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Interannual changes in the zooplankton community structure on the southeastern Bering Sea shelf during summers of 1994–2009

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ABSTRACT

On the southeastern Bering Sea shelf, mesozooplankton plays an important role in material transfer between primary producers and fisheries resources. The biomass of mesozooplankton in this region is known to vary annually, but little is known about annual changes in community structure and species composition. In the present study, regional and long-term changes in abundance, biomass and community structure of copepods and chaetognaths on the shelf were evaluated based on NORPAC net samples collected during summers of 1994–2009. During the study period, regime shifts occurred from high interannual variability regime (1994–1999) to low interannual variability regime with high temperature (2000–2005), then to a low interannual variability regime with low temperature (2007–2009). A total of 24 calanoid copepod species belonging to 21 genera were identified from samples. Copepod abundance ranged from 150 to 834,486 inds. m^{-2}, was greatest on the Middle shelf, and was higher in cold years, than in warm years. Copepod biomass ranged from 0.013 to 150 g DM m^{-2}, and was also higher in cold years than in warm years. Based on the results of cluster analysis, the copepod community was divided into six groups (A–F). The regional and interannual distributions of each group were distinct. Interannual changes in abundance of the dominant copepod on the Outer shelf and Middle shelf were highly significant ($p < 0.0001$), and their abundances were negatively correlated with temperature and salinity. Interannual changes in copepod community that occurred between cold and warm years are thought to have been caused by differences in the magnitude and timing of the spring phytoplankton bloom between the two regimes. Abundance and biomass of the chaetognath *Parasagitta elegans* ranged from 30 to 15,180 inds. m^{-2} and from 11 to 1559 mg DM m^{-2}, respectively. Chaetognath abundance was significantly correlated with the abundance of the dominant copepods ($p < 0.0001$). Differences in cold and warm years may also affect recruitment of walleye pollock. We conclude that on the southeastern Bering Sea shelf, the magnitude and timing of primary production, which is related to climate change, may significantly affect how it is transferred through the food web.

1. Introduction

The southeastern Bering Sea shelf is characterized by high biological productivity, has large amounts of phytoplankton, zooplankton, benthos, fishes, seabirds and marine mammals, and is an important fishing ground of walleye pollock (*Theragra chalcogramma*) (Springer, 1992; Springer et al., 1996). Recently, this region has undergone large biological/environmental changes (Jin et al., 2009; Stabeno et al., 2010). In 1997, a coccolithophore (*Emiliania huxleyi*) bloom was observed (Napp and Hunt, 2001; Stockwell et al., 2001; Sukhanova and Flint, 1998), and mass mortality of short-tailed shearwaters (*Puffinus tenuirostris*) occurred near the Pribilof Islands (Baduini et al., 2001). In 1998, a climate regime shift was reported (McFarlane et al., 2000), and the biomass of the jellyfish *Chrysaora melanaster* was observed to peak (Brodeur et al., 2008). To describe the effect of climate regime shifts on lower to higher trophic levels, Hunt et al. (2002) proposed the Oscillation Control Hypothesis (OCH). In 2006, a climate regime shift from a warm period to cold period was reported, and the OCH was revised based on observations during this period (Hunt et al., 2011).

In the Bering Sea ecosystem, mesozooplankton are important because they connect primary production to higher trophic level production. In the mesozooplankton fauna of this region, the

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dominant taxon is Copepoda, and various studies have been conducted on their biology and ecology. They include studies of seasonal variations of community structure during spring and summer (Smith and Vidal, 1986), interannual variations in their total wet-weight biomass (Hunt et al., 2008; Napp et al., 2002; Sugimoto and Tadokoro, 1997, 1998), seasonal and spatial variations in community structure (Kang et al., 2006), and the effects of El Niño and La Niña on biomass and production (Coyle and Pinchuk, 2002). However, most studies of long-term variations in mesozooplankton have treated only wet-weight biomass data without examining the species caught or separating sub-regions or domains. In studies of species and zooplankton community structure, the study areas have been narrow, and the study periods have been short. Consequently, information on long-term changes in mesozooplankton community and their species composition is extremely scarce.

The second most abundant taxonomic group in the Bering Sea mesozooplankton biomass is chaetognaths (Coyle and Pinchuk, 2002). They are carnivores, prey upon small zooplankton and fish larvae, contribute to vertical fluxes to deep water (Brodeur and Terazaki, 1999), and sometimes account for nearly 50% of the prey of walleye pollock larvae (Brodeur and Wilson, 1996). Thus, chaetognaths are important because of their role linking lower to higher trophic levels. However, little is known about their long-term variation in the Bering Sea.

In the present study, regional and long-term changes in abundance, biomass and community structure of copepods and chaetognaths are evaluated based on samples collected over the southeastern Bering Sea shelf during the summers of 1994–2009. Long-term data on copepods and chaetognaths are compared with hydrographic data, and we discuss possible mechanisms controlling interannual variations in mesozooplankton community structures and species composition.

Table 1
Calanoid copepod species collected in the southeastern Bering Sea during summers of 1994–2009. Major region of occurrence is also shown for each species. •: Large oceanic copepods that have a diapause phase in deep layer (Miller et al., 1984). Region abbreviations are: I: Inner shelf, M: Middle shelf, O: Outer shelf, S: Slope and B: Basin.*: Rare species (occurred only < 2% of the whole stations) omitted from data for cluster analysis (cf. Fig. 4).

Species	Major region of occurrence
Acartia longiremis (Lilljeborg, 1853)	I, M, O
A. tumida Willey, 1920	M, O
*_Aetideopsis rostrata_ Sars, 1903	B
*_Aetideus pacificus_ Brodsky, 1950	B
Calanus spp.	M, O, S, B
Candacia columbiae Campbell, 1929	S, B
Centropages abdominalis Sato, 1913	I, M
Epilabidocera amphitrites (McMurrich, 1916)	I
•_Eucalanus bungii_ Giesbrecht, 1892	O,S,B
Eurytemora herdmani Thompson and Scott, 1897	I
Gaetanus intermedius Wolfenden, 1905	S,B
G. simplex Brodsky, 1950	S,B
Heterorhabdus tanneri (Giesbrecht, 1895)	S,B
Metridia pacifica Brodsky, 1950	O,S,B
Microcalanus pygmaeus (Sars, 1900)	M,O
•_Neocalanus cristatus_ (Kröyer, 1848)	O,S,B
•_N. flemingeri_ Miller, 1988	O, S, B
•_N. plumchrus_ (Marukawa, 1921)	O,S,B
Paraeuchaeta elongata (Esterly, 1913)	B
Pleuromamma scutullata Brodsky, 1950	S,B
Pseudocalanus spp.	I, M, O, S, B
*_Racovitzanus antarcticus_ Giesbrecht, 1902	B
Scolecithricella minor (Brady, 1883)	O, S, B
*_S. ovata_ (Farran, 1905)	B
Tortanus discaudatus (Thompson and Scott, 1897)	I
Undinopsis pacificus Brodsky, 1950	O,S

2. Material and methods

2.1. Field sampling

Sampling was conducted over the southeastern Bering Sea shelf during 1994–2009 between 24 June and 8 August on board the T/S Oshoro-Maru of the Faculty of Fisheries, Hokkaido University. For each year, samples were collected within a two week period. Zooplankton samples were collected by vertical hauls of flowmeter-equipped NORPAC nets (45 cm mouth diameter, 0.335 mm mesh; Motoda, 1957) from 150 m depth or near the bottom (where the depth was shallower than 150 m) to the surface. Zooplankton samples were immediately preserved with 5% formaldehyde-seawater buffered with sodium tetraborate. In addition, temperature and salinity were measured with a CTD (Neil Brown, Mark IIIB during 1994–2001 and Seabird SBE-911*plus* during 2002–2009). Water samples from the CTD rosette were filtered through GF/F filters, extracted with acetone or DMF and chlorophyll *a* concentration was measured using a fluorometer (Turner Designs, Inc.).

The number of sampling stations in any one year was 9–49 (total=96), and the total number of samples was 428 (Fig. 1). Based on the bottom depth, the southeastern Bering Sea shelf was divided into three regions: Inner shelf (< 50 m), Middle shelf (50–100 m) and Outer shelf (100–200 m) (Coachman and Charnell, 1979; Coachman, 1986). Areas with depth of 200–1000 m and > 1000 m were classified as Slope and Basin, respectively. Six stations on the Outer shelf and six on the Middle shelf were sampled every year of the study (Fig. 1), so only the data from these twelve stations were used to analyze long-term changes.

2.2. Sample analysis

Based on the biomass of the samples, subsamples were created with a Motoda plankton splitter (Motoda, 1959), and the subsamples were examined under a stereomicroscope.

Copepods were staged and identified to the lowest possible taxonomic level. For copepods, the most important genus in this region (*Calanus*) is reported to be mixture of *Calanus glacialis* and *Calanus marshallae* (Nelson et al., 2009). We could not distinguish

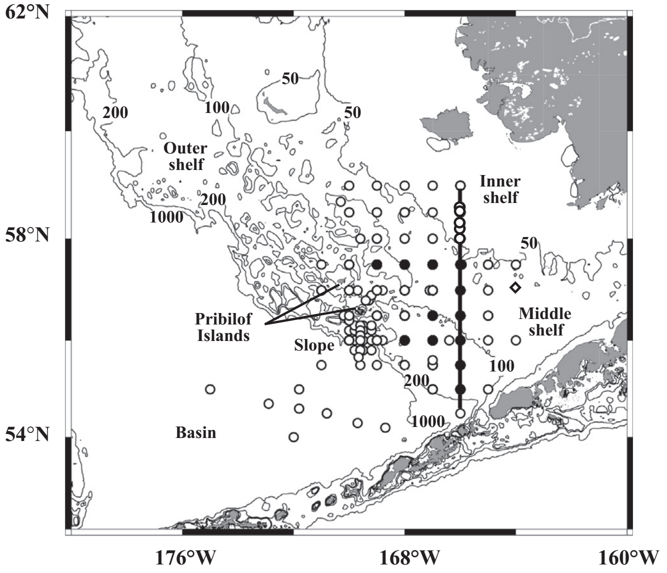

Fig. 1. Location of the sampling stations in the southeastern Bering Sea during the summers of 1994–2009 (circles). Solid symbols denote stations where sampling was conducted in all years from 1994–2009, providing the data used for annual comparisons. Line indicates 166°W transect where the hydrographic data were analyzed (cf. Fig. 2).

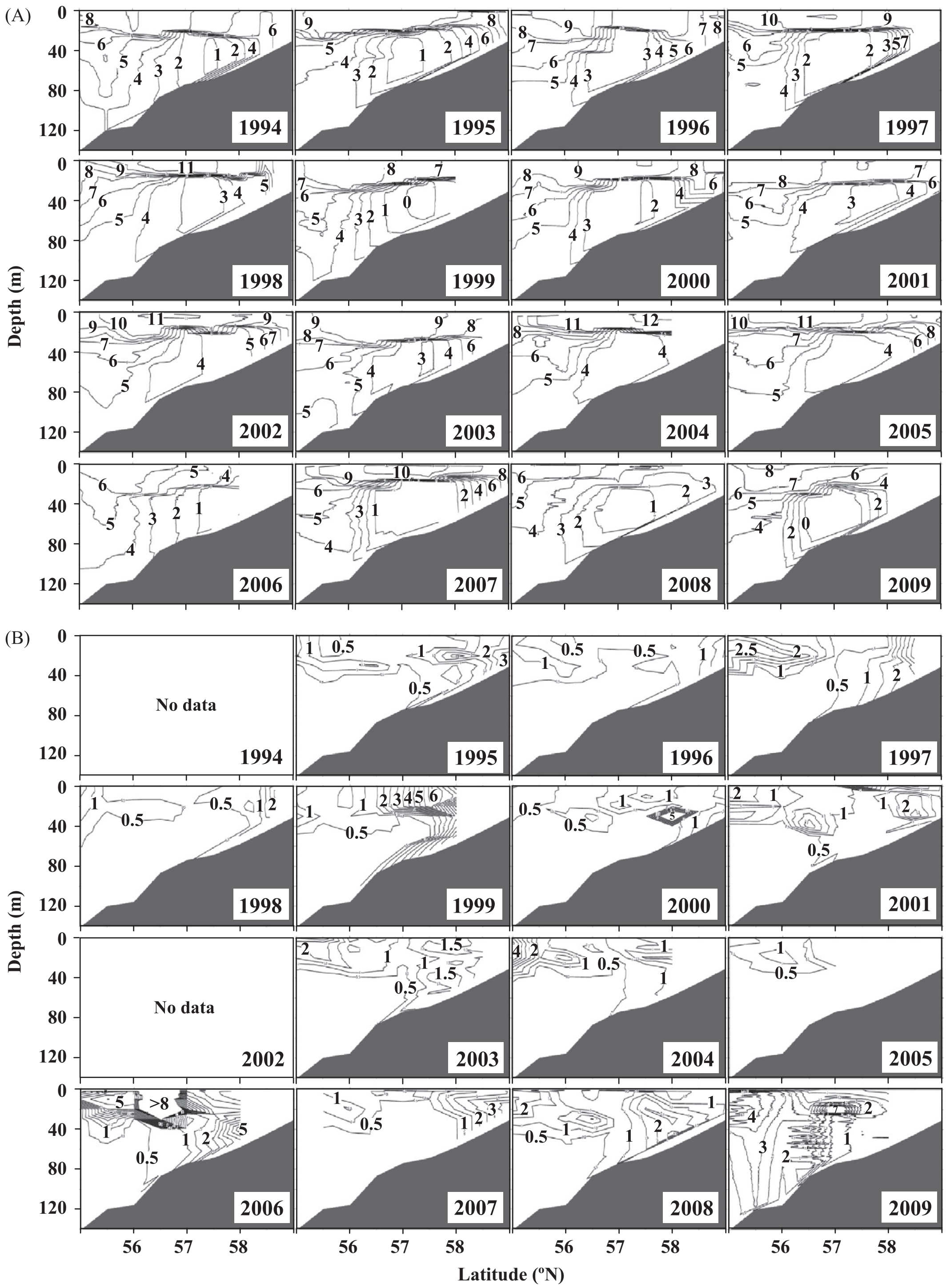

Fig. 2. (A) Temperature and (B) chlorophyll *a* stations along 166°W during summers of 1994–2009.

the two species and treated them as "*Calanus* spp.". For biomass estimation, copepods were separated into four groups: *Calanus* spp., *Neocalanus* spp., *Eucalanus bungii* and other copepods. One hundred individuals in each group were chosen randomly for measurement of total lengths (TL, μm) by ocular micrometer. Dry mass (DM, μg) was estimated using the following equations derived for organisms from the Oyashio region (Imao, 2005):

Calanus and *Neocalanus* spp. (less lipids)
$$\log_{10} \mathrm{DM} = 2.48 \log_{10} \mathrm{TL} - 6.00 \quad (1)$$

Calanus and *Neocalanus* spp. (more lipids)
$$\log_{10} \mathrm{DM} = 3.00 \log_{10} \mathrm{TL} - 7.70 \quad (2)$$

E. bungii $\log_{10} \mathrm{DM} = 3.16 \log_{10} \mathrm{TL} - 9.16 \quad (3)$

Other copepods $\log_{10} \mathrm{DM} = 2.62 \log_{10} \mathrm{TL} - 6.40 \quad (4)$

For *Calanus* spp. and *Neocalanus* spp., lipid accumulation was separated into two: less lipids ($<20\%$ of prosome volume) and more lipids ($\geq 20\%$ of prosome volume). Then Eqs. (1) and (2) were applied for less and more lipid specimens, respectively. The total

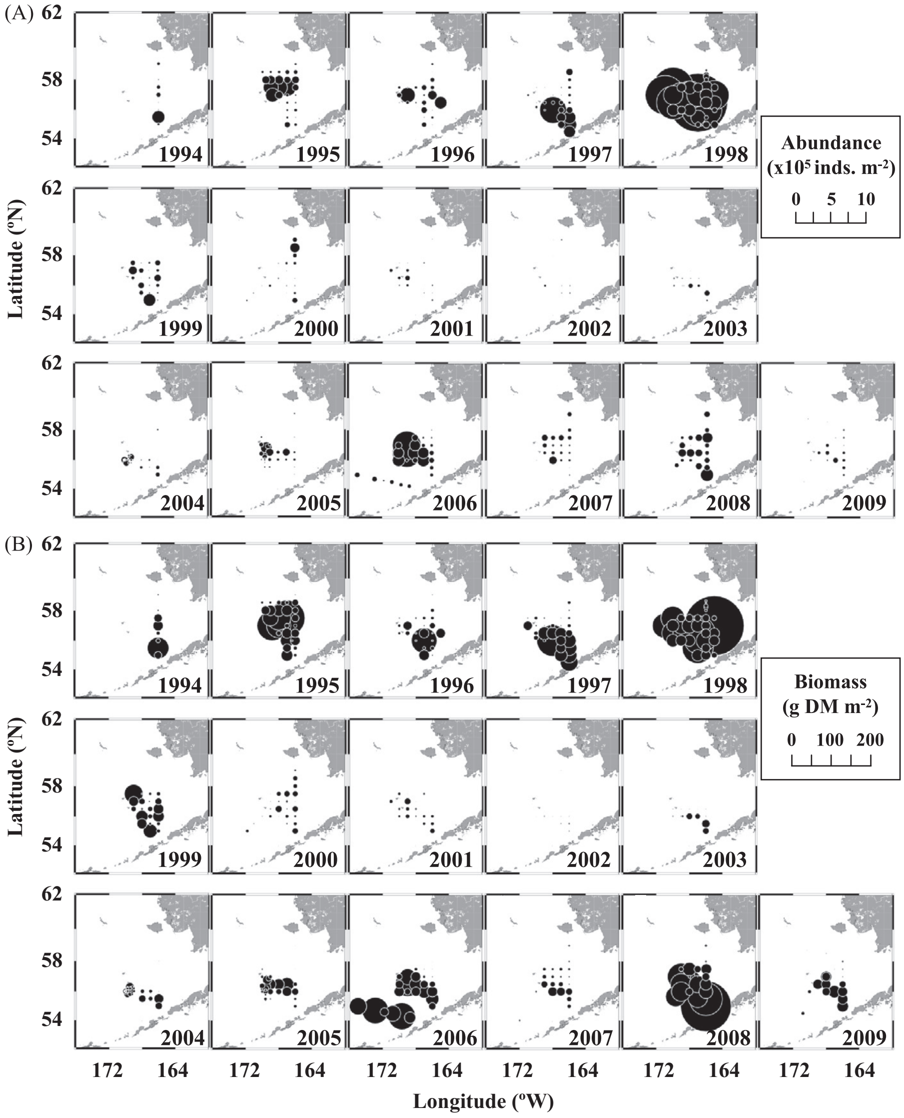

Fig. 3. Regional variations in (A) copepod abundance and (B) biomass in the southeastern Bering Sea during summers of 1994–2009.

biomass of copepods (mg DM m^{-2}) was estimated by multiplying the average individual mass (mg DM $inds.^{-1}$) by the abundance (inds. m^{-2}).

Chaetognaths were identified to species based on the samples collected during 1996–2009. The total length (TL, mm) of the dominant chaetognath, *P. elegans*, was measured using a ruler for large individuals (TL≥10 mm) and an ocular micrometer for small specimens (TL < 10 mm). Specimens were classified according to McLaren (1969), Sameoto (1973) and Zo (1973): Stage I (juveniles), Stage II (immature) and Stage III (mature). To estimate DM, ash-free dry mass (AFDM, mg) was estimated from the TL using the following equation (Mumm, 1991):

$$\mathrm{AFDM} = 0.0002\mathrm{TL}^{2.6924} \quad (5)$$

Dry mass was estimated as DM = AFDM/0.9 (Båmstedt, 1986).

2.3. Data analysis

Zooplankton samples were collected day and night. Since the depths of most sampling stations were < 150 m and the sampling was conducted throughout the water column, day–night differences in abundance and biomass were expected to be small. There were no significant differences between day and night abundance or biomass of copepods and chaetognaths for all years ($p = 0.06$–0.93, *U*-test). Thus, no day-night conversions were done for abundance or biomass.

To examine community structure, we conducted cluster analysis and nonmetric multidimensional scaling (NMDS) ordination. Abundance data (*X*: inds. m^{-2}) of each species were transformed to $\log_{10}(X+1)$ prior to analysis to reduce the bias of abundant species. Rare species which occurred only < 2% of the whole stations were eliminated from the data for analysis (cf. Table 1). 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. The NMDS ordination was carried out to delineate the sample groups on the two-dimensional map. All of these analyses were carried out using BIOSTAT II software (Sigma Soft).

To evaluate environmental factors that may have influenced sample groups determined by cluster analysis, nonmetric multidimensional scaling (NMDS) ordination was carried out to delineate the sample groups in two-dimensional space. We then

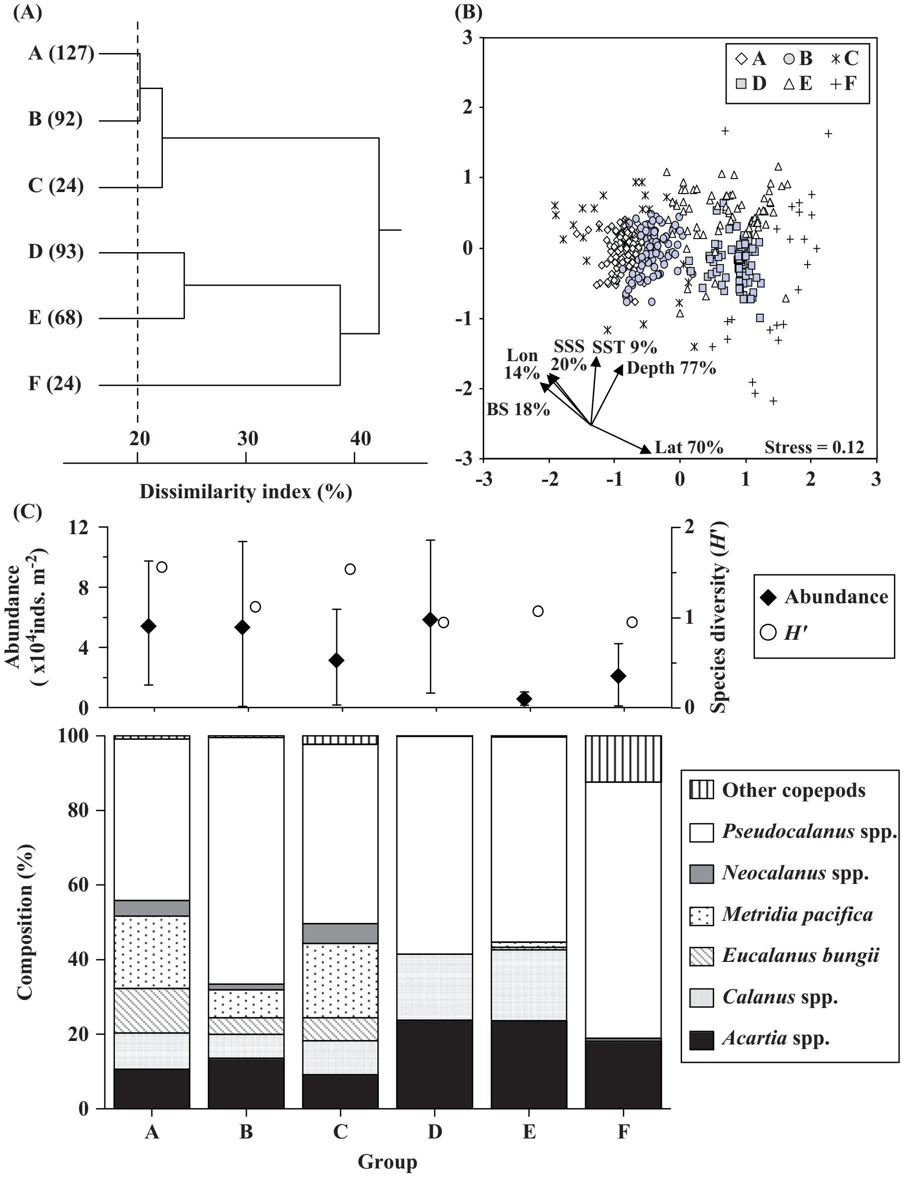

Fig. 4. Copepod assemblages: (A) dendrograms from the cluster analysis based on copepod abundance. Six groups (A–F) were identified with dissimilarity at 20% (dashed line). Numbers in the parentheses indicate quantity of stations included in each group. (B) Nonmetric multidimensional scaling plots of the six groups, with arrows and percentages indicating directions of environmental parameters and coefficient of determinations (r^2), respectively. Lat: latitude, Lon: longitude, SSS: sea surface salinity, SST: sea surface temperature, BS: bottom salinity. (C) Mean abundance with standard deviations and species diversity (H') (upper) and taxonomic composition of each group (lower).

conducted multiple-regression analysis ($Y=aX_1+bX_2+c$) with the hydrographic data (Y: latitude, longitude, depth, sea surface and bottom temperature and sea surface and bottom salinity) are the dependent variables and two-dimensional NMDS as independent variables (thus, axis 1 as $X1$ and axis 2 as X_2) (a, b, c are fitted constants). Shannon's diversity index (H') in each group was calculated using the equation:

$$H' = -\sum n_i/N \times \ln n_i/N \tag{6}$$

where n_i is the abundance (inds. m^{-2}) of the ith species, and N is the total copepod abundance (inds. m^{-2}) in the group (Shannon and Weaver, 1949).

To evaluate factors affecting the variability of copepod abundance, two-way ANOVA with year and station as independent variables was used. To determine which factors controlled annual changes in copepod abundance, correlation analysis was done between the abundance of dominant copepods and three factors: water temperature (throughout whole water column, in upper layer and in lower layer), salinity and chlorophyll a (whole water column).

For *P. elegans*, cohort analysis was done based on the TL histogram data from the Middle shelf using Microsoft Excel Solver (Aizawa and Takiguchi, 1999).

To evaluate what factors controlled the interannual changes in chaetognath abundance, we tested for correlations between the chaetognath abundance for the Outer shelf and Middle shelf and four factors: water temperature (whole water column, upper and lower layer), salinity (whole water column), chlorophyll a (whole water column) and abundance of the dominant copepods.

3. Results

3.1. Hydrography

In all years, a thermocline was present 20–30 m, and the bottom temperature of Middle shelf ranged between 0 and 4 °C, but was higher for the Inner and Outer shelves (Fig. 2A). The Middle shelf, bottom temperature was about 4 °C during 2001–2005, and lower (0–3 °C) during 2007–2009. Owing to Stabeno et al. (2012), there were three regimes in depth-averaged ocean temperature: cold; 1995, 1997, 1999, 2007–2009, average; 1996, 2000, 2006, and warm; 1998, 2001–2005. Our results confirmed this pattern (Fig. 2A).

The peak of summer chlorophyll *a* at each station varied between 0.5 and 25.4 mg m^{-3}, and chlorophyll *a* was high above the thermocline and on the Inner shelf (Fig. 2B). The peak of chlorophyll *a* was low (ca. 1 mg m^{-3}) during the warm regime (2001–2005).

3.2. Copepods

Regional and interannual changes in total copepod abundance and biomass were observed (Fig. 3). Copepod abundance ranged from 150 to 834,486 inds. m^{-2}, and was greatest on the Middle shelf (Fig. 3A). Copepod abundance was high during cold years (1995, 1997, 1999 and 2007–2009), and low in warm years (2001–2005) (Fig. 3A). Copepod biomass ranged from 0.013 to 150 g DM m^{-2}, and was highest on the Outer and Middle shelves (Fig. 3B). The biomass peak occurred in more oceanic waters than

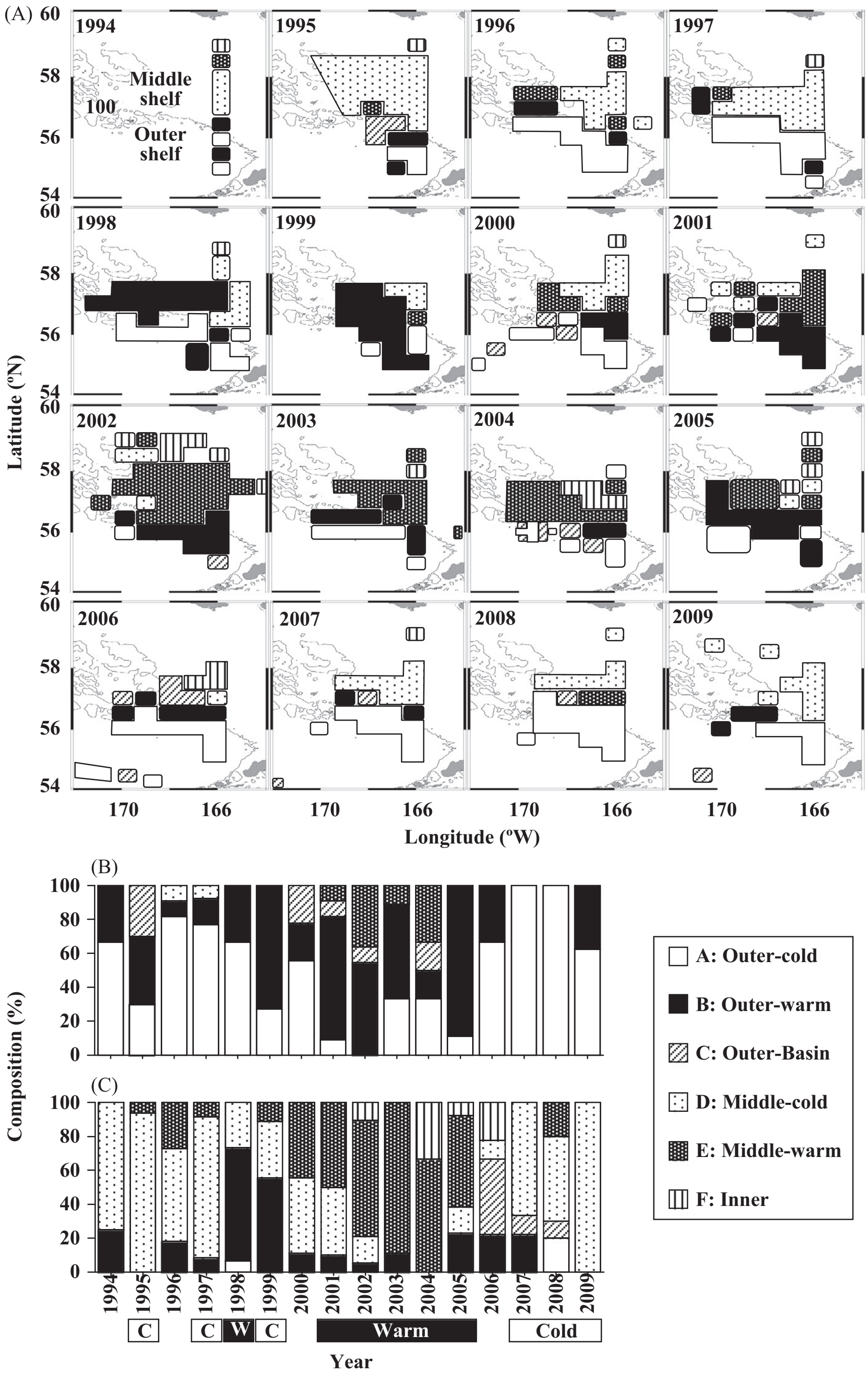

Fig. 5. (A) Spatial and temporal distribution of six copepod communities identified from Bray–Curtis dissimilarity analysis. Annual distribution of groups on the (B) Outer shelf and (C) Middle shelf.

the abundance peak due to the dominance of large-sized oceanic copepods. Copepod biomass and abundance were both high in cold years and low in warm years.

Throughout the study period, 24 calanoid copepod species from 21 genera were identified (Table 1). *Pseudocalanus* spp. was the most numerous, and *Calanus* spp. was dominated the copepod biomass. Large-sized oceanic copepods that diapause at depth (i.e., *E. bungii*, *Metridia pacifica*, *Neocalanus cristatus*, *Neocalanus flemingeri* and *Neocalanus plumchrus*) were collected on the Outer shelf, on the Slope and in the Basin (Table 1).

Based on abundance of each species, cluster analysis divided the copepod community into six groups (A–F). The groups contained 24–127 stations (Fig. 4A). From multiple-regression analysis, environmental factors that were significantly related with the group separation were latitude, longitude, depth, sea surface temperature, sea surface salinity and bottom salinity. The most important factors were latitude and depth; they determined 70–77% of the variability of the copepod community (Fig. 4B). Mean copepod abundance was highest in group D and lowest in group E (Fig. 4C). Species diversity was higher in groups A and C ($H'=1.6$) than in groups B, D, E and F ($H'=1.0$–1.1). These group-specific differences in species diversity were caused by their species composition. For groups A–C, *Pseudocalanus* spp. and large, oceanic copepods (*M. pacifica*, *E. bungii*, *Neocalanus* spp.) were abundant (Fig. 4C). For groups D and E, species diversity was lower, and the species compositions were similar; they were comprised of *Pseudocalanus* spp. (55–58%), *Acartia* spp. (24%) and *Calanus* spp. (18–19%). In group F, the proportion of *Calanus* spp. decreased, and the main species were *Pseudocalanus* spp. (69%), and *Acartia* spp. (18%). Endemic species, such as *Epilabidocera amphitrites*, *Eurytemora herdmani* and *Tortanus discaudatus*, were also observed (Fig. 4C, Table 1).

Table 2
Variance analysis (two-way ANOVA) on year-to-year and station-to-station differences in abundance (inds. m^{-2}) of dominant copepod taxa on Outer and Middle shelf of the southeastern Bering Sea during summers of 1994–2009.

Domain	Species	*F*-value *df*1, *df*2	
		Year$_{15,30}$	Station$_{2,30}$
Outer shelf			
	Acartia spp.	2.136^{*}	1.215^{ns}
	Calanus spp.	1.259^{ns}	3.027^{ns}
	Eucalanus bungii	1.402^{ns}	2.610^{ns}
	Metridia pacifica	2.060^{*}	1.464^{ns}
	Neocalanus spp.	5.228^{***}	1.956^{ns}
	Pseudocalanus spp.	1.190^{ns}	0.194^{ns}
Middle shelf			
	Acartia spp.	6.574^{****}	2.798^{ns}
	Calanus spp.	6.026^{****}	3.745^{*}
	Pseudocalanus spp.	5.791^{****}	0.195^{ns}

ns: not significant.
* $p < 0.05$.
*** $p < 0.001$.
**** $p < 0.0001$.

The regional and interannual distributions of each group were clearly separated (Fig. 5A). Composition of group A was greater in cold years (1995, 1997, 1999 and 2007–2009) on the Outer shelf, and that of group B was greater in warm years (1998, 2001–2005) on the Outer shelf, and group C was seen mainly on the Outer shelf and in the Basin, but also on the Middle shelf in 2006–2008 (Fig. 5B). Group D was mainly observed in cold years on the Middle shelf, group E was seen in warm years on the Middle shelf, and group F was centered on the Inner shelf (Fig. 5A).

Two-way analysis of variance (ANOVA) on annual and geographical differences in abundance of the dominant copepods showed significant interannual changes for *Acartia* spp., *M. pacifica* and *Neocalanus* spp. on the Outer shelf (Table 2). Significant station-to-station differences were detected only for *Calanus* spp. on the Middle shelf. All dominant copepods on the Middle shelf (*Acartia* spp., *Calanus* spp. and *Pseudocalanus* spp.) showed highly significant interannual changes in abundance ($p < 0.0001$, Table 2).

Correlation analysis was used to evaluate which environmental parameters were related to the interannual changes in copepod abundance. Abundances of the three dominant copepods on the Middle shelf, which all showed high interannual variability, were strongly negatively correlated with temperature and salinity (Table 3).

3.3. Chaetognaths

Two chaetognath species (*P. elegans* and *Eukrohnia hamata*) were collected. *P. elegans* dominated the chaetognath fauna, composing 84% of the total chaetognath abundance and 89% of the chaetognath abundance on the Middle shelf. For this reason, *E. hamata* was not included in the subsequent analysis of chaetognaths.

P. elegans abundance ranged from 30 to 15,180 inds. m^{-2}, and was highest on the Middle shelf (Fig. 6A). Abundance was low during 2000–2004 and high during 1996–1999 and 2005–2009. *P. elegans* biomass varied from 11 to 1559 mg DM m^{-2} (Fig. 6B). Biomass was low during 2002–2004 and high during 1996–1999 and 2005–2009. Differences in the timing of the abundance and

Table 3
Correlation coefficients (r) between abundance of dominant copepods and various environmental parameters in the southeastern Bering Sea during summers of 1994–2009.

Domain	Species	Temperature ($n=91$)			Salinity ($n=91$)	Chlorophyll *a* ($n=45$)
		Whole water column	Upper layer	Lower layer	Whole water column	Whole water column
Outer shelf						
	Acartia spp.	0.207^{*}	0.149	0.186	−0.140	0.067
	Calanus spp.	-0.423^{****}	−0.101	-0.406^{***}	-0.294^{**}	0.192
	Eucalanus bungii	0.138	−0.143	0.307^{**}	0.517^{****}	0.071
	Metridia pacifica	-0.231^{*}	-0.258^{*}	−0.105	0.076	0.370^{*}
	Neocalanus spp.	-0.285^{**}	-0.404^{***}	−0.108	0.252^{*}	0.369^{*}
	Pseudocalanus spp.	−0.159	−0.142	−0.044	−0.028	0.341^{*}
Middle shelf						
	Acartia spp.	-0.410^{***}	−0.146	-0.431^{****}	-0.506^{****}	−0.111
	Calanus spp.	-0.448^{****}	-0.340^{**}	-0.457^{****}	-0.407^{***}	−0.126
	Pseudocalanus spp.	-0.567^{****}	-0.292^{**}	-0.539^{****}	-0.484^{****}	−0.037

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.
**** $p < 0.0001$.

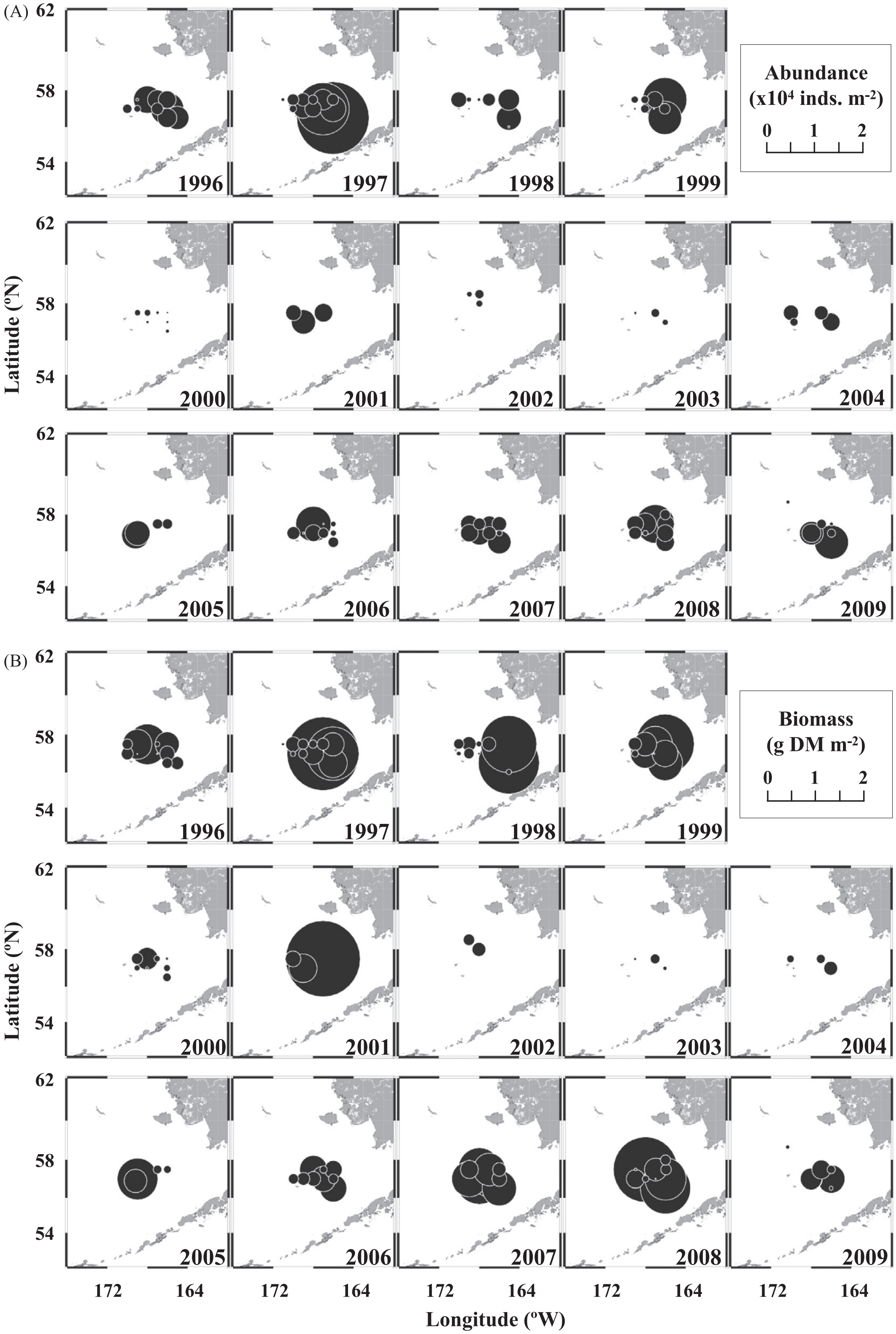

Fig. 6. Regional variations in *Parasagitta elegans*: (A) abundance and (B) biomass during summers of 1996–2009.

biomass peaks might have been caused by interannual changes in *P. elegans* body-size composition.

In every year, *P. elegans* TL composition on the Middle shelf had two or three cohorts (Fig. 7). The small-sized cohort was dominated by Stage I (juveniles), the middle-sized cohort by Stage II (immature), and the large-sized cohort by Stage III (mature) individuals. Stage III was not observed in 2003 or 2004 (Fig. 7). The average TL of the small-sized cohort (Stage I) was significantly larger (3.5–8.5 mm) during 1996–2005 than those (2.5–5.5 mm) during 2006–2009 (Fig. 7) ($p < 0.05$, *U*-test).

P. elegans abundance on the Outer shelf was positively correlated with dominant copepod abundance (*Acartia* spp., *Calanus*

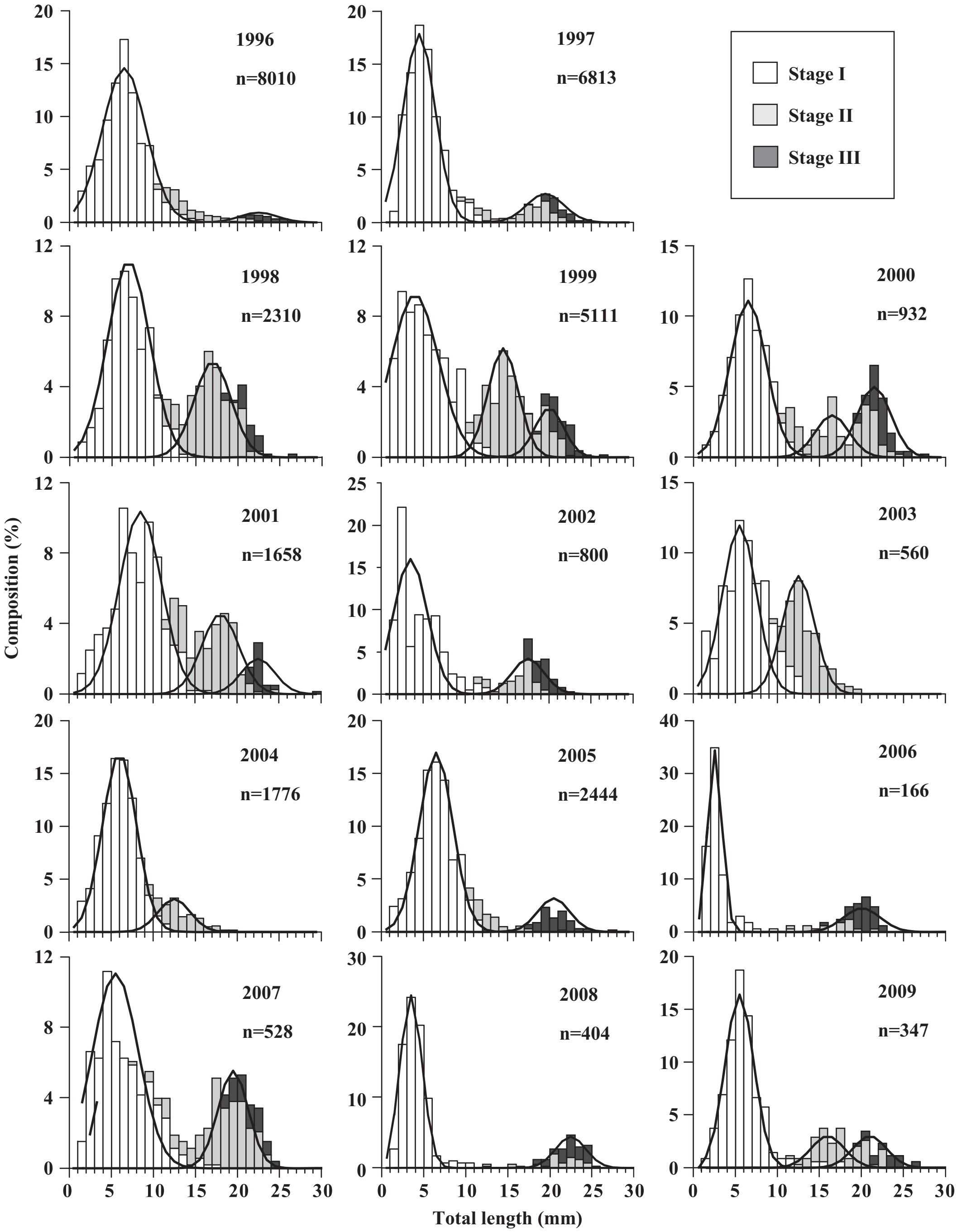

Fig. 7. Annual patterns of *Parasagitta elegans* length frequency on Middle shelf during summers of 1996–2009. *n*: number of measured specimens.

spp. and *Pseudocalanus* spp.), but not with environmental factors (Table 4). On the Middle shelf, *P. elegans* had a highly significant positive correlation with dominant copepod abundance ($p < 0.0001$) and significant negative correlations with temperature and salinity. Thus on the Middle shelf, *P. elegans* abundance was high when temperature and salinity were low, and low when temperature and salinity were high, which is similar to the pattern observed in copepod abundance (Table 4).

4. Discussion

The copepod community on the Bering Sea shelf showed large interannual differences across the shelf (Fig. 5A). The major environmental factors that were related to the copepod community were latitude and depth (Fig. 4B), and species diversity was highest on the Outer shelf because of the occurrence of the oceanic copepods in addition to the shelf copepods (Fig. 4C). These findings correspond well with the horizontal distribution of copepod community structure reported by Cooney and Coyle (1982). These cross-shelf differences in copepod species may be related to the occurrence of frontal structures (Coachman and Charnell, 1979; Coachman, 1986). The large number of oceanic species on the Middle shelf in 1998 (Fig. 5C) may be caused by the transportation of oceanic copepods by strong cross-shelf advection (Stabeno et al., 2001) (Fig. 1). Stabeno et al. (2012) also reported the transport of oceanic species during warm years.

Long-term changes in zooplankton on the southeastern Bering Sea shelf based upon wet-weight biomass have been reported (Sugimoto and Tadokoro, 1997, 1998; Napp et al., 2002). Recently,

Table 4
Correlation coefficients (r) between abundance of chaetognath *Parasagitta elegans* and various parameters (water temperature, salinity and copepod abundance) on the Outer shelf and Middle shelf in the southeastern Bering Sea during summers of 1996–2009.

Parameters	Outer shelf	Middle shelf
Temperature		
Whole water column	–0.137	-0.519^{****}
Upper layer	–0.057	-0.301^{**}
Lower layer	–0.057	-0.547^{****}
Salinity		
Whole water column	–0.172	-0.513^{****}
Copepods		
Acartia spp.	0.343^{**}	0.563^{****}
Calanus spp.	0.431^{****}	0.503^{****}
Eucalanus bungii	0.129	–
Metridia pacifica	0.195	–
Neocalanus spp.	0.093	–
Pseudocalanus spp.	0.291^{**}	0.566^{****}

–: not applicable.

** $p < 0.01$.

**** $p < 0.0001$.

Hunt et al. (2008) also reported that the zooplankton wet mass was lower in the early 2000s than in the late 1990s. This corresponds with the interannual changes in copepod abundance and biomass observed in the present study (Fig. 3). In the present study, the copepod community greatly varied between cold years (1995, 1997, 1999 and 2007–2009) and warm years (1998, 2001–2005) on both the Outer and Middle shelves. In warm years, oceanic species decreased on the Outer shelf, but showed no change on the Middle shelf, and the abundance of all copepod species drastically decreased on both the Outer and Middle shelf (Fig. 5). Thus, these findings clearly indicate that both the wet mass and copepod community structure showed interannual changes on the southeastern Bering Sea shelf (Fig. 8).

Physical and biological changes have occurred in the southeastern Bering Sea shelf over the last two decades (Fig. 8). During the 1997 El Niño/Southern Oscillation (ENSO) event, there were anomalous atmospheric conditions over the southeastern Bering Sea shelf (Overland et al., 2001), a warm surface layer, a bloom of the coccolithophorid *E. huxleyi* (Sukhanova and Flint, 1998) and mass mortality of short-tailed shearwaters (*P. tenuirostris*) (Baduini et al., 2001). Short-tailed shearwaters prey on large zooplankton, especially adult euphausiids (Hunt et al., 1996), and the starvation of shearwaters that occurred during the summer of 1997 may have been due to low densities of adult euphausiids (Stockwell et al., 2001) or difficulty in finding prey patches due to low water transparency caused by the coccolithophore blooms (Lovvorn et al., 2001). Thus, the mass mortality of short-tailed shearwaters may not have been related with the pattern of mesozooplankton abundance and biomass described in this study.

Coccolithophore (*E. huxleyi*) blooms in recent times were first observed in this region in September 1997 (Vance et al., 1998). Large-scale coccolithophore blooms were also observed in June 1998 and 2000 (Sukhanova and Flint, 1998; Iida et al., 2002, 2008, 2012). As an ecological consequence of coccolithophores, negative effect for short-tailed shearwaters and their nutritional values for copepods should be considered. Information in the literature regarding ingestion of coccolithophores by copepods is contradictory. For example, Huskin et al. (2000) state that *E. huxleyi* is difficult to digest and has low nutritional value, it is not a preferred food item for *Calanus* species. However, Nejstgaard et al. (1997) reported that about 75% of the carbon consumed by *Calanus finmarchicus* during an *E. huxleyi* bloom came from *E. huxleyi* ($>30\times10^{6}$ cells L^{-1}), and high abundance of *Calanus* spp. was observed on the Inner shelf during a coccolithophore bloom (Coyle and Pinchuk, 2002). The latter observations suggest that coccolithophore production may have little effect on *Calanus* spp. In fact, years of coccolithophore blooms (1997, 1998 and 2000) did not correspond with years of low copepod abundance or biomass (Fig. 8B). This discrepancy between coccolithophore blooms and copepod abundance could be explained if coccolithophorids are ingested by *Calanus* species (Nejstgaard et al., 1997) and have some nutritional value. As the other possible cause, turbid waters of coccolithophore bloom may provide copepods refuge from visual predators (Lovvorn et al., 2001).

During the study period, there were cold (1995, 1997, 1999, 2007–2010), average (1996, 2000, 2006) and warm years (1998, 2001–2005) (Fig. 2A). During cold and warm years, the timing and magnitude of the spring bloom differ (Stabeno et al., 2001; Hunt et al., 2002, 2011). During cold years, the sea ice remains during the severe winter storms, and ice-edge blooms occur. In warm years, the sea ice melts before the spring storms, and strong wind mixing delays the start of the bloom until stratification occurs when the thermocline develops. From long-term (1960–2005) simulation modeling, Jin et al. (2009) reported that in cold years ($PDO < -1$), phytoplankton blooms start early, last long and are large, while in warm years ($PDO > 1$), they occur later with short pulses and are small. These differences in bloom timing between cold and warm years have also been recorded in mooring observations in this region (Hunt et al., 2011).

Copepod abundance and biomass on both the Outer shelf and Middle shelf were high during cold years (1995, 1997, 1999 and 2007–2009) and low during warm years except 1998 (2001–2005) (Fig. 3, Table 3). The dominant copepod, *Calanus* spp., has an extended spawning period; it starts well before the spring phytoplankton bloom (February) and ends in May; however the survival rate of early developmental stages depends on whether they encounter a phytoplankton bloom or not, and recruitment of copepodid stages increases if they encounter early ice associated blooms, which are highly productive (Baier and Napp, 2003). Low temperatures in cold years may also lead to greater abundance of the small copepods *Pseudocalanus* spp. and *Acartia* spp. especially in the Middle shelf (Table 3). Cold temperature may provide the longer growing season and high primary productivity of ice-edge blooms, sufficient food condition for copepods, resulting in increased abundance of both large and small copepods.

In this study, copepod abundance on both the Outer and Middle shelf was negatively correlated with temperature (Table 3). In contrast, on the Inner shelf, positive correlations were reported between spring temperatures and the abundance of three copepods (*Calanus* spp., *Pseudocalanus* spp. and *Acartia* spp.), and between summer temperatures and two copepods (*Pseudocalanus* spp. and *Acartia* spp.) (Coyle and Pinchuk, 2002). This suggests that the response of copepods to temperature may vary between the Outer-Middle shelf (negative, this study), and the Inner shelf (positive, Coyle and Pinchuk, 2002). In this study, differences between cold and warm years on the Middle shelf were observed in copepod abundance, but not in species composition (groups D and E in Fig. 4C). This is partly because both large and small copepods were abundant in cold years and less abundant in warm years (Table 3). Coyle et al. (2008) compared the summer zooplankton community on the Middle shelf between a cold (1999) and warm year (2004), and reported that the dominant species shifted from large species in the cold year to small species in the warm year. However, this phenomenon was not observed during the 16 years of the present study. Our results showed that both large- and small-sized copepods showed a clear negative correlation with habitat temperature (Table 3).

Similar to copepods, the biomass of the jellyfish *C. melanaster* is high in cold years and low in warm years (Brodeur et al., 2008).

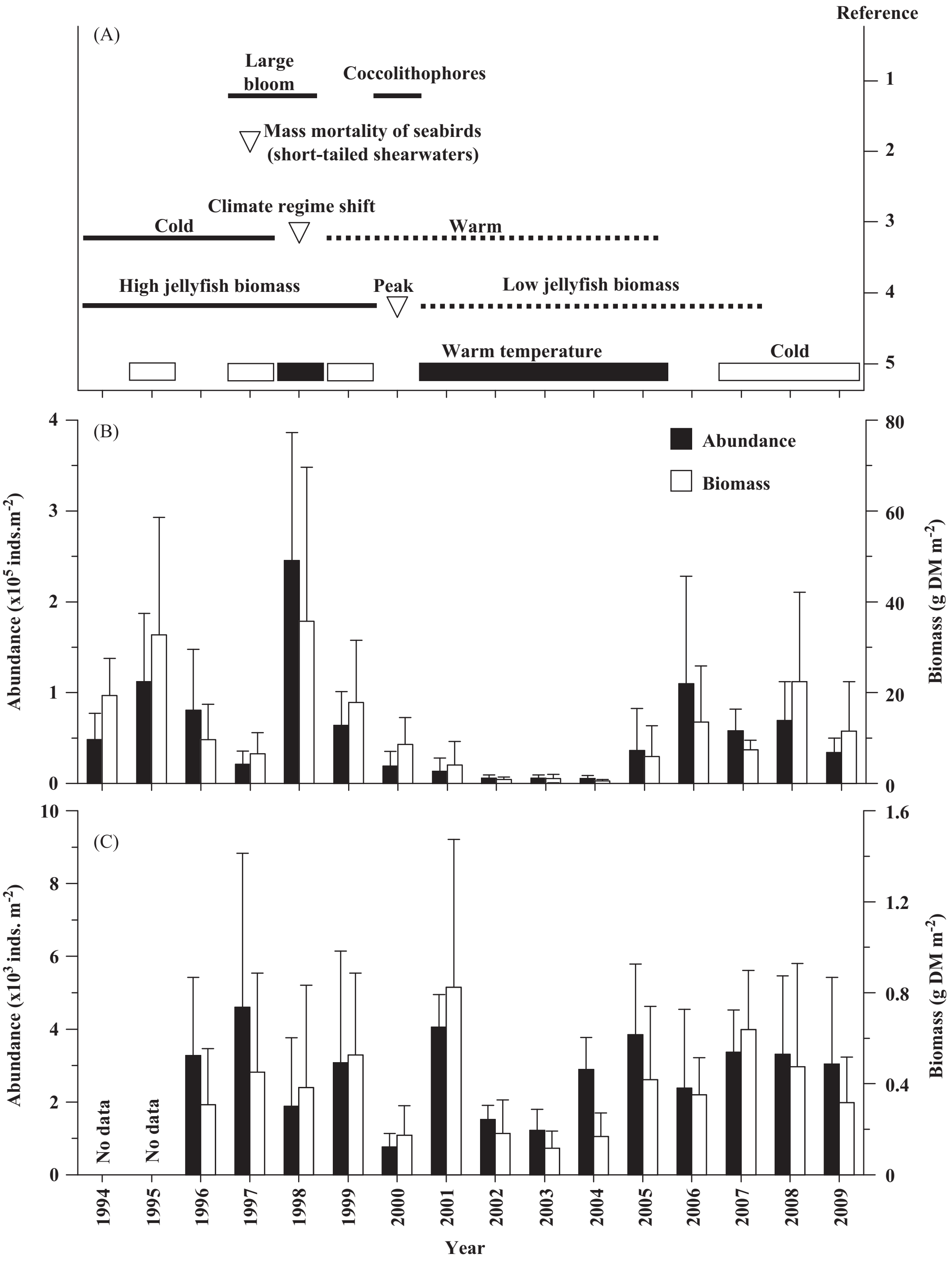

Fig. 8. (A) Annual changes in biological/environmental conditions, (B) copepod abundance and biomass and (C) chaetognath (*Parasagitta elegans*) abundance and biomass on Middle shelf of the southeastern Bering Sea during summers of 1994–2009. Values are means and error bars indicate standard deviations. For references in (A), 1: Sukhanova and Flint (1998), Iida et al. (2002,2008), 2: Baduini et al. (2001), 3: McFarlane et al. (2000), 4: Brodeur et al. (2008), Hunt et al. (2010), 5: Stabeno et al. (2012).

The increase in cold years may be due to improved feeding conditions for polyps (mass sinking of phytoplankton after ice-edge bloom), and subsequent abundant food (copepods) for pelagic medusae may improve survival and growth (Brodeur et al., 2008). In contrast, oceanic blooms in warm years are less productive and provide less food (sinking phytoplankton) for polyps, as well as less food (copepods) for planktonic medusae, resulting in low growth and survival of polyps and medusae.

Interannual changes in chaetognath abundance and biomass were somewhat similar to the changes in copepods (Fig. 8). This may be an example of bottom-up control on predatory chaetognath abundance by prey (copepods) abundance. Chaetognaths in this region change their food items and size at maturity between cold and warm years; in cold years, they prey on large *Calanus* spp. and mature at large size, while in warm years, they feed on small *Pseudocalanus* spp. and mature at small size (Baier and Terazaki, 2005). The TL of most mature (Stage III) individuals in the present study was >20 mm in cold years (1997, 1999 and 2007–2009), and <20 mm in warm years (1998, 2001, 2002 and 2005), and no mature individuals were observed in the warm years 2003 and 2004 (Fig. 7). These facts support the finding of Baier and Terazaki (2005), who reported that sufficient food conditions in cold years result in a large size at maturity, while food limitation in warm years induces small size at maturity.

For the early life history stages of walleye pollock, an important fisheries resource in this region, food conditions differ between cold and warm years (Napp et al., 2000; Hunt et al., 2011). In cold years, there may be a mismatch between the production of pollock larvae and their prey (Napp et al., 2000), but an early start of the ice-edge bloom and high abundance of lipid-rich prey for age-0 fish (copepods and euphausiids) results in high survival rates and low cannibalism (Hunt et al., 2011). In warm years, the late start of the open-water bloom results in a low abundance of lipid-rich prey for the age-0 pollock and chaetognaths. Under this food-limited condition, growth and survival of walleye pollock juveniles decrease, and the proportion of cannibalism may increase. This results in a decrease in recruitment (Hunt et al., 2011, Heintz et al., 2013). Thus, the timing and magnitude of primary production related with climate change affects production through the entire food web structure on the southeastern Bering Sea shelf.

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