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# Changes in the population structure of *Calanus sinicus* during summer–autumn in the southern Yellow Sea

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## Abstract

*Calanus sinicus* is a calanoid copepod widely distributed in coastal waters of China and Japan, and over-summering strategies may have major impacts on their population dynamics which in turn affect local marine food web structure. The abundance, stage composition, and sex composition of the planktonic copepod *C. sinicus* were studied from August to October 2002 in the southern Yellow Sea to understand how its population recovers from the over-summering state. Results showed that *C. sinicus* had low reproduction in August due to high temperature, except in waters near the Cheju Island with rich food and moderate bottom temperature, but the reproduction rates here decreased in September–October as food availability declined. When temperature dropped in September–October, *C. sinicus* actively propagated in coastal shallow waters. However, reproduction rates of *C. sinicus* individuals inhabiting the Yellow Sea Cold Water Mass (YSCWM) remained low during the three months of the study. The percentage of *C. sinicus* females was high during the reproductive period, which suggests that the sex composition of adult *C. sinicus* may reflect whether or not the population is in the reproductive mode. Numerous fifth copepodite stage (CV) *C. sinicus* aggregated in the YSCWM in a suspended developmental stage during the three months of this study, and they potentially served as the parental individuals for population development when conditions became optimal for reproduction later in the year.

**Key words:** *Calanus sinicus*, stage composition, sex composition, population structure, Yellow Sea Cold Water Mass, life history strategy

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## 1 Introduction

Copepods account for the greatest proportion of the total mesozooplankton biomass in the pelagic realm of the oceans and are the most abundant metazoans on the earth (Siokou-Frangou et al., 2010; Sun et al., 2010; Kiørboe, 2011; Huo et al., 2012). Copepods occupy a pivotal position in marine food webs (Turner, 2004; Sampey et al., 2007). They have evolved many life history strategies, such as dormancy, diurnal vertical and seasonal migration, and alternative reproductive models (Bonnet et al., 2005; Niehoff, 2007; Baumgartner and Tarrant, 2017), to adapt to the environment and maintain their populations. Their population dynamics are sensitive to environmental changes (Beaugrand et al., 2002; Hays et al., 2005; Chivers et al., 2017), therefore understanding copepod population dynamics, key species in particular, can provide insights on marine ecosystem health and the potential impacts of climatic changes.

*Calanus sinicus* is widely distributed in shelf waters of the Northwest Pacific Ocean (Chen, 1964; Hulsemann, 1994). This ecologically important copepod is primarily herbivorous (Yang, 1997), and it serves as one of the major food sources of many commercially important fishes (Uye et al., 1999; Meng, 2003). *Calanus sinicus* was one of the target species of the China-GLOBEC Program (Sun, 2005), and understanding its population dynamics was a major focus of the study.

High summer temperature has detrimental effects on *C. sinicus* survival (Huang and Zheng, 1986; Pu et al., 2004a; Zhang et al., 2007). *Calanus sinicus* is common from late autumn to spring in waters of the Taiwan Strait and South China Sea (Lin and Li,

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1984; Chen, 1992; Hwang and Wong, 2005; Zhang and Wong, 2013). In the Yellow Sea, *C. sinicus* occurs throughout the year with two seasonal peaks in spring and autumn (Chen, 1964; Anon, 1977). The Yellow Sea Cold Water Mass (YSCWM), which is located near bottom of the central region of the Yellow Sea with low temperature and high salinity (Su and Weng, 1994), provides a refuge for *C. sinicus* to survive through summer (Wang et al., 2003).

Intensive studies of the over-summering strategy of *C. sinicus* in the Yellow Sea have been conducted (Li et al., 2004; Pu et al., 2004b; Sun, 2005). Low temperature and scarce food in the YSCWM induce diapause of *C. sinicus* at the fifth copepodite stage (CV) through the summer (Li et al., 2004; Pu et al., 2004b). During this period, *C. sinicus* has low metabolic and developmental rate and high survival rate (Li et al., 2004; Pu et al., 2004a), which helps maintain the population under adverse environmental conditions. However, what happens to the population between the over-summering period and the autumn peak period and its main trigger(s) have not been investigated.

In the Yellow Sea, the population structure of *C. sinicus* has only been studied for the whole region (Chen, 1964) or for a single month (Pu et al., 2004a; Wang et al., 2009), while few researches focus on monthly changes of population structure in specific regions. In this study, ten stations spanning the southern Yellow Sea were sampled from August to October. Pu et al. (2004b) divided the ten stations into three regions—the northwest costal region, the YSCWM region, and the southeast region, as both physical environment and the ecological and physiological features of *C. sinicus* significantly differed among three regions in August 2002. In the present study, we focused on changes in the population structure of *C. sinicus* in different regions of the southern Yellow Sea when the YSCWM gradually decays.

To investigate how the *C. sinicus* population recovers from the over-summering state, we examined the abundance, stage composition, and sex composition of *C. sinicus* in regions with different environments. Our objectives are to: (1) explore the population structure changes of *C. sinicus* from August to October among different regions, and (2) test the hypothesis that appropriate temperature together with high food condition could induce over-summering *C. sinicus* to reproduce, which may provide insights on the population dynamics of this copepod.

## 2 Materials and methods

A transect (about 516 km total length) in the southern Yellow Sea with ten sampling stations was sampled in August 16–20, September 24–26, and October 22–24, 2002 (Fig. 1). At each station, zooplankton samples were collected using a 50-cm mouth diameter net with 160-μm mesh size, and the sampling times were random (day or night) because of ship-time constraints. The nets were towed vertically from about 4 m above the bottom to the sea surface at ~1 m/s. Samples were preserved in 5% neutral formalin seawater solution immediately after the nets were retrieved. To determine the characteristics of the vertical distribution of *C. sinicus*, water samples were taken at different depths (0, 5, 10, 20, 35, 50, 75 and 2–5 m from the bottom) at each station using a 59-L steel sampler, and the collected samples were filtered through a 38-μm mesh net (Liu et al., 2003). The retained copepods were preserved in 5% neutral formalin seawater solution. Each stage (from egg to adult) of *C. sinicus* collected by both samplers was identified and counted under a dissecting microscope in the laboratory. The abundance of *C. sinicus* at each station collected with the zooplankton net was expressed as ind./m$^2$. Based on the filtered water volume, the abundance of *C. sinicus* at each water depth was expressed as ind./m$^3$. The number of adult *C. sinicus* at each station collected by net was much larger than that using the steel sampler, so the sex composition was calculated based on net samples.

At each station, vertical temperature and salinity profiles were obtained by lowering a Sea-Bird CTD instrument (SBE-19) from the sea surface to near the sea bed. At the same time, water samples were taken at each depth (0, 10, 20, 30, 50, and 2–5 m from the bottom), then 500 mL of seawater from each depth were filtered onto a Whatman GF/F filter. Chlorophyll *a* concentration (Chl *a*) was determined fluorometrically using a Turner Designs Fluorometer after the filters were extracted with 90% aqueous acetone for 24 h.

The abundances of all stages (from egg to adult) of *C. sinicus* collected by net were used for detrended correspondence analys-

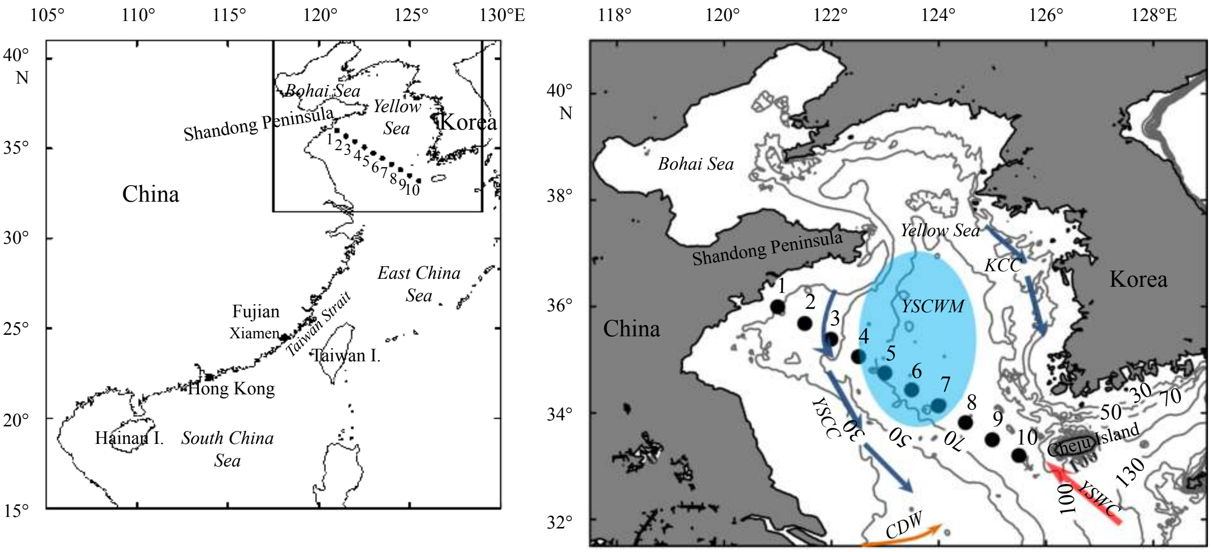

**Fig. 1.** Map of the study area and locations of the ten sampling stations. Contour lines indicate water depth (m). The arrows indicate the Yellow Sea Warm Current (YSWC), Yellow Sea Coastal Current (YSCC), Korean Coastal Current (KCC), and Changjiang Diluted Water (CDW); and the Yellow Sea Cold Water Mass (YSCWM) is indicated by shaded area.

is (DCA). Results showed that the longest gradient of all ordination axes was less than 3.0, which suggested that using linear method (redundancy analysis) is a better choice to summarize relations between multiple response variables and several predictors (Lepš and Šmilauer, 2003). Then the biotic and abiotic variables were subjected to redundancy analysis (RDA). The positions of sample points, and angles between arrows of stages and environmental variables in the ordination diagram could help identify relationships among the stations, the developmental stages of *C. sinicus*, and the environmental variables. Both DCA and RDA were conducted using Canoco 4.5.

## 3 Results

### 3.1 *Environmental conditions*

Figure 2 shows the vertical profiles of temperature, salinity and Chl *a* along the transect. In August, sea surface temperature (SST) at all stations was higher than 25°C, and a strong thermocline existed between 16 m and 40 m water depth. The YSCWM was located at the bottom of the central Yellow Sea, and two cold water masses with temperatures lower than 10°C were present at Stas 4 and 6–7. In September, SST dropped to 23°C, the mixed layer depth descended, and the thickness of the thermocline decreased to approximately 26–38 m depth. The water masses with temperatures lower than 10°C also got smaller. SST continued dropping in October and the thermocline became thinner, with the upper limit dropping to about 35 m depth. However, the influence of the Yellow Sea Warm Current water kept the sea bottom water temperature at stations near the Cheju Island relatively high (11–17°C) during all three months (Fig. 2a).

The water mass with salinity higher than 33 had the greatest spatial range in August, as it spanned Stas 4–10. As time progressed, the distribution of this water mass gradually decreased, spanning Stas 5–10 at the sea bottom in September and Stas 7–10 in October. Chl *a* concentration was low in the YSCWM (usually less than 0.2 mg/m$^3$). The Chl *a* concentration of the upper water was lower at the central part of the transect than at stations inshore and near the Cheju Island. The highest Chl *a* concentration (>4 mg/m$^3$) occurred at the 10 m water stratum at Sta. 9 in August.

### 3.2 *Abundance and stage composition of Calanus sinicus*

Figure 3 shows that the largest proportion of *C. sinicus* eggs occurred at Sta. 2 in August. From Sta. 2 to the central part of the transect (Stas 5–7) in August, the proportion of eggs decreased quickly, and the CV stage gradually dominated the population. The abundance of *C. sinicus* was relatively high along Stas 8–10 in August, and the proportion of eggs gradually increased with closer proximity to the Cheju Island. The abundance of *C. sinicus* was higher at Stas 2–6 in September compared with that in August, but it decreased at the other stations. In September, the proportion of eggs was higher at Stas 4–7 than that in August, and the proportion of CV was much lower at stations in the YSCWM and higher at inshore stations (Stas 1–2) than that in August. The abundance of *C. sinicus* was lower in October than in September as a whole, and adults occupied a greater proportion of the population in October than in the other two months. Eggs and nauplii dominated the population of *C. sinicus* at Stas 3–5 in October, and CV became the dominant developmental stage at Stas 6–7.

Figure 4 shows the sex composition of adult *C. sinicus*. No adults were sampled at Sta. 1 throughout the study. Overall, the proportion of females gradually increased from August to October. Females accounted for ⩽60% of adult *C. sinicus* at Stas 2–6 in August, Stas 5 and 9 in September, and Sta. 5 in October. The proportion of females at all other stations was higher than 77% throughout the study.

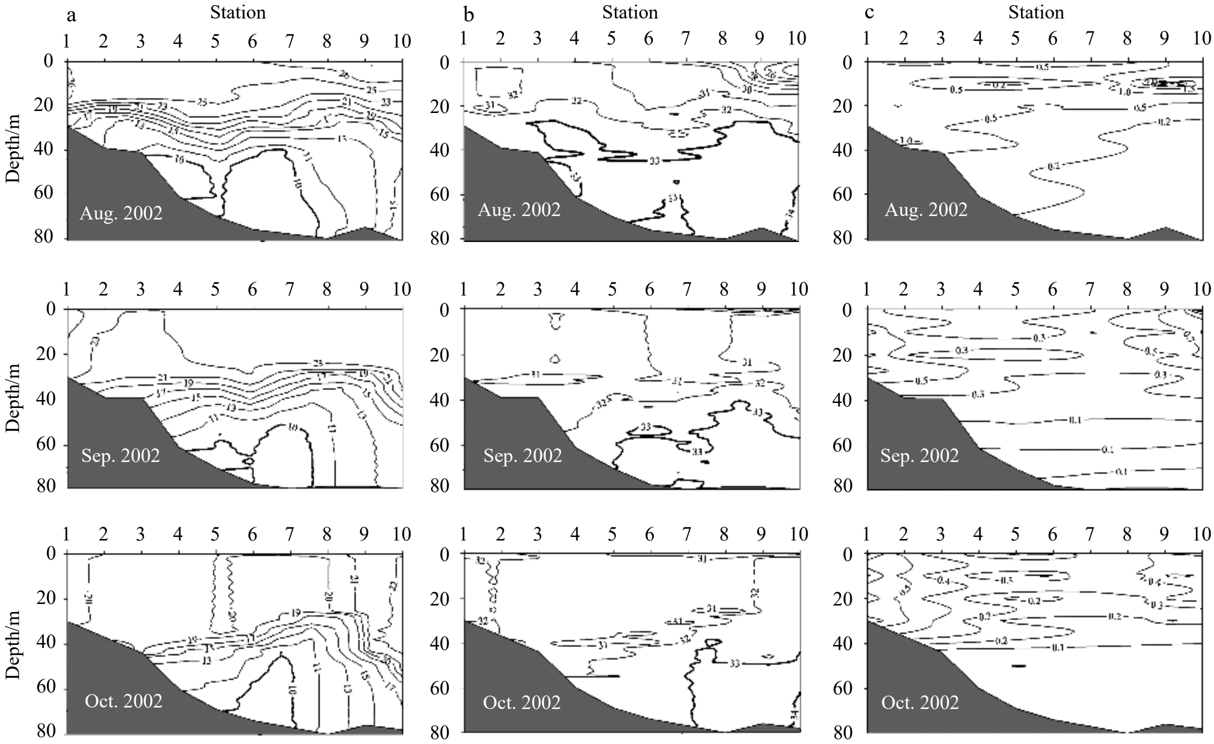

**Fig. 2.** Vertical profiles of temperature (a, °C), salinity (b), and chlorophyll *a* concentration (c, mg/m$^3$) along the transect from August to October 2002.

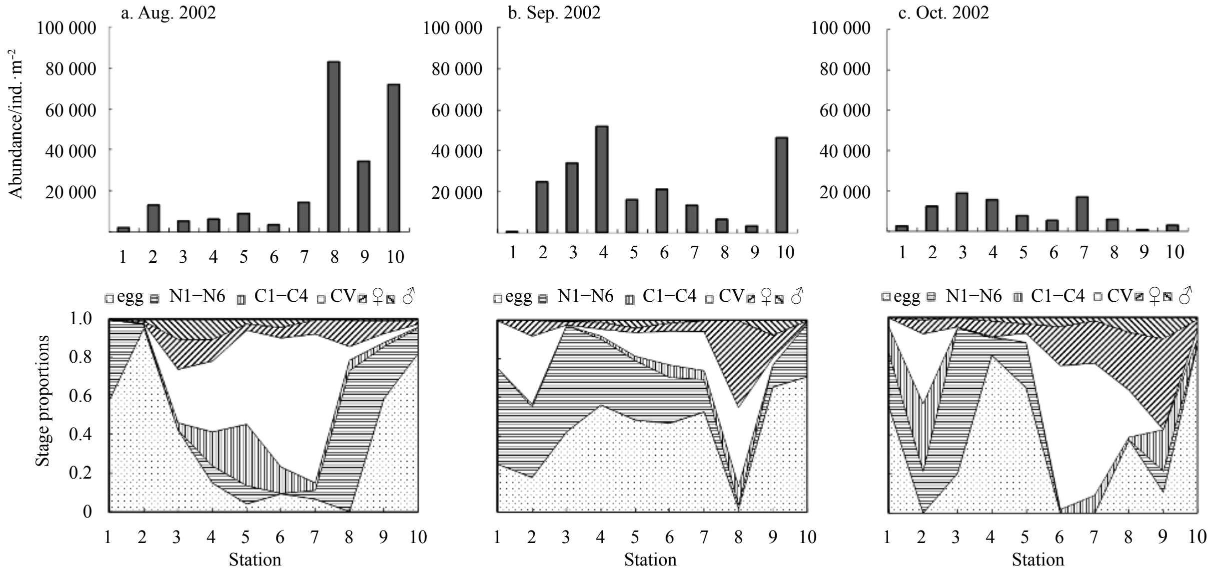

**Fig. 3.** Abundance and stage composition of *Calanus sinicus* along the transect in the Yellow Sea. a. August 2002, b. September 2002 and c. October 2002.

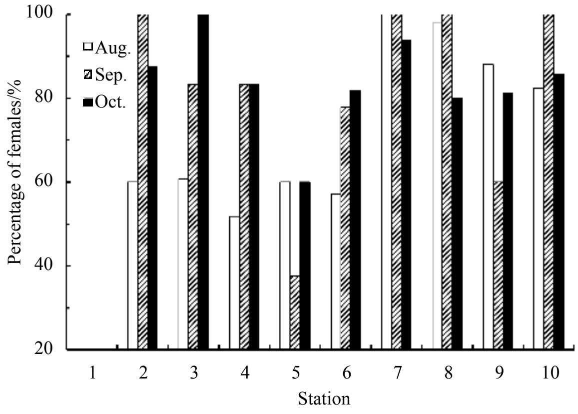

**Fig. 4.** Sex composition of adult *Calanus sinicus* along the transect from August to October 2002.

### 3.3 *Relationship between environmental factors and the abundance of Calanus sinicus*

RDA (Fig. 5) and Fig. 6 revealed that *C. sinicus* eggs and nauplii had a similar distribution pattern, and both developmental stages showed a positive relationship with SST. *Calanus sinicus* eggs and nauplii mostly occurred above the thermocline at Stas 8–10 in August–September, and in the coastal region (Stas 1–4) in September–October. Copepodid and adult *C. sinicus* had a similar distribution pattern, and both were negatively correlated with sea bottom temperature (SBT) and positively correlated with sea bottom salinity (SBS). The stations in the central part of the southern Yellow Sea (Stas 5–7) aggregated in Fig. 5, and were characterized by high SBS, low SBT, and high abundance of copepodid and adult *C. sinicus*. While other stations were widely distributed in the figure, with Stas 4 and 8 being located close to Stas 5–7. Stations 1–3 were characterized by low SBS, high SBT, and high Chl *a* concentration.

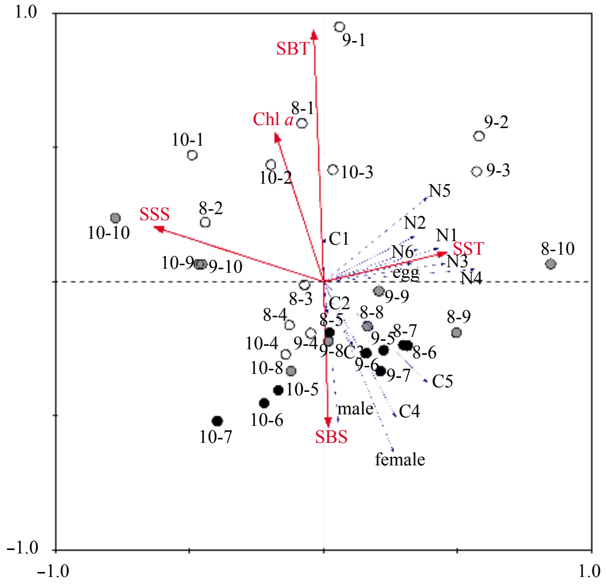

**Fig. 5.** Redundancy analysis results. The bold arrows represent the environmental factors, sea surface temperature (SST), sea bottom temperature (SBT), sea surface salinity (SSS), and sea bottom salinity (SBS); and chlorophyll *a* concentration (Chl *a*) represents the mean value for the water column calculated by trapezoidal integration. The thin arrows represent the developmental stages of *Calanus sinicus*, and the circles represent all stations. The number before "-" indicates month, and the number after indicates station. Different circle types represent stations in different regions.

## 4 Discussion

### 4.1 *Abundance changes of Calanus sinicus*

The changes of *C. sinicus* abundance exhibited different patterns spatially and monthly in the surveyed area. In the northwest coastal region (Stas 1–4), water had shallow depth, and the column was relatively well mixed. Since the upper thermal limit for *C. sinicus* is about 23°C (Huang and Zheng, 1986; Huang et al., 1993), the high SST and thin layer of cold bottom water in August in this region negatively affected the survival of *C. sinicus*, causing low abundances of all developmental stages (Figs 3 and 6). As

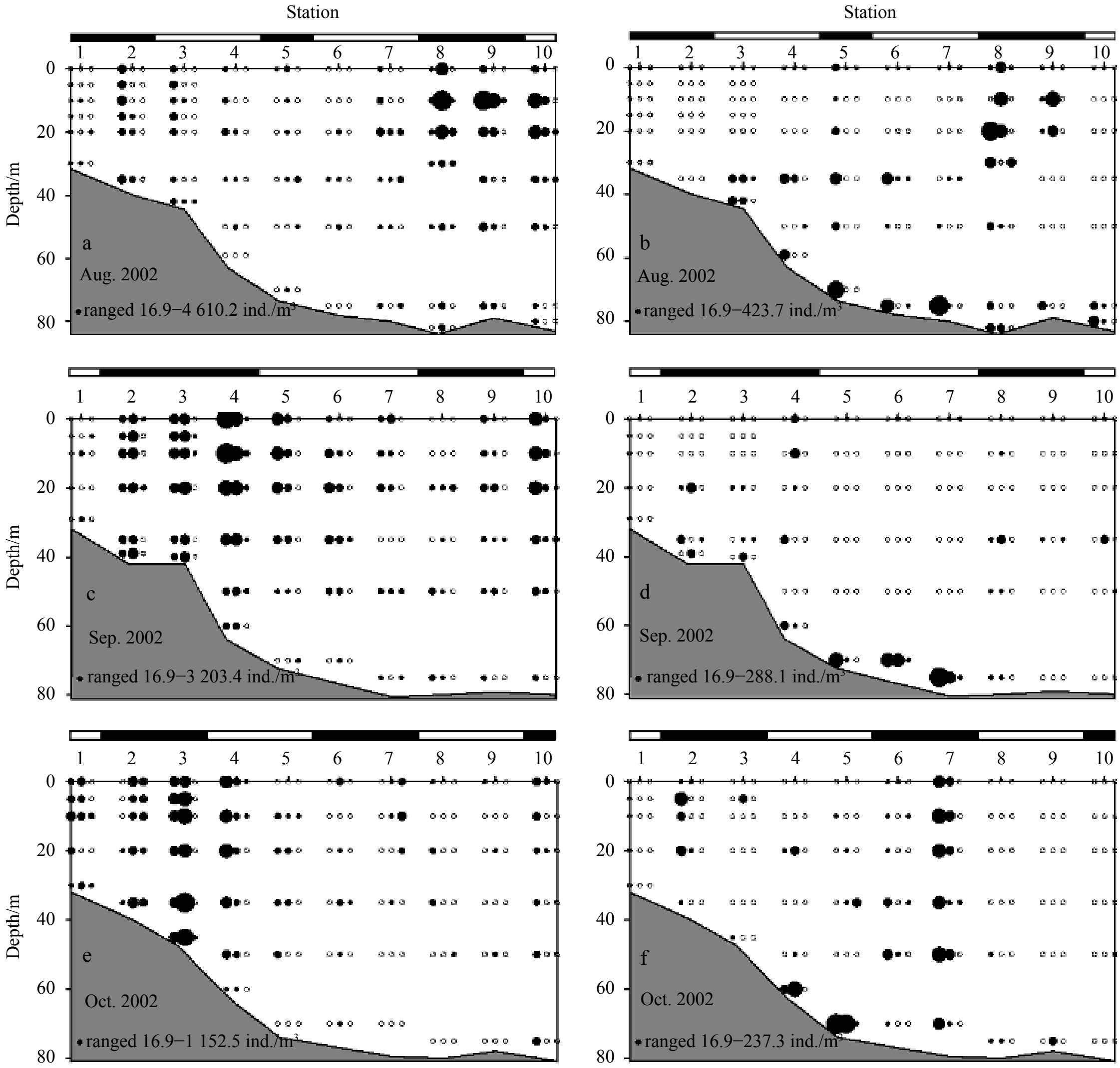

**Fig. 6.** Vertical distribution of *Calanus sinicus* (ind./m$^3$) in the southern Yellow Sea during August (a and b), September (c and d), and October (e and f) 2002. Eggs (left), N1–N6 (middle), and C1–C4 (right) of *C. sinicus* are shown in a, c and e. CV (left), female (middle), and male (right) of *C. sinicus* are shown in b, d and f. The white and black bars indicate day and night, respectively. Open circles represent that no individuals were sampled. Solid circle size represents abundance, which increases linearly with the pie area, and the range is shown in each figure.

the temperature decreased in September and October in this region (Fig. 2), conditions became beneficial for *C. sinicus* recruitment (Fig. 6), resulting in high abundance in the coastal region (Figs 3 and 6). The decreased abundance of *C. sinicus* in October might be due to the relatively high rate of mortality in shallow water (Uye, 2000).

The YSCWM is a prominent feature in the central part (Stas 5–7) of the southern Yellow Sea in summer (Su and Weng, 1994). Cold water with scarce food in the YSCWM induces *C. sinicus* CVs to remain suspended development (Li et al., 2004; Pu et al., 2004b), resulting in dominance of this stage in this region (Fig. 6). *Calanus sinicus* abundance exhibited relatively stable at Stas 5–7 from August to October (Figs 3 and 6). In the individual-based model of *C. sinicus* population dynamics in the central Yellow Sea, the population peaks in May–June and December–January (Wang et al., 2014b). The stable structure of the YSCWM maintains the *C. sinicus* population in summer–autumn, thus individuals are ready to reproduce when the environment becomes suitable during autumn–winter.

In the southeast region (Stas 8–10), the cool bottom water did not mix with hot surface water because of the thermocline, meanwhile, it was warmed by the Yellow Sea Warm Current (Pang and Hyun, 1998), resulting in moderate SBT in this region. Bottom water at the favorable temperature can increase molting rates of *C. sinicus*, induce reproduction (Pu et al., 2004b; Zhang et al., 2007), and protect *C. sinicus* from the hot SST. The suitable bottom water temperature and high Chl *a* concentration in August in the southeast region induced *C. sinicus* to recruit, resulting in high abundance of eggs and nauplii (Fig. 6). Along the same transect sampled in August 22–24, 2001, the abundance of *C. sinicus* in this region with lower Chl *a* concentration was less than that in this study (Pu et al., 2004a), suggesting the important role of food availability to *C. sinicus* population (Zhou et al., 2016). As the Chl *a* concentration decreased in September–October, the egg production rate of *C. sinicus* decreased (Uye and Murase, 1997), as well as the abundance of *C. sinicus* (Figs 3 and 6). In addition, horizontal transport by the Yellow Sea Warm Current may also affect the abundance of *C. sinicus* in this region in

September–October (Lü et al., 2013).

Tidal fronts in the Yellow Sea affect the distribution of Chl *a* concentration and *C. sinicus* population (Liu et al., 2002). Stations 4 and 8 were located at the edge of the YSCWM, with temperature fronts in the bottom layer (Fig. 2). The abundance of *C. sinicus* was high at Sta. 4 in September and at Sta. 8 in August, and high Chl *a* concentration occurred in the vicinity of the two stations (Figs 2 and 3), concurring with the findings in tidal front region (Liu et al., 2003). Stations 4 and 8 had similar environmental features but different abundances and population structures of *C. sinicus* compared with stations in the central part of the southern Yellow Sea (Stas 5–7) (Figs 3 and 5), suggesting the effects of hydrodynamics on copepod population.

### 4.2 *Sex composition of adults*

Sex ratio is a parameter that affects both the growth rates and the evolutionary trajectories of wild populations (Sapir et al., 2008). Although the sex ratio of CV *C. sinicus* is nearly 1:1, the female:male ratio of adult *C. sinicus* is very high during the reproductive mode (Chen, 1964). This pattern indicates that adult male individuals have a relatively short life span and that mass death occurs after maturation and mating (Lin and Li, 1984).

In the present study, the percentage of females was relatively low at Stas 2–6 in August and at Sta. 5 during all three months (Fig. 4), when the reproduction rates of *C. sinicus* were very low due to high temperature in August and the effect of the YSCWM, respectively (Pu et al., 2004b; Zhang et al., 2007). And *C. sinicus* actively propagated at Stas 8–10 in August and at Stas 2–4 in September–October (Fig. 6), when the percentage of females was relatively higher (Figs 4 and 6). These results indicate that the sex composition of adult *C. sinicus* may reflect whether or not the population is in the reproductive mode. The sex composition of adult *C. sinicus* at Stas 6–7 was not similar to that at Sta. 5, which may indicate that CV individuals at different stations in the YSCWM are not fully synchronous in development.

There is evidence in other copepods that sex determination depends on the environmental conditions experienced by individuals (Korpelainen, 1990). The skewed sex ratio of *C. sinicus* during periods of high reproduction may also be environmental sex determination, which needs more investigations in future studies to confirm.

### 4.3 *Life history strategies of Calanus sinicus during summer–autumn*

*Calanus sinicus* CVs dominated and remained suspended development in the YSCWM region (Stas 5–7) in August–October as an over-summering strategy, similar to over-wintering dormant *Calanus finmarchicus* (Hirche, 1996), to bridge periods of environmental harshness. However, when the appropriate environment appeared, *C. sinicus* outside the YSCWM actively propagated at Stas 8–10 in August and at Stas 2–4 in September–October, suggesting that the *C. sinicus* population can respond rapidly to environmental changes, and once exposed to favorable conditions, the population will quickly develop and expand (Wang, 2009).

Besides temperature, food availability is also an important factor that influences copepod reproduction (Uye and Murase, 1997; Ceballos and Álvarez-Marqués, 2006; Huo et al., 2008). In this study, *C. sinicus* reproduced actively only when temperature and prey availability were both appropriate. Interannual variability in phytoplankton blooms illustrates that the Chl *a* concentration is relatively high from September to May in the northwest coastal region, while high Chl *a* levels occur in March–May and after October in the central part of the southern Yellow Sea (Xu et al., 2013). Therefore, food availability in November–December induces *C. sinicus* to propagate in the central part of the southern Yellow Sea during a second reproductive period (Zhang et al., 2005).

Compared with individuals in the coastal region, *C. sinicus* in the YSCWM region have longer prosome length, higher dry weight, greater oil sac volume, and higher total lipid content (Pu et al., 2004b; Wang et al., 2009; Wang et al., 2014a). *Calanus sinicus* in the coastal region must actively feed to meet their metabolic needs and fuel reproduction during summer–autumn (Huo et al., 2008; Wang et al., 2014a), but the successful recruitment may be low as the deleterious effects of high temperature on egg production and hatching and the high mortality rate in shallow water (Uye, 2000; Zhang et al., 2007). Therefore, *C. sinicus* individuals in the YSCWM region may be more important for population development in autumn–winter because of high abundance, good physiological status, and ideal environmental conditions.

*Calanus sinicus* eggs and nauplii were abundant in September–October in the coastal region, which indicates that *C. sinicus* had entered in the reproductive period in this region. In contrast, the reproduction rates of *C. sinicus* in the YSCWM region are still low in September–October. When the YSCWM gradually decays in November–December, the Chl *a* concentration in the area is high (Xu et al., 2013), allowing *C. sinicus* CVs to molt, quickly propagate, and produce a peak of adults in November–December and a peak of eggs in December–January (Wang et al., 2014b). The new generation goes through winter and becomes the parental population during the spring reproductive period.

Prior to this study, what happens to the *C. sinicus* population between the over-summering period and the second reproductive period in autumn–winter in the Yellow Sea was poorly understood. The results of this study fill this gap, and confirm that appropriate temperature together with high food condition can induce reproduction of over-summering *C. sinicus*, resulting in asynchronous reproductive periods among different regions. Our study provides a better understanding of the population dynamics and life history strategies of *C. sinicus* in the Yellow Sea. How variations in the sex ratios take place, however, still needs further work.

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