abundant species (Table 2). The largest number of stations were clustered to group B ( $n = 45$ ). Since the including sample number is the greatest, distributed widely, biomass and NBSS slope settled medium, we treated that group B was the normal hydrographic condition and zooplankton community in the Chukchi Sea during summer.

Group C, which was observed to the north of Lisburne Peninsula during 2008, was predominated by barnacle larvae (*B. crenatus*) that composed 84% of the zooplankton abundance (Table 2). This anomalous species composition of group C might be a result of the sampling period in 2008 (7–13 July: two-week to one-month earlier than the other year [24 July–13 August]). The sampling period of 2008 might be matched with the release timing of barnacle larvae. Concerning the release timing of barnacle larvae, laboratory-rearing studies show that the amount of food concentration (phytoplankton) in ambient water is an important factor to determine release timing (Clare *et al.*, 1984; Clare and Walker, 1986). Field studies also suggest

that onset of the phytoplankton bloom is a key factor stimulating the release of barnacle larvae (Barnes, 1957; Crisp, 1962). In the Chukchi Sea, the phytoplankton bloom is reported to occur from spring to summer (Wang *et al.*, 2005), and the barnacle larvae may release at that period. Since most of the primary productivity in this region derived from ice-edge bloom (Hunt *et al.*, 2011), early sampling period in 2008 may imply nearby the bloom. Thus, the earlier sampling period in 2008 than the other years may have allowed the collection of barnacle larvae in meroplankton form just after the release timing by benthic adults.

Group D dominated to the north of Lisburne Peninsula during 2007 (Figure 6). Hydrographic information in this area in 2007 shows that the sea ice reduction started early (Markus *et al.*, 2009), and the amount of the Pacific Water through the Bering Strait into the Chukchi Sea was greatest during 1991–2007 (Mizobata *et al.*, 2010; Woodgate *et al.*, 2010). In this study, significantly higher sea surface salinity in 2007 would be caused by the greater intrusion of Pacific Water at that year (Figure 2). In terms of temperature, the highest sea surface temperature in 2007 (Figure 2) would be caused by the early timing of sea ice reduction (Markus *et al.*, 2009), and intensive solar heating by a stationary presence of anticyclonic circulation over the Chukchi Sea at that year (Mizobata *et al.*, 2010; Vanin, 2010).

The zooplankton community of group D is characterized by low abundance and biomass of most taxa/species, especially for juvenile stages (C1–C4) of *Pseudocalanus* spp. (Tables 1 and 2). These results may be related to the strength of water-column stratification. For instance, Simpson-Hunter's index (Simpson and Hunter, 1974) between 10 and 20 m depth was significantly greater for group D ( $11.01 \pm 8.19$ ) than the other groups (0.82–3.16) (one-way ANOVA,  $p < 0.0001$ ). High temperature condition of group D in 2007 may induce open-water bloom which starts later and ends with short pulse (Hunt *et al.*, 2011). Under such food limited condition, it may be difficult even for small copepods (*Pseudocalanus* spp.) to increase number of generations per year. Since developmental time of calanoid copepods is inversely correlated with temperature (e.g. Corkett and McLaren, 1978), the high temperature condition in group D may provide faster development of *Pseudocalanus* spp., thus induce low abundance of their juveniles (C1–C4) there.

In conclusion, characteristics of zooplankton community in the Chukchi Sea greatly varied with region. Zooplankton community to the south of Lisburne Peninsula was highly productive, and had little interannual variability. This high productivity may be caused by the continuous inflow of Pacific Water containing high nutrients. The zooplankton community to the north of Lisburne Peninsula greatly

varied with year, which may be related to interannual changes in sea ice extension and the release timing of benthic larvae.

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## Figure legends

Figure 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.

Figure 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.

Figure 3. Comparison between OPC ( $Y$ ) and directly measured data ( $X$ ) in term of abundance (a) and wet mass (b). Solid, dot and long-short dot lines indicates the regressions on whole samples, normal samples (open circles) and phytoplankton dominated samples (solid triangles), respectively. Long dashed lines indicate positions of 1:1.

Figure 4. Horizontal distribution of abundance (a) and biomass (b) of mesozooplankton in the Chukchi Sea during July–August of 1991, 1992, 2007 and 2008, analyzed by OPC.

Figure 5. Results of cluster analysis based on mesozooplankton biovolume size spectra in the Chukchi Sea (a). Four groups (A–D) were identified at 55 and 73% Bray-Curtis dissimilarity connected with UPGMA. Numbers in the

parentheses in (a) indicate number of stations which each group contain. NMDS plots of each group (b). Arrows and percentages in (b) indicate directions of environmental parameters and coefficient of determination ( $r^2$ ), respectively. BD: bottom depth, BS: bottom salinity, BT: bottom temperature, Lat: latitude, Lon: longitude, ST: surface temperature. Mean biomass and size composition (ESD in mm) of each group (c).

Figure 6. Horizontal distributions of each group identified from cluster analysis on mesozooplankton biovolume size spectra (cf. Figure 5a) in the Chukchi Sea during July–August of 1991, 1992, 2007 and 2008.

Figure 7. Mean normalized biomass size spectra (NBSS) of four groups identified from cluster analysis on mesozooplankton biovolume size spectra (cf. Figure 5a) in the Chukchi Sea during July–August of 1991, 1992, 2007 and 2008. Numbers in the parentheses indicate number of stations belonging to each group. For the dominant zooplankton species in each group (cf. Table 2), mean (symbols) and standard deviation (bars) data on each developmental stage are shown in the panel.

Figure 8. Vertical distribution of temperature, salinity, dissolved inorganic nitrogen (DIN) and chlorophyll *a* at four groups identified from cluster analysis on

mesozooplankton biovolume size spectra (cf. Figure 5a) in the Chukchi Sea during July–August of 1991, 1992, 2007 and 2008. Symbols and bars indicate mean values and standard deviations at 10 m intervals.

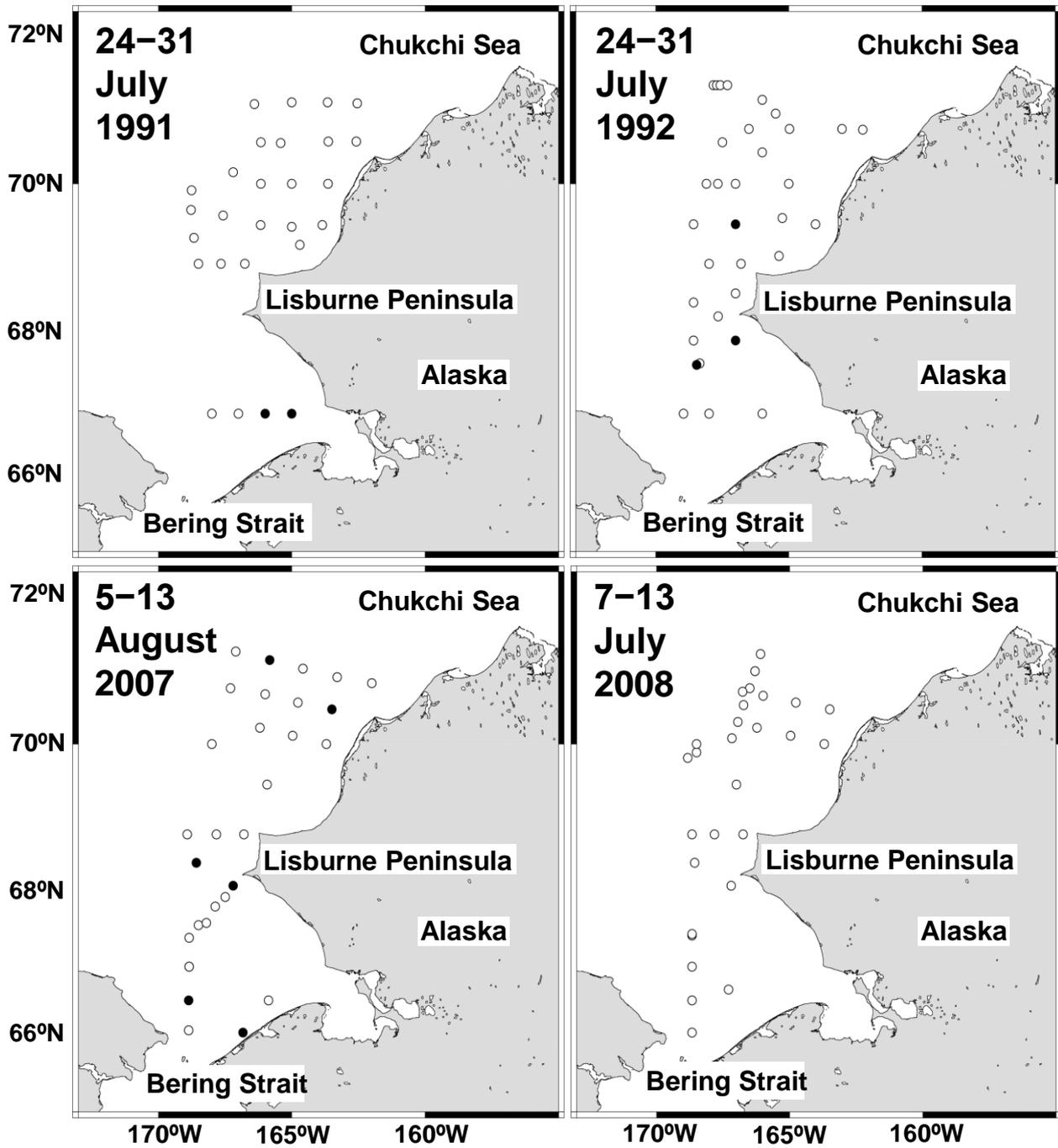


Figure 1 (Matsuno et al.)

**(a) Temperature**

**(b) Salinity**

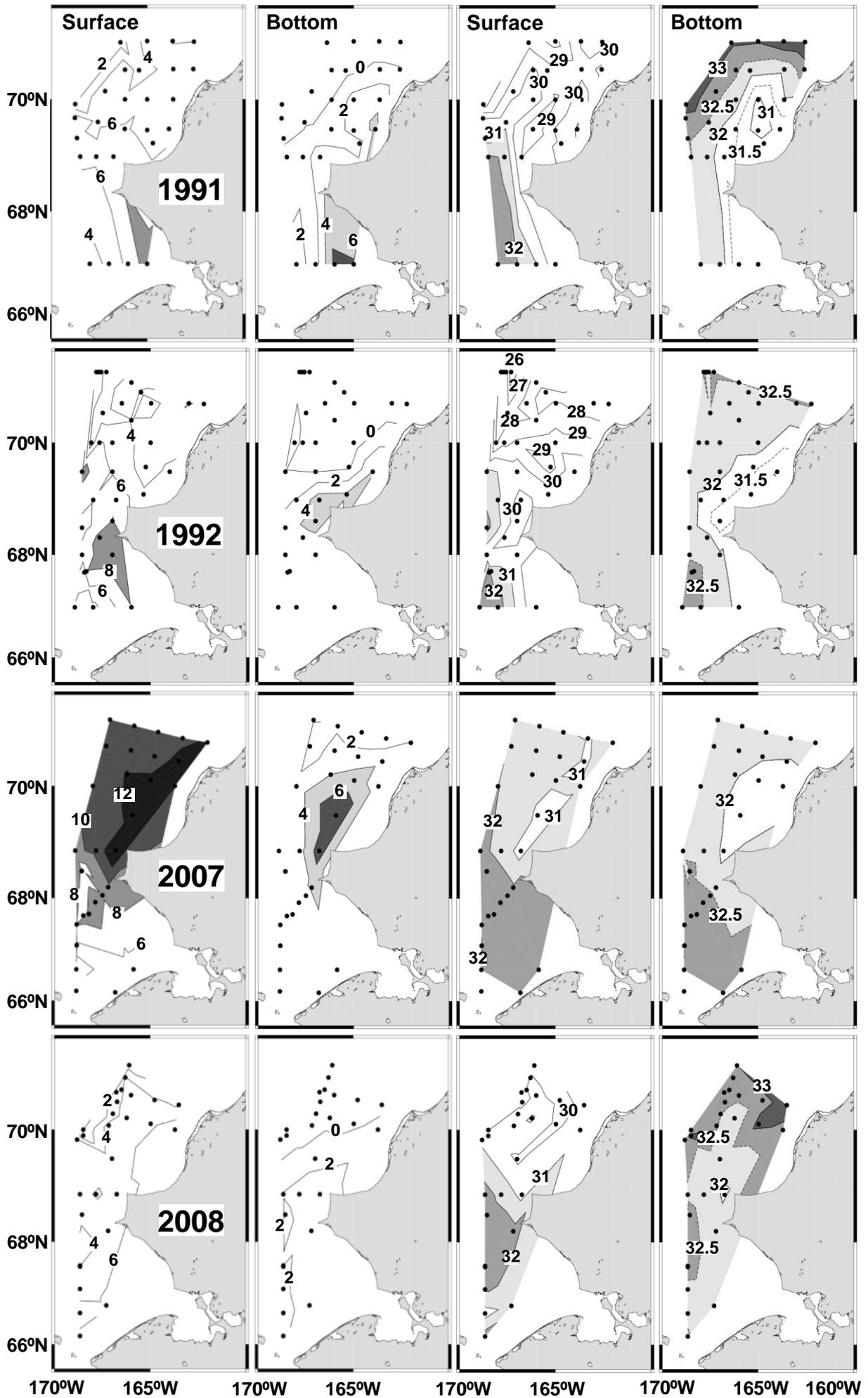


Figure 2 (Matsuno et al.)

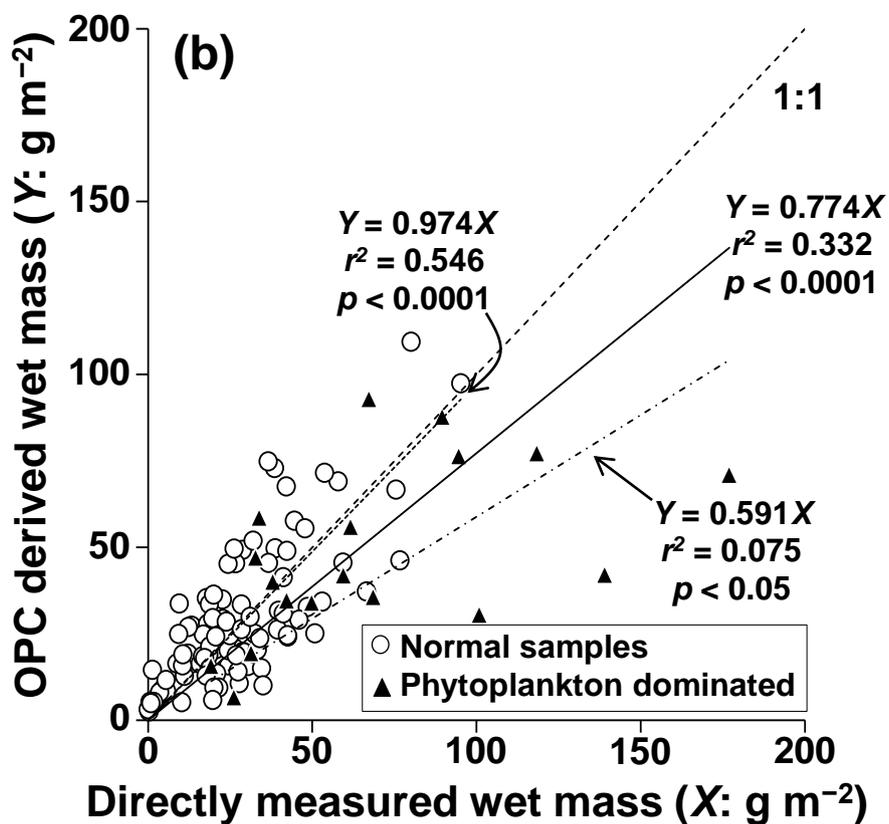
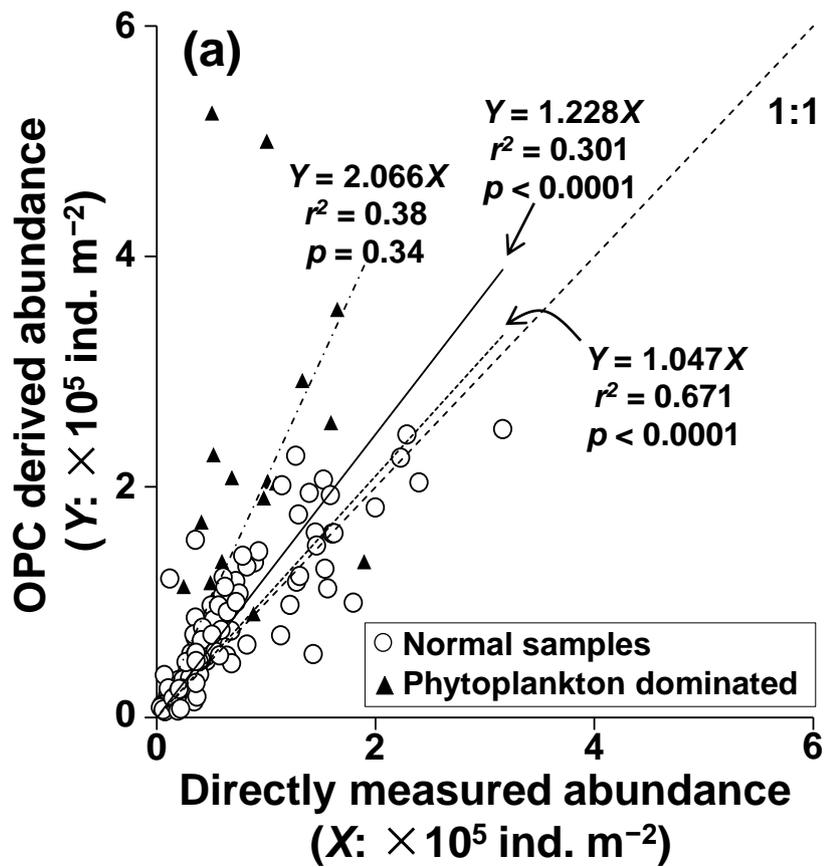


Figure 3 (Matsuno et al.)

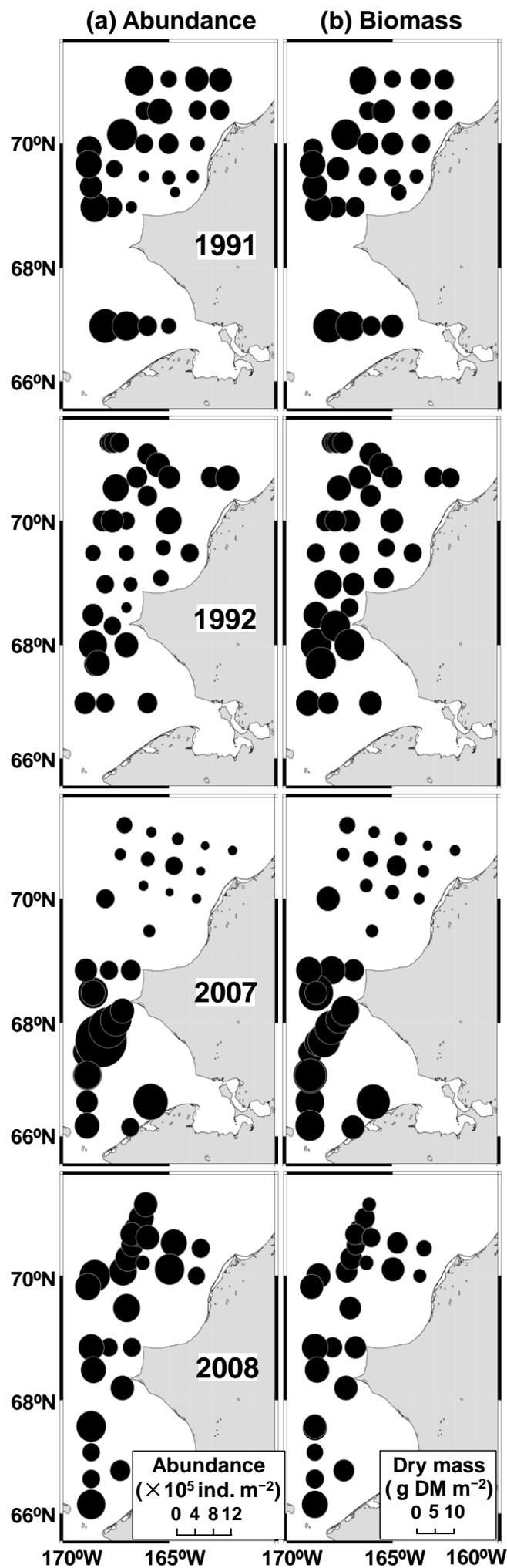


Figure 4 (Matsuno et al.)

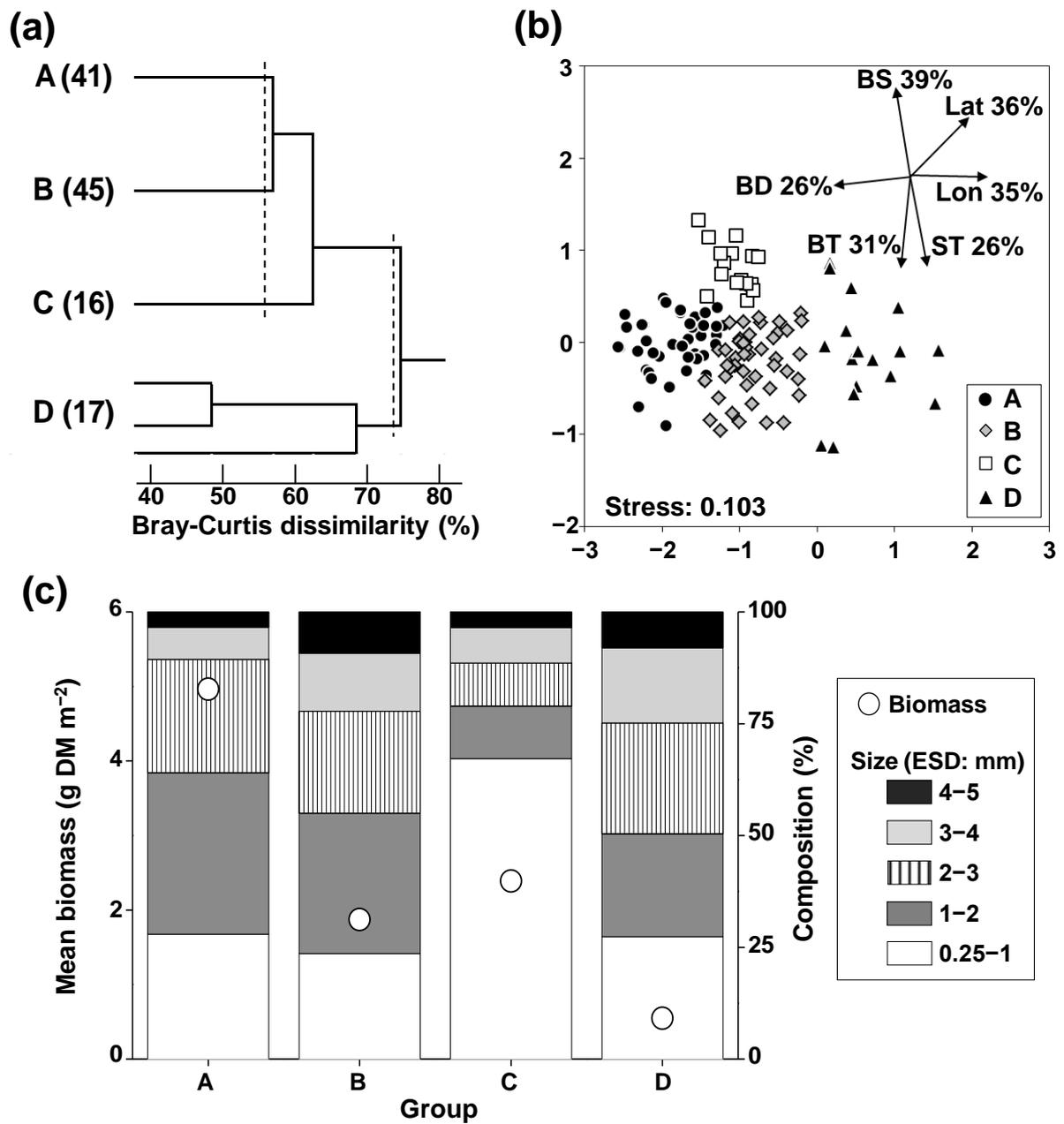


Figure 5 (Matsuno et al.)

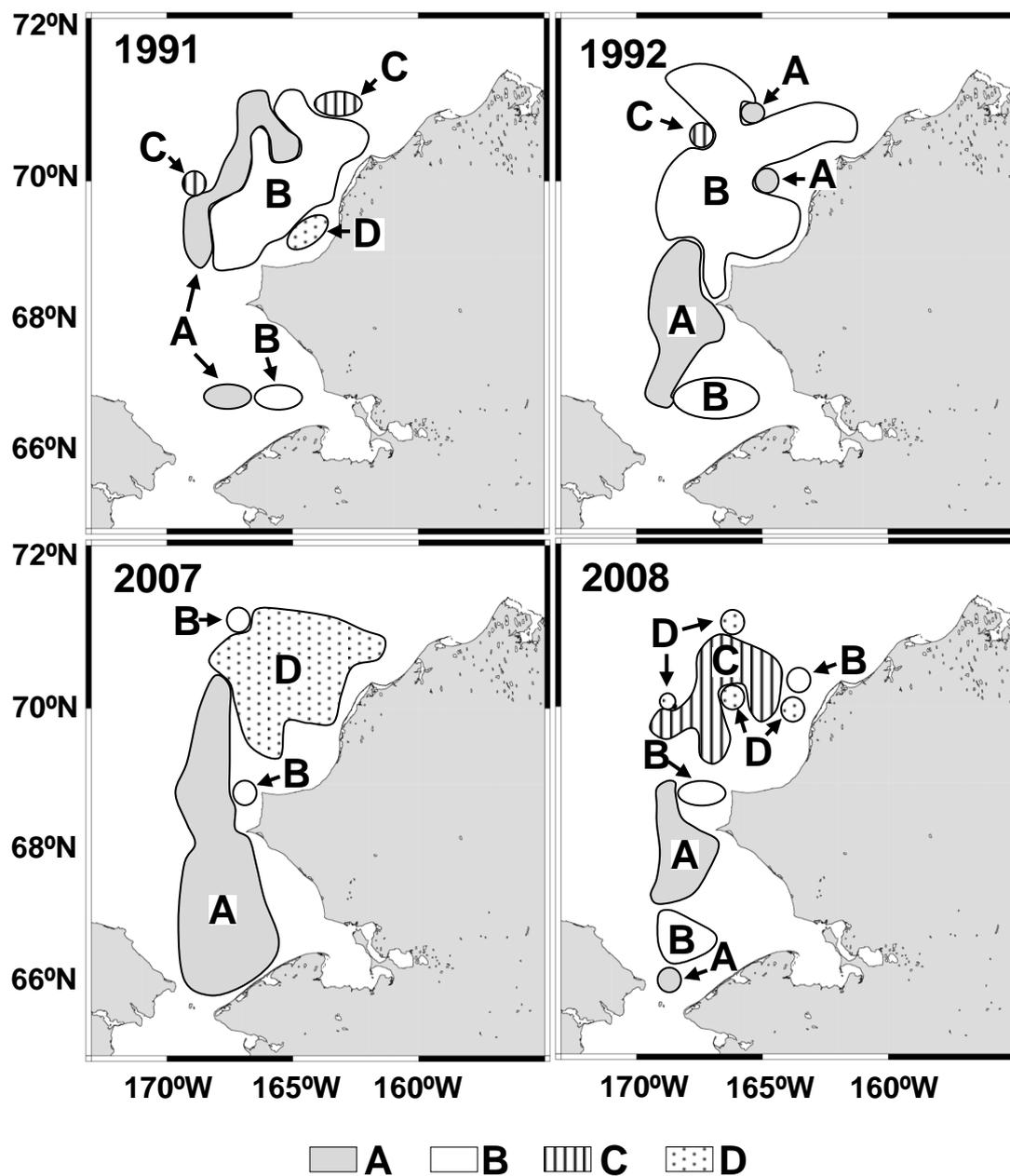


Figure 6 (Matsuno et al.)

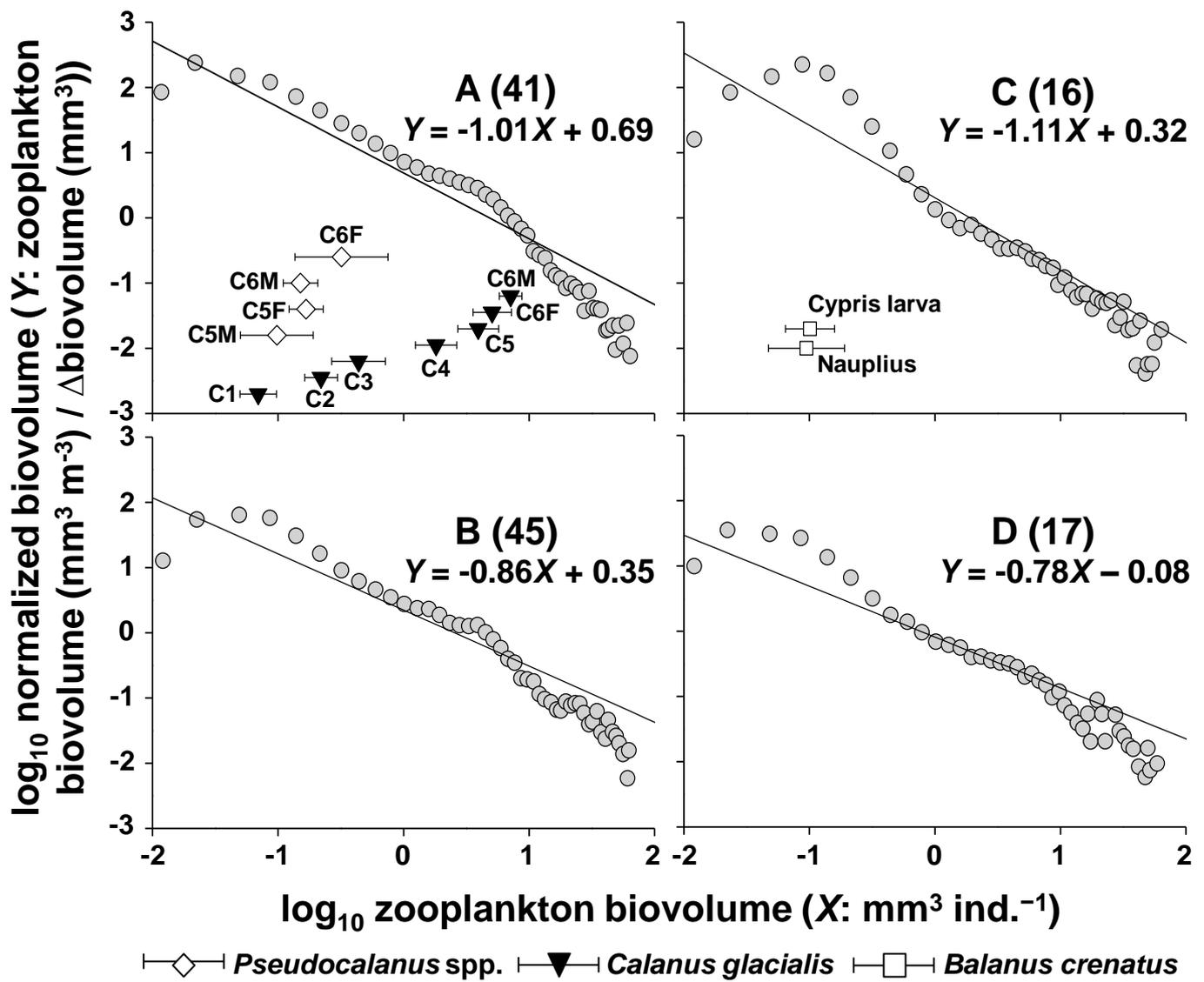


Figure 7 (Matsuno et al.)

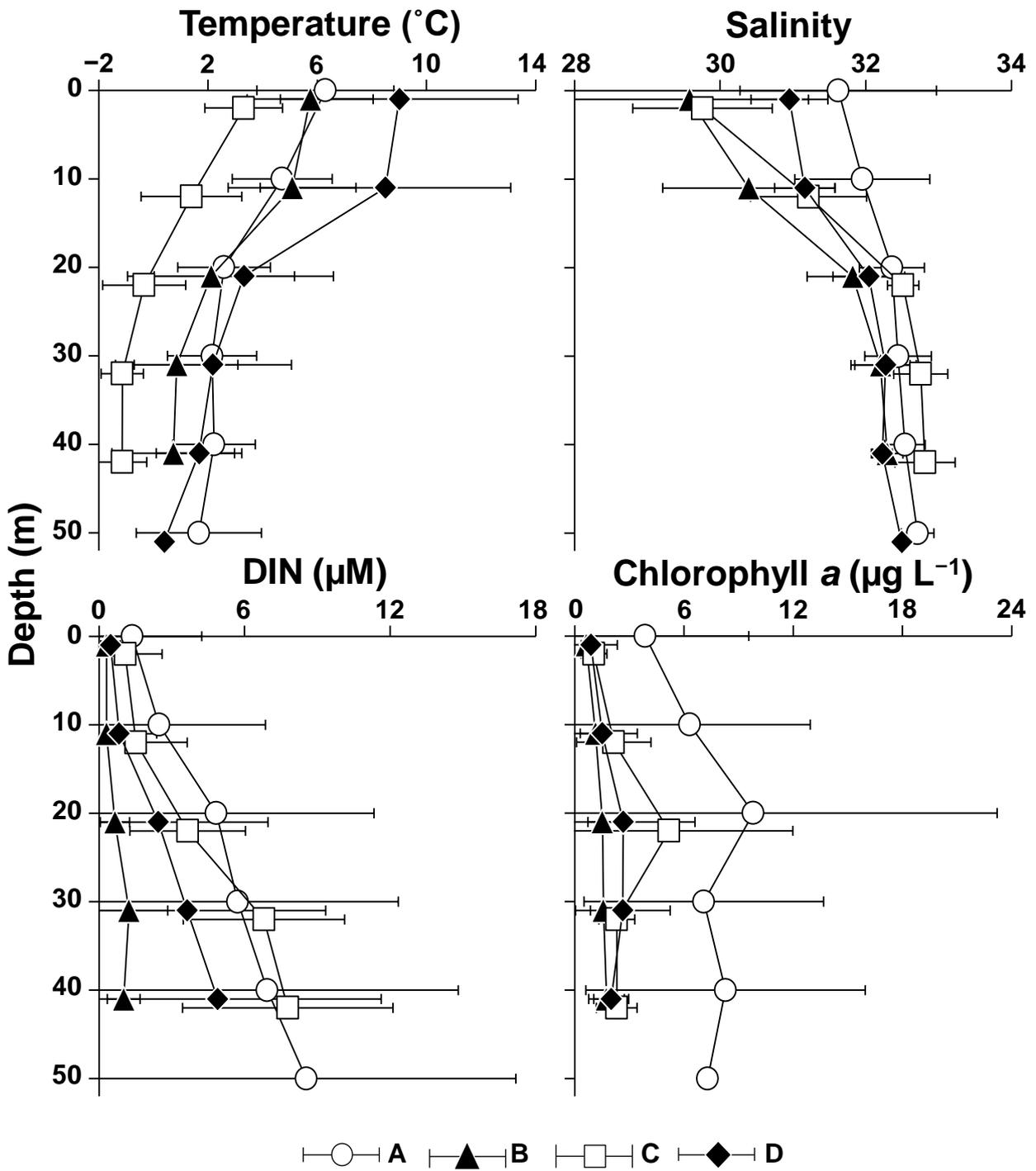


Figure 8 (Matsuno et al.)

Table 1. Comparison of zooplankton abundance, biomass and slope ( $a$ ) of NBSS ( $Y = aX + b$ ) at each group identified by Q-mode analysis (cf. Figure 5a) in the Chukchi Sea during July–August of 1991, 1992, 2007 and 2008. Differences between groups were tested by one-way ANOVA and post-hoc test by Fisher's PLSD. Any groups not connected by the underlines are significantly different ( $p < 0.05$ ). Values are mean  $\pm$  sd. Numbers in the parentheses indicate number of stations belonging to each group. \*\*\*:  $p < 0.0001$ .

Parameters	Groups				one-way ANOVA	Fisher's PLSD			
	A (41)	B (45)	C (16)	D (17)		D	B	C	A
Total abundance ( $\times 10^5$ ind. $m^{-2}$ )	1.94 $\pm$ 1.88	0.54 $\pm$ 0.23	1.52 $\pm$ 0.45	0.22 $\pm$ 0.26	***	D	B	C	A
Total biomass (g DM $m^{-2}$ )	4.96 $\pm$ 1.93	1.87 $\pm$ 0.49	2.39 $\pm$ 0.64	0.55 $\pm$ 0.18	***	D	B	C	A
Slope of NBSS ( $a$ )	-1.01 $\pm$ 0.12	-0.86 $\pm$ 0.11	-1.11 $\pm$ 0.08	-0.78 $\pm$ 0.20	***	C	A	B	D

Table 2. Comparison of zooplankton abundances in the four groups identified by Q-mode analysis (cf. Figure 5a) in the Chukchi Sea during July–August of 1991, 1992, 2007 and 2008. Values are mean abundance in each region. Differences between groups were tested by one-way ANOVA and post-hoc test by Fisher's PLSD. Any regions not connected by the underlines are significantly different ( $p < 0.05$ ). Numbers in the parentheses indicate number of stations included in each region. \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.0001$ , NS: not significant.

Species	Abundance (ind. m <sup>-2</sup> )				one-way ANOVA	Fisher's PLSD			
	A (41)	B (45)	C (16)	D (17)					
<i>Acartia hudsonica</i>	50	26	16	55	NS				
<i>Acartia longiremis</i>	333	161	169	290	NS				
<i>Acartia tumida</i>	24	2	0	0	NS				
<i>Calanus marshallae</i>	46	37	0	2	NS				
<i>Calanus glacialis</i>	3 426	2 954	1 032	1 093	*	C	D	<u>B</u>	A
<i>Centropages abdominalis</i>	5 245	91	17	226	**	C	B	<u>D</u>	A
Cyclopoida	1 542	439	196	306	**	C	D	<u>B</u>	A
<i>Eucalanus bungii</i>	4 029	725	23	227	***	C	D	<u>B</u>	A
<i>Eurytemora herdmani</i>	4	0	15	8	NS				
<i>Epilabidocera amphitrites</i>	0	2	0	3	NS				
<i>Gaidius brevispinus</i>	1	0	0	0	NS				
<i>Metridia pacifica</i>	3 851	648	45	55	*	C	D	<u>B</u>	A
<i>Microcalanus pygmaeus</i>	323	21	14	19	NS				
<i>Neocalanus cristatus</i>	36	13	4	30	NS				
<i>Neocalanus flemingeri</i>	83	49	15	11	NS				
<i>Neocalanus plumchrus</i>	210	114	64	123	NS				
<i>Pseudocalanus</i> spp. (C1–C4)	3 952	2 567	4 415	1 817	*	D	B	<u>A</u>	C
<i>Pseudocalanus acuspes</i>	2 923	1 296	1 147	929	**	D	C	<u>B</u>	A
<i>Pseudocalanus major</i>	1 184	307	309	238	NS				
<i>Pseudocalanus mimus</i>	668	449	415	340	NS				
<i>Pseudocalanus minutus</i>	3 151	1 972	2 214	1 060	NS				
<i>Pseudocalanus newmani</i>	5 022	1 724	1 426	2 001	**	C	B	<u>D</u>	A
<i>Scolecithricella minor</i>	59	6	0	38	NS				
<i>Tortanus discaudatus</i>	0	0	12	17	NS				
Amphipoda	33	0	0	0	NS				
Appendicularia	7 429	3 978	2 939	2 226	**	D	C	<u>B</u>	A
<i>Balanus crenatus</i> (nauplius and cypris larva)	34 160	26 419	96 070	24 698	***	D	B	<u>A</u>	C
Bivalvia larva	374	13	21	24	NS				
Chaetognatha	1 125	667	565	689	NS				
<i>Clione limacina</i>	50	40	2	11	NS				
Echinoidea larva	1 066	11	0	12	**		<u>B</u>	D	A
Eubrachyura zoea	125	75	116	73	NS				
Euphausiacea	2 566	769	107	1 110	NS				
<i>Evadne</i> spp.	146	33	0	4	NS				
Hydrozoa	2 347	603	284	1 294	NS				
Isopoda	40	55	190	3	**	D	<u>A</u>	B	C
<i>Limacina helicina</i>	65	135	74	40	NS				
Polychaeta	5 362	1 657	2 644	839	*	D	B	<u>C</u>	A
Total copepods	36 158	13 603	11 549	8 888	***	D	C	<u>B</u>	A
Total zooplankton	91 046	48 059	114 561	39 911	***	D	B	<u>A</u>	C

Table 3. Result on analysis of covariance (ANCOVA) for slope ( $a$ ) of NBSS ( $Y = aX + b$ ). As independent variables, intercept ( $b$ ) of NBSS and zooplankton group (cf. Figure 5a) were applied. df: degree of freedom, SS: sum of squares. \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , NS: not significant.

Parameter	df	SS	F-value	$p$
Intercept	1	0.120	8.841	**
Group	3	0.140	3.440	*
Group×Intercept	3	0.018	0.451	NS
Error	111	1.510		

Table 4. Comparison on the slope ( $a$ ) of NBSS ( $Y = aX + b$ ) on mesozooplankton community from various locations. Numbers in the parentheses indicate range of slope.

Location/Region	Unit	Size range (mm)	Slope	References
Gulf of St. Lawrence (Open Water)	Biovolume	0.25–2	–0.47	Herman and Harvey (2006)
Barents Srea	Biovolume	0.25–14	–0.63 (–0.44 ~ –0.91)	Basedow <i>et al.</i> (2010)
Tasman Sea	Biovolume	0.11–3.3	–0.69 (–0.59 ~ –0.78)	Baird <i>et al.</i> (2008)
Gulf of St. Lawrence (Estuary)	Biovolume	0.25–2	–0.90	Herman and Harvey (2006)
Coral Sea	Biovolume	0.11–3.3	–0.97 (–0.94 ~ –0.99)	Baird <i>et al.</i> (2008)
South West Coral Sea	Wet mass	0.25–2.5	–1.00 (–0.49 ~ –1.31)	Suthers <i>et al.</i> (2006)
North Iberian Shelf	Carbon	0.25–17	–1.11 (–0.90 ~ –1.21)	Nogueira <i>et al.</i> (2004)
North Pacific Ocean	Carbon	0.18–4.0	–1.13	Rodriguez and Mullin (1986)
Northwest Atlantic Ocean	Carbon	0.07–8.0	–1.14 (–1.09 ~ –1.17)	Quinones <i>et al.</i> (2003)
California Current	Carbon	0.2–3.3	–1.43 (–0.53 ~ –1.96)	Huntley <i>et al.</i> (1995)
Australian Estuary	Wet mass	0.25–1.6	–1.89 (–0.72 ~ –3.06)	Moore and Suthers (2006)
California Bright	Biovolume	0.025–4.0	–2.30	Napp <i>et al.</i> (1993)
Chukchi Sea (A: south in all years)	Biovolume	0.25–5	–1.01 (–0.69 ~ –1.24)	This study
Chukchi Sea (B: north in 1991/1992)	Biovolume	0.25–5	–0.86 (–0.59 ~ –1.09)	This study
Chukchi Sea (C: north in 2008)	Biovolume	0.25–5	–1.11 (–1.00 ~ –1.30)	This study
Chukchi Sea (D: north in 2007)	Biovolume	0.25–5	–0.78 (–0.48 ~ –1.27)	This study