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

Kohei Matsuno*, Atsushi Yamaguchi, and Ichiro Imai

Laboratory of Marine Biology, Graduate School of Fisheries Science, Hokkaido University, 3 1 1 Minatomachi, Hakodate, Hokkaido 041 8611, Japan

Corresponding author: tel: +81 138 405543; fax: +81 138 405542; e-mail: k.matsuno@fish.hokudai.ac.jp.

An optical plankton counter was used to examine the regional characteristics of the zooplankton communities in the Chukchi Sea during the 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 zooplankton biovolume in equivalent spherical diameter (ESD) in 48 bins, one every 0.1 mm between 0.25 and 5.0 mm, a Bray–Curtis cluster analysis classified zooplankton communities into four groups (A–D). No changes were observed in zooplankton communities south of the Lisburne Peninsula (group A) throughout the 4 years, but there were differences north of the Peninsula, with group B (normal, intermediate biomass) observed in 1991/1992, group D (low biomass) in 2007, and group C (predominance of barnacle larvae) in 2008. Analysis of the normalized biomass size spectra for the groups indicated that groups A and C were very productive, so the zooplankton community south of the Lisburne Peninsula was consistently highly productive, which may be because of the continuous inflow of Pacific Water rich in nutrients. Zooplankton communities north of the Lisburne Peninsula varied greatly from year to year, which may be related to interannual changes in sea-ice extent.

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 consists mainly of a shallow shelf (depth <50 m), and recent observations show it to have demonstrated the most dramatic reduction in sea ice anywhere within the Arctic Ocean (Shimada *et al.*, 2001, 2006). It is believed that the reduction in sea ice in the Chukchi Sea is attributable to the increased inflow of warm Pacific Water passing through the Bering Strait (Shimada *et al.*, 2006). Based on satellite observations from 1991 to 2007, both the volume and the temperature of the Pacific Water that passed through the Bering Strait were highest in 2007 when the sea-ice extent was least (Woodgate *et al.*, 2010). Sea surface temperature (SST) in the Chukchi Sea is normally 4–6°C, yet it reached 12°C in 2007 (Vanin, 2010). This anomalously high temperature is considered to be the combined effect of early sea-ice retreat (Markus *et al.*, 2009) and intense solar heating (Mizobata *et al.*, 2010; Vanin, 2010). Such recent and drastic changes in the hydrography of the region are considered to have a great effect on the marine ecosystem, especially the plankton community (Grebmeier *et al.*, 2006; Hunt and Drinkwater, 2007).

Zooplankton are important secondary producers in the marine ecosystem and a vital link between phytoplankton and fish or marine mammals (Lowry *et al.*, 2004; Wassmann *et al.*, 2006). The southern Chukchi Sea is reported to have high primary production enhanced by the inflow of Pacific Water rich in nutrients (Sambrotto *et al.*, 1984; Springer and McRoy, 1993). As Pacific Water also transports zooplankton inhabiting the Bering Sea, its inflow strongly influences the spatial distribution of zooplankton biomass and species composition in the Chukchi Sea (Springer *et al.*, 1989; Hopcroft *et al.*, 2010; Matsuno *et al.*, 2011). The zooplankton community of 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), and there have been reports too of an occasional outbreak of small barnacle larvae (*Balanus crenatus*) after phytoplankton blooms (Barnes, 1957; Crisp, 1962).

The zooplankton size spectrum can aid evaluation of marine ecosystem structure (Sheldon *et al.*, 1972; Kerr, 1974), and provide information on growth rates and metabolic activity of the zooplankton (Platt and Denman, 1977, 1978). Although important, size measurements on zooplankton by microscopic observation are time-consuming, and it is difficult to obtain accurate measurements manually. To overcome these problems, Herman (1988) developed an optical plankton counter (OPC) that measures zooplankton size and number quickly and accurately, and it has been applied in various marine ecosystems (Herman, 1992; Huntley *et al.*, 1995; Nogueira *et al.*, 2004; Baird *et al.*, 2008). Normalized biomass size spectra (NBSS) analysis (Platt and Denman, 1978) of zooplankton size-spectrum data from OPC measurements has been used to evaluate the marine ecosystem structure from many locations around the world (e.g. Nogueira *et al.*, 2004; Herman and Harvey, 2006; Basedow *et al.*, 2010). NBSS analysis can be used to evaluate whether bottom-up or top-down controls are dominant in marine ecosystems (Moore and Suthers, 2006; Suthers *et al.*, 2006; Finlay *et al.*, 2007). Despite their importance, few studies have been made on zooplankton size spectra in the Chukchi region, so to fill this gap, we combined OPC measurements and NBSS analyses to evaluate the zooplankton characteristics in the Chukchi Sea.

OPC analysis was carried out on preserved zooplankton samples collected in the Chukchi Sea during the summers of 1991/1992 (when sea-ice coverage was relatively broad) and 2007/2008 (when the sea ice was much 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 equivalent spherical diameter (ESD). The NBSS analysis was performed on each clustered group to evaluate summer zooplankton productivity in the Chukchi Sea and the results in terms of ecosystem characteristics were compared with those for other oceanic regions.

Material and methods

A total of 119 zooplankton stations was occupied by the TS "Oshoro-Maru" in the Chukchi Sea ($66°00'-71°11'$N $162°02'-168°58'$W; Figure 1) during 24–31 July 1991 ($n = 27$), 24–31 July 1992 ($n = 33$), 5–13 August 2007 ($n = 31$), and 7–13 July 2008 ($n = 28$). Samples were collected by day or night by vertical tows with a NORPAC net (mouth diameter 45 cm, mesh size 0.335 mm) from 5 m above the seabed (the depths of most stations were ~50 m). The volume of water filtered through the net was estimated by a flowmeter (Rigosha Co. Ltd) mounted on the net ring. The volume of water filtered through the net ranged from 2.1 to 10.1 m^3 (mean $\pm$ s.d.: 5.5 $\pm$ 1.6 m^3). This large range of filtered volume was caused by the differences in net towing depth (25–63 m, mean 45 m), which was influenced by the bottom depth at each station. Once on board, samples were preserved immediately in 5% v/v borax buffered formalin. At each station, temperature and salinity were measured by a conductivity–temperature–depth probe (Neil Brown, Mark 3B in 1991 and 1992, and Sea-Bird Electronics Inc. SBE 911 Plus in 2007 and 2008). These hydrographic data are published elsewhere (Hokkaido University, 1992, 1993, 2008, 2009).

OPC analysis

In the laboratory on land, 1/2–1/8 aliquots of the zooplankton samples, obtained with a Motoda box splitter (Motoda, 1959), were used for the OPC measurements (OPC-1L: Focal Technologies Corp.). The OPC measures the number of particles within 4096 size categories between 0.250 and 20 mm ESD with a precision of 0.001–0.021 mm. As we collected samples by vertical hauls of a NORPAC net, large plankton such as giant jellyfish (Brodeur *et al.*, 2008) or euphausiids (Ashjian *et al.*, 2010) were not collected quantitatively. Because of this, only data on meso-zooplankton in the size range 0.25–5.0 mm ESD from the OPC analysis were used. To evaluate accurate size and number, the measurements were made using adequate flow rate (10 l min^{-1}) and particle density (<10 counts s^{-1}), according to the procedures of Mullin *et al.* (2000) and Yokoi *et al.* (2008). In addition to whole sample measurements, OPC measurements were conducted on individual copepodid stages of the dominant copepods (*C. glacialis* and *Pseudocalanus* spp.) and the barnacle larvae (*B. crenatus*) taken from the samples.

Abundance and biomass

Abundance per square meter (N, ind. m^{-2}) at each ESD size category was calculated from the equation $N = (nD)/(sF)$, where n is the number of particles (=zooplankton individual), s the split factor of each sample, F the filtered volume of the net (m^3), and D the net-towed depth (m).

Zooplankton wet mass (WM) for 4096 size categories was calculated from the ESD data by assuming the relative density of zooplankton to be equal to that of seawater (1 mg mm^{-3}). WM was converted to dry mass (DM) assuming that the water content of zooplankton was 90% (DM = 0.1 × WM), as shown by Matsuno *et al.* (2009). For comparison with OPC-derived biomass, direct WM measurements were made for 1/2 aliquots of all samples. Samples were filtered on preweighed 100 μm mesh, and weighed with a precision of 10 mg. During these WM measurements, samples dominated by phytoplankton were noted (19 out of 119 samples).

As zooplankton sampling was conducted during July–August (the Arctic summer), daytime sampling accounted for 91% of all sampling stations (Figure 1). Day–night comparisons of zooplankton abundance and biomass also showed no significant differences (*U*-test, $p = 0.15$–0.39), so no day–night conversion for abundance or biomass was made.

Cluster analysis

To evaluate spatial and temporal changes in zooplankton biovolume size spectra, cluster analysis was applied. Before the analysis, biovolume data on 1761 categories between 0.25 and 5.0 mm ESD were binned into 48 size classes at 0.1 mm ESD intervals (0.25–0.30, 0.30–0.40, ..., 4.90–5.00 mm). Based on these biovolume data, similarities between the samples were evaluated by Bray–Curtis methods (Bray and Curtis, 1957). To group 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). Non-metric multidimensional scaling (NMDS) ordination was carried out to delineate the sample groups on a two-dimensional map. All these analyses were carried out using BIOSTAT II software (Sigma Soft).
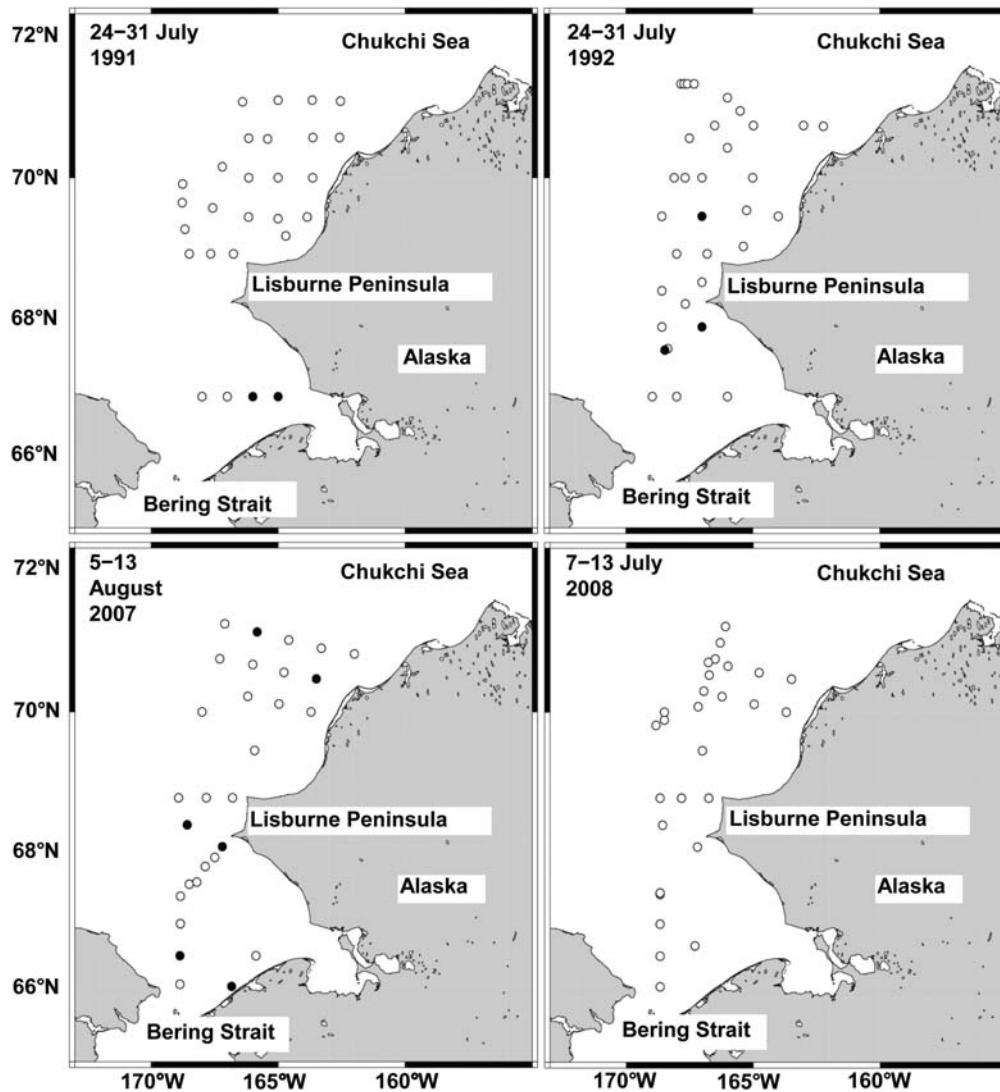
Figure 1. Location of the sampling stations in the Chukchi Sea during July/August of 1991, 1992, 2007, and 2008. Open and solid symbols denote stations where sampling was conducted by day and by night, respectively.

To clarify which environmental parameters (latitude, longitude, depth, SST, salinity, bottom temperature, salinity) had significant relationships with the zooplankton groupings, multiple regressions ($y = ax_1 + bx_2 + c$, where y is the environmental variable and x_1 and x_2 are axes 1 and 2 of NMDS, respectively) were made using StatView (SAS Institute Inc.).

Normalized biomass size spectra

Based on the OPC data, the NBSS was calculated following the procedure of Suthers *et al.* (2006). Zooplankton biovolume (B, $mm^3\, m^{-3}$) was calculated in each of the 48 size classes. To calculate the x-axis of the NBSS [$\log_{10}$ zooplankton biovolume ($mm^3\, ind.^{-1}$)], B was divided by the abundance of each size class (ind. m^{-3}) and converted to $\log_{10}$. To calculate the y-axis of the NBSS [$\log_{10}$ normalized biovolume ($mm^3\, m^{-3}$)/Δbiovolume (mm^3)], B was divided by the biovolume interval between consecutive size classes [Δbiovolume (mm^3)] and converted to $\log_{10}$. Based on these data, an NBSS linear model was

calculated (Platt and Denman, 1978): $y = ax + b$, where a and b are the slope and the intercept of NBSS, respectively.

Statistical analysis

Based on the zooplankton groups clustered based on their size spectra, inter-group differences in hydrography (SST, surface salinity, bottom temperature, bottom salinity) and zooplankton data (abundance, biomass, and slope of NBSS) were tested using one-way analysis of variance (ANOVA) and Fisher's protected least-squares difference (PLSD) method. To evaluate the abundant zooplankton species in each group, taxonomic data on the same samples (Matsuno *et al.*, 2011) were also used for analyses using one-way ANOVA and Fisher's PLSD. To clarify the factors that governed the slope of the NBSS, an analysis of covariance (ANCOVA) was conducted using Statview, with the intercept of the NBSS and zooplankton group as independent variables.
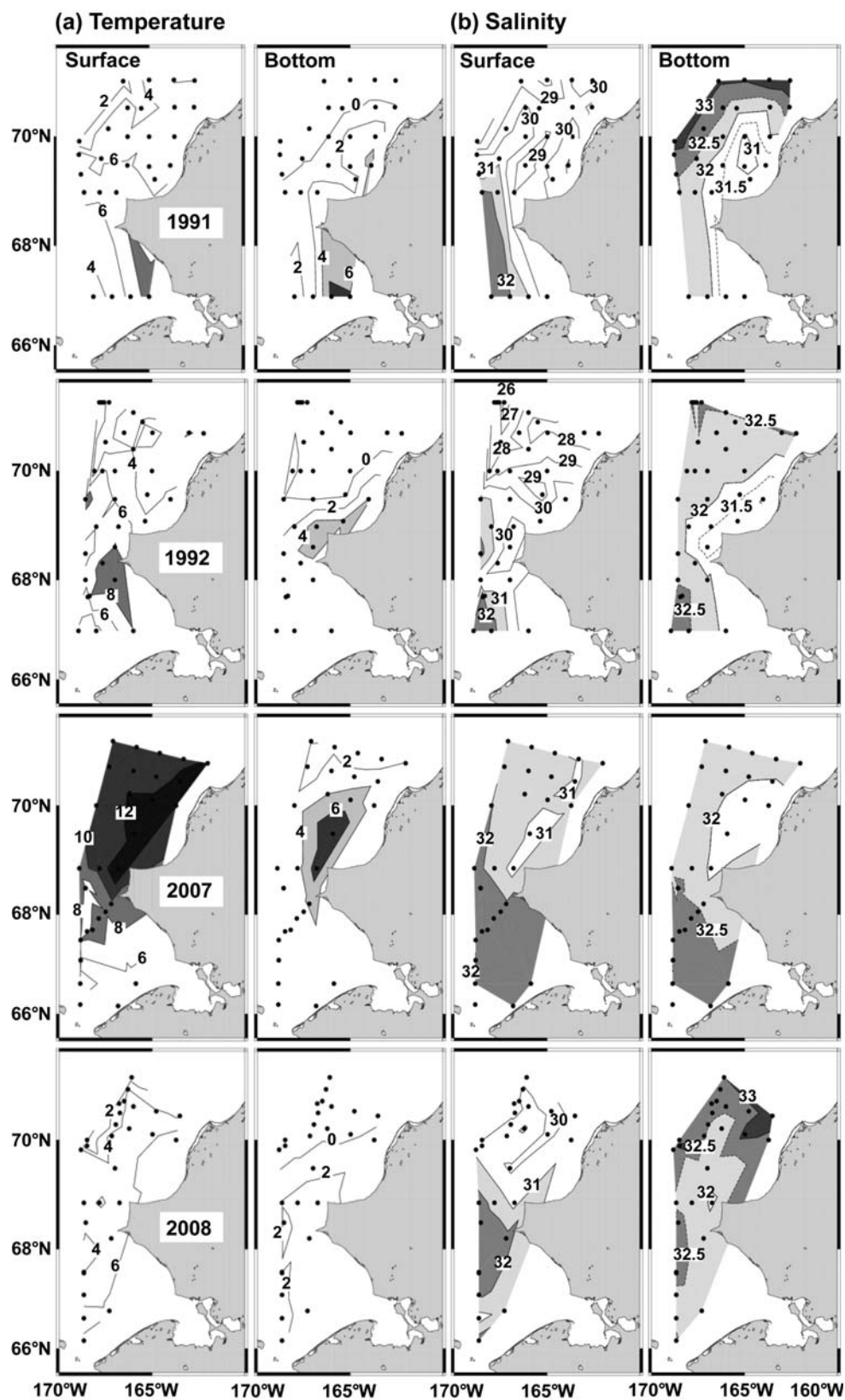
Figure 2. (a) Temperature and (b) salinity at the sea surface (left of each pair of columns) and the bottom (right of each pair of columns) of stations in the Chukchi Sea during July/August of 1991, 1992, 2007, and 2008.
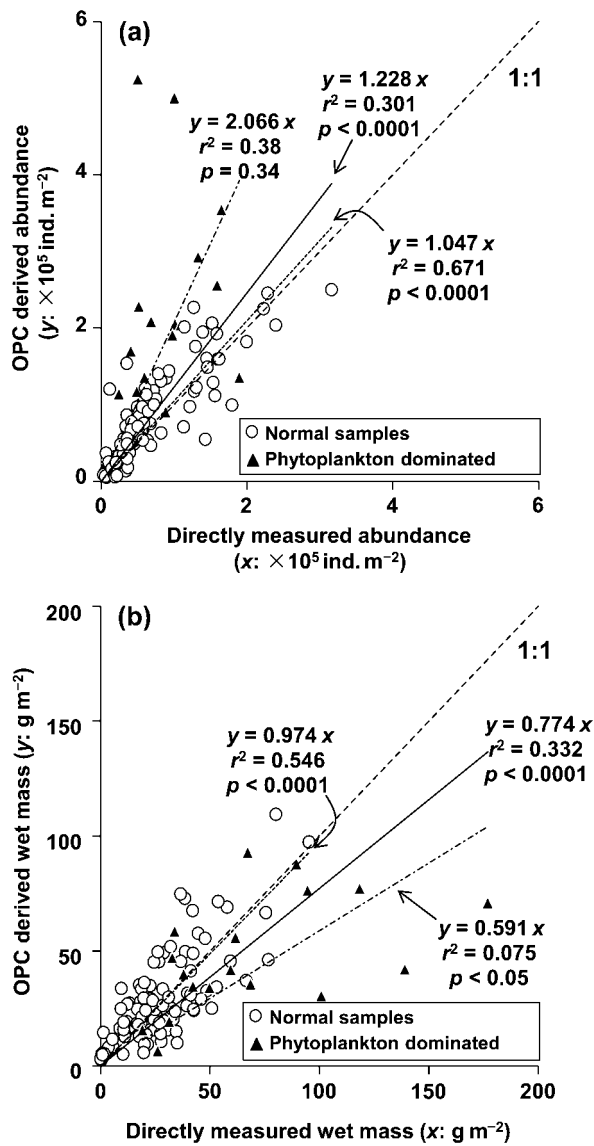
Figure 3. Comparison between OPC-measured (*y*) and directly measured data (*x*) in terms of (a) abundance and (b) WM. Solid, short-dashed, and dashed-dotted lines indicate the regressions on whole samples, normal samples (open circles), and phytoplankton-dominated samples (solid triangles), respectively. Long-dashed lines indicate positions of 1:1.

Results

Hydrography

SST and bottom temperature ranged from -0.9 to $14.0°C$ and -1.7 to $8.0°C$, respectively (Figure 2a). The SST values in 2007 were $3.9-14.0°C$ (mean $9.7°C$), and were significantly higher than in the other 3 years (-0.9 to $9.6°C$, mean $4.8°C$; one-way ANOVA, $p < 0.0001$). In 2007, differences in temperature between the sea surface and the bottom (surface–bottom values) were significantly higher, especially north of the Lisburne Peninsula ($4.4-11.0°C$, mean $8.7°C$), than those in the other years ($0.1-8.6°C$, mean $4.1°C$; one-way ANOVA, $p < 0.0001$).
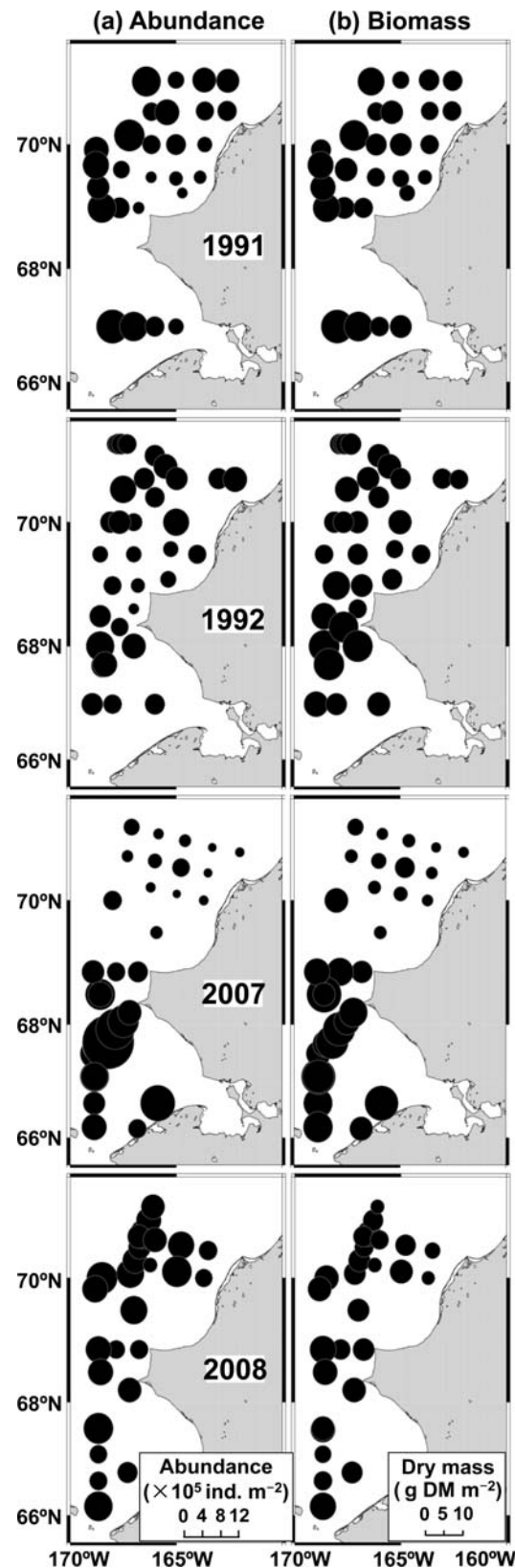

Figure 4. Horizontal distribution of (a) abundance and (b) biomass of mesozooplankton in the Chukchi Sea during July/August of 1991, 1992, 2007, and 2008, analysed by OPC.
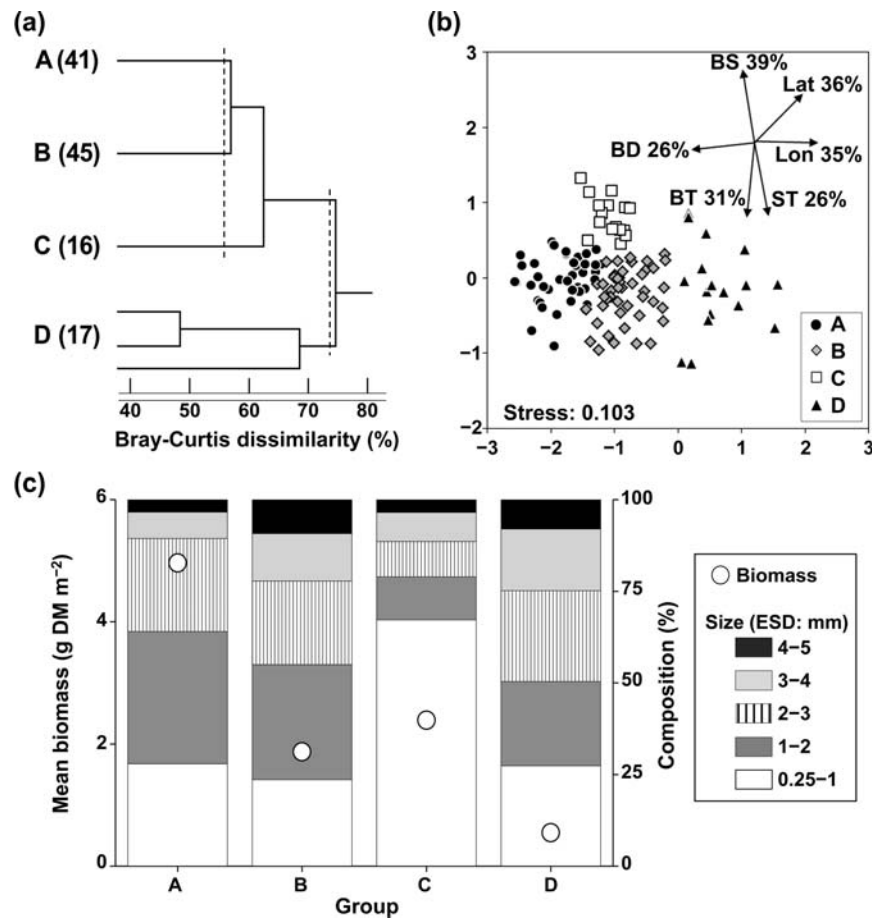
Figure 5. (a) Results of cluster analysis based on mesozooplankton biovolume size spectra in the Chukchi Sea. Four groups (A–D) were identified at 55 and 73% Bray–Curtis dissimilarity connected with UPGMA. Numbers in parenthesis indicate the number of stations each group contained. (b) NMDS plots of each group. Arrows and percentages indicate directions of environmental parameters and coefficients of determination (r^2), respectively. BD, bottom depth; BS, bottom salinity; BT, bottom temperature; Lat, latitude; Lon, longitude; ST: surface temperature. (c) Mean biomass and size composition (ESD, mm) of each group.

Table 1. Comparison of zooplankton abundance, biomass, and slope (*a*) of NBSS ($y = ax + b$) of each group identified by Q-mode analysis (cf. Figure 5a) in the Chukchi Sea during July/August of 1991, 1992, 2007, and 2008.

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

Differences between the 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 ± s.d. Numbers in parenthesis are the number of stations belonging to each group.
***$p < 0.0001$.

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 in the other 3 years (one-way ANOVA, $p < 0.0001$). There was no interannual variability in bottom salinity (Figure 2b).

Characteristics of OPC measurements

Comparisons of abundance (ind. m^{-2}) and WM (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
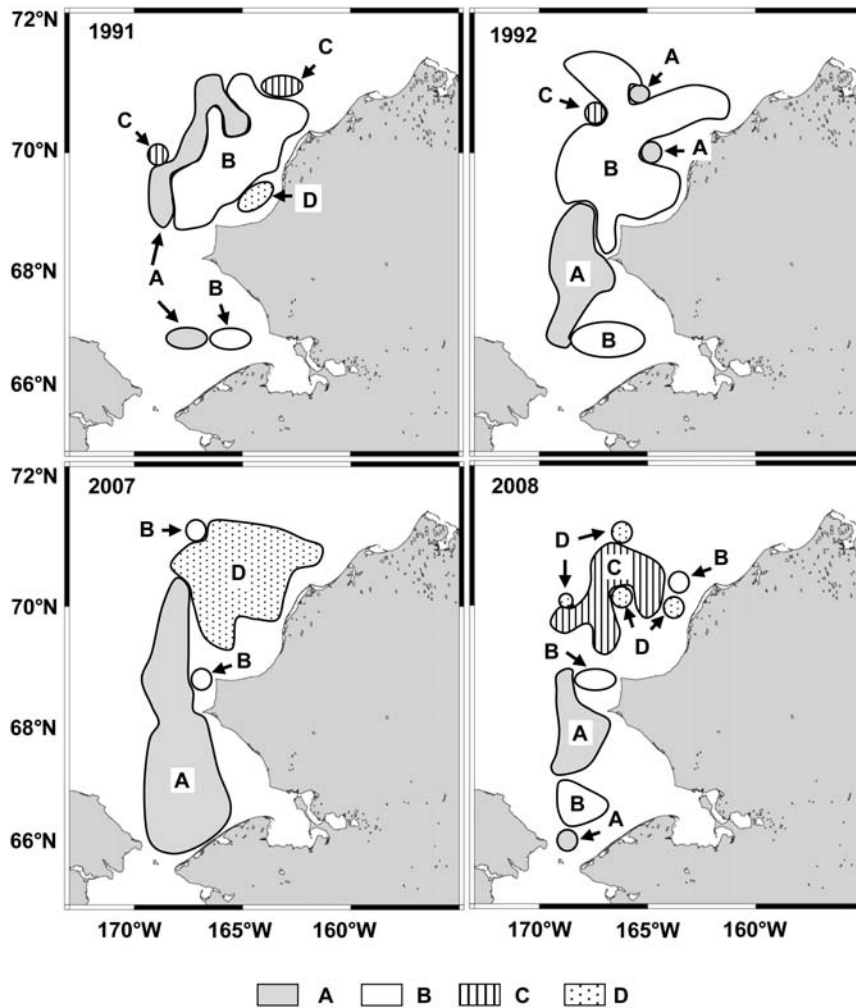
Figure 6. Horizontal distributions of each group identified from cluster analysis on mesozooplankton biovolume size spectra (cf. Figure 5a) in the Chukchi Sea during July/August of 1991, 1992, 2007, and 2008.

underestimated zooplankton biomass (Figure 3b). As 19 samples were dominated by phytoplankton, elimination of those data ($n = 100$, normal sample) provided substantial matches between OPC-derived and directly measured data (slope 0.974–1.047; Figure 3).

Zooplankton abundance, biomass, and community

Zooplankton abundance ranged from 5000 to 1 171 000 ind. m^{-2} (mean 111 002). There was little regional difference in abundance between 1991, 1992, and 2008, but abundance was less north of the Lisburne Peninsula in 2007 relative to the south (Figure 4a). Zooplankton biomass ranged from 0.2 to 10.9 g DM m^{-2} (mean 3.1; Figure 4b). Similar to abundance, biomass changed little regionally in 1991, 1992, and 2008, but it was lower north of the Peninsula in 2007 (Figure 4b).

Based on the biovolume in the 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 variables showing significant relationships on the NMDS ordination were latitude, longitude,

depth, SST, bottom temperature, and bottom salinity (Figure 5b). The mean abundances were higher for groups A and C (152 000–194 000 ind. m^{-2}) than for groups B and D (22 000–54 000 ind. m^{-2}; Table 1). The mean biomass also had a similar pattern, higher for group A (4.96 g DM m^{-2}) than for group D (0.55 g DM m^{-2}; Table 1). In terms of size composition, the dominance of the smallest size class (0.25–1 mm) in group C was marked (Figure 5c).

The distribution and occurrence of each zooplankton group had clear spatial and interannual patterns (Figure 6). South of the Lisburne Peninsula, group A dominated throughout the study period, but north of the Peninsula, dominant groups varied by year: group B in 1991 and 1992, group D in 2007, group C in 2008 (Figure 6).

The dominant taxa differed by the group. Various copepods (*C. glacialis*, *Centropages abdominalis*, Cyclopoida, *E. bungii*, *M. pacifica*, *Pseudocalanus acuspes*, *Pseudocalanus newmani*), Appendicularia, Echinoidea larvae, and Polychaeta were abundant in group A (Table 2). There was no species showing especially high abundance in group B. Group C was characterized by a few large

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.

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

Values are mean abundance in each region. Differences between the 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 ($p < 0.05$). The numbers in parenthesis indicate the number of stations included in each region. N.S., not significant.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.0001$.

copepods and many barnacle larvae (*B. crenatus*). Group D was characterized by the low abundance of the juvenile stages (C1– C4) of *Pseudocalanus* spp. (Table 2).

Normalized biomass size spectra

The ANCOVA revealed significant relationships: between the NBSS slope and both the intercept ($p < 0.01$) and the group ($p < 0.05$), although the interaction of group and intercept had no significant relationship with slope (Table 3). The slope of the NBSS for each group ranged from -0.78 to -1.11 (Table 1). Results of the mean NBSS for each group are shown in Figure 7. Significant inter-group differences were observed in the slopes of the NBSS (Table 1), with C > A > B > D (Table 1).

Table 3. Result of the ANCOVA for the slope (*a*) of NBSS ($y = ax + b$), with the intercepts (*b*) of NBSS and zooplankton group (cf. Figure 5a) applied as independent variables.

Parameter	d.f.	SS	F-value	p-value
Intercept	1	0.120	8.841	*
Group	3	0.140	3.440	**
Group × intercept	3	0.018	0.451	N.S.
Error	111	1.510	–	–

d.f., degrees of freedom; SS, sum of squares.
N.S., not significant.
*$p < 0.01$.
**$p < 0.05$.

Discussion

Abundance, biomass, and NBSS

As is characteristic of the OPC measurement method, abundance was overestimated for the samples dominated by phytoplankton (Figure 3a). This overestimation is most likely caused by the OPC detection of large chain-forming diatoms. Because of the presence of the phytoplankton, the zooplankton abundance estimates obtained using the OPC method may be higher than that obtained by microscopic observation (Herman, 1992; Herman and Harvey, 2006). Interestingly, the reverse pattern (underestimation) was the case for biomass in the phytoplankton-dominated samples (Figure 3b). Biomass calculated by direct measurement inevitably includes phytoplankton debris in the phytoplankton-dominant samples. As OPC detects particles of much larger sizes (>250 μm), that method's biomass estimates may be lower than the values obtained by direct measurement (Matsuno *et al.*, 2009).

Although 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 remaining samples (normal, $n = 100$), in terms of both abundance and biomass (Figure 3). These facts suggest that the OPC analysis is an adequate method for estimating zooplankton abundance and biomass in the region.

NBSS analysis, based on zooplankton biovolume size spectra, has been applied to evaluate marine ecosystem structure worldwide (Herman and Harvey, 2006; Baird *et al.*, 2008; Basedow *et al.*, 2010). The slope of NBSS is an important index in evaluating marine ecosystem structure and its productivity (Rodriguez and
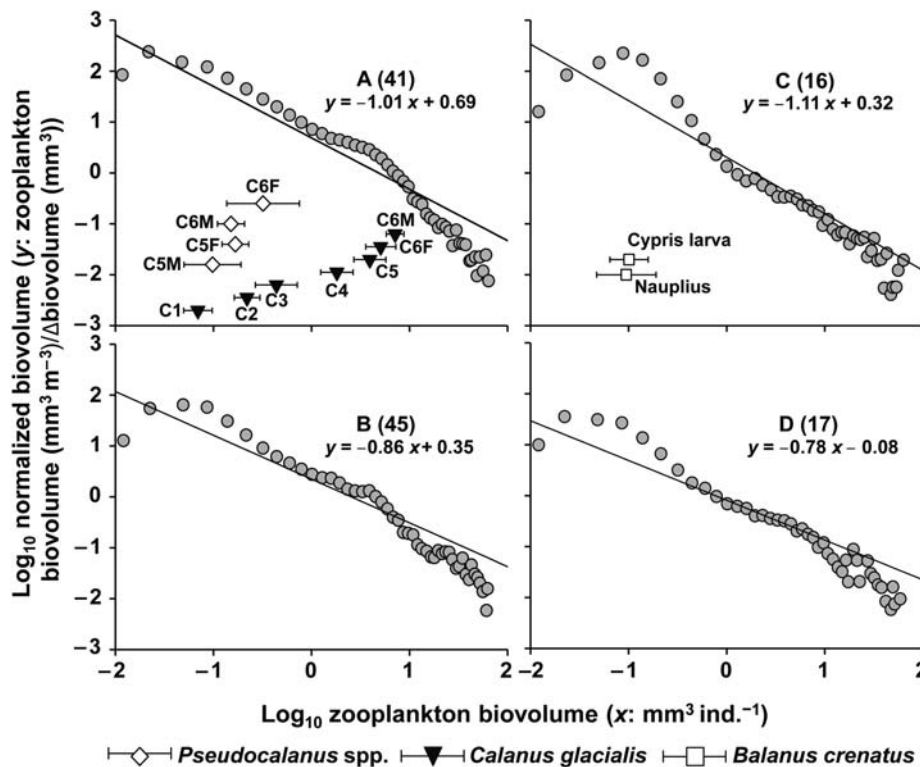
Figure 7. Mean NBSS of four groups identified from cluster analysis on mesozooplankton biovolume size spectra (cf. Figure 5a) in the Chukchi Sea during July/August of 1991, 1992, 2007, and 2008. Numbers in parenthesis indicate the number of stations belonging to each group. For the dominant zooplankton species in each group (cf. Table 2), the mean (symbols) and standard deviation (bars) data for each developmental stage are shown in the panel.

Table 4. Comparison of the slope (*a*) of NBSS ($y = ax + b$) on the mesozooplankton community at various locations.

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 Sea	Biovolume	0.25–14	−0.63 (−0.44 to −0.91)	Basedow et al. (2010)
Tasman Sea	Biovolume	0.11–3.3	−0.69 (−0.59 to −0.78)	Baird et al. (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 to −0.99)	Baird et al. (2008)
Southwest Coral Sea	Wet mass	0.25–2.5	−1.00 (−0.49 to −1.31)	Suthers et al. (2006)
North Iberian Shelf	Carbon	0.25–17	−1.11 (−0.90 to −1.21)	Nogueira et al. (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 to −1.17)	Quinones et al. (2003)
California Current	Carbon	0.2–3.3	−1.43 (−0.53 to −1.96)	Huntley et al. (1995)
Australian Estuary	Wet mass	0.25–1.6	−1.89 (−0.72 to −3.06)	Moore and Suthers (2006)
California Bight	Biovolume	0.025–4.0	−2.30	Napp et al. (1993)
Chukchi Sea (A, south in all years)	Biovolume	0.25–5	−1.01 (−0.69 to −1.24)	This study
Chukchi Sea (B, north in 1991/1992)	Biovolume	0.25–5	−0.86 (−0.59 to −1.09)	This study
Chukchi Sea (C, north in 2008)	Biovolume	0.25–5	−1.11 (−1.00 to −1.30)	This study
Chukchi Sea (D, north in 2007)	Biovolume	0.25–5	−0.78 (−0.48 to −1.27)	This study

Numbers in parenthesis indicate the range of slopes.

Mullin, 1986; Splures and Munawar, 1986). Sheldon et al. (1972) reported that the slope of the NBSS for stable marine ecosystems is −1, and that slopes higher and lower than −1 indicate ecosystems with high or low productivity, respectively (cf. Rodriguez and Mullin, 1986; Splures and Munawar, 1986). Slopes of NBSS in each group were in the order D < B < A < C, the slopes of groups A and C were higher than −1, and those of groups B and D were lower than −1 (Table 1). Hence, groups A and C were likely highly productive, whereas groups B and D were less productive. Group A was dominated by *Pseudocalanus* spp. and *C. glacialis*, and group C by barnacle larvae (Figure 7).

Comparisons of the slopes of the NBSS from the present study and previous studies worldwide are shown in Table 4. The slope of group C (−1.11) was close to values from the North Pacific Ocean (−1.13) and the Atlantic Ocean (−1.14), but that of group A (−1.01) was similar to those from coral seas (−0.97 to −1.00). As the area south of the Lisburne Peninsula was occupied by group A throughout the 4 years (Figure 6), the zooplankton community there is considered to be associated with a highly productive ecosystem, caused by the continuous inflow of Pacific Water. North of the Lisburne Peninsula, groups B and D, with more moderate slopes (−0.78 to −0.86), were found in 1991/1992 and 2007, and group C, with a steep slope (−1.11), in 2008 (Figure 6). As mentioned below, mass recruitment of meroplankton (barnacle larvae) was the cause of the high production of group C. Therefore, we conclude that the zooplankton community and its productivity north of the Lisburne Peninsula are highly variable from year to year.

Zooplankton community
The distribution and the 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* for each group are shown in Figure 8. Group A was common south of the Lisburne Peninsula, and area characterized by higher SST, nutrient concentration, and chlorophyll *a*. North of the Lisburne Peninsula, dominant groups varied by year, group B in 1991/1992, group C in 2008, and group D in 2007 (Figure 6). Temperature profiles for each group varied greatly, with temperatures in C < B < D (Figure 8). Within the three groups, group D

was characterized by high SST and relatively high salinity, with a strong thermocline around 15 m (Figure 8).

The zooplankton community of group A was dominated by both small and large zooplankton (Table 2). The continuous inflow of Pacific Water rich in nutrients implies high primary production south of the Lisburne Peninsula (Sambrotto et al., 1984; Springer and McRoy, 1993), although primary production north of the Lisburne Peninsula was less than to the south (Hill and Cota, 2005). During 2007, there was a dramatic increase in large Pacific copepods south of the Lisburne Peninsula (Matsuno et al., 2011). In the present study, the abundance of the Pacific copepods (E. bungii and M. pacifica) of group A was significantly greater than in the other groups (Table 2). In addition to the Pacific copepods, both Arctic copepods (C. glacialis) and small copepods (C. abdominalis, Cyclopoida, P. acuspes, and P. newmani) were more abundant in group A than in the other groups (Table 2). This may have been caused by the invasion of Pacific copepods through the inflow of Pacific Water, and by the abundance of Arctic copepods and small neritic copepods, whose nutrition may be supported by high primary production south of the Lisburne Peninsula.

Group B was found north of the Lisburne Peninsula during 1991/1992 (Figure 6). The temperature conditions associated with that group were between those of groups D (2007) and C (2008) in the same region (Figure 8). In terms of the zooplankton community, the abundance of most of the species/taxa in group B was moderate, with none especially abundant (Table 2). The largest number of stations were clustered in group B (*n* = 45). As the number of stations was highest and their spatial distribution greatest, and because the biomass and NBSS slope and temperatures were intermediate, we conclude that stations in group B represented "normal" hydrographic and zooplankton community conditions in the Chukchi Sea during summer.

Group C, which was found north of the Lisburne Peninsula during 2008, was dominated by barnacle larvae (B. crenatus), which constituted 84% of the zooplankton then (Table 2). The anomalous species composition of group C might be a result of the difference in sampling period in 2008 [7–13 July: 2 weeks to 1 month earlier than the other years (24 July–13 August)], if it matched the timing of release of barnacle larvae in that year but not the others. In terms of the timing of release of barnacle
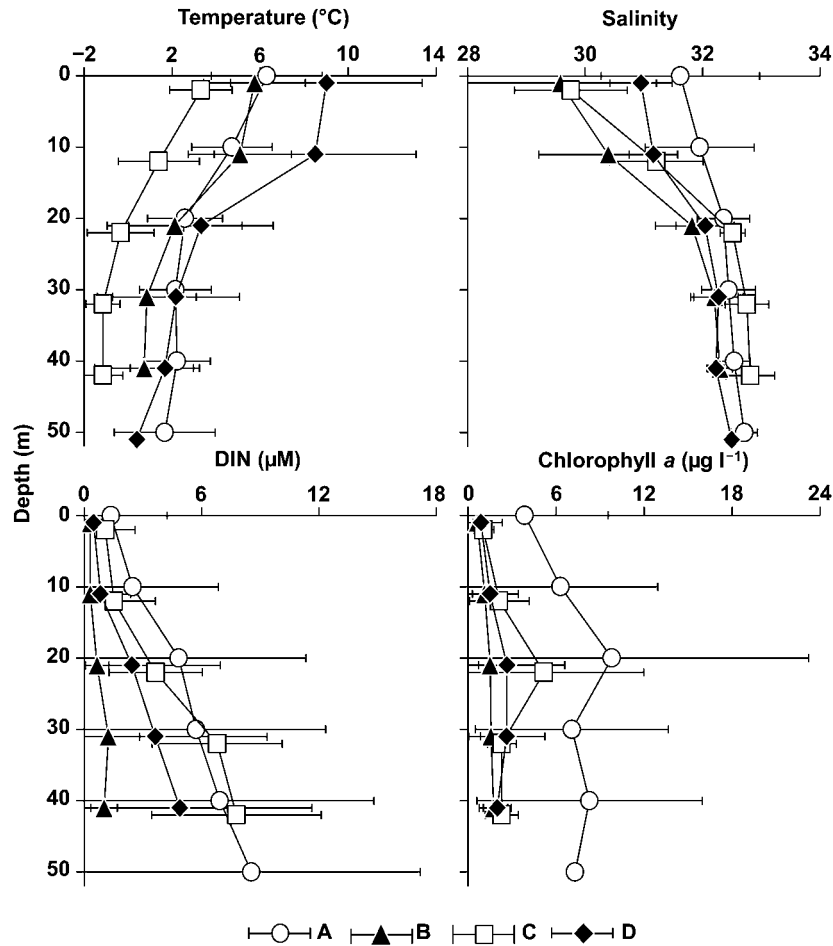
Figure 8. Vertical distribution of temperature, salinity, dissolved inorganic nitrogen (DIN), and chlorophyll *a* of the four groups identified from cluster analysis on mesozooplankton biovolume size spectra (cf. Figure 5a) in the Chukchi Sea during July/August of 1991, 1992, 2007, and 2008. Symbols and bars indicate the mean values and standard deviations at 10 m intervals.

larvae, laboratory-rearing studies show that food concentration (phytoplankton) in ambient water is an important factor in determining the timing (Clare and Walker, 1986). Field studies also suggest that the onset of the phytoplankton bloom is a key factor stimulating the release of barnacle larvae (Barnes, 1957; Crisp, 1962). In the Chukchi Sea, phytoplankton blooms from spring to summer (Wang *et al.*, 2005), and the barnacle larvae may be released during that period. As most of the primary productivity in the region is derived from ice-edge blooms (Hunt *et al.*, 2011), the early sampling in 2008 may have been closer to the bloom peak, just after the release of barnacle larvae by the benthic adults.

Group D dominated north of the Lisburne Peninsula during 2007 (Figure 6). Hydrographic information for that area in 2007 shows that the sea-ice reduction started early (Markus *et al.*, 2009), and the volume of Pacific Water passing through the Bering Strait into the Chukchi Sea was greatest during the period 1991–2007 (Mizobata *et al.*, 2010; Woodgate *et al.*, 2010). In this study, significantly higher sea surface salinity in 2007 was caused by greater intrusion of Pacific Water (Figure 2). In terms of temperature, the highest SST, in 2007 (Figure 2), was caused by the early retreat of sea ice (Markus *et al.*, 2009) and intense solar heating by a stationary presence of anticyclonic

circulation over the Chukchi Sea (Mizobata *et al.*, 2010; Vanin, 2010).

The zooplankton community of group D was 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, e.g. the stratification from surface to bottom was significantly greater for group D (4.59 ± 3.08) than for the other groups (0.94–1.66; one-way ANOVA, $p < 0.0001$). High temperature conditions associated with group D in 2007 may have led to an open-water bloom, which would have started later and ended after a short pulse of primary production (Hunt *et al.*, 2011). Thereafter, food limitation may have made it difficult for small copepods (*Pseudocalanus* spp.) to produce a second generation. As the developmental time of calanoid copepods is inversely correlated with temperature (Corkett and McLaren, 1978), the high temperatures associated with group D may have allowed faster development of *Pseudocalanus* spp., and hence less abundance of their juveniles (C1–C4).

To conclude, the characteristics of the zooplankton community in the Chukchi Sea varied greatly by region and among years. The zooplankton community south of the Lisburne Peninsula was very productive, with little interannual variability. This high

productivity may be caused by the continuous inflow of Pacific Water rich in nutrients. The zooplankton community north of the Lisburne Peninsula varied greatly by year, which may be related to interannual changes in the sea-ice extent and the timing of release of benthic larvae.

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