Zoological Studies **49**(4): 492-503 (2010)

Zoological Studies

Unexpected Dominance of the Subtropical Copepod *Temora turbinata* in the Temperate Changjiang River Estuary and Its Possible Causes

Guang-Tao Zhang[1], Song Sun[1,*], Zhao-Li Xu[2], and Qi-Long Zhang[1]

[1]*Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China*
[2]*East China Sea Fisheries Research Institute, Chinese Academy of Fisheries Sciences, Shanghai 200090, China*

(Accepted May 14, 2008)

Guang-Tao Zhang, Song Sun, Zhao-Li Xu, and Qi-Long Zhang (2010) Unexpected dominance of the subtropical copepod *Temora turbinata* in the temperate Changjiang River estuary and its possible causes. *Zoological Studies* **49**(4): 492-503. The zooplankton community in the Changjiang (Yangtze) River estuary (CRE) was sampled quarterly in 2004, the 1st yr after the Three Gorges Reservoir was impounded to a water level of 135 m, in order to investigate possible changes in the community structure after freshwater control upstream at the dam. Zooplankton assemblages were consistent with previous studies in all seasons except summer. A tropical-subtropical copepod species, *Temora turbinata*, was found to be the most abundant zooplankton species in this area for the 1st time in Aug. 2004, while previously dominant species, such as *Calanus sinicus*, *Euchaeta concinna*, and *Labidocera euchaeta*, decreased in abundance and appearance frequency. From historical data, *T. turbinata* was never dominant in this area before 2003. It was present only in summer, in accordance with the northerly invasion of the Taiwan Warm Current (TWC). In this study, the range of the Changjiang River Diluted Water was found to have shrunk in summer, and the TWC occupied a larger area of both the bottom and surface layers, compared to the long-term average. Our results indicate that *T. turbinata* in the CRE area was recruited from the southern part of the East China Sea by the TWC. Its unexpected dominance suggests a northward extension of warm-water species resulting from global warming, although it appeared immediately following water control at the Three Gorges Reservoir. http://zoolstud.sinica.edu.tw/Journals/49.4/492.pdf

Key words: *Temora turbinata*, Three Gorges Reservoir, Taiwan Warm Current, Global warming, Northward extension.

In the past several decades, the Changjiang (Yangtze) River estuary (CRE) has attracted the attention of many scientists from different countries. At first, this area was known as a traditional fishing ground. River runoff carried abundant mineral nutrients, which in turn stimulated high primary production (Guo and Pan 1992). The estuary is known as the spawning ground of many commercially important species, such as hairtail (*Trichiurus japonicus*), anchovy (*Engraulis japonicus*), and crabs. Second, the freshwater discharge, known as the Changjiang River Diluted Water (CRDW), is thought to be of great importance to current patterns in the East China Sea (ECS), and its effects can reach as far as Jeju I., Korea (Ichikawa and Beardsley 2002). Third, a common concern is how the construction of the Three Gorges Dam (TGD) will influence this area. The TGD was begun in 1994 and is scheduled for completion in 2009. Its reservoir was filled to the 135 m water level on 12 June 2003 and contained approximately 12.3 × 10^9 m^3 of water, and when filled to the final 175 m water level will contain 39.3 × 10^9 m^3 (Zhang et al. 2003). According to the original scheme, through water control at the reservoir, freshwater discharge to the estuary will increase from Jan. to June, a proper level will be maintained in the flood season, i.e., summer, and it

*To whom correspondence and reprint requests should be addressed. Tel: 86-532-82898598. Fax: 86-532-82868008. E-mail:sunsong@qdio.ac.cn

will decrease after Oct.

Zooplankton biomass in the CRE is highest in the flood season, approximately from July to Sept., and lowest in the dry season, from Nov. to Apr. Zooplankton in the estuary is highly diverse, and usually are divided into 3 or 4 groups (Gao and Zhang 1992). Since freshwater species can be found only inside the river mouth and are usually scarce, they were neglected in some investigations focusing on marine species. Estuarine species live near the river mouth, where salinity varies from 6 to 20 practical salinity units (PSU). Oceanic species from the Yellow and East China Seas usually appear at offshore stations, accompanying the invasion of different currents. Shelf species live between these 2 parts, and those from neritic areas of both the Yellow and East China Seas can be observed in this area. The most important species in this area is *Calanus sinicus*, which commonly appears in shelf seas of China, Japan, and Korea. In previous studies, it was dominant in this area year-round, especially in spring and early summer (Xu and Chen 2007). Some tropical-subtropical species, such as *Temora turbinata* and *Rhincalanus nasutus*, can be observed in this area from June to Sept., but they are usually scarce and unimportant in the ecosystem.

Since both the seasonal and geographical distributions of zooplankton are affected by river discharge, it was proposed that water control at the Three Gorges Reservoir (TGR) would substantially influence the zooplankton community. However, it is not possible to predict the influence because of the complexity of the estuary ecosystem. Quarterly samplings were carried out in 2004, in order to inspect zooplankton assemblages after initiation of water control at the TGR, and zooplankton assemblages were also compared to those of previous investigations from 1958-1959 to 2002, to evaluate possible changes.

MATERIALS AND METHODS

Field investigations

Quarterly investigations were carried out at the same set of stations (Fig. 1) during 29 Feb.- 9 Mar., 24-31 May, 31 Aug.- 4 Sept., and 3-8 Nov. 2004. Temperature and salinity were respectively measured with a reversing thermometer (with an accuracy of 0.01°C; GB 13195-1991, [Watanabe Keiki, Japan]) and a portable salinometer (with an accuracy of 0.01‰) at different depths (0, 5, 10, 20, and 30 m). Salinity was measured in PSU. Zooplankton were sampled at each station by vertically towing a net from the bottom to the surface (with a mesh size of 505 μm, a mouth opening of 0.5 m^2, a length of 2 m). Specimens were preserved with 5% formalin seawater and enumerated in the laboratory.

Dominance index

The abundance at each station was calculated with total numbers divided by the volume of water filtered. The dominance index (Y) was calculated by the following formula (Dufrene and Legendre 1997):

$$Y = (n_i / N) \times f_i ;$$

where n_i represents the abundance of the ith species, N is the total abundance of the community, and f_i is the appearance frequency at all of the stations investigated. Rather than employing statistical analyses, a subjective constant of 0.02 was adopted in this study as the criterion for a dominant species.

RESULTS

Environmental conditions

Water temperatures varied 7.96-12.19°C in Feb., 16.11-22.60°C in May, 20.69-28.20°C in Aug., and 19.11-22.76°C in Nov. In Feb. and Nov., since fresh water is colder than oceanic water, the water temperature decreased from neritic to oceanic stations by about 2°C, but in May and Aug. it was found to increase seawards. Thermal stratification was observed at deep stations in May and Aug., while in Feb. and Nov. water temperatures were similar in the surface and bottom layers at all stations. In Aug., cold bottom water was found to have invaded northwestwards to 32°N (Fig. 2).

In our investigation, the influence of the CRDW was largest in May, when the surface salinity was < 30 PSU at all investigated stations, and smallest in Feb., with a saline front appearing at 122.2°E (Fig. 3). Salinities in Feb. were almost the same in the surface and bottom layers, but they were much lower in the surface than in the bottom layer in the other 3 mo, since the diluted water mainly spreads in the surface layer. A salinity of > 32 PSU was observed in the surface layer only in the east of the investigation area in Aug. and in the northeast in Nov., while in bottom layers, it was found in the east during all seasons and occupied much larger areas than in the surface layer.

Zooplankton community

Evident seasonal variations were observed in both species number and total zooplankton abundance. Including planktonic larvae of benthic fauna, totally 65 taxa were recorded in Feb., 89 in May, 123 in Aug., and 81 in Nov. Average zooplankton abundances at each station were 111.1 individuals (ind.)/m^3 in Feb., 254.2 ind./m^3 in May, 725.3 ind./m^3 in Aug., and 107.5 ind./m^3 in Nov. Copepods are the most important zooplankton group in this area. In Feb., 26 copepod species were recorded, accounting for 96.7% of total zooplankton abundance. In May, 23 copepod species accounted for 43.5% of the total abundance, 58 species accounted for 52.3% in Aug., and 36 species accounted for 78.2% in Nov.

Dominant species

In 2004, dominant zooplankton species in the CRE could be divided into 3 groups:

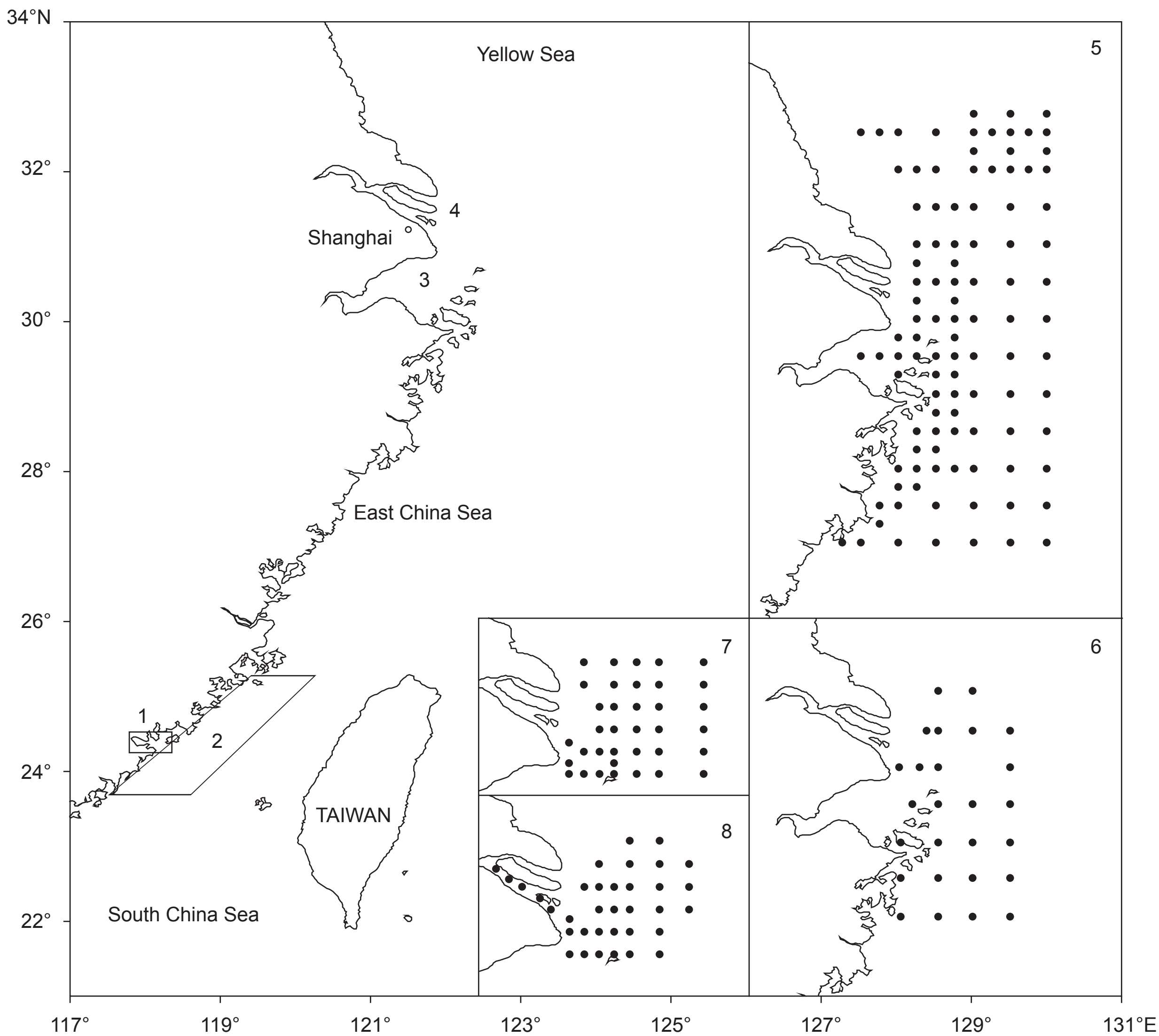

Fig. 1. Map showing sampling stations during the 4 investigations included in this study, and the locations cited in the text. In the map, **1** represents the Jiulong River estuary investigated by Huang and Chen (1985), **2** is the area from Dongshan I. to Meizhou Bay included in Lin and Lian (1988), **3** is Hangzhou Bay, **4** is the Changjiang River estuary investigated in this study, **5** shows the sampling sites during the 1958-1959 investigation, **6** shows those in 2002, **7** shows stations investigated, during 1986-1987 and **8** indicates sampling sites in 2004.

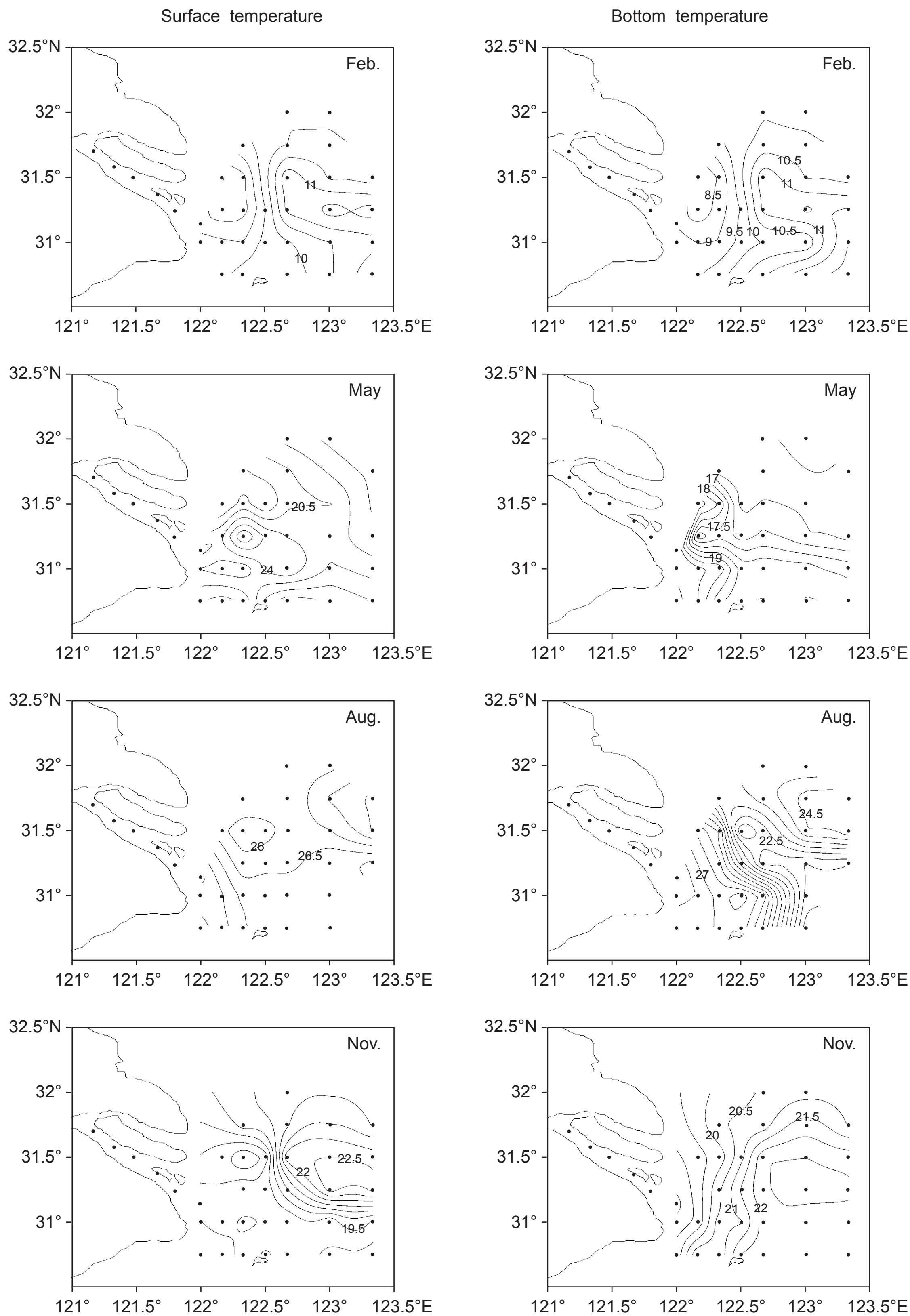

Fig. 2. Isoline maps of surface and bottom temperatures (°C) in the Changjiang River estuary in 2004. Black dots represent measuring sites. As there was only a single row of stations inside the Changjiang River, they were not included in this isoline map. Temperatures at these stations varied from 9.0 to 28.2°C.

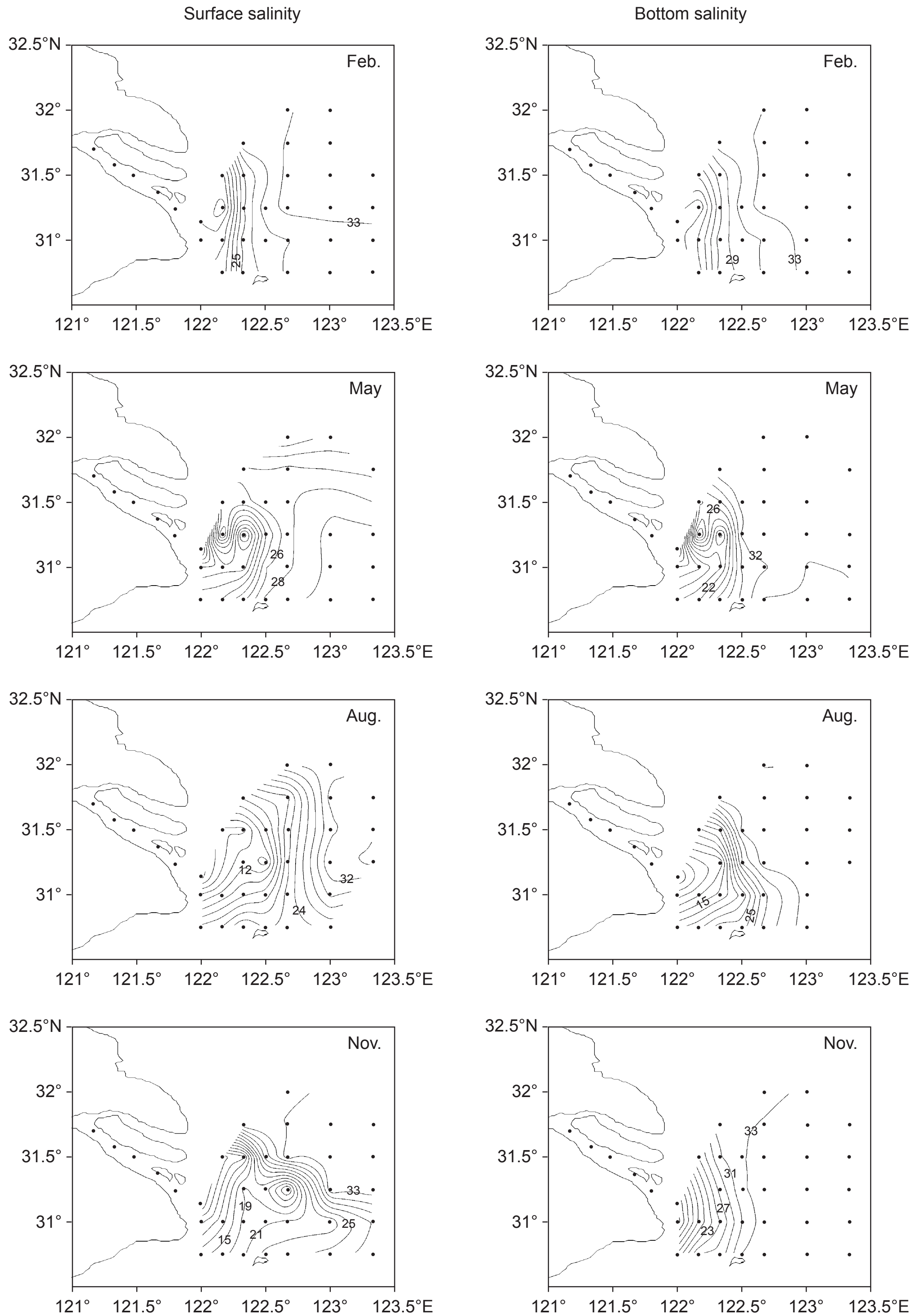

Fig. 3. Isoline maps of surface and bottom salinities in the Changjiang River estuary in 2004. Black dots represent measuring sites. As there was only a single row of stations inside the Changjiang River, they were not included in the isoline map. Salinities at these stations were all < 5 PSU.

species restricted to estuarine areas such as *Sinocalanus* spp.; species found mainly in neritic areas such as *Labidocera euchaeta*, *Acartia pacifica*, *Pseudoeuphausia* spp., *Sagitta nagae*, *Centropages dorsispinatus*, *Temora turbinata*, and *Diphyes chamissonis*; and oceanic species which invade into neritic areas, such as *Calanus sinicus*, *Euchaeta concinna*, *Sagitta enflata*, *Paracalanus* spp., *Oncaea venusta*, and *Doliolum denticulatum*. *Calanus sinicus* was the most predominant species in Feb. and May, with the highest *Y* values of 0.11 and 0.26, while in Nov. its *Y* value was similar to that of *Paracalanus* spp. and *E. concinna* (Table 1).

Most of those species were recorded as being dominant in previous observations, except for *T. turbinata* and *Paracalanus* spp. (Table 2). *Temora turbinata*, which had been recorded but was never dominant in the estuarine area, was found to be the predominant zooplankton species in Aug. 2004 in this study, with the highest dominance index of 0.09. It was captured at 29 of 35 total stations, and the highest abundance of 439.2 ind./m^3 was recorded as far north as 31.5°N, with an inter-station average of 81.9 ind./m^3. The distribution range had expanded compared to former studies, and *T. turbinata* was found even at stations inside the Changjiang River (Fig. 4). During the 1961 investigation, no individuals of the *Temora* genus were recorded at 30°50'-32°N and 121°50'-122°20'E (Chen et al. 1995). In that study, *T. turbinata* was not observed in Feb. or May, and appeared at only 2 stations in Nov. with an abundance no higher than 0.2 ind./m^3. Three *Paracalanus* species, *P. parvus*, *P. aculeatus*, and *P. crassirostris*, were recorded in the estuarine area. Since copepodites of these 3 species are difficult to differentiate, they were identified as *Paracalanus* spp. in this study, which might have increased their abundance and dominance index in the statistical analysis.

Among the 4 mo investigated in this article, zooplankton assemblages changed more evidently in Aug. than in the other 3 mo. Not only was *T. turbinata* recorded as the most predominant species for the first time, but also some previously recorded dominant species, such as *C. sinicus*,

Table 1. Dominant zooplankton species and their dominance index (*Y*) in the Changjiang River estuary during quarterly investigations in 2004

Taxon	Aug. 2004	Nov. 2004	Feb. 2004	May 2004
Copepoda				
Calanus sinicus		0. 13	0. 11	0. 26
Labidocera euchaeta		0. 03	0. 02	
Centropages dorsispinatus	0. 07			
Paracalanus spp.	0. 04	0. 13		
Sinocalanus tenellus			0. 08	
S. sinensis			0. 07	
Euchaeta concinna		0. 14		
Temora turbinata	0. 09			
Acartia pacifica	0. 08			
Oncaea venusta			0. 06	
Chaetognath				
Sagitta enflata	0. 08			
S. nagae		0. 04		
Sagitta larvae				0. 10
Siphonophora				
Diphyes chamissonis				0. 04
Euphausidii				
Pseudoeuphausia sinica		0. 02		
Decapods				
Decapoda larvae	0. 03	0. 03		0. 06
Thaliceae				
Doliolum denticulatum	0. 03			
Other				
Brachyura larvae				0. 02

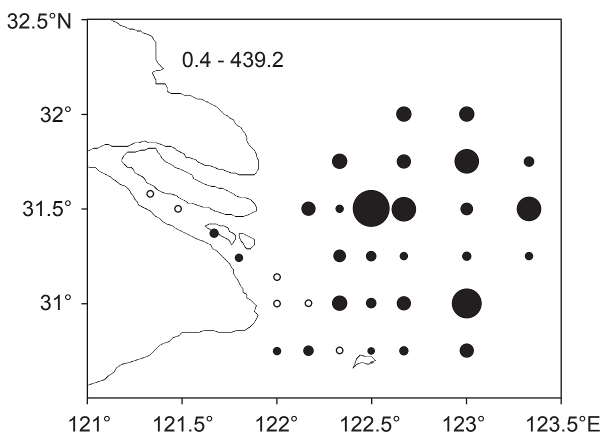

Fig. 4. Geographical distribution of *Temora turbinata* in Aug. 2004, the 2nd summer after water control began at the Three Gorges Reservoir. Open circles represent stations at which no *T. turbinata* was captured, and the sizes of the filled circles are in proportion (linearly) to the abundances of *T. turbinata* (individuals (ind.)/m^3).

E. conncina, and *L. euchaeta*, were no longer dominant, as their dominance index decreased to < 0.02 (Table 1). Among these 3 species, *C. sinicus* used to be dominant in this area year-round, and it was the most predominant species in Aug. 1986 and 2002. *Labidocera euchaeta* was recorded as dominant in Aug. 1959 and 1986, with respective dominance indices of 0.09 and 0.03. Although no *Euchaeta* species was recorded as dominant, large numbers of *Euchaeta* larvae were observed in Aug. 1959 and 2002.

DISCUSSION

Zooplankton assemblages were consistent with previous studies in all seasons except summer, when *T. turbinata* unexpectedly prospered. This is the first time that it was found to be a dominant species in the temperate CRE. During monthly sampling from Sept. 1955 to Dec. 1956 and Aug. 1985 to July 1986, *T. turbinata* was

Table 2. Dominant zooplankton species and their dominance index (*Y*) in the Changjiang River estuary in Aug. in this and 3 previous studies

Taxon	Aug. 1959	Aug. 1986	Aug. 2002	Aug. 2004
Copepoda				
Calanus sinicus	0. 06	0. 11	0. 50	
Labidocera euchaeta	0. 09	0. 03		
Tortanus vermiculus	0. 03			
Centropages dorsispinatus		0. 03		0. 07
Paracalanus spp.				0. 04
Euchaeta larvae	0. 12		0. 04	
Temora turbinata				0. 09
T. discaudata			0. 02	
Acartia pacifica		0. 04	0. 04	0. 08
Chaetognath				
Sagitta betodi	0. 13			
S. enflata	0. 09	0. 06	0. 05	0. 08
S. nagae		0. 09		
Siphonophora				
Muggiaea atlantica		0. 04		
Diphyes chamissonis		0. 03		
Cladocera				
Penilia avirostris		0. 03		
Euphausidii				
Pseudoeuphausia latifrons	0. 03			
Decapods				
Lucifer intermedius	0. 02	0. 03	0. 03	
Decapoda larvae				0. 03
Thaliceae				
Doliolum denticulatum				0. 03

observed in the CRE in 7 different months during 1958-1959 and 4 mo in 1985-1986, but completely disappeared in the other months (Fig. 5). In the 5 mo in 1958-1959, when *T. turbinata* was much more abundant in the estuary, it was found to mainly be distributed in the southern portion of the ECS (Fig. 6). In 1959, no individual was captured to the north of 32°N, but it had invaded as far north as 33.5°N in Sept. 1958. The highest abundance found in the ECS was 68.1 ind./m^3, far less than the 439.1 ind./m^3 recorded in this study. The frequency of capturing *T. turbinata* at various stations in this area was no higher than 41% during 1955-1956, and < 28% during 1985-1986. As stations in Aug. 2002 were limited to the east of 122°E and expanded southwards (all locations mentioned in this paragraph are marked in figure 1), the frequency was as high as 81%, but the abundance at each station was no more than 38.0 ind./m^3. The highest abundance during 1955-1956 was found in Sept. 1956 of 68.0 ind./m^3, and that during 1985-1986 was only 2.0 ind./m^3.

Temora turbinata has been found to be predominant in mesozooplankton communities in various environments around the world, but usually in tropical and subtropical areas (Goswami and Padmavati 1996, Lopez-Salgado and Suarez-Morales 1998, Ara 2002, Dunbar and Webber 2003). In seas around China, it is common in coastal and estuarine areas in the southern part of the ECS and the South China Sea. In the Jiulong River estuary (Fujian, China), the population size of *T. turbinata* peaks from Apr. to June. Its abundance was about 11-100 ind./m^3 in this period, but < 10.0 ind./m^3 the rest of the year (Huang and Chen 1985). From Dongshan I. to Meizhou Bay on the west side of the Taiwan Strait, its abundance was > 25.0 ind./m^3 in May, with a maximum of 250.0 ind./m^3 (Lin and Lian 1988), and on the east side of the strait, it was the predominant zooplankton species in the same month, with an average abundance of 65.0 ind./m^3 (Lan et al. 2004). In the northern part of the Taiwan Strait and southern part of the ECS, it was predominant in Aug. (Hsieh et al. 2005). It can be found in the northern part of the ECS and the Yellow Sea in summer, but at very low abundances (Zheng et al. 1982).

In previous studies, *T. turbinata* was suggested to be a tropical-subtropical species of shelf-oceanic environments (Lopez-Salgado

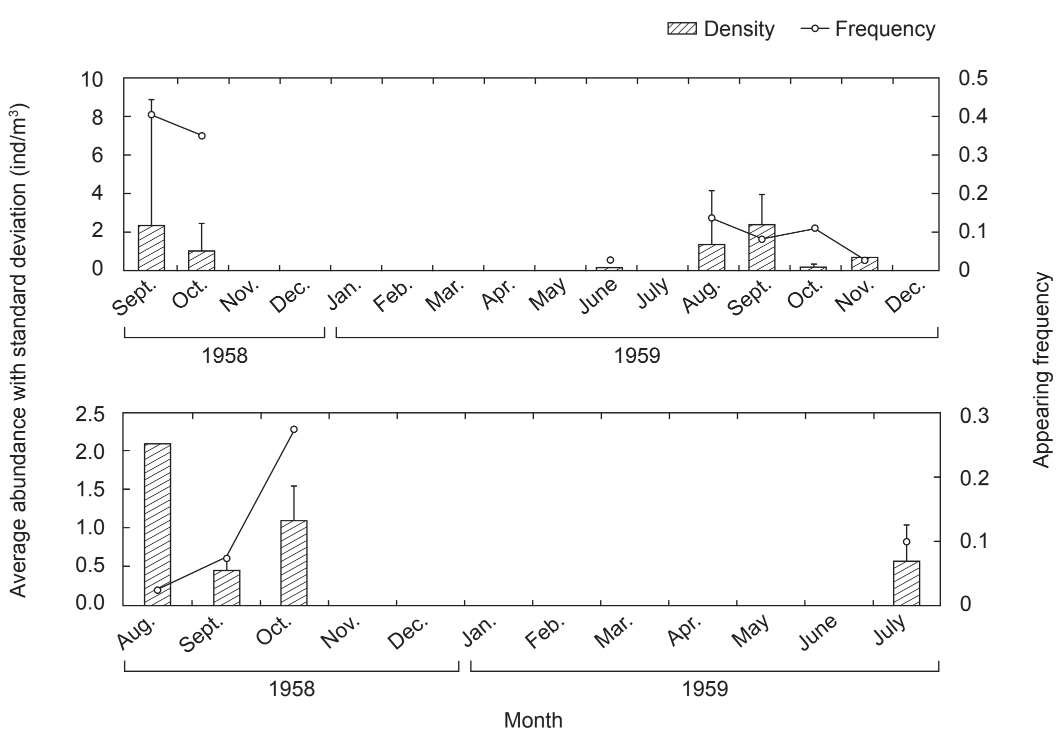

Fig. 5. Annual variations in *Temora turbinate* in the Changjiang River Estuary. The histogram represents the average abundance (individuals (ind.)/m^3) among all stations at which *T. turbinata* appeared, and the error bar represents the standard deviation. Circles represent the frequency at which *T. turbinata* was captured at all stations. As the 1958-1959 investigation covered a large area, only stations within 30-32°N and 121.25-124°E were included in this figure.

and Suarez-Morales 1998). Temperatures below 16.5°C appear to be less than optimal for the successful growth and reproduction of this species. However, it can be transported considerable distances in the open ocean, due to its tolerance of a wide range of environmental conditions (Vervoort 1965, Bradford 1977). In the CRE, *T. turbinata* cannot recruit locally, and was most possibly transported from southern parts of the seas around China every year, since it can be found only in summer in this area but perennially in the south. Population maintenance is impossible in winter, when water temperatures are as low as 5°C, far lower than its optimal temperature of 16.5°C, and its abundance usually peaks after Aug. in this area, later than the Apr.-June period in the Jiulong River estuary. In our investigation in 2004, it dramatically decreased in Nov. and was not recorded in the estuary in Feb. or May. In the Jiulong River estuary, it can be found year-round, even though its abundance decreases dramatically after summer. In the northern part of the Taiwan

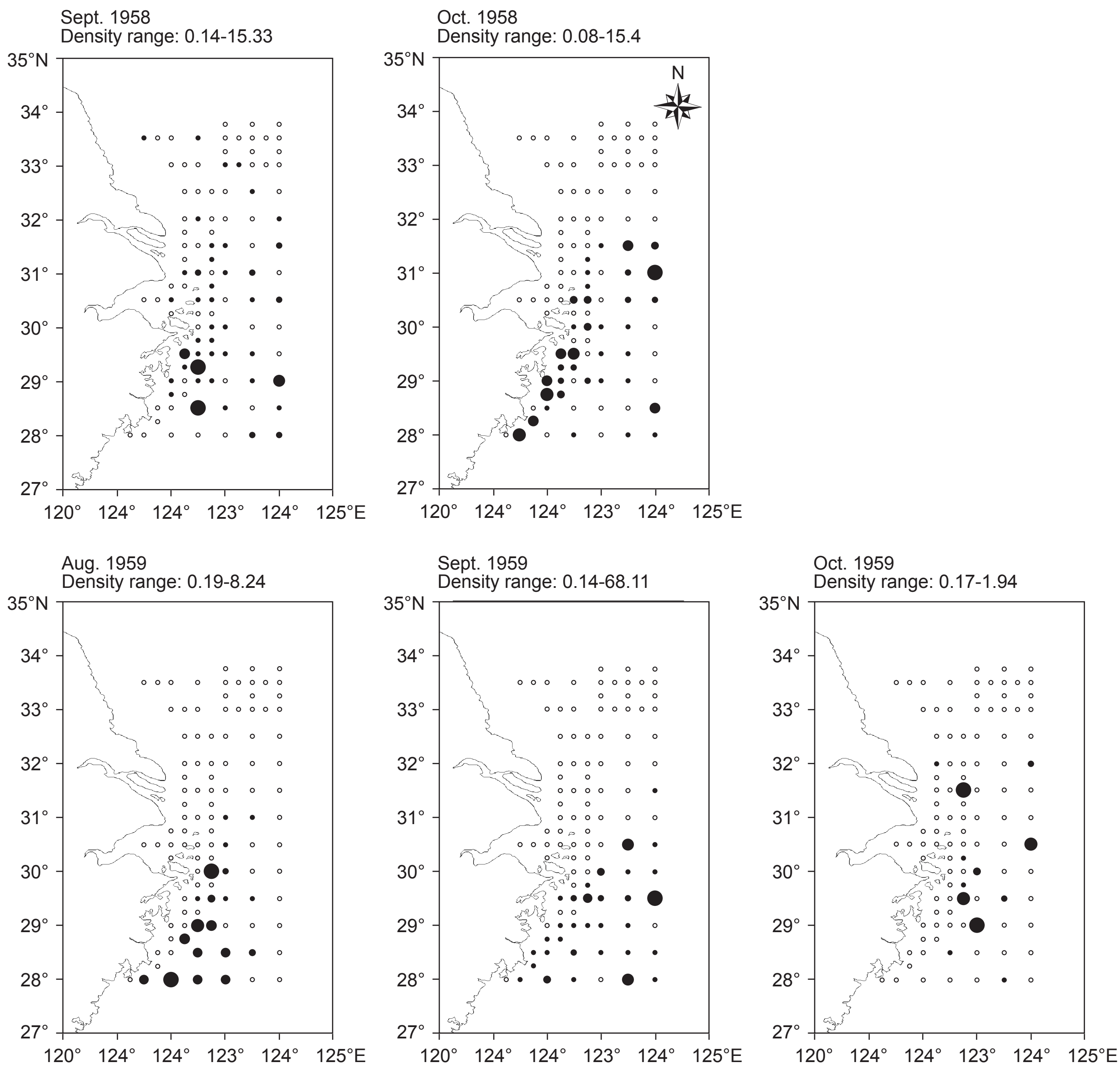

Fig. 6. Geographical distribution of *Temora turbinata* in peak months of Aug. to Oct. Open circles represent stations at which no *T. turbinata* was captured, and the sizes of the filled circles are in proportion (linearly) to the abundances of *T. turbinata* (individuals (ind.)/m^3).

Strait, it was predominant in Aug. (Hsieh et al. 2005), which is later than in the Jiulong River estuary but similar to results in this area.

Additionally, judging from the current patterns, transportation of this species from the south to the CRE is reasonable. In summer, both the Taiwan Warm Current (TWC) and the coastal current in the southern portion of the estuary flow northwards (Zhang and Wang 2004), which might introduce *T. turbinata* from both sides of the Taiwan Strait to the investigation area. Usually, the northerly invasion of the TWC, especially that in the surface-water layer, is counteracted by the CRDW. It may reach further north when freshwater discharge is low. In Aug. 1998, when the discharge was greatest in the past 20 yr at 77,100 m^3/s, the CRDW expanded southeastwards at the mouth, before turning towards the north-northeast (Guo et al. 2000). The CRDW occupied most of the surface areas and reached as far east as 127°E in that year, while salty TWC water invaded only in the bottom layer as a narrow band to 31°N. The freshwater discharge was only 39,500 m^3/s in Aug. 2000, when the CRDW expanded towards the north-northeast directly at the river mouth (Zhu et al. 2003). In our study, the freshwater discharge was 40,290 m^3/s in Aug. 2004 (JR Zhu, pers. comm.), smaller than the long-term average of 43,000 m^3/s in Aug. but a little higher than that in Aug. 2000. The physical environments were quite similar in these 2 yr, when salty water invaded westwards to 123°E in the surface layer and northwestwards to 32°N in the bottom layer. The TWC bottom water can also be distinguished by its low temperature, consistent with that determined by the high salinity (Fig. 2).

Besides introducing more *T. turbinata* into the estuarine area, the northerly invasion of the TWC also influences other aspects of the zooplankton assemblages in the CRE. First, in such circumstances, zooplankton from north and east, such as *C. sinicus*, *L. euchaeta*, and *E. concinna*, will have less opportunity to enter the estuarine area. *Calanus sinicus* is the dominant species in the Bohai, Yellow, and East China Seas. In summer, it is known to decrease in most areas but is concentrated in the Yellow Sea Cold Water Mass area (Zhang 1989, Wang et al. 2003). In previous studies, the Yellow Sea Mixed Water, characterized by a low bottom temperature, can invade the estuarine area from the northeast, but it could not be distinguished in this study. *Labidocera euchaeta* is a neritic species mainly distributed in the northern part of the estuary, and *E. concinna* is an oceanic species in deep areas of the ECS. Second, invasion by the TWC can also change the physical environments. Uye (1988) suggested that the respective lower and upper thermal limits for embryonic development of *C. sinicus* were 5 and 23°C, and other authors have concluded that *C. sinicus* thrives at 10-20°C (Huang and Zheng 1986). *Calanus sinicus* is thought to be able to survive the hot summer in the Yellow Sea because of the cold bottom refuge and stable vertical structure, which ensures that it avoid hot surface temperatures through a flexible diel vertical migration (Zhang et al. 2007). However, both the surface and bottom temperatures might be disturbed by an invasion of the TWC. The most notable difference is that the bottom temperature at most stations in this study increased above 23°C, which is known to be deleterious to *C. sinicus* (Huang and Zheng 1986, Pu et al. 2004, Zhang et al. 2005), but *T. turbinata* is known to be able to adapt to high temperatures (27-30°C) (Hopcroft and Roff 1998).

However, transport by the TWC itself cannot explain the prosperity of *T. turbinate* in this area. First, the maximum abundance observed here is even higher than those in the Taiwan Strait, the suggested region of origin. This indicates that the population was likely recruited endemically after introduction. Second, the freshwater discharge was even lower in Aug. 2000 than in Aug. 2004. Although physical environments were quite similar in these 2 yr, a dominant species shift was not observed in Aug. 2000 (Xu and Shen 2005). *Temora turbinata* was absent from all samples in 2000, while *L. euchaeta*, *C. sinicus*, and *E. concinna* were found as dominants although with lower *Y* values (Xu et al. 2005).

Although it was recorded immediately after water control at the TGR was initiated, the dominant species shift did not likely result from changes induced by freshwater discharge. First, we cannot be sure that the low freshwater discharge in Aug. 2004 was induced by water control at the TGR. According to the original scheme, the river discharge ought to be constant from July to Sept. The water level of the TGR reached 135 m in June 2003, and reports about its precise impacts on freshwater discharge and physical environments in the estuary area are still unavailable. Second, the prevalence of *T. turbinata* should become established over a long period rather than in a single month. Quarterly sampling in our investigation missed the period when the *T. turbinata* population was increasing.

Since the maximum abundance observed here was even higher than values from the Taiwan Strait, the population should include individuals transported from elsewhere and those also recruited locally.

In our opinion, the prosperity of *T. turbinata* in the CRE is another case of a northward extension of warm-water species resulting from global warming. In previous studies, it was suggested that changes in the biogeography of copepods can be explained by climate change or their impact on phytoplankton through food chain effects (Beaugrand et al. 2002, Piontkovski and Landry 2003, Richardson and Schoeman 2006). According to inter-annual SST variations, the CRE has entered a warm period since 1986 (Zhou et al. 2005). The SST anomaly in 2004 was positive, indicating that it was also a warm year (XY Zhou, pers. comm.). *Temora turbinata* is present year-round within a temperature range of 18.6-29.6°C (Ara 2002). In the CRE, water temperatures fall into this range from approximately June to Oct. However, in warm years, e.g., with annual maximum SSTs, this period may be obviously prolonged by a month as global warming continues. Thus, it is possible that *T. turbinata* can survive a longer time and produce a larger population locally. Invasion or substitution by *T. turbinata* has been recorded in various areas. Although those mechanisms are still not completely understood due to limited physical and biological background data, further studies on *T. turbinata* will be meaningful to the ecology of this species, and in detecting how global climate changes are influencing biogeography.

Acknowledgments: We acknowledge support from the Three Gorges Project Construction Committee in the project, the 3 Gorges Project, and the Estuary Ecology and Environment (SX2001-018). We thank Prof. J.R. Zhu, S.W. Gao, and Dr. W.W. Xian for their help with specimen identification and field sampling. Financial support from the Science and Technology Ministry of China (973-G1999043708 and 2006CB400606) to S. Sun is also acknowledged.

REFERENCES

Ara K. 2002. Temporal variability and production of *Temora turbinata* (Copepoda: Calanoida) in the Cananeia Lagoon estuarine system, Sao Paulo, Brazil. Sci. Mar. **66:** 399-406.

Beaugrand G, PC Reid, F Ibañez, JA Lindley, M Edwards. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science **296:** 1692-1694.

Bradford JM. 1977. Distribution of the pelagic copepod *Temora turbinata* in the New Zealand coastal waters, and possible trans-Tasman population continuity. NZ J. Mar. Freshw. Res. **11:** 131-144.

Chen YQ, ZL Xu, YL Wang, FX Hu, H Hu, GC Gu. 1995. An ecological study on zooplankton in plume front zone of Changjiang (Yangtze) River estuarine area. I. Biomass distribution of dominant species. J. Fish. Sci. China **2:** 49-63. (in Chinese with English abstract)

Dufrene M, P Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. **67:** 345-366.

Dunbar FN, MK Webber. 2003. Zooplankton distribution in the eutrophica Kingston Harbour, Jamaica. Bull. Mar. Sci. **73:** 343-359.

Gao SW, HQ Zhang. 1992. On the ecology of zooplankton in the Changjiang River estuary. Stud. Mar. Sin. **33:** 201-216. (in Chinese with English abstract)

Goswami SC, G Padmavati. 1996. Zooplankton production, composition and diversity in the coastal waters of Goa. Indian J. Mar. Sci. **25:** 91-97.

Guo BH, EM Zou, XJ Xiong, WM Huang. 2000. Seasonal variation of water exchange between the Yellow and East China Sea. Acta Oceanol. Sin. **Supplement:** 13-23. (in Chinese with English abstract)

Guo YJ, YL Pan. 1992. Primary productivity in the Changjiang River estuary. Stud. Mar. Sin. **33:** 191-199. (in Chinese with English abstract)

Hopcroft RR, JC Roff. 1998. Zooplankton growth rates: the influence of female size and resources on egg production of tropical marine copepodites. Mar. Biol. **132:** 79-86.

Hsieh CH, CS Chen, TS Chiu. 2005. Composition and abundance of copepods and ichthyoplankton in Taiwan Strait (western North Pacific) are influenced by seasonal monsoons. Mar. Freshwater. Res. **56:** 153-161.

Huang JQ, BY Chen. 1985. Composition and distribution of planktonic copepods in the Jiulong River estuary. Taiwan Strait **4:** 79-87. (in Chinese with English abstract)

Huang JQ, Z Zheng. 1986. The effects of temperature and salinity on the survival of some copepods from Xiamen Harbour. Oceanol. ET Limnol. Sin. **17:** 161-167. (in Chinese with English abstract)

Ichikawa H, RC Beardsley. 2002. The current system in the Yellow and East China Seas. J. Oceanogr. **58:** 77-92.

Lan YC, CT Shih, MA Lee, HZ Shieh. 2004. Spring distribution of copepods in relation to water masses in the northern Taiwan Strait. Zool. Stud. **43:** 332-343.

Lin YH, GS Lian. 1988. Ecological studies of planktonic copepods in the west part of the Taiwan Strait. J. Oceanogr. Taiwan Strait **7:** 248-253. (in Chinese with English abstract)

Lopez-Salgado I, E Suarez-Morales. 1998. Copepod assemblages in surface waters of the western Gulf of Mexico. Crustaceana **71:** 312-330.

Piontkovski SA, MR Landry. 2003. Copepod species diversity and climate variability in the tropical Atlantic Ocean. Fish. Oceanogr. **12:** 352-359.

Pu XM, S Sun, B Yang, P Ji, YS Zhang, F Zhang. 2004. The combined effects of temperature and food supply on *Calanus sinicus* in the southern Yellow Sea in summer. J. Plankton Res. **26:** 1049-1057.

Richardson AJ, DS Schoeman. 2006. Climate impact on plankton ecosystems in the Northeast Atlantic. Science

305: 1609-1612.

Uye SI. 1988. Temperature-dependent development and growth of *Calanus sinicus* (Copepoda: Calanoida) in the laboratory. Hydrobiologia **167/168:** 285-293.

Wang R, T Zuo, K Wang. 2003. The Yellow Sea Cold Bottom Water - an oversummering site for *Calanus sinicus* (Copepoda, Crustacea). J. Plankton Res. **25:** 169-183.

Vervoort W. 1965. Pelagic Copepoda. Part II. Copepoda Calanoida of the families Phaennidae up to and including Acartiidae, containing the description of a new species of Aetidaidae. Atlantide Rep. **8:** 9-216.

Xu ZL, BJ Chen. 2007. Seasonal distribution of *Calanus sinicus* (Copepoda, Crustacea) in the East China Sea. Acta Oceanol. Sin. **26:** 150-159.

Xu ZL, XQ Shen. 2005. Zooplankton biomass and its variation in water near Changjiang Estuary. Resources Environ. Yangtze Basin **14:** 282-286. (in Chinese with English abstract)

Xu ZL, XQ Shen, SW Ma. 2005. Ecological characters of zooplankton dominant species in the waters near the Changjiang estuary in spring and summer. Mar. Sci. **29:** 13-19. (in Chinese with English abstract)

Zhang GT, S Sun, B Yang. 2007. Summer reproduction of the planktonic copepod *Calanus sinicus* in the Yellow Sea: influences of high temperature and cold bottom water. J. Plankton Res. **29:** 179-186.

Zhang GT, S Sun, F Zhang. 2005. Seasonal variation of reproduction rates and body size of *Calanus sinicus* in the southern Yellow Sea, China. J. Plankton Res. **27:** 135-143.

Zhang JB. 1989. Marine Atlas of Bohai Sea, Yellow Sea, East China Sea: biology. Beijing: China Ocean Press. (in Chinese with English abstract)

Zhang JS, NS Zhao, XB Mao. 2003. Analysis on the impoundment process of Three Gorges Reservoir up to EL 135 m. Water Power **12:** 19-21. (in Chinese with English abstract)

Zhang QL, F Wang. 2004. Climatological analysis of water masses in Zhoushan fishing ground and adjacent region. Oceanol. ET Limnol. Sin. **35:** 48-54. (in Chinese with English abstract)

Zheng Z, SJ Li, S Li, BY Chen. 1982. Distribution of planktonic copepods in the Taiwan Strait. Taiwan Strait **1:** 69-77. (in Chinese with English abstract)

Zhou XY, DB Hu, CZ Wang, XJ Hu, SK Yao. 2005. Seasonal and inter-annual SST variation in the Changjiang River estuary. Period. Ocean Univ. China **35:** 357-362. (in Chinese with English abstract)

Zhu JR, PX Ding, DX Hu. 2003. Observation of the diluted water and plume front of the Changjiang River estuary during August 2000. Oceanol. ET Limnol. Sin. **34:** 249-255. (in Chinese with English abstract)