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Seasonal size composition and abundance distribution of *Euphausia pacifica* in relation to environmental factors in the southern Yellow Sea

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Abstract

The seasonal size structure and spatial abundance distributions of *Euphausia pacifica* populations were investigated in the central part of southern Yellow Sea from August 2009 to May 2010. The abundance and biomass of *E. pacifica* were higher in spring and summer, and lower in autumn and winter. The mean abundance and biomass (calculated by carbon) were 74.94 ind./m^3 and 8.23 mg/m^3, respectively. Females with total length (*TL*) ranging between 10 and 19 mm in summer had a substantial contribution to the population biomass, whereas larvae of *TL* of 3–7 mm in spring were the main contributor to the population abundance. The sex ratio (female:male) showed a female bias in four seasons. Its value peaked in summer, and then decreased in autumn, spring, and winter successively. Cohort analysis revealed that the length-frequency distribution of *E. pacifica* could be characterized as one group with large animals (mean TL>12 mm) accompanied by one or two subgroups of small individuals (mean TL<7 mm). Regarding the spatial distribution, juveniles and adults of *E. pacifica* tend to concentrate in relatively deep water with low temperature (~11°C) and high salinity (>32), whereas its larvae showed more abundance in inshore water with rich chlorophyll *a*, low salinity (<32), and warm temperature (>11°C), especially in summer and autumn. Associations changed seasonally between stage-specific abundance and environmental factors.

Key words: spatial distribution, size composition, biomass, *Euphausia pacifica*, Yellow Sea

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1 Introduction

Within the North Pacific Ocean, *Euphausia pacifica* Hanson is a predominant and widely distributed temperate species of euphausiid krill (Boden et al., 1955; Brinton et al., 2000). It is not only the primary phytoplankton grazer (Ohman, 1984), but also a key trophic link between primary production and top predators. An interesting feature of the species population is flexible seasonality, such as, the species have spawning durations that range from one single season in February or May in the Toyama Bay of Japan (Iguchi et al., 1993), to two or more continuous seasons extending from March-September off the Oregon coast (Feinberg and Peterson, 2003), May through August in the Gulf of Alaska (Pinchuk et al., 2008), or April-May and August-September in the Oyashio region (Kim et al., 2009) to year-round off of the southern California (Brinton, 1976). In addition, the longevity of *E. pacifica* varies from 6 months in southern California to 2 years in the North Pacific (Siegel and Nicol, 2000). Moreover, the biomass of the species varies from 38 mg/m^3 in Baja California to 2 025 mg/m^3 off the Saanich Island, Canada as compiled by Taki (2006).

The Yellow Sea, surrounded by the Chinese Mainland and Korean Peninsula, is a highly active marine ecosystem, but it has been intensively altered by human activities. In the central part of the region, *E. pacifica* is the only dominant species of euphausiid throughout the year (Cai, 1986; Wang et al., 2003; Yoon et al., 2006). It is not only the key second producer accounting for over 60% of the total biomass of large crustacean zooplankton (Sun et al., 2011), but also one of the major prey items for upper trophic level fishes (Xue et al., 2004; Zhang, 2007). Thus, there have been numerous studies of *E. pacifica* in the Yellow Sea, including studies of seasonal spatial distributions (Yoon et al., 2000, 2006; Wang et al., 2003), population structure and reproduction (Sun et al., 2011; Feinberg et al., 2013), and vertical distribution and diurnal vertical migration (Wang and Zuo, 2004; Liu and Sun, 2010). Some unique characteristics of *E. pacifica* in the Yellow Sea have been clarified, such as having the largest brood size and smallest total length of females (Feinberg et al., 2013), and two spawning seasons from March to late June and early August of summer (Sun et al., 2011). Despite the importance of *E. pacifica* in the Yellow Sea, comprehensive information on its

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body size data is absent, even though it is essential to appreciate its lifecycle (Taki, 2004, 2006; Kim et al., 2009, 2010). In this study, we performed a more concerted analysis on the seasonal size variations of *E. pacifica* in the southern Yellow Sea, based on recent field data of four consecutive seasons from August 2009 to May of 2010. First, we examined the seasonal patterns of stage-specific abundance in relation to environmental variables and characterized the population structure of the species. Second, we explored the seasonal size distribution of *E. pacifica* based on length-frequency cohort analysis, which might be helpful in the further research of the euphausiid lifecycle in the Yellow Sea.

2 Data and methods

2.1 *Field sampling*

Four cruises were conducted separately during late summer (August 21 to September 3, 2009), mid-autumn (October 11 to 24, 2009), mid-winter (January 5 to 20, 2010), and late spring (May 17 to 27, 2010) onboard the R/V *Beidou* in the central part of the Yellow Sea. Water depth of sampled stations ranged mostly between 50 m and 80 m, with a mean value of 63 m. The samplings were continuous along zigzag-cruising survey transects illustrated at more than thirty stations (Fig. 1). The sampling time interval between adjacent stations was 4–6 h. At each station, the euphausiid samples were towed vertically from 2 m above the bottom to the surface mainly with a conical plankton net of 500 μm mesh size and 80 cm mouth diameter. Considering the net efficiency, data of small specimens (body length<2 mm) were supplemented from samples collected using a 160 μm mesh size conical plankton net (50 cm mouth diameter). Collections of euphausiids were preserved in 5% buffered formalin seawater immediately after coming on deck. Temperature and salinity were obtained with a Seabird 19-plus CTD profiler. The chlorophyll *a* (Chl *a*) concentration of surface seawater at each station was measured fluorometrically (Turner Designs AU-10) using standard technique (Strickland and Parsons, 1972).

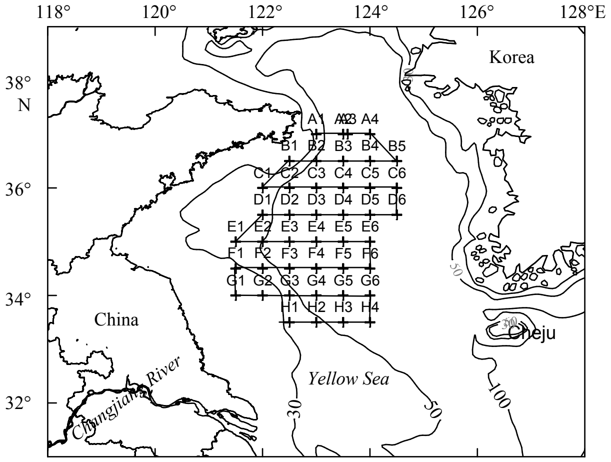


Fig. 1. Map of transects and stations sampled in the central part of the southern Yellow Sea.

2.2 *Biological measurements*

Euphausia pacifica samples were sorted, measured, and staged under 20× Nikon stereoscopic microscopes in the lab. When a given stage was abundant, the samples were divided with aliquots splitter until the last subsample contained at least 30 individuals of each given stage. Nauplius, calyptopis, and furcilia of larval stages were identified, and their total length (*TL*, mm) was measured according to Suh et al. (1993). Adult were distinguished from juveniles regardless of the presence of a thelycum in female or a petsma in male. No eggs were observed due to technical difficulties. The *TL* of juveniles and adults was defined as the lateral distance from the tip of the rostrum to the distal end of the telson (excluding spines) to the nearest 0.1 mm. Abundance was presented as the number per cubic meter of water (ind./m^2). The individual biomass (carbon content, *C*) of *E. pacifica* was estimated from the empirical equation between length and dry weight (*DW*, mg): $DW=9.954\times10^{-4}\ TL^{3.156}$ (Iguchi and Ikeda, 1995), and the carbon content conversion factor of 0.375–0.432 (Iguchi and Ikeda, 1998).

2.3 *Statistical analysis*

Due to uneven spatial distribution of stage-specific data, analysis of variance (ANOVA) was conducted to test the differences of stage-specific abundance among seasons, locations, and sampling time.

For the cohort analysis of size distribution, the "Mixdist" package in the R statistical software (http://cran.r-project.org) was applied by fitting finite mixture distribution models (Macdonald and Green, 1988). The range of *TL* from 0.5 to 25.3 mm was binned into 1–26 size classes by 1 mm increments. No separation of data into stages or sex was made when fitting the normal distribution curve. The original abundance data (as frequency data) were averaged over stations for each survey, then root transformed to acquire the most optimal model fit with $p>0.5$ in analysis of variance of the fitting model.

Canonical correspondence analysis (CCA) was conducted using CANOCO 5.0 (Ter Braak et al., 2012) to determine the best explanatory environmental variables for the stage-specific abundance of *E. pacifica*. For valid matrics, only stations where at least two developmental stages of *E. pacifica*, or only developmental stages that occurred in at least two stations in any month, were included in the analysis. The environment variables included sampling time (day/night), surface seawater temperature (SST), bottom seawater temperature (BST), and surface seawater salinity (SSS), bottom seawater salinity (BSS), and Chl *a* concentration.

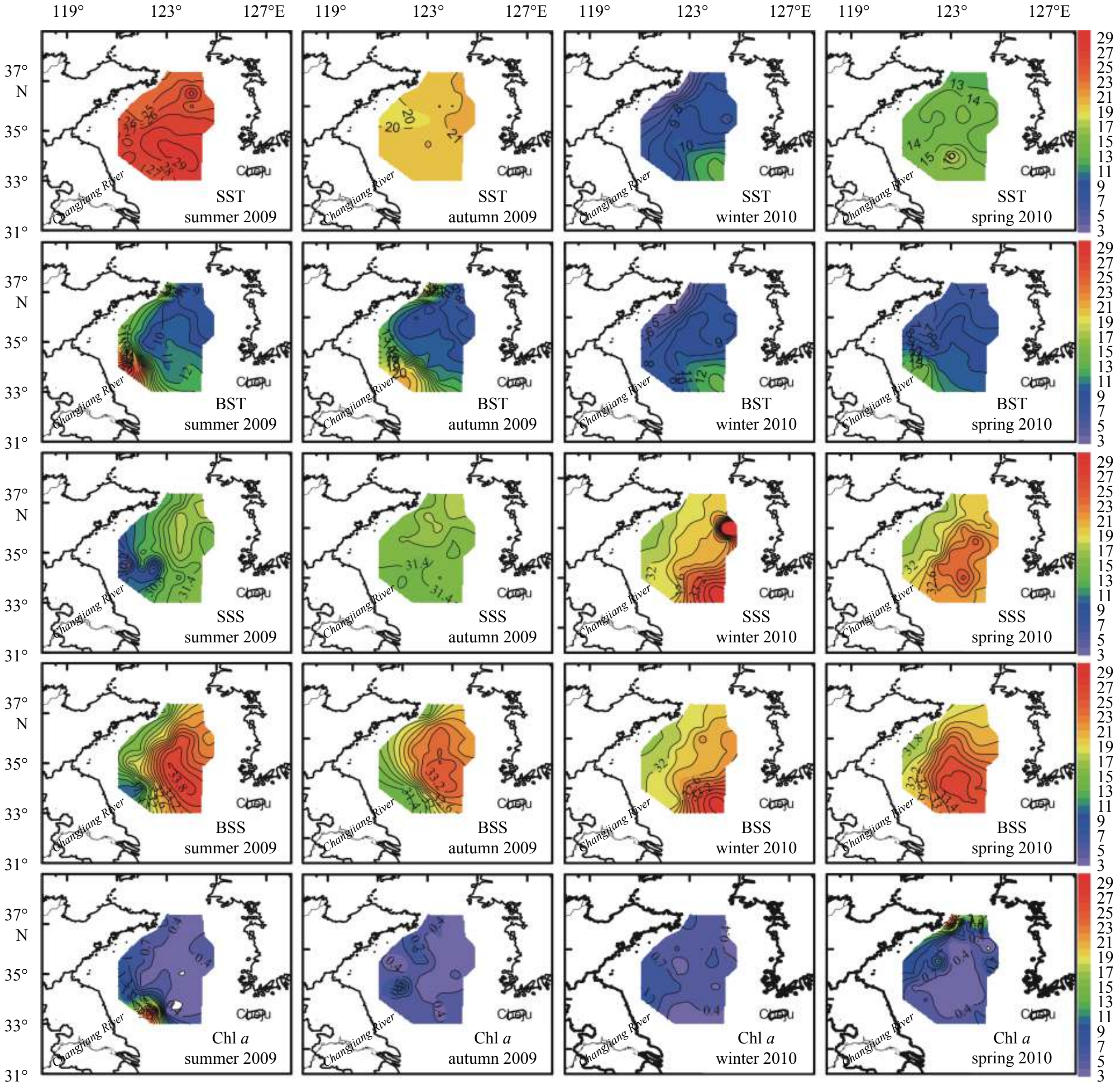
3 Results

3.1 *Hydrography*

During late spring to autumn, there was pronounced stratification in the survey area, as a result of warm (>10°C) and low saline (<32) surface seawater, and cold (<10°C) and high saline (>33) bottom seawater (Fig. 2). In winter, there was little difference intemperature and salinity between the surface and bottom water. Very high saline sea water (>34) was confined to stations in the southeastern corner of the survey area. The Chl *a* concentration was lower (<0.7 mg/m^3) in the central part, while it was relatively higher (>2.5 mg/m^3) in the northern part area in spring and the southern part in summer.

3.2 *Abundance, sex ratio and biomass*

The stage-specific abundances of *E. pacifica* had no significant differences between the sampling times (Kruskal-Wallis, $p>0.05$). Thus, all the data were pooled in the following analysis. The mean value of *E. pacifica* total abundance over four seasons was (74.94±189.35) ind./m^3. The seasonal mean abundance varied significantly (ANOVA, $p<0.001$). It peaked in spring, then dropped in summer, autumn and winter successively (Table 1).



SST summer 2009
SST autumn 2009
SST winter 2010
SST spring 2010
BST summer 2009
BST autumn 2009
BST winter 2010
BST spring 2010
SSS summer 2009
SSS autumn 2009
SSS winter 2010
SSS spring 2010
BSS summer 2009
BSS autumn 2009
BSS winter 2010
BSS spring 2010
Chl *a* summer 2009
Chl *a* autumn 2009
Chl *a* winter 2010
Chl *a* spring 2010

Fig. 2. Surface seawater temperature (SST, °C), bottom seawater temperature (BST, °C), surface seawater salinity (SSS), bottom seawater salinity (BSS), and Chl a concentration (mg/m^3) in the central part of the Yellow Sea during summer and autumn 2009, and winter and spring 2010.

Table 1. Mean abundance (ind./m^3) and biomass (mg/m^3) of *E. pacifica* larvae, juveniles and adults in summer and autumn 2009, and winter and spring 2010 in the southern Yellow Sea

	Season	Female	Male	Juvenile	Furcilia	Calyptopis	Nauplius	Total
Abundance	summer	8.44±19.59	0.84±1.34	0.84±2.54	1.33±3.76	0.78±2.65	<0.01	12.24±21.11
	autumn	0.73±1.00	0.43±0.63	<0.01	0.12±0.51	0.12±0.72	<0.01	1.39±1.91
	winter	0.84±1.00	0.79±0.85	0.02±0.05	0.10±0.30	<0.01	<0.01	1.75±1.79
	spring	0.46±2.11	0.37±1.21	4.61±11.06	243.98±270.61	21.25±32.04	0.54±3.36	271.22±292.50
Biomass	summer	11.74±27.21	1.34±2.23	0.44±1.63	0.03±0.06	<0.01	<0.01	13.65±29.03
	autumn	1.46±2.27	0.90±1.53	<0.01	<0.01	<0.01	<0.01	2.36±3.63
	winter	1.49±1.63	1.40±1.57	0.01±0.03	0.01±0.05	<0.01	<0.01	2.91±3.07
	spring	0.68±1.39	0.53±1.34	1.47±3.61	10.36±13.37	0.07±0.12	<0.01	13.11±14.30

The estimated biomass of *E. pacifica* was higher in summer and lower in autumn, with a mean of (8.23±17.41) mg/m^3 over four seasons.

Sex ratios (female:male) of *E. pacifica* were female-biased with a mean of 1:0.21 throughout the four seasons. It was 1:0.09 in summer, 1:0.58 in autumn, 1:0.76 in spring and 1:0.95 in winter. The differences in sex ratios among the four seasons were significant (ANOVA, $p<0.001$).

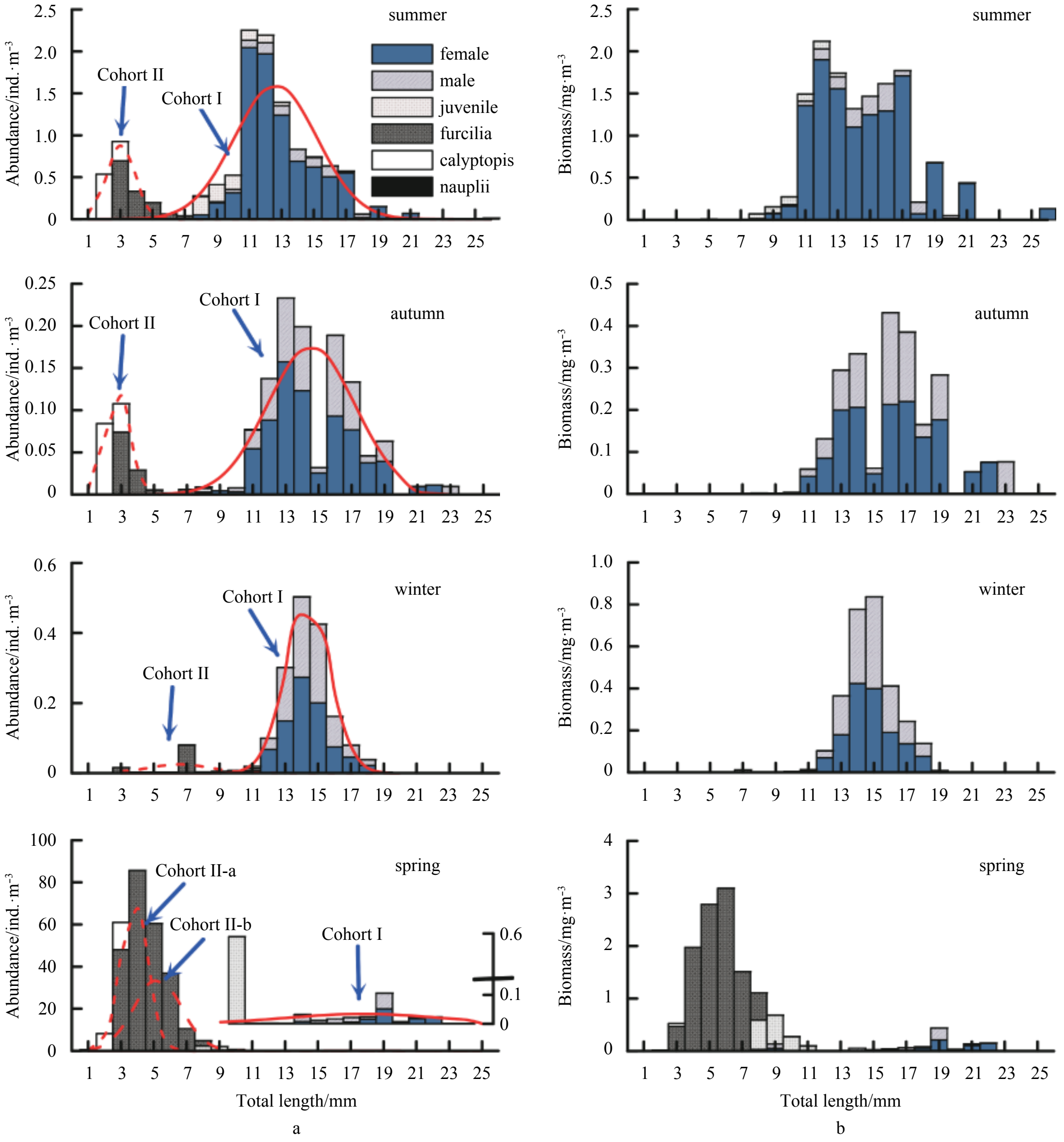
3.3 *Size composition of E. pacifica*

Maximum *E. pacifica* sizes were found to be 22.05 mm for males in autumn and 25.03 mm for females in summer. The euphausiid size width of 3–19 mm in winter was relatively narrow with the lowest size upper limit over the study period. The *TL* of males occupied smaller size classes of 8–19 mm, whereas females were distributed mostly over a larger *TL* size width of 17–24 mm. As shown in Table 1 and Fig. 3a, furcilia and calyptopis of larvae with *TL* of 3–7 mm were the main contributors to the total abundance in spring. Adults with *TL*>10 mm were over 85% of the total abundance from summer to winter. Notably, females in summer accounted for 72% of the season's total abundance. Similar to total abundance, females with *TL*>10 mm in summer and furcilia of larvae with *TL*<7 mm in spring were the main contributors to the total biomass (Fig. 3b).

Cohort analysis results (Figs 3a and 4) revealed a bimodal fitted pattern for *E. pacifica* size distributions, with one large size (mean length>12 mm) mature group (Cohort I) and a small size (<6 mm) immature group (Cohort II) in summer, autumn and winter. However, in spring, the immature group Cohort II can be divided further into two subgroups, Cohort II-a and II-b. According to the mode means illustrated in Fig. 4, the individuals from similar cohorts were larger in spring and winter, and smaller in summer and autumn. The *TL* of stage-specific *E. pacifica* changed seasonally. Of the stages, females showed a sharp *TL* fluctuation, with the largest in spring and the smallest in summer.

3.4 *Spatial distribution*

The stage-specific abundance of *E. pacifica* varied seasonally and geographically (Fig. 5). In spring, furcilia and calyptopis of larvae were abundant in the north of the area, especially at Sta. D4, adults were most dense in the center part of the area. In summer juveniles and female concentrated in the central of study area, while larvae were more abundant at Stas F1, G2, G3, and



a

b

Fig. 3. Length-frequency distributions and stage compositions of *E. pacifica* abundance (a) and biomass (b) in the central part of the southern Yellow Sea during August and October 2009, and January and May 2010. Hypothetical abundance distribution curves of each cohort are superimposed on the figure in a.

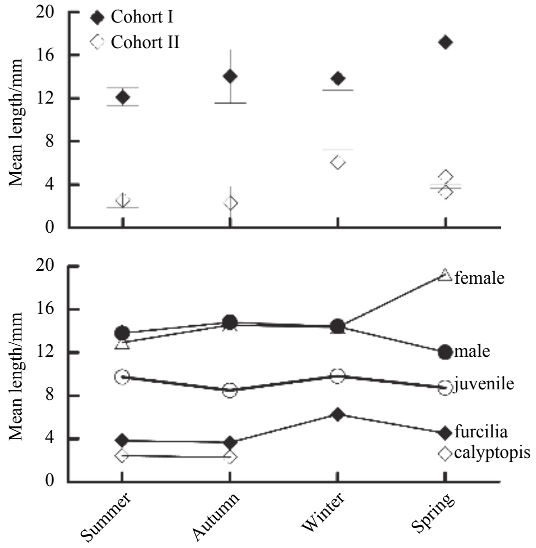


Fig. 4. Seasonal variability of mean total length of each stage and cohort of *E. pacifica* estimated by length-frequency distributions in Fig. 3a. Error bars: standard deviation.

H2. In autumn and winter, the density center of *E. pacifica* moved to the southern part of the area, which was mainly contributed to by females and juveniles.

Associations between stage-specific abundance and environmental factors changed with the season in regard to CCA results (Fig. 6). From the vector distances on the plots (Fig. 6), BST showed the highest variance and was very close to larvae in summer and autumn. Chl *a* had noticeable loadings only in spring and winter. The relative vector distributions of adults and larvae had slight relevance between them. Significant correlations (Table 2) included the abundance of the larva (including furcilia, calyptopis and nauplius) correlated with Chl *a* and BSS positively, and with BSS and SSS negatively in summer. The abundance of females and males correlated positively with both water temperature and salinity in winter, while it only correlated positively with BSS in autumn. Additionally, males were negatively correlated with Chl *a* in winter. There was also a positive correlation between juvenile abundance and BSS in spring.

4 Discussion

4.1 *Sampling time*

Euphausiids conduct strong vertical migration in pelagic wa-

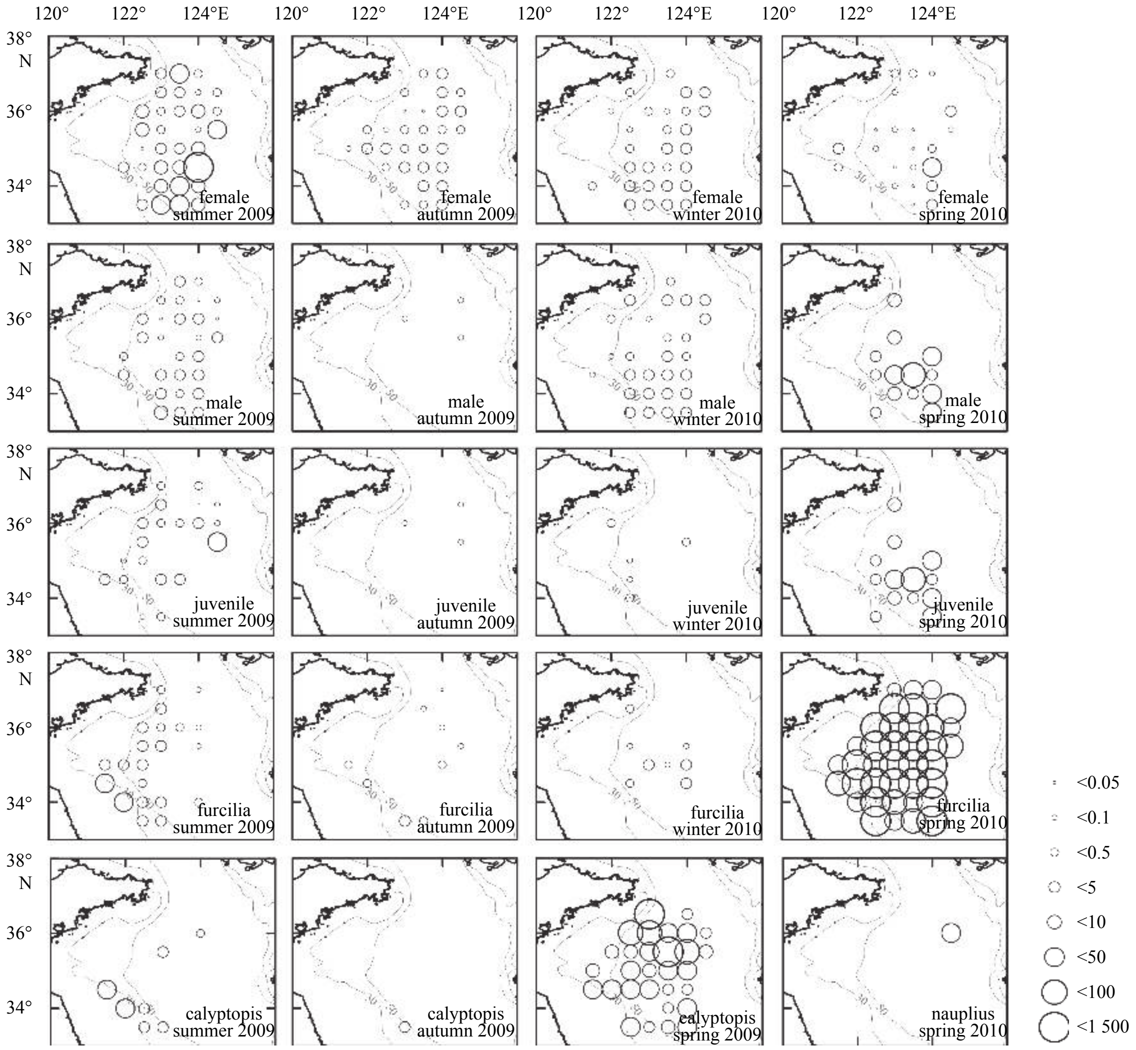


Fig. 5. Spatial abundance (ind./m^3) distributions of *E. pacifica* nauplii, calyptopis and furcilia, juveniles, females, and males in the central part of the southern Yellow Sea during August and October 2009, and January and May 2010.

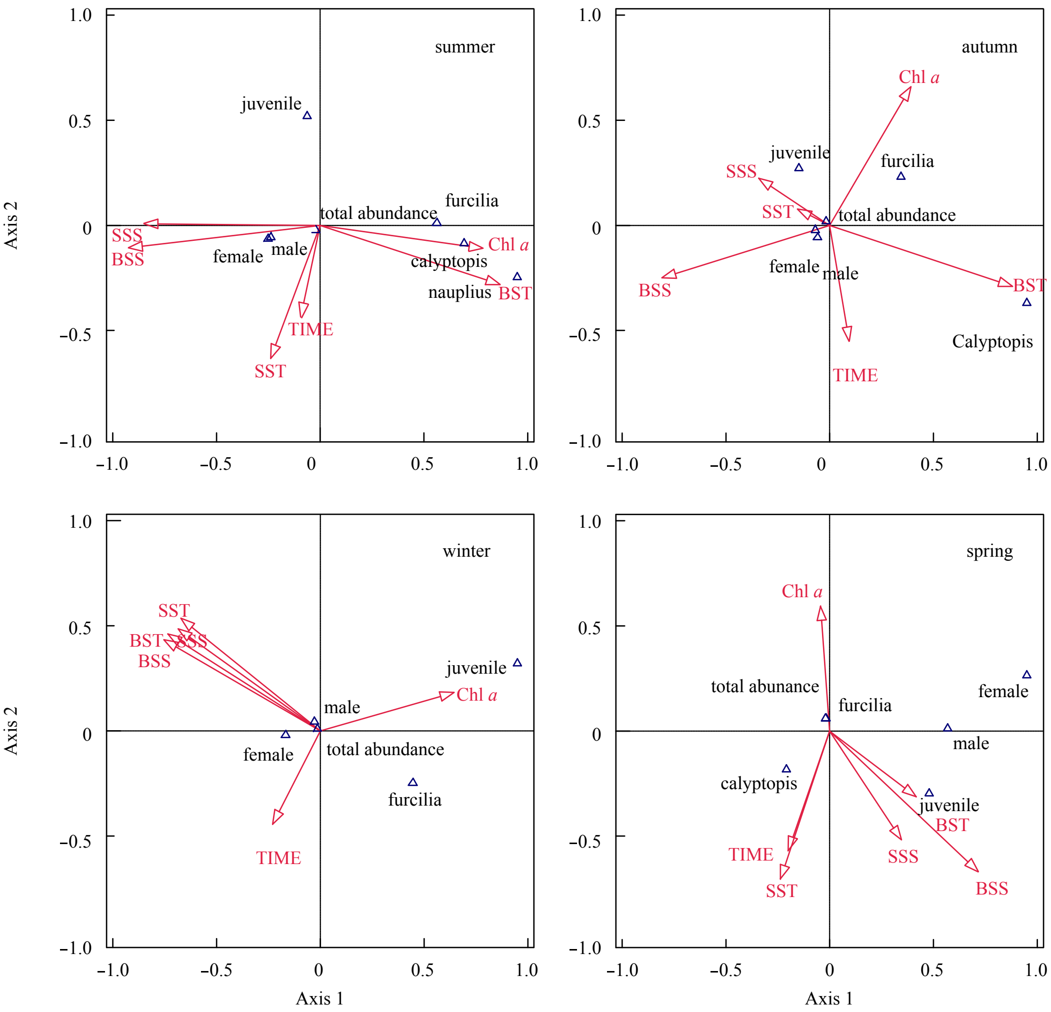


Fig. 6. CCA diagram of *E. pacifica* abundances and environmental factors in the central part of the southern Yellow Sea. SST represents surface seawater temperature, BST bottom seawater temperature, SSS surface seawater salinity, BSS bottom seawater salinity, TIME sampling time, and Chl *a* chlorophyll *a*.

ters (Liu and Sun, 2010). We note the existing biases by the sampling time and the potential impacts on abundance estimates for *E. pacifica* (Yoon et al., 2000; Taki, 2008, 2010). Thus, variance analysis among sampling times was performed before the spatial abundance and size distribution analysis. The sampling time may not present obvious influences on the results for the following two reasons. First, our samples being randomly collected over a broad study region during the day and at night may blur the day/night patterns in contrast to frequent sampling at fixed sites. Second, our sampling of the whole water column covering most water layers of *E. pacifica* distribution is likely to mitigate the potential variance from vertical diurnal migration.

4.2 *Stage and size composition*

In the southern Yellow Sea, the population recruitment of *E. pacifica* usually occurs intensely and extensively in spring, as the species' spawning season begins as early as March and ends between June and early August (Sun et al., 2011). From our results, in May of late spring, the abundance of *E. paciifca* peaked, female individuals in our samples were often observed to be gravid and larger compared to other seasons. Also, there was relatively high proportion of adult males, which could benefit reproduction. In addition, calyptopis and furcilia of larvae were abundant throughout the study area, and were the major components of the population. The median developmental time from egg to calyptopis is less than 18 d (Ross, 1981; Feinberg et al., 2006), and that from egg hatching to the late furcilia stage is about 38–43 d at 8°C or 10.5°C (Ross, 1981; Feinberg et al., 2006). Considering the above, May of late spring in this study could be in the season of later spawning and rapid population recruitment of *E. pacifica*, consistent with Sun et al. (2011). The remarkable female-biased sex ratio in summer may result from high mortality of males after the end of reproduction season (Taki, 2010).

In contrast, from summer to winter, *E. pacifica* was far lower in abundance than those in spring (Table 1), and its adults were smaller than those in spring (Cohort I in Fig. 4). The small adults may be due to seasonal growth stagnation and slow development, which has also been observed in the Japanese Sea and Yellow Sea (Iguchi et al., 1993; Yoon et al., 2000; Taki, 2004). The long period of slow development has been suggested to be advantageous for individuals to overwinter and reach the adult stage at a larger size for reproduction in the following year (Feinberg et al., 2006). In addition, most of the late furcilia from summer to winter in Cohort II were unlikely to have originated from eggs hatched during the concurrent month, given the 38–43 d of

Table 2. Pearson's correlations between the abundance of stage specific *E. pacifica* and environmental variables

Stage	Season	Chl *a*	SST	SSS	BST	BSS
Total abundance	summer	–0.04	0.24	–0.08	0.03	0.09
	autumn	–0.09	0.19	–0.27	0.01	0.21
	winter	–0.40[1]	0.42[1]	0.40[1]	0.42[1]	0.51[1]
	spring	–0.26	0.11	0.14	–0.17	0.13
Female	summer	–0.17	0.27	0.10	–0.14	0.29
	autumn	–0.16	0.28	–0.17	–0.22	0.49[1]
	winter	–0.34	0.50[1]	0.39[1]	0.50[1]	0.53[1]
	spring	–0.06	–0.18	0.06	0.08	0.23
Male	summer	–0.21	0.14	0.10	–0.15	0.16
	autumn	–0.15	0.20	–0.16	–0.17	0.40[1]
	winter	–0.45[1]	0.35	0.43[1]	0.35[1]	0.48[1]
	spring	–0.08	–0.08	0.16	0.06	0.23
Juvenile	summer	–0.07	–0.13	0.02	–0.18	0.02
	autumn	–0.06	0.30	0.12	–0.24	0.07
	winter	0.26	–0.20	–0.17	–0.24	–0.18
	spring	–0.18	0.10	0.36[1]	0.16	0.47[1]
Furcilia	summer	0.50[1]	–0.03	–0.59[1]	0.61[1]	–0.62[1]
	autumn	0.02	–0.03	–0.19	0.28	–0.25
	winter	0.01	–0.12	–0.10	–0.12	–0.08
	spring	–0.19	0.24	–0.06	–0.22	–0.10
Calyptopis	summer	0.40[1]	–0.04	–0.62[1]	0.61[1]	–0.60[1]
	autumn	0.02	–0.03	–0.19	0.28	–0.25
	winter	–	–	–	–	–
	spring	–	–	–	–	–
Nauplius	summer	0.86[1]	–0.17	–0.07	0.10	–0.11
	autumn	–	–	–	–	–
	winter	–0.19	0.24	–0.06	–0.22	–0.10
	spring	–	–	–	–	–

Note: [1] Significant at p<0.05.

development needed (Ross, 1981; Feinberg et al., 2006). Thus, it seems that the period from summer to winter cannot be rapid growing period for the *E. pacifica* population in the southern Yellow Sea.

Even if cohort analysis provides a synoptic depiction of the population structure, the limitations on determining the age and growth rate exist given the long and uneven sampling intervals (2–4 months) in this study. A single size bin may contain individuals that differ in age by several months and perhaps even longer. Overlapping could increase with extension of the spawning time (Yoon et al., 2000). Therefore, more frequent sampling or alternative biochemical aging techniques like lipofuscin (Harvey et al., 2010) may be needed for further research on the *E. pacifica* lifespan in the Yellow Sea.

4.3 *Biomass estimation*

The biomass of *E. pacifica* has been evaluated in many regions (Iguchi and Ikeda, 1999; Siegel and Nicol, 2000; Taki, 2006; Kim et al., 2009). Our estimated mean biomass of *E. pacifica* in the central part of the Yellow Sea was higher than that off of northeastern Japan and the downstream California Current, but lower than that near the Saanich Island, Toyama Bay, off of Oregon in the upstream California Current (Taki, 2006), and the Oyashio region (Kim et al., 2009). Moreover, it was approximately 1.5 times greater than value estimated by Sun et al. (2010) for the same region. Our higher value may be due to individuals with *TL*<5mm in May and August not being included in Sun et al. (2010). Our results indicate that *E. pacifica* could contribute up to 50% of the total zooplankton biomass in the southern Yellow Sea as estimated by Huo et al. (2012). The high biomass percentage of *E. pacifica* as a secondary producer indicates the importance of the species for higher trophic predators in the Yellow Sea marine ecosystem.

4.4 *Correlations with environmental factors*

Associations changed seasonally between stage-specific abundance and environmental factors. In the Yellow Sea, temperature and salinity have been suggested to be the primary factors influencing spatial patterns of *E. pacifica* (Yoon et al., 2000; Sun et al., 2011). Our results showed that juveniles and adults tend to aggregate in the central part of the study region, and correlated negatively with BST and positively with BSS in summer and autumn. The distribution pattern was consistent with previous observations (Yoon et al., 2000, 2006; Wang et al., 2003; Wang and Zuo, 2004), which have been explained as a strategy for *E. pacifica* to avoid thermal damage of the surface water (Iguchi et al., 1993; Sun et al., 2011). But in winter and spring, adults tended to distribute in relatively warm (9–14°C) waters of the study area. Similarly, *E. pacifica* adults have been reported to limit their extension to <8°C of the northern water in February (Yoon et al., 2006). Unlike adults, the furcilia and calyptopis of larvae were more abundant in warmer (>11°C), less saline (<32) water, verifying their inclination to be in the upper water layer (Liu and Sun, 2010). Surface water conditions have remarkable influence on the juvenile distribution in spring. Moreover, the Chl *a* concentration had some impact on the *E. pacifica* distribution. As shown in Figs 5 and 2, high abundance of *E. pacifica* larvae often occurred in Chl *a*-rich waters, similar to the findings by Yoon et al. (2000) and Sun et al. (2011), and especially in summer, larvae had a remarkably positive correlation with Chl *a*.

5 Conclusions

Euphausia pacifica is a major contributor to the total zooplankton biomass in the Yellow Sea pelagic ecosystem, and showed seasonal variations in regard to size structure and stage composition. A female-biased sex ratio remained throughout the study period. Larvae in spring and adults in summer became the largest contributors to population abundance and biomass, respectively. In *E. pacifica* population, larger individuals presented in winter and spring, and smaller in summer and autumn.

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