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Seasonal occurrence of *Calanus sinicus* in the northern South China Sea: A case study in Daya Bay

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ABSTRACT

Calanus sinicus is a calanoid copepod species that is distributed broadly in the continental shelf waters of the Northwest Pacific Ocean. This study aims to understand the seasonal variations of the distribution and abundance of *C. sinicus* in Daya Bay from the northern South China Sea (nSCS) and to explore its possible seasonal occurrence based on current and historical data. Monthly surveys of the species were conducted in Daya Bay, a subtropical bay in the nSCS, during the period between May 2013 and April 2014. *C. sinicus* was present from January to May, and disappeared after June. The spatial pattern of *C. sinicus* in the bay was characterized by its distribution into the southwestern part of the bay in January, bay-wide spread in February, patchiness in March and virtual retreat from the bay mouth in April. Reproduction occurred from January to April at a low rate. Adults were mostly abundant in January and declined to a minimum in April. The percentage of early developmental stages increased from 54.1% in January to 90.1% in April, as collected by a fine mesh size. Based on historical data from Daya Bay and from the coastal waters of the nSCS, *C. sinicus* was carried into the nSCS from the East China Sea by the China Coastal Current during the northeastern monsoon period and survived from December to October of the next year. The summer coastal upwelling may provide suitable refuges for the species in the nSCS by limiting the adverse effects caused by high temperatures. Our results confirm the viewpoint that *C. sinicus* could exist in the nSCS in summer and fall.

1. Introduction

Calanus sinicus is a planktonic copepod species with a wide geographical distribution in the continental shelf waters of China, Japan and Korea (Chen, 1992; Kang et al., 2007; Uye, 2000). It is an ecologically important copepod species in the shelf ecosystems of the Northwest Pacific because its eggs, larvae and adults provide a wide size spectrum of food items for commercially important fish stocks in the near-shore spawning and nursing grounds (Zhu and Iverson, 1990). As we face a changing environment, it is crucial to understand the climate-driven impacts on this key species because of its relevance to important fish stocks (Kang et al., 2007; Sun et al., 2002). Climate variability on inter-annual and inter-decadal scales has significantly affected the dynamics of copepods in the Northeast Pacific (Batchelder et al., 2013; Liu and Peterson, 2010; Liu et al., 2015). For example, the abundance and biomass of subarctic copepod *Neocalanus plumchrus* and *Neocalanus cristatus* were significantly negatively correlated with sea surface temperature and water transport in the Northern California Current (Liu and Peterson, 2010; Liu et al., 2015). For *C. sinicus*, increasing water temperature was one of the main reasons for the higher abundance of *C. sinicus* in the Yellow Sea in the 1990s compared to the 1980s (Kang et al., 2007).

Along the coastal waters of China, the distribution of *C. sinicus* ranges from the Bohai Sea, the Yellow Sea and the East China Sea in the north to the northern part of the South China Sea (nSCS), and it even extends to the coast of Vietnam in the south, with breeding centres located in the coastal waters of the Yellow Sea and East China Sea (Chen, 1964, 1992). It accounts for as much as 80% of the total zooplankton biomass in the Yellow Sea and East China Sea (Chen, 1964). *C. sinicus* occurs year-round from the central and northern areas of the Taiwan Strait to the Inland Sea of Japan (Huang et al., 2002; Lin and Li, 1984; Uye, 2000; Wang et al., 2003; Zhang et al., 2005), and seasonally from the southern Taiwan Strait to the coastal waters of Hainan Island (Hwang and Wong, 2005; Yin et al., 2011; Zhang and Wong, 2013). It is carried into the coastal waters of the nSCS from population centres by the China Coastal Current during the northeast monsoon period in winter and spring and can then be used as a biological indicator for the intrusion of cold water into the nSCS (Hwang and Wong, 2005). The species vanishes in the nSCS as the water temperature increases with the shift of the seasonal monsoon from the northeast to the southwest during summer and fall and appears again when the monsoon patterns reverse (Hwang and Wong, 2005; Zhang and Wong, 2013). However, recent

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studies have reported that *C. sinicus* can exist in the southern Taiwan Strait (Guo et al., 2011), near Hong Kong (Zhang et al., 2009), and around Hainan Island (Yin et al., 2011; Zhang et al., 2009) from late June to early September.

Temperature is an important factor in regulating the distribution of *C. sinicus* in the northwest Pacific Ocean (Uye, 2000), and temperatures >23 °C are considered to be stressful to the species in the laboratory (Uye, 1988). In the field, 26–27 °C is suggested as the upper thermal limit for the species (Wang et al., 2003). Although the surface water temperature is higher than 27 °C in the coastal waters of the nSCS during summer, *C. sinicus* are still found sporadically in the area (Guo et al., 2011; Yin et al., 2011; Zhang et al., 2009). Hence, the notion that *C. sinicus* is carried by the China Coastal Current into the nSCS during winter and spring and disappears in summer and autumn is worthy of reconsideration.

Daya Bay is a semi-enclosed bay that is located in the nSCS (Fig. 1); it is characterized by a mild subtropical climate with the northeast monsoon prevailing from October to April and the southwest monsoon from May to September (Xu, 1989). Low salinity water enters the bay, forced by the northeast monsoon that drives the winter coastal current southwestward from the Taiwan Strait to the nSCS shelf (Su, 2004). An intrusion of low temperature and high salinity waters into the bay dominates along the bottom from the coastal upwelling in the nSCS during summer (Li et al., 1990). In this system, the hydrographic, chemical and biological parameters have been monitored seasonally at 12 fixed stations during winter (January), spring (April), summer (July) and fall (October) since the 1990s (Wang et al., 2008). A recent monthly survey was carried out in the bay from May 2013 to April 2014 as an intensive case study to understand the seasonal occurrence of the species in the nSCS.

Our hypothesis is that the occurrence of *C. sinicus* in the nSCS is associated with the local hydrographic conditions. The objective of this study is to document the seasonal abundance and distribution of *C. sinicus* in Daya Bay and to explore the possible influence of environmental conditions on its seasonal occurrence. This research may provide new insights into the mechanisms underlying the population recruitment and sustainability of *C. sinicus* in the coastal waters of the nSCS.

2. Materials and methods

Daya Bay is located between 114°30′ and 114°50′E and 22°30′ and 22°50′N, with an area of 600 km^2 (Fig. 1). No major rivers discharge into it, and most of its water originates from the South China Sea. Its current is mostly controlled by tides (Xu, 1989). Its water depth ranges from 6 to 16 m, with an average of 10 m. Ecological monitoring has been carried out at 12 fixed stations by scientists from Marine Biology Research Station at Daya Bay, Chinese Academy of Sciences during early January, April, July and October since the 1990s, including temperature, salinity, chlorophyll *a*, nutrients, phytoplankton, zooplankton and benthos (Wang et al., 2008). A Water Quality Monitoring System (The Hach Company, Loveland, CO, USA) was employed to collect the data for the water depth, surface and bottom temperature, and salinity at all stations. Water samples were pre-filtered through a 200-μm mesh to remove large abiotic particles or zooplankton, and they were then filtered with 0.45-μm cellulose filters to analyse chlorophyll *a* (Chl *a*). The material left in the filters was measured after extraction with acetone (90% v/v) in the dark for 24 h at 4 °C (Parsons et al., 1984), using a Turner Design 10 fluorometer. Zooplankton was collected by vertical hauls from within 1 m of the bottom to the surface using a plankton net (50-cm mouth diameter, 505-μm mesh size). The filtered water volume

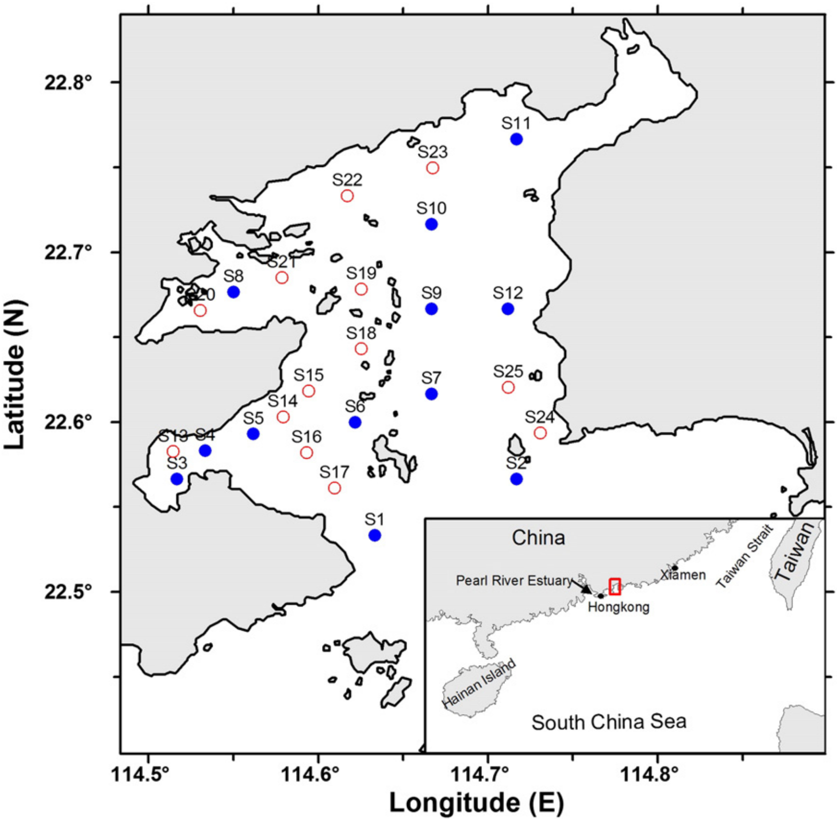

Fig. 1. Location of Daya Bay in the northern South China Sea (shown in the large map), and the sampling sites in Daya Bay (●-fixed station for ecological monitoring, labelled S1–S12, ○-additional station in the monthly survey, from S13 to S25).

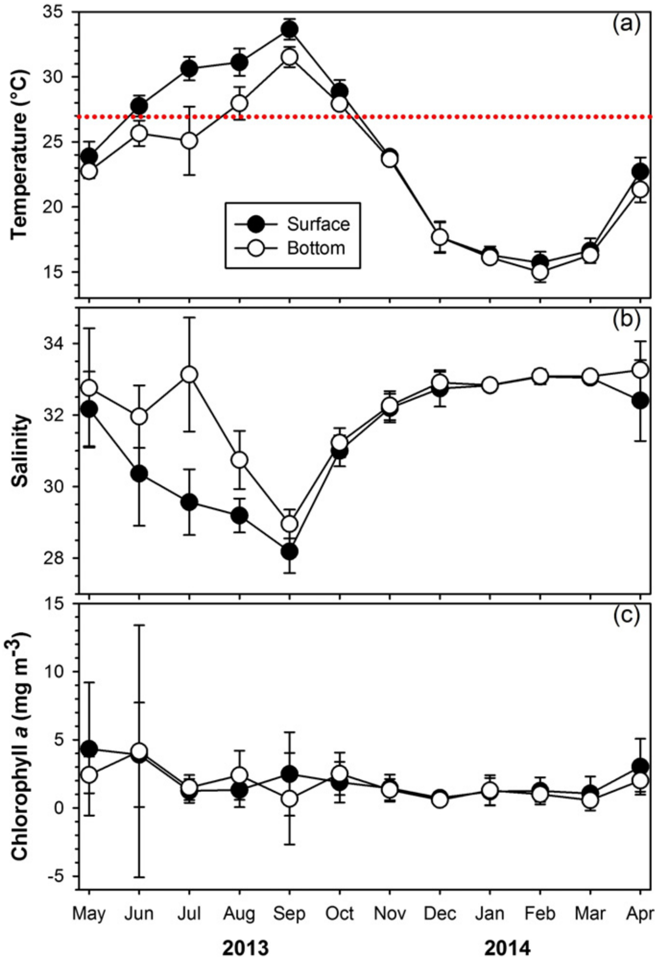

Fig. 2. Seasonal variations in the water temperature (a), salinity (b) and chlorophyll *a* concentration (c) at the surface and bottom layers in Daya Bay from May 2013 to April 2014. Values represent the average of 25 sampling stations. Bars denote standard errors. The dotted line represents the temperatures >27 °C.

was determined by the rope length multiplied by the mouth area. The samples were preserved in a 5% formalin-seawater solution for species identification in the laboratory.

Sampling was also conducted monthly from May 2013 to April 2014 at 25 stations (including the 12 fixed stations). The method of measuring environmental factors (temperature, salinity and Chl *a*) was identical to that of the ecological monitoring surveys. Zooplankton collections were taken by two types of conical plankton nets. One of the net mesh sizes was the same as that used in monitoring, and another net was equipped with a 160-μm mesh opening (30 cm mouth diameter) to effectively catch the full range of developmental stages of *C. sinicus*. In the laboratory, the nauplii (NI–NV), copepodite (CI–CV), as well as adult males and females of *C. sinicus* were identified under a stereomicroscope according to the descriptions of Li and Fang (1983). The counts were converted to abundances expressed as the number of individuals per cubic metre (ind. m^{-3}).

A one-way analysis of variance (ANOVA) was used to examine the difference between surface and bottom environmental parameters, followed by Kruskal–Wallis test or Dunn's multiple comparison test, which was conducted by using Sigmaplot 11.0, with a significance level of 0.05. The long-term variation of *C. sinicus* was analysed from 1998 to 2009. Pearson correlation tests between copepod abundance and temperature, salinity and Chl *a* were conducted to understand which factors influence their distribution.

3. Results

3.1. Environmental conditions

A seasonal variation in temperature and salinity was observed for both the surface and bottom layers (Fig. 2). The surface temperature increased from 15.71 °C in February to 33.65 °C in September, while salinity showed the lowest values in September and the highest in February and March (Fig. 2a–b). The temperature in the surface layer increased markedly after June, with temperatures >27 °C. The difference in temperature between the surface and bottom became more evident from April to September, especially from June to August ($F = 95.820$, $p < 0.001$). Similarly, salinity stratification also appeared from April to September, with the most significant difference in July ($H = 28.785$, $p < 0.001$). The decline of the stratification process began in October. The difference in Chl *a* between the surface and bottom was not significant ($p = 0.291$), with their average concentrations were 1.99 ± 1.84 mg m^{-3} and 1.70 ± 1.85 mg m^{-3}, respectively. The peaks of the Chl *a* concentration were found in spring (May–June 2013 and April 2014) and autumn (September–October, 2013) (Fig. 2c).

3.2. Seasonal abundance

C. sinicus showed a clear seasonal pattern of abundance in Daya Bay (Fig. 3). It was found in May 2013 and from January to April 2014. High abundances were recorded in January (14.0 ind. m^{-3}), collected by 505-μm nets, and February (63.9 ind. m^{-3}), collected by 160-μm nets. *C. sinicus* occurred in all of the samples collected using 505-μm nets in January, while it dominated the study area in February sampled by 160-μm nets (Table 1). Though the abundance of *C. sinicus* in the 160-μm samples was higher than that of the 505-μm samples, the percentage of its abundance to total zooplankton for the latter was higher than the former (Table 1). It dropped abruptly in terms of abundance and frequency during May (Fig. 3, Table 1).

3.3. Spatial distribution

The abundance of *C. sinicus* collected using 160-μm nets was integrated across all developmental stages to illustrate its spatial distribution during January to April. The spatial pattern of *C. sinicus* varied seasonally from January (Fig. 4a), February (Fig. 4b), and March (Fig. 4c) to April (Fig. 4d). It first occurred in the southwestern part of the bay in January, spread into most parts of the survey area in February, assembled into three high-value centres in March, and mostly retreated

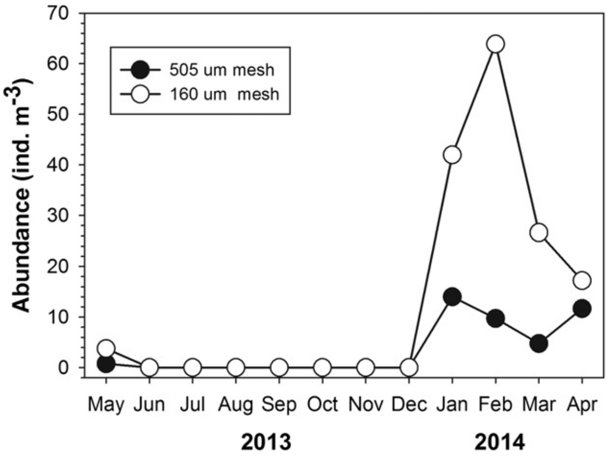

Fig. 3. Average of seasonal abundance (ind. m^{-3}) of *Calanus sinicus* in Daya Bay from May 2013 to April 2014.

Table 1
The frequency (%) and percentage (%) of *Calanus sinicus* during the period in which *Calanus sinicus* was present, in both 505-μm and 160-μm mesh nets.

Year	Month	505 μm net Frequency (%)	Percentage (%)	160 μm net Frequency (%)	Percentage (%)
2014	January	100	16.43	64	0.41
	February	93	11.02	100	1.18
	March	87	10.62	56	4.24
	April	40	20.96	36	0.06
2013	May	7	0.02	8	0.02

to the bay mouth in April. *C. sinicus* abundance differed between the southern and northern parts (stations divided by 22.65°N) and western and eastern parts (stations divided by 114.65°E) from January to April. Its abundance in the southern bay and the western bay was generally higher than that in the northern and the eastern (Fig. 5). The distribution of *C. sinicus* in Daya Bay suggests that the appearance of *C. sinicus* might be first in the western bay and then extended from south to north and from west to east. The abundance of *C. sinicus* was negatively correlated with salinity and Chl *a* in January, and it was negatively correlated with temperature and positively correlated with salinity in April. No significant relationships between abundance and temperature or salinity were found in February and March (Table 2).

3.4. Population structure

The abundance and stage composition of *C. sinicus* taken by 505-μm nets and 160-μm nets, respectively, were compared. Copepodites II–V and adults were the dominant developmental stages in the 505-μm samples (Fig. 6a–b), and nauplii III–V, copepodites I–V, and adults in the 160-μm samples (Fig. 6d–e). Adults occurred abundantly in January and declined to a minimum in April in both the 505-μm and 160-μm samples. The abundance and percentage of CI, CII and CIII increased from 25.3% in January to 59.8% in February and decreased from 37.3% in March to 17.7% in April, while the CIV and CV individuals dominated

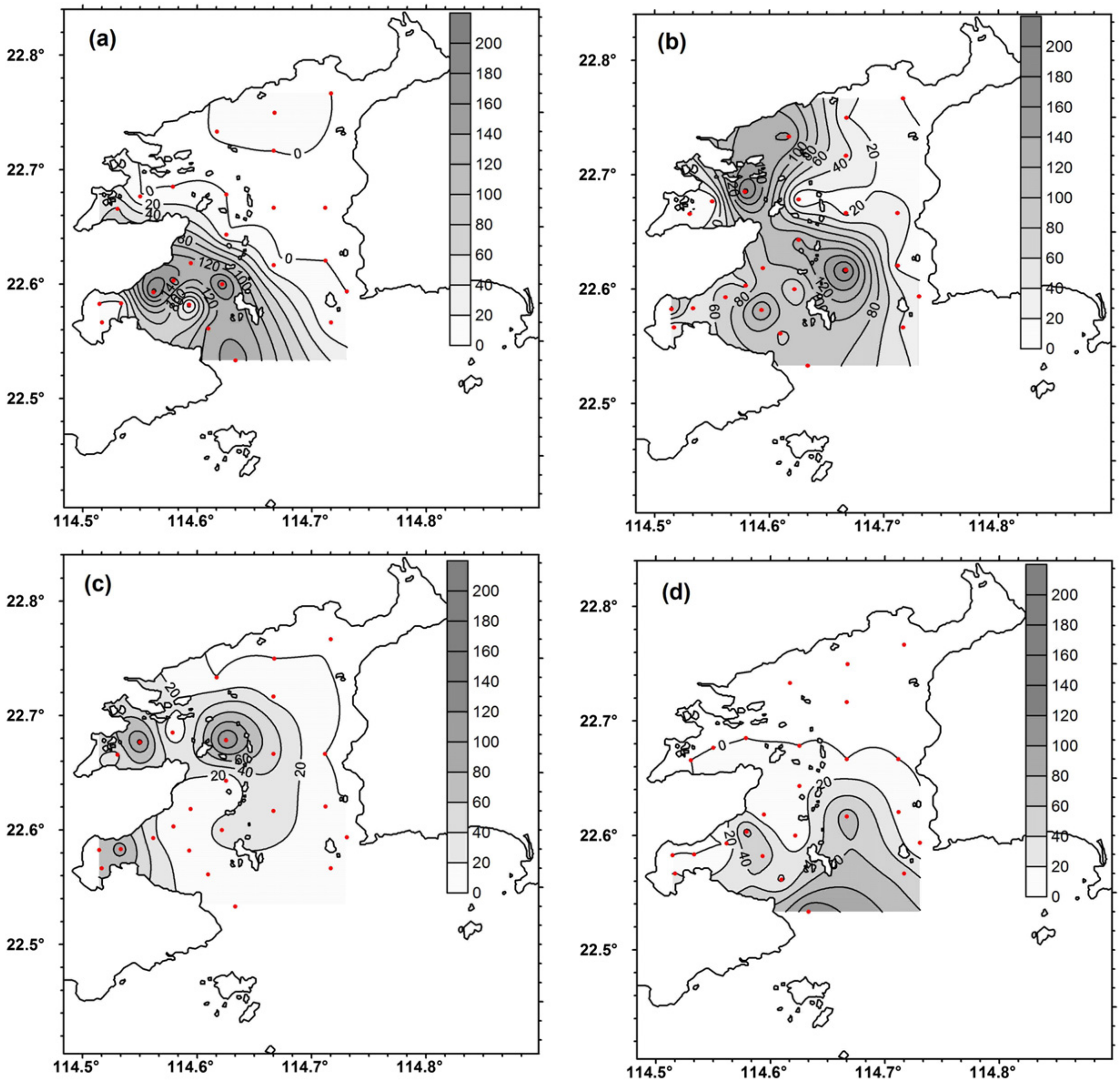

Fig. 4. Spatial distribution of the abundance of *Calanus sinicus* (ind. m^{-3}) in Daya Bay during January (a), February (b), March (c), and April (d) 2014, collected by 160-μm nets.

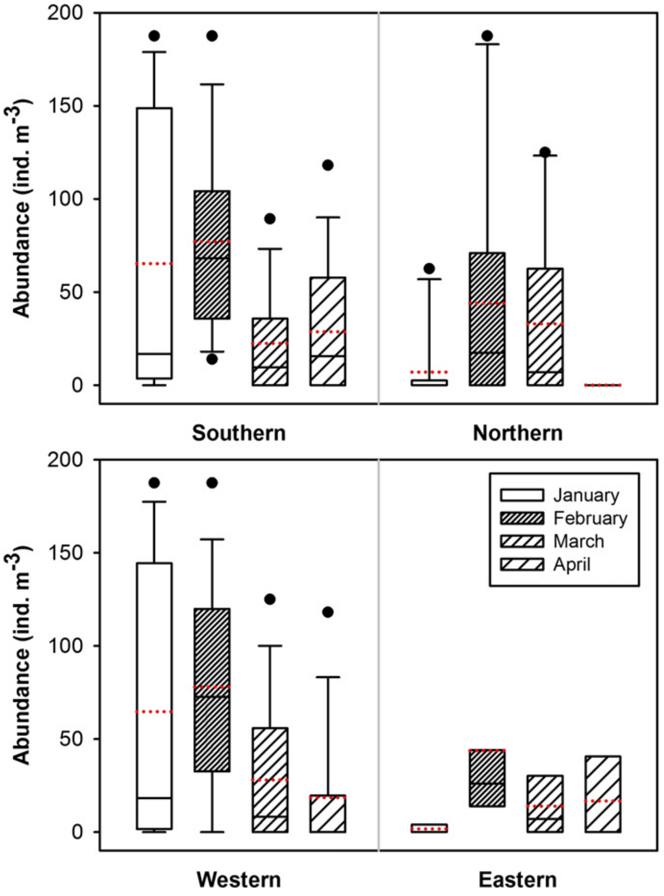

Fig. 5. The abundance of *Calanus sinicus* in the southern and northern, and western and eastern parts of Daya Bay in January, February, March, and April 2014. The solid line through the box is the sample median, and the dotted line is the sample average; the limits of the box are the 25th and 75th percentile. The whiskers are the 10th and 90th percentiles. Outliers are shown by single points.

in April in contrast to the relatively low values from January to March (Fig. 6b). All of the developmental stages of the species were observed in the 160-μm samples, and their abundance varied monthly, with the early stages NIII–CIII increasing from 54.1% in January to 77.9% in February and from 84.0% in March to 90.1% in April (Fig. 6e). The sex ratio of females/males was variable between the 505-μm and 160-μm samples, with a higher ratio in February for the 505-μm samples and in April for the 160-μm samples (Fig. 6c and f).

Table 2
Pearson correlation coefficients with *p*-values (in parentheses) for *Calanus sinicus* abundance and sea surface temperature, salinity, and chlorophyll *a* (Chl *a*). Significant relationships are in bold.

Year	Season	Temperature	Salinity	Chl *a*
2014	January	0.212(0.309)	**−0.536(<0.01)**	**−0.437(<0.05)**
	February	−0.086(0.683)	0.089(0.673)	−0.363(0.075)
	March	−0.326(0.112)	0.018(0.933)	0.026(0.904)
	April	**−0.570(<0.01)**	**0.513(<0.01)**	−0.193(0.592)
1998–2009	January	−0.003(0.983)	−0.067(0.611)	−0.069(0.605)
	April	−0.221(0.105)	**0.294(<0.05)**	−0.101(0.465)
	July	**0.866(<0.001)**	−0.151(0.628)	0.024(0.940)
	October	−0.364(0.336)	−0.567(0.112)	0.803(0.054)

3.5. Inter-annual variations

The occurrence of *C. sinicus* varied from 1998 to 2009 in Daya Bay (Fig. 7). The species always occurred in January and April and occasionally in July or October. In some years, such as 1998, 2003, 2004, and 2009, it could be found in very low numbers in October. The abundance of *C. sinicus* showed the highest values in January 2008. In the study area, temperature fluctuated seasonally with relatively low temperatures in January and April and high temperatures in July and October (Fig. 8a). Different annual trends of salinity were also observed in the surface and bottom layers (Fig. 8b). The difference in salinity between the surface and bottom layers was highest in July 1998. The seasonal mean concentration of Chl *a* was relatively constant, at approximately 1–3 mg m^{-3} in January and April, but it was more variable in July and October (Fig. 8c). Its abundance was high at temperatures ranging from 15 to 24 °C and salinities from 32 to 34 in January and April (Fig. 9a–b). Interestingly, it also appeared in July or October with temperatures of ~29 °C, such as in 1998, 2003, and 2004. A significantly positive correlation between *C. sinicus* and salinity in April and temperature in July was found (Table 2). *C. sinicus* seems to be concentrated in a range from 1 to 3 mg m^{-3} for Chl *a* in January and April (Fig. 9c), and no significant correlations among these factors were found from 1998 to 2009 (Table 2).

4. Discussion

This study focuses on the seasonal variations in the distribution and abundance of *C. sinicus* in Daya Bay based on a combination of field and historical data. Our results show that *C. sinicus* was present from January to May in 2013 and 2014 and that it was also observed occasionally in July and October from 1998 to 2009. We discuss the possible reasons for its seasonal occurrence in Daya Bay and even in the nSCS on the basis of comparable previous results.

4.1. Seasonal occurrence of C. sinicus in Daya Bay

Firstly, the source population of *C. sinicus* in Daya Bay is originated from the East China Sea by the China Coastal Current during the northeast monsoon period. Monthly samplings in our study reveal that *C. sinicus* is present from January to May during the northeast monsoon period and that it disappears when the southwest monsoon prevails in Daya Bay. The geographical distribution and abundance of *C. sinicus* are summarized monthly from the north to south along the coastal waters of the northwest Pacific Ocean (Fig. 10). It takes place throughout the year in the northern Yellow Sea (Yang et al., 2012; Yin et al., 2013a), the Kii Channel, the Inland Sea of Japan (Uye, 2000), the East China Sea (Chen, 1964; Xu and Chen, 2007; Xu et al., 2011) and the northern Taiwan Strait (Huang et al., 2002), with the peaking from April to July (Fig. 10). However, it occurs from January to April or May towards the south in the southern Taiwan Strait (Huang et al., 2002) and around Hong Kong coastal waters (Hwang and Wong, 2005). Generally, the abundance of *C. sinicus* declines from the north to south, with the exception of the Kii Channel (Fig. 10b) because this species was sampled by fine mesh size in comparison with other waters. The seasonal occurrence of this species off Taiwan, Hong Kong and the northwest coastal waters of the SCS is associated with the southwestward movement of cold water along the Chinese coast (Hwang and Wong, 2005; Yin et al., 2011; Zhang and Wong, 2013). Daya Bay lies on the northern coast of SCS, connecting the East China Sea and nSCS through the Taiwan Strait. Therefore, the entrance of *C. sinicus* into Daya Bay is caused by the tidal advection of the China Coastal Current during winter. On the other hand, the appearance of *C. sinicus* in Daya Bay may exclude its potential recruitment from its egg because its resting egg has been not found in the adjacent waters of Day Bay (Chen et al., 2015).

Secondly, after its transport into Daya Bay, the spatial distribution of *C. sinicus* may be influenced by the tidal current in the bay. The tide in

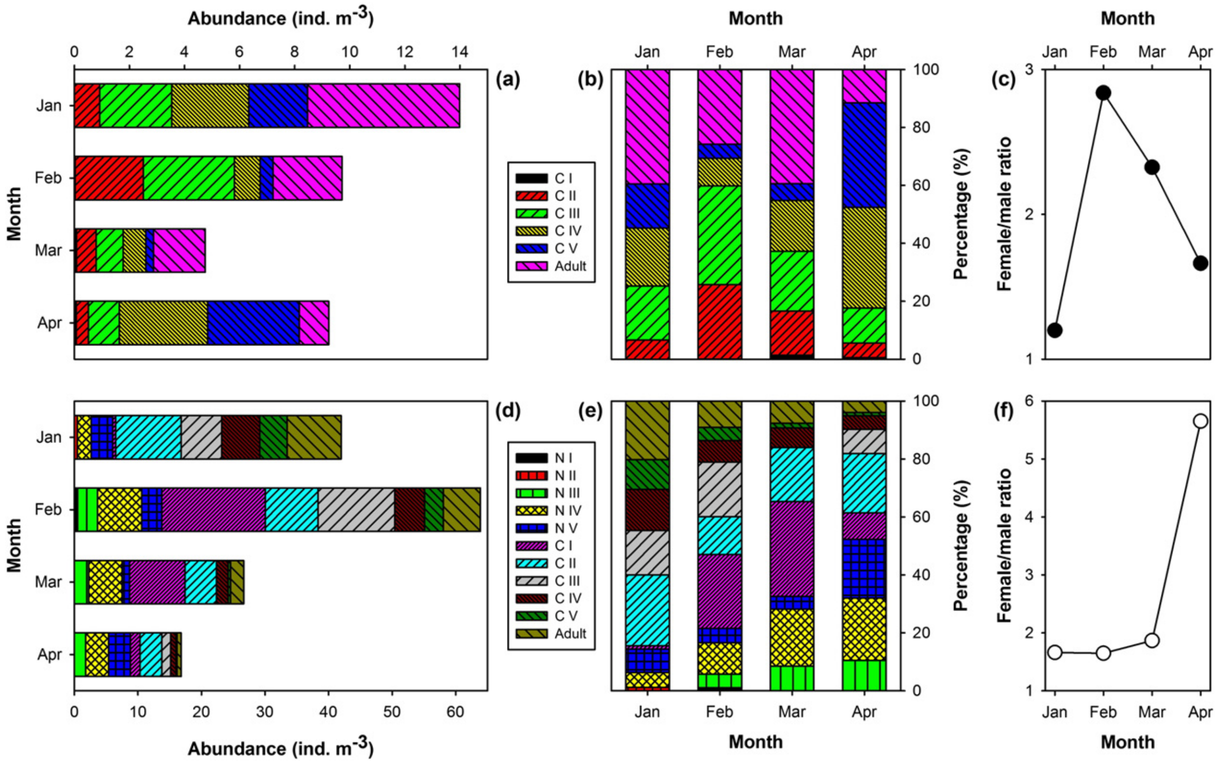

Fig. 6. Temporal changes in the abundance (a and d), percentage (b and e) and sex ratio (c and f) of *Calanus sinicus*, collected by 505-μm and 160-μm nets, from January to April 2014 in Daya Bay. Values represent the average of 25 sampling stations.

Daya Bay is mainly irregular semidiurnal (Xu, 1989). The horizontal tidal flow obviously reciprocates in a south–north direction (Wu et al., 2007). The distribution pattern of *C. sinicus* in Daya Bay suggests that *C. sinicus* may first be transported to the southern part of Daya Bay, which connects to the shelf waters of the nSCS, and then to the western, central and northern areas from January to April, which enhances proliferation through tidal currents (Wu et al., 2007; Xu, 1989). It displays a patchy distribution in March and retreats towards the bay mouth in April. This virtual withdrawal is probably due to the decreasing source population and the increasing temperature after March.

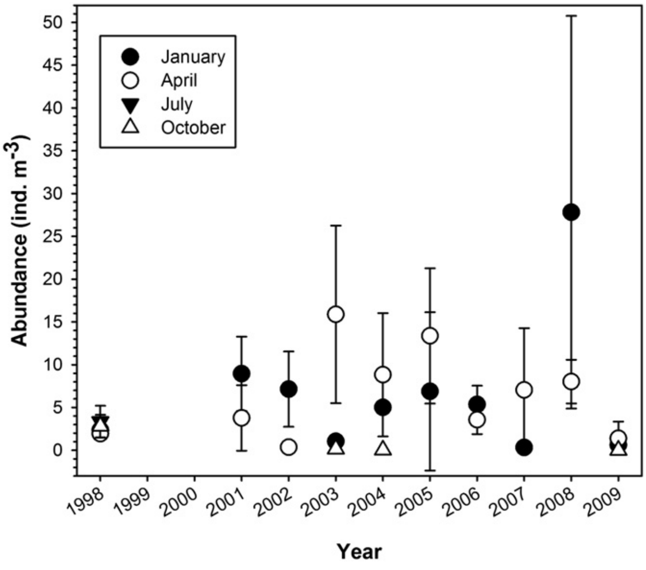

Fig. 7. Variability in abundance (ind. m^{-3}) of *Calanus sinicus* during January, April, July, and August from 1998 to 2009 in Daya Bay. Values represent the average of 12 sampling stations. Bars denote standard errors.

Finally, the duration of *C. sinicus* in Daya Bay was influenced by temperature and transport of source population. Temperature is one of the main factors determining the period of *C. sinicus*' existence in Daya Bay. The thermal range is suggested as being between 1 and 27 °C for the survival of *C. sinicus* and 5 and 23 °C for population reproduction (Uye, 1988; Wang et al., 2003). The surface temperature increases dramatically from April until September, when the southwesterly monsoon prevails in Daya Bay. It exceeds the upper limit of *C. sinicus*' survival tolerance from June to October and then results in its disappearance. The absence of *C. sinicus* at high temperatures after May is also supported by its seasonal occurrence in Xiamen Harbour, where it disappears in June when the temperature warms to 24 °C (Lin and Li, 1984). No individuals remain after May in the coastal waters of Hong Kong when the water temperature is >25 °C (Hwang and Wong, 2005; Zhang and Wong, 2013). While the decreased surface temperature is suitable for *C. sinicus*' survival, it is still absent in Daya Bay from November to December, which suggests that it may not yet have reached the northern part of the SCS from the East China Sea. The transportation and development of *C. sinicus* populations may vary annually and regionally. The appearance of *C. sinicus* was first observed in December 2002 (Hwang and Wong, 2005) and 2003 (Zhang and Wong, 2013) in the coastal waters of Hong Kong, while it occurred in January 2014 in Daya Bay, although the distance is much shorter between Daya Bay and the source population region than between the coastal waters of Hong Kong and this region.

The reproduction rate of *C. sinicus* in Daya Bay may be affected by high temperatures. The percentage composition of CI–CIII of *C. sinicus* observed in Xiamen Harbour during the reproductive season was approximately 40–50% (Lin and Li, 1984). In this study, approximately 18–60% of the CI–CIII composition was observed from January to April (Fig. 6b). Analysis of the proportions of developmental stages reveals that all stages occur continuously. The female/male ratio from the 160-μm samples is <6.0, much lower than the 11.39 reported in August

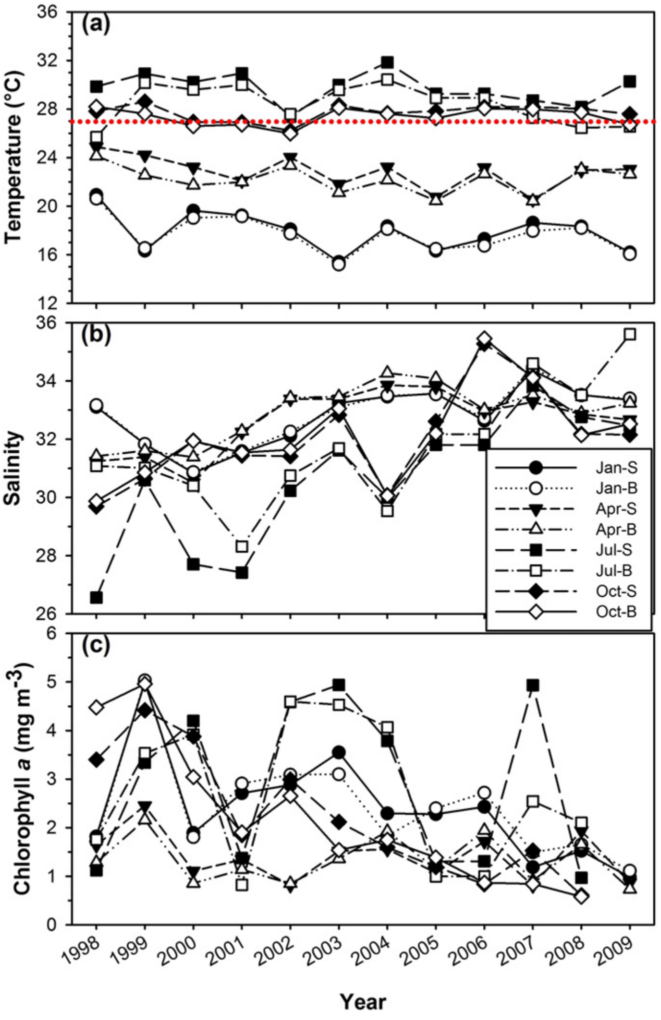

Fig. 8. Variability in water temperature (a), salinity (b), and chlorophyll *a* concentration (c) in the surface and bottom layers of Daya Bay during January, April, July, and August from 1998 to 2009. Values represent the average of 12 sampling stations. The dotted line represents the temperature >27 °C.

1999 in the Yellow Sea Cold Bottom Water (Wang et al., 2003), which suggests that during the period of the northeast monsoon, *C. sinicus* inhabiting Daya Bay may reproduce at low temperatures, but at a lower rate. The increase in abundance in February may be the result of local reproduction after horizontal transport into the bay, but declines drastically in April when temperatures exceed its ideal range (Uye, 1988; Wang et al., 2003; Zhang et al., 2005). The effects of temperature on the local reproduction of *C. sinicus* in Daya Bay need to be studied further.

Compared to water temperature, salinity and Chl *a* concentrations seem to not be limiting factors in the spatial and seasonal patterns of *C. sinicus* in Daya Bay. In January, the southern part of the bay was characterized by low salinity and Chl *a* concentrations as a result of the China Coastal Current (Xu, 1989). In April, *C. sinicus* moves towards the western and southern parts of the bay, where a significant phytoplankton bloom was observed in the upper-water layers. Its peak abundance, from January to March, also appeared at least three months before the peak in Chl *a* concentration. The highest Chl *a* concentration was found from April to June, but the highest *C. sinicus* abundance appeared in February, although the proportion of early developmental stages increased significantly. Therefore, increases in the Chl *a* concentrations could not support the existence of *C. sinicus* after May.

High proportions of early stages were recorded from January to April. However, the contribution of *C. sinicus* to the total abundance of zooplankton decreased from April to May (Table 1), which was due to the increasing numbers of other species from the mesozooplankton community, such as *Pseudevadne tergestina*, *Penilia avirostris*, *Parvocalanus crassirostris* and *Paracalanus parvus* after April (unpublished data). Cladoceran species may break out in a short time in Daya Bay when the temperature and food concentrations are favourable (Li et al., 2014). Similarly, *C. sinicus* is replaced by small species, such as *Paracalanus* sp., *Acartia omorii*, and *Oithona davisae*, in shallow inshore waters (<20 m) of the Inland Sea of Japan, despite the temperature and salinity seeming to be appropriate for its survival (Uye, 2000).

4.2. Seasonal occurrence of *C. sinicus* in the nSCS

One interesting finding in this study is that *C. sinicus* in Day Bay could survive in July and October in some years when the surface temperatures were higher than 27 °C in the coastal waters of the nSCS. *C. sinicus* was also observed in the southern Taiwan Strait from June to early September during 1988, 1994, 2005 and 2006 (Guo et al., 2011). It was also found around the east of Hainan Island from late August to early September in 2004 and 2006 (Yin et al., 2011; Zhang et al., 2009). It has been suggested to be an indicator species of upwelled cold waters in these regions in summer (Guo et al., 2011; Yin et al., 2013b). Chen (1992) suggested that *C. sinicus* disappeared from June to October along the coasts of the nSCS when the water temperatures increased rapidly in spring, while these findings indicate that it is also prevalent in summer with low abundances based on the same mesh size (Table 3).

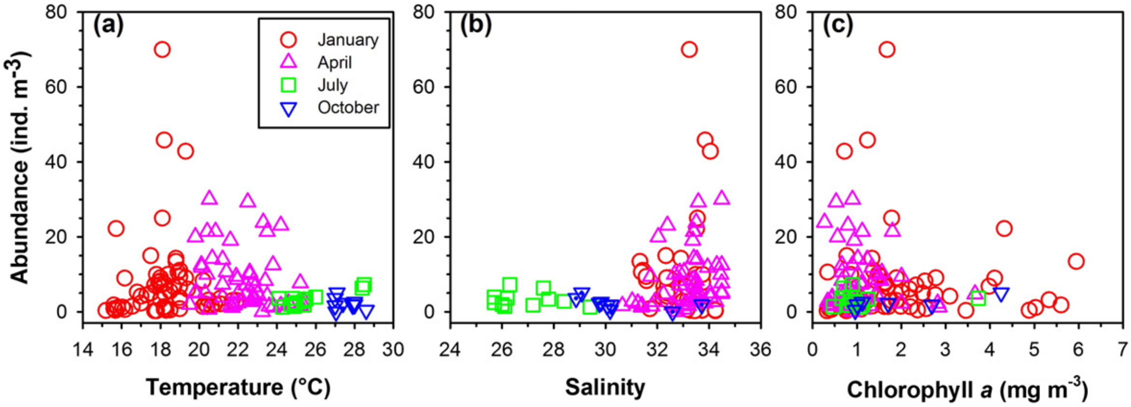

Fig. 9. Abundance of *Calanus sinicus* (ind. m^{-3}) in relation to the surface temperature (a), salinity (b), and chlorophyll *a* concentration (c) during 1998–2009. $n = 59$ in January; $n = 55$ in April; $n = 12$ in July 1998; in October, $n = 6$ in 1998, $n = 1$ in 2003, $n = 1$ in 2004 and $n = 1$ in 2009. Bottom temperature data are used in July 1998.

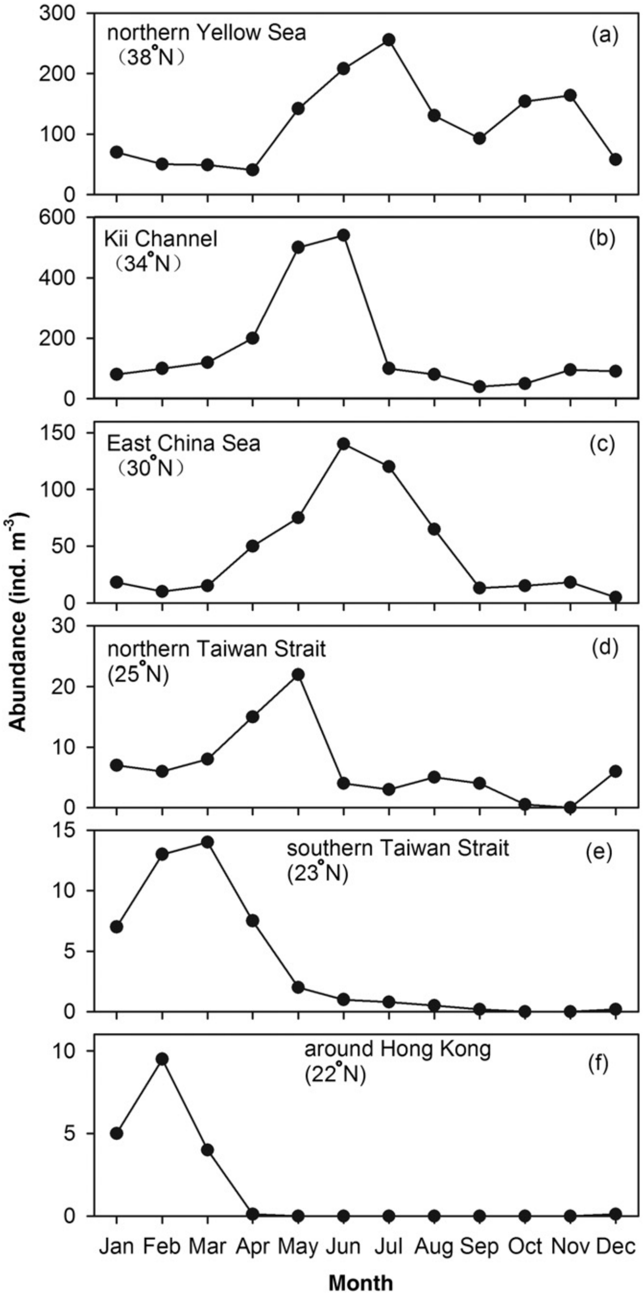

Fig. 10. Monthly change in mean abundance of *Calanus sinicus* in (a) the northern Yellow Sea (modified from Yang et al., 2012; Yin et al., 2013a), (b) the Kii Channel, the Inland Sea of Japan (Uye, 2000), (c) the East China Sea (Chen, 1964; Xu and Chen, 2007; Xu et al., 2011), (d) the northern Taiwan Strait (Huang et al., 2002), (e) the southern Taiwan Strait (Huang et al., 2002), and (f) around Hong Kong waters (Hwang and Wong, 2005). Note difference in abundance scales between panels (a)–(f).

The occurrence of *C. sinicus* in the nSCS recorded occasionally during summer may be associated with coastal upwelling events. Coastal upwelling is a common seasonal phenomenon from June to September in the nSCS. The summer coastal upwelling is induced at many places along the coast of the nSCS, including the Yuedong-Taiwan Bank upwelling (Hong et al., 2009; Jing et al., 2009, 2011; Fig. 11B), the Qiongdong upwelling (Su and Pohlmann, 2009; Jing et al., 2011; Fig. 11C), and the Vietnam upwelling (Liu et al., 2012; Fig. 11D). Zooplankton in coastal upwelling ecosystems, such as the California Current (Roemmich and McGowan, 1995), the Benguelan upwelling (Verheye and Richardson, 1998) and the Peruvian upwelling (Ayón et al., 2004) have been influenced by these upwelling events because they supply cold, nutrient-rich water to the surface and support high levels of biological productivity. In the southern Taiwan Strait, the stations with relatively abundant *C. sinicus* during summer are within well-recognized upwelling regions near the coast and Taiwan Bank (Guo et al., 2011; Hong et al., 2009). In the upwelling area east of Hainan Island, *C. sinicus* is present in high abundance in the inshore waters in summer with temperatures <27 °C (Jing et al., 2009; Yin et al., 2011; Zhang et al., 2009). There are no quantitative data on *C. sinicus* in the Vietnam coastal upwelling region to date. *C. sinicus* is not found in the Pearl River estuary or Hong Kong coastal waters in summer (Hwang and Wong, 2005; Li et al., 2006; Zhang and Wong, 2013). Therefore, *C. sinicus* could maintain a number of populations in these coastal upwelling regions or adjacent waters in the nSCS due to the low temperatures from the upwelled cold water.

An observation of *C. sinicus* from Daya Bay in July 1998, with an abundance range from 1.3 to 7.3 ind. m^{-3} recorded at all stations (S1-S12), may also be a result of the influence of adjacent coastal upwelling. The intrusion of cold water from the coastal upwelling into Daya Bay happens in summer every year along the bottom and then enhances water stratification (Li et al., 1990). Generally, the lowest temperature in July is >27 °C in most years, but was marked by a dramatic decrease, with temperatures of <26 °C in July 1998 (Fig. 8a). A positive correlation was also found between *C. sinicus* and bottom water temperature during July. The coastal upwelling events in the nSCS were significantly strengthened during the summer of 1998 following the El Niño event (Jing et al., 2011). This may explain why *C. sinicus* was present in July 1998, but not in other years until 2009, because the low bottom temperature may provide an over-summering refuge for the species. Cold water resulting from strong upwelling events would be suitable for *C. sinicus*' survival in Daya Bay or, to a certain extent, in the coastal waters of the nSCS during summer or fall.

The survival of *C. sinicus* populations in the coastal upwelling regions or the adjacent coastal upwelling waters of the nSCS during summer is very similar to its over-summering strategy in the Yellow Sea Cold Bottom Water area (YSCBW, Fig. 11A). The YSCBW is traditionally defined as a bottom pool of the remnant Yellow Sea winter water resulting from summer stratification with the temperature ≤10 °C (He et al., 1959). Although *C. sinicus* exists in the southern Yellow Sea throughout the year, its abundance decreases in July and August due to unfavourably high temperatures (Chen, 1964). However, a relatively high abundance of the fifth copepodite stage and adult *C. sinicus* occurs in summer in the central and southern Yellow Sea (Wang et al., 2003), where low temperatures and low food availability in the YSCBW help it to maintain a much lower developmental rate and higher survival rate (Pu et al., 2004; Sun et al., 2002). *C. sinicus* could still survive in these coastal upwelling regions of the nSCS to avoid thermal damage, although its abundance is relatively low during August–September in the southern Taiwan Strait (Guo et al., 2011), near Hainan Island (Yin et al., 2011; Zhang et al., 2009), and in Daya Bay. High abundance of *C. sinicus* in the YSCBW during may be resulted from its finer mesh size and lower bottom water temperature than that in the coastal upwellings of the nSCS (Table 3). The occurrence of *C. sinicus* in the coastal upwelling regions in the nSCS relies on cold bottom waters, which may be the reason why it can persist in both the nSCS and the Yellow Sea Cold Bottom Water area during summer and fall.

5. Conclusions

Based on the above analysis, it can be concluded that the seasonal occurrence of *C. sinicus* in the nSCS is closely associated with the China Coastal Current in winter and coastal upwelling in summer or fall. The species is carried into the nSCS by the China Coastal Current during the northeast monsoon and generally disappears during the period of the prevailing southwest monsoon. *C. sinicus* can maintain itself at a low population level in coastal upwelling regions or the adjacent waters of the nSCS during summer because coastal upwellings can provide a suitable habitat for *C. sinicus* to avoid the damage caused by high

Table 3
Summary of abundance (ind. m^{-3}) with average or range of *Calanus sinicus* in coastal upwelling regions from the northern South China Sea during June–October, with comparable data for the Yellow Sea Cold Bottom Water.

Region	Season	Year	Abundance (ind. m^{-3})	Net mesh (μm)	Source
Yellow Sea Cold Bottom Water	August	1999	345.7	300	Wang et al. (2003)
Southern Taiwan Strait	Late June–early July	2006	6.26	505	Guo et al. (2011)
	July	2005	8.22	505	Guo et al. (2011)
	Late August–early September	1988	2.46	505	Guo et al. (2011)
	Late August–early September	1994	1.43	505	Guo et al. (2011)
East Hainan Island	Middle July–early August	2006	13.74	505	Yin et al. (2011)
	Late August–early September	2004	9.4–13.9	500	Zhang et al. (2009)
Daya Bay	July	1998	3.33	505	This study
	October	1998	2.83	505	This study
	October	2003	0.16	505	This study
	October	2004	0.035	505	This study
	October	2009	0.01	505	This study

temperatures. However, questions remain. For instance, what explains the existence of *C. sinicus* in Daya Bay in October 1998, 2003, 2004, and 2009 without any obvious cold-water intrusion? Does *C. sinicus* reproduce in the summer coastal upwelling regions of the nSCS? How does *C. sinicus* respond to the variability of coastal upwelling due to long-term climate change? Until now, little information has been available on the long-term distribution pattern and seasonality of *C. sinicus* in the shelf waters of the nSCS. The answers to these questions are of significance for re-evaluating the geographic distribution and ecological role of *C. sinicus* in the shelf ecosystems of the Northwest Pacific Ocean.

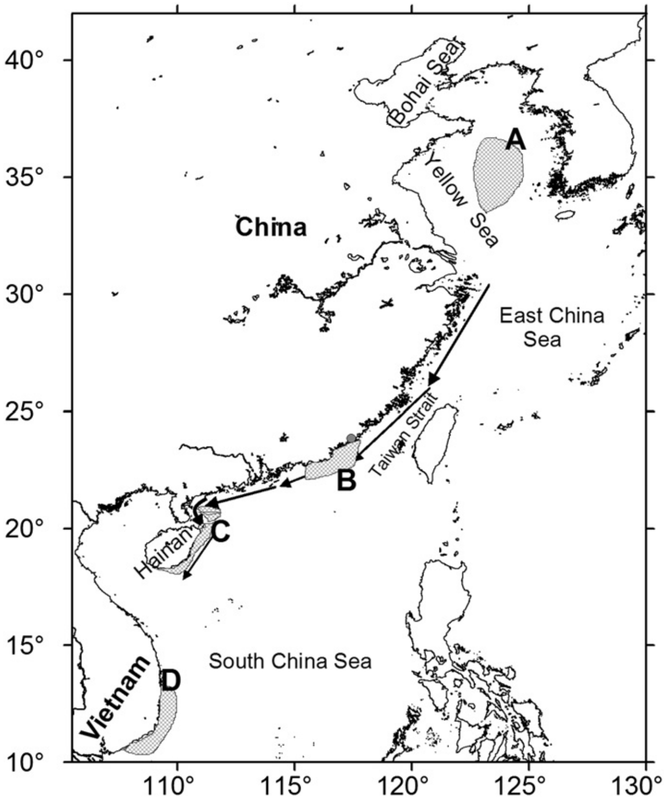

Fig. 11. Schematic diagram of the China Coastal Current (solid line with arrow) during the period of the northeast monsoon and identified coastal upwelling regions (B–D) during the southwest monsoon. The arrows represent the coastal current direction. The shadowed areas A, B, C, and D represent the Yellow Sea Cold Bottom Water, Yuedong-Taiwan Bank coastal upwelling, Qiongdong coastal upwelling, and Vietnam coastal upwelling.

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