

# Breeding places, population dynamics, and distribution of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in the Yellow Sea and the East China Sea

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Received: 5 August 2014 / Revised: 16 March 2015 / Accepted: 25 March 2015 / Published online: 23 April 2015  
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**Abstract** In East Asian waters, concern about giant jellyfish blooms, including *Nemopilema nomurai* (Cnidaria: Scyphozoa: Rhizostomeae), has increased in recent decades. Based on surveys in 2012 and 2013, as a part of the Chinese Jellyfish 973 Program, we investigated the life cycle in situ of the planktonic stages of this species in the Yellow Sea and the East China Sea. We found the following results: (1) Offshore of the Changjiang River is one of its principal breeding places, and is the area where the pelagic stages of *N. nomurai* appear earliest in the YS and ECS. (2) The general distribution pattern of pelagic stages of *N. nomurai* described previously in the YS and ECS is confirmed from the 2012 and 2013 surveys: From this small area (31.50–33.00°N,

122.00–122.75°E) usually in late May and early June, it expanded into the 31.5–36°N sea area (aggregating in 32–34°N) in June, then continued to expand northward and southward to 30–37°N by August, and then shrank to 34–37°N in October. (3) The biomass and abundance of *N. nomurai* in 2012 both in June and August were higher than those in 2013. (4) We confirmed that almost all pelagic stages of *N. nomurai* in the YS and ECS were confined north of 30°N. The breeding places, population dynamics, and mechanism of formation of the distribution pattern of *N. nomurai* in the YS and ECS in recent years are presented.

**Keywords** Jellyfish bloom · Population dynamics · Biomass · Abundance · Life cycle

Guest editors: Song Sun, Xiaoxia Sun & Ian Jenkinson / Giant Jellyfish Blooms and Ecosystem Change

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## Introduction

In recent decades, the ecological roles of jellyfish in marine ecosystems have attracted increasing concern worldwide (e.g., Arai, 2001; Lynam et al., 2005; Purcell, 2005, 2007). Some evidence points to a general worldwide increase of jellyfish, associated with over-fishing, eutrophication, climate change, and species invasions (reviewed in Purcell et al., 2007). Other evidence, however, suggests that any global increase in jellyfish may be not as robust as previously thought (Condon et al., 2013), despite clear evidence for increases locally, as in the Bering Sea, the Mediterranean, and northern Gulf of Mexico (Graham,

2001; Mills, 2001; Brodeur et al., 2002). In East Asian waters, particularly the Sea of Japan, and both Korean and Chinese coastal seas, jellyfish including *Nemopilema nomurai* (Cnidaria: Scyphozoa: Rhizostomeae) have been more intensively studied in recent decades (e.g., Kawahara et al., 2006; Uye, 2008; Zhang et al., 2012; Xu et al., 2013; Yoon et al., 2014).

Mass occurrences of *N. nomurai* in the Yellow Sea (YS) and the East China Sea (ECS) took place in 2003, and in 2006, 2007, 2009, 2012 (Yan et al., 2004; Ding & Cheng, 2005; Li et al., 2007; unpublished data cited in our “Discussion” section). Previously, mass occurrences took place in the Sea of Japan in 1920, 1958, and 1995, which is about once every 40 years (Kishinouye, 1922, Shimomura, 1959, Yasuda, 2004), but since 1995 “explosions” (Uye, 2008) of *N. nomurai* mass occurrences have occurred in this area, including in 2002, 2003, 2006, 2007, and 2009 (Kawahara et al., 2006; Xu et al., 2013). In Korean waters, by comparison, for the period 2005–2013, the highest abundance was recorded in 2005, followed by 2007 and 2009, and the least abundance was in 2008 and 2010–2013 (Yoon et al., 2014). In brief, the abundance of this species in recent years in East Asia waters has varied from year to year and has not always shown an increasing trend.

*Nemopilema nomurai* is one of the largest jellyfish species, and can attain a bell diameter of ~2 m and a wet weight of ~200 kg (Kishinouye, 1922, Omori & Kitamura, 2004). Like other jellyfish, *N. nomurai* frequently shows diurnal vertical movement, sometimes migrating between depths of over 100 m and the surface (Honda et al., 2009). So far studies of *N. nomurai* have been done on life cycle, growth, and mass occurrence in the Sea of Japan (e.g., Kawahara et al., 2006; Uye, 2008); transport of organic matter (Yamamoto et al., 2008); induction of gonadal maturation and spawning, oocyte size, and maturity (Ohtsu et al., 2007; Toyokawa et al., 2010); the roles of podocysts (Kawahara et al., 2013); physical and biological processes affecting the occurrence around Cheju Island (Yoon et al., 2008); and simulated behavior of the giant jellyfish *N. nomurai* by a particle-tracking experiments in the (ECS) and the Sea of Japan (Moon et al., 2010). Many of these cited papers have repeated a widely held belief that “The *N. nomurai* population appearing in the Sea of Japan is transported from coastal areas along China and the western

Korean Peninsula (i.e. the Bohai, Yellow and northern East China Seas)” (Uye, 2008). The first aim of the present work has been to conduct surveys to test this hypothesis, and to refine it should the findings show this to be necessary. To do this, we have improved the existing baseline of knowledge on the life cycle of *N. nomurai* in China coastal seas (e.g., Cheng et al., 2005; Ding & Cheng, 2005, 2007; Li et al., 2007; Zhang et al., 2012), including the initial population and its development, biomass increase, and decay in the Yellow sea (YS) and the ECS.

The second aim of this study is to improve understanding of the life cycle of *N. nomurai* in situ in Chinese and nearby coastal seas. Wild ephyrae of *N. nomurai* were first recorded offshore of the Changjiang river estuary by Toyokawa et al. (2012). However, it is still not clearly known where and when the ephyra begins to appear in the northern ECS. Based on the results of our surface count surveys and bottom trawl surveys in recent years (Zhang et al., 2012), preliminary conclusions on the population dynamics of this species in 2006–2007 have been that young medusae always appear first in the northern ECS in late May and early June, especially offshore of the Changjiang river estuary, and then the distribution expands to the whole YS and northern ECS in summer, before gradually shrinking northward to a small sea area, and disappearing in autumn and winter. Using these previous conclusions as a hypothesis, the third principal aim of the present study has been to examine what inter-annual differences occur in the population dynamics, the occurrence, the spatial distribution pattern, and the biomass; in relation to this, we also determined if there still were no medusae south of 30°N in the ECS, i.e., the condition we observed in 2006–2007. To summarize, the investigation reported here has had three principal aims: (1) to obtain data to support or counter the previous conclusion that the area offshore of the Changjiang River is the earliest ephyrae releasing place, (2) to investigate the population dynamics, including the annual expansion and shrinkage of the geographical distribution of medusae, and (3) to re-examine the southern boundary of this species. This work has been based primarily on cruise surveys conducted in 2012 and 2013, and also in the context of all our previous data as a part of National Basic Research Program (China Jellyfish Project 973 Program).

## Materials and methods

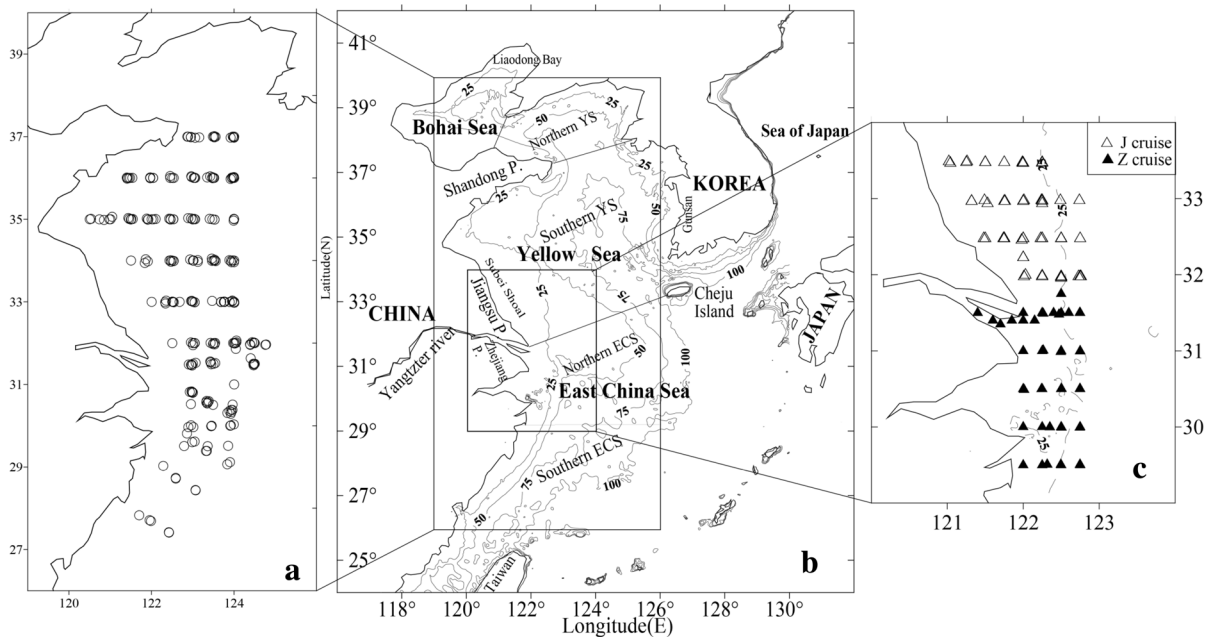
### Study area

The YS and ECS are semi-enclosed by the contiguous lands of China in the west and Korea in the east, being temperate marginal seas in the northwest Pacific Ocean. They are connected topographically, but divided subjectively by a line from the Yangtze River mouth to Cheju Island (Fig. 1). These two relatively shallow seas are strongly affected by monsoons, massive river runoff, tides, and the Kuroshio Current. Combination of these characteristics causes various circulation regimes and different water masses. Generally, in spring–summer, currents tend to flow counterclockwise in the southern YS, while a coastal current also flows from south to north at the offshore edge of Subei Shoal (Su, 1998), and in the ECS, despite the weak south-eastward current running along the 50 m isobath off the Changjiang River, the main direction of the whole current system i.e., Taiwan Current and other branches of the Kuroshio Current are all northeast (Fig. 2) (Ichikawa & Beardsley, 2002; Guan & Fang, 2006; Yang et al., 2012). In autumn–winter time, the current is not exactly same

with spring–summer current, and one of the differences is that the Yellow Sea Warm Current generally exists northwestward in the center of the southern YS (Su, 1998). Some hydrology characteristics in the YS and ECS are given by Wei et al. (2015).

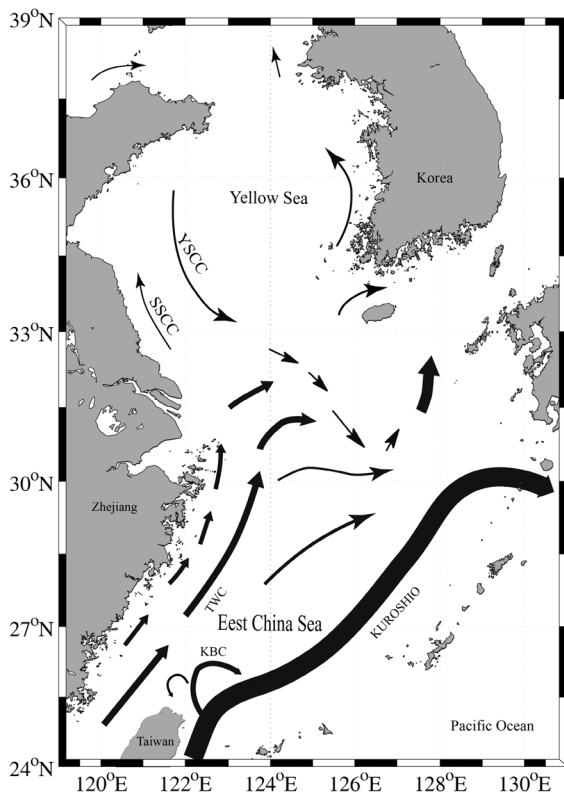
### Breeding place

Based on our previous survey results from 2006 to 2009, the young medusa of *Nemopilema nomurai* first began to occur in the northern ECS (but not yet in other parts of the YS or the Bohai Sea) especially close offshore of the Changjiang River. In order to seek the conspicuous juvenile stages of *N. nomurai* as early as possible, two cruises being undertaken, the “Jiangsu offshore” (J) cruise and the “Zhejiang offshore” (Z) cruise, by two fishing boats “Zhe Pu Yu 23012” and “Su Ru Yu Yun 288”. On the cruises, sampling was carried out in May and early June 2013 (Fig. 1c; Table 1). During J cruise, 66 samples (one sample at each station) were collected from off Jiangsu province, and some stations were repeated several times from May 3 through June 8, 2013. Almost simultaneously, on Z cruise, 62 samples were collected from off Zhejiang province, and similarly some stations were



**Fig. 1** Map (b) of study area, isobaths (gray line) of 25, 50, 75, and 100 m in coastal water. Sampling stations of surveys for population dynamics and distribution pattern of *Nemopilema*

*nomurai* from 2012 to 2013 (a) and for early planktonic larvae in May and early June 2013, some of the stations were surveyed several times (c)



**Fig. 2** Current system distribution pattern of average residual current during spring–summer (April–September) in the Yellow Sea and East China Sea (drawn according to Su, 1998; Guan & Fang, 2006; Ichikawa & Beardsley, 2002; Yang et al., 2012). YSCC Yellow Sea Coastal Current, SSCC Subei Shoal Coastal Current, TWC Tai Wan Current, KBC Kuroshio Branch Current

repeated several times from May 3 to May 31, 2013. A conical plankton net (0.8 m mouth diameter, 500  $\mu\text{m}$  mesh size) was towed obliquely for 10 min from near the bottom to the surface, where the boat speed varies from 1.5 to 4.0 knots. According to the morphology of the earliest stages of *N. nomurai* described by Kawahara et al. (2006), ephyrae, metephyrae, and juvenile medusae of *N. nomurai* were enumerated in the field, and the standard bell diameter (for ephyrae and metephyrae: width from lappet tip to lappet tip) was measured on board using a stereomicroscope, and then preserved in 5% neutralized formalin seawater solution. A Seabird SBE-25 CTD was deployed to determine temperature and salinity.

#### Population dynamics and distribution pattern

Aiming to follow the trail of biomass increase and decay of *N. nomurai* in 2012 and 2013, 6 bottom trawl

surveys were conducted in the YS and ECS aboard the R/V *Beidou* in June, August and October 2012, June, August and September 2013 (Table 1). Survey stations varied somewhat from cruise to cruise due to the weather conditions (total stations are shown in Fig. 1a). The trawling method and biomass calculation of *N. nomurai* as a by-catch in bottom trawl surveys has been described by Zhang et al. (2012). The bell diameter of each medusa from subsamples was measured. A Seabird SBE-25 CTD was deployed to determine temperature and salinity at every station during all cruises. The synchronous temperature and salinity data in 2012 and 2013 in the YS and ECS are given by Wei et al. (2015). Variation shown around the mean of all units in this paper ( $\pm$ ) represents SD.

#### Validation of distribution bound of *N. nomurai*

To investigate whether the southern limit of distribution of *N. nomurai* in the ECS still remained to the north of 30°N, the presence or absence data of *N. nomurai* caught as by-catch sampled in bottom trawl surveys described above in 2012 and 2013 were also analyzed (Fig. 1; Table 1).

## Results

### Initial breeding place

The results of the investigations on J cruise and Z cruise in May and June, 2013 (Fig. 3; Table 2), showed a total of 58 early pelagic larvae (ephyra, metephyrae, and juvenile medusae) of *N. nomurai* occurring in the area (122.00–122.75°E, 31.50–33.00°N) from May 3 to June 8, 2013. Among them, 39 ephyrae and metephyrae were found, comprising 67% of the total pelagic *N. nomurai* larvae. Two metephyrae (Bell diameter (BD) measuring 25 and 10 mm, respectively) were initially found at stations (122.75°E, 31.48°N) and (122.51°E, 31.51°N) on May 4, 2013, and then a single ephyra (BD 5 mm) was taken at station (122.25°E, 32°N) on May 6, 2013. The abundance sampled was very low during the period investigated, and pelagic larvae occurred in only 14 samples out of 128, with only occasional ephyrae/metephyrae presenting in samples from station (122.25°E, 32.99°N) and station (122.75°E,

**Table 1** Cruise dates, areas, and sampling method

Survey purpose	Year	Date	Survey range	Survey sea area	Sampling method
Breeding place	2013	May 3–June 8	32.00–33.50°N, 121.00–122.75°E	Jiangsu offshore	Zooplankton net (500 µm mesh size)
		May 3–31	29.50–31.50°N, 121.50–122.75°E	Zhejiang offshore	
Population development and distribution pattern, validation of distribution bound	2012	June 11–29	27.42–37.00°N, 120.50–124.50°E	SYS and ECS	Bottom trawl (10 cm mesh size cod-end with a 2.4-cm-mesh liner)
		October 9–26	30.02–37.00°N, 121.13–124.40°E		
	2013	June 17–29	27.41–37.01°N, 121.40–124.50°E		
		August 13–September 2	29.50–36.99°N, 120.85–124.78°E		
Previous study survey	2006	June 1–13	27.90–33.10°N, 122.40–125.00°E	ECS	Bottom trawl
		August 19–September 12	27.80–39.00°N, 120.50–125.00°E	YS and ECS	
		October 2–November 3	27.80–36.50°N, 121.00–125.00°E	SYS and ECS	
	2007	May 6–15	26.90–32.00°N, 121.20–124.00°E	ECS	SYS and ECS
		August 15–September 3	31.00–37.00°N, 121.20–124.51°E		
	2008	July 9–13	34.00–35.80°N, 120.00–121.00°E	SYS	SYS
		August 9–12	34.00–36.00°N, 120.00–122.00°E		
	2009	July 29–August 27	27.80–36.50°N, 120.50–125.00°E	SYS and ECS	
	2011	August 12–August 30	26.45–36.99°N, 120.51–125.51°E	SYS and ECS	Surface water observing

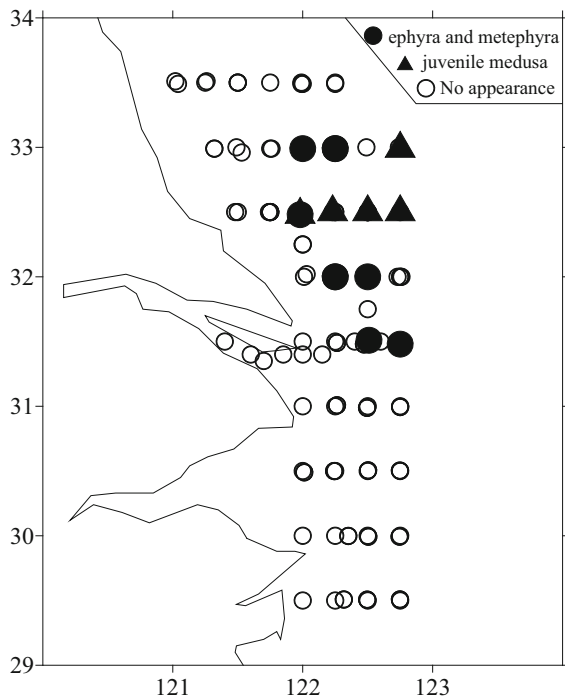
SYS Southern Yellow Sea, ECS East China Sea, YS Yellow Sea

32.5°N) with 32 and 12 individuals being taken on May 30 and on June 6, respectively. No jellyfish larva of any form was found in the southern area surveyed or in the northernmost section.

The temperature and salinity at each station where early pelagic stages appeared in May and early June 2013 are shown in Table 2. On average, the temperature and salinity of the surface and bottom water were 17.3 °C, 15.6 °C, 27.8, and 31.0, respectively.

#### Population dynamics and distribution pattern

In 2012, the biomass of *N. nomurai* increased from  $(9,512 \pm 18,998 \text{ kg km}^{-2})$  in June to  $(26,698 \pm 34,867 \text{ kg km}^{-2}, P < 0.01)$  in August, then dramatically decreased to  $(79 \pm 154 \text{ kg km}^{-2}, P < 0.01)$  in October. However, the abundance of the population increased non-significantly from June  $(2,051 \pm 3,274 \text{ ind. km}^{-2})$  to August  $(3,793 \pm 7,498 \text{ ind. km}^{-2}, P > 0.05)$ , then dramatically decreased to just a few



**Fig. 3** Stations with occurrence of ephyrae and metephyrae (black circles), juvenile medusa (black triangles) of *Nemopilema nomurai* and stations (circles) investigated at which no “early pelagic larvae” were found in May and early June at offshore of Jiangsu and Zhejiang Province

medusae over the whole cruise in October ( $P < 0.01$ ). On the other hand, the population of this species has been growing from smaller bell diameter ( $41 \pm 18$  cm,  $n = 745$ ) in June to significantly larger BD ( $63 \pm 21$  cm,  $n = 965$ ,  $P < 0.001$ ) in August, then they decayed in October. Only 11 medusae were sampled on the October cruise, and were rather fragmentary, which prevented us measuring their BD. With regard to distribution pattern of BD, generally *N. nomurai* was smaller in the northern part ( $34\text{--}36^\circ\text{N}$ ) than in the southern sections ( $31\text{--}34^\circ\text{N}$ ) in June 2012 ( $P < 0.05$ ), and a similar situation was presented in August 2012 ( $P < 0.05$ ) (Fig. 4).

Compared to 2012, biomass and abundance of *N. nomurai* dramatically increased from ( $391 \pm 1,360$  kg km<sup>-2</sup>,  $154 \pm 341$  ind km<sup>-2</sup>) in June to ( $11,388 \pm 14,634$  kg km<sup>-2</sup>,  $P < 0.001$ ,  $688 \pm 1,057$  ind km<sup>-2</sup>,  $P < 0.01$ ) in August, and continued to increase non-significantly to ( $16,026 \pm 37,822$  kg km<sup>-2</sup>,  $P > 0.05$ ,  $1,395 \pm 3,512$  ind km<sup>-2</sup>,  $P > 0.05$ ) in September, 2013. The biomass and abundance of *N. nomurai* in 2012 in both June and August were

significantly higher than that in 2013 (both  $P < 0.01$ ). The distribution area was mainly limited to  $31.5\text{--}34^\circ\text{N}$  in June 2013, which is smaller in extent than the area occupied in June 2012, while they increased and expanded to the same whole survey area in August 2013. It seems the biomass distribution pattern of this species in the area  $30\text{--}32^\circ\text{N}$  had already begun to shrink northward in September 2013, although at this time this species was distributed over the same area as in August. Correspondingly, the BD significantly increased from ( $32 \pm 20$  cm,  $n = 375$ ) in June to ( $83 \pm 21$  cm,  $n = 416$ ,  $P < 0.001$ ) in August, and then non-significantly decreased to ( $72 \pm 20$  cm,  $n = 526$ ,  $P > 0.05$ ) in September in 2013. The distribution pattern of medusa size in 2013 was similar to that in June 2012, *N. nomurai* was smaller in the northern than in the southern part of the studied area in June 2013 ( $P < 0.05$ ), while the medusa size was almost uniform in August and September 2013, which was dissimilar to the situation in August 2012 (Fig. 5).

The distribution pattern of *N. nomurai* surveyed in 2012 was generally similar to that in 2013 in the YS and the ECS (Figs. 4, 5), from the small area of occurrence usually in May, medusae of *N. nomurai* distributed into the  $31.5\text{--}36^\circ\text{N}$  sea area (aggregating in  $32\text{--}34^\circ\text{N}$ ) in June, then the distributional area continued to expand northward and southward, covering  $30\text{--}37^\circ\text{N}$  in August, and then shrank northward to a small sea area in October. In short, the annual cycles of development and distribution were basically similar, but with quantitative differences.

Average temperatures and salinities of surface and bottom water from June to October in 2012 and 2013 in the study area are shown in Table 3. The distribution of temperature and salinity in detail is given by Wei et al. (2015) There was no significant difference in the average temperature at the surface or at the bottom between these 2 years (ANOVA,  $P > 0.05$ ), while the average salinity in June and August 2013 was higher than that in June and August 2012 except for the average bottom salinity in August (ANOVA,  $P < 0.01$ ).

#### Validation of distribution bound of *N. nomurai*

According to the stations at which *N. nomurai* occurred in June, August, September, and October, 2012 and 2013 (Figs. 4, 6), we found that almost all *N. nomurai* occurred north of  $30^\circ\text{N}$ . So the southern

**Table 2** Time and location of earliest observation of pelagic larvae of *Nemopilema nomurai* with temperature and salinity in May and early June 2013

Date (2013)	Longitude and latitude	Early pelagic <i>Nemopilema nomurai</i> larvae	Individual number	Temperature (°C)		Salinity		Bell diameter (mm)
				Surface	Bottom	Surface	Bottom	
May 4	122.75°E, 31.48°N	Metephyra	1	15.1	13.0	28.0	32.7	25
May 4	122.51°E, 31.51°N	Metephyra	1	16.5	12.7	13.0	33.1	10
May 6	122.25°E, 32.00°N	Ephyra	1	16.4	14.0	17.2	29.5	5
May 14	122.25°E, 32.00°N	Metephyra	1	15.5	15.1	29.7	29.8	10
May 14	122.50°E, 32.00°N	Ephyra	1	15.4	13.8	30.5	31.8	7
May 30	122.25°E, 32.99°N	Ephyra, metephyra	32	16.5	16.4	31.4	31.4	2–18
May 30	122.00°E, 32.99°N	Ephyra	1	17.0	16.8	31.4	31.4	7
May 31	121.98°E, 32.48°N	Metephyra	1	17.8	16.0	29.1	30.5	18
May 31	122.23°E, 32.50°N	Juvenile medusa	1	17.7	16.1	29.2	30.5	50
June 1	122.50°E, 32.50°N	Juvenile medusa	2	17.4	16.6	30.5	30.7	68, 104
June 5	122.25°E, 32.99°N	Metephyra	1	17.7	17.0	31.0	31.1	13
June 5	122.75°E, 32.99°N	Juvenile medusa	1	18.1	14.1	30.6	31.1	58
June 6	121.98°E, 32.48°N	Juvenile medusa	2	20.3	17.6	28.7	30.3	90, 110
June 6	122.75°E, 32.50°N	Juvenile medusa	12	20.8	18.6	28.4	30.9	60–140

distribution bound of *N. nomurai* was north of 30°N at that time.

## Discussion

### Breeding place

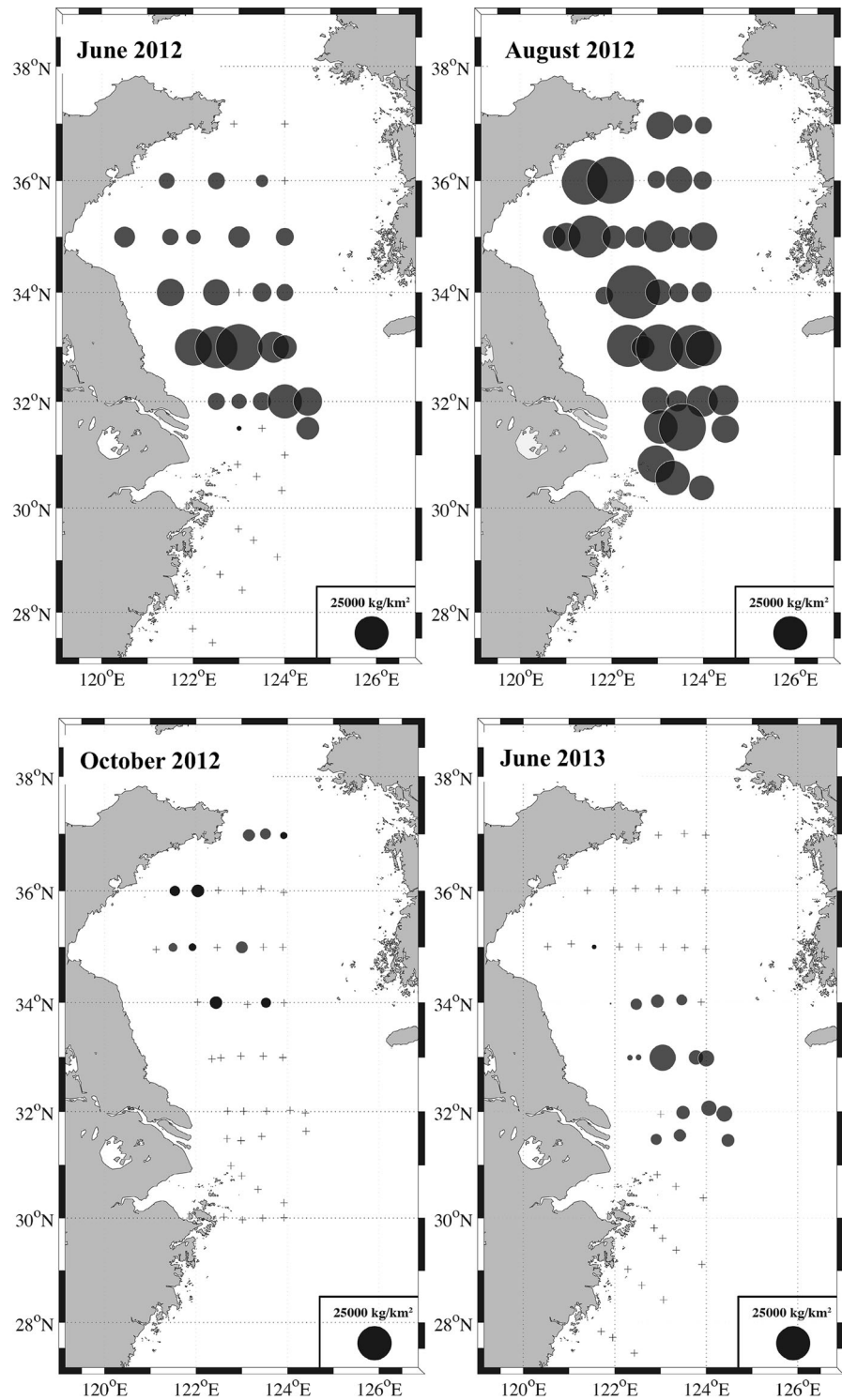
From laboratory-rearing experiments, Kawahara et al. (2006) found that newly liberated ephyrae grew to metephyrae (BD: 8–14 mm), advanced metephyrae (BD: 14–18 mm), and young medusae (BD: 40–110 mm) by 10, 20, and 40–50 day post-liberation, respectively. Despite variable conditions in the field, according to the time and the stages of *N. nomurai* we sampled (Table 2), it is reasonable to extrapolate that the pelagic *N. nomurai* larvae occurring in this area (122.00–122.75°E, 31.50–33.00°N) in 2013 had been liberated during the last few days of April, when temperature in the water column was increasing from ca. 12 to 18°C. Our conclusion thus in part supports the reports by Kawahara et al. (2006) that strobilation and ephyra liberation take place in April, May, and June.

As for the temperature and salinity at stations where ephyrae and metephyrae occurred, the surface temperature and salinity varied from 15 to 18°C and from 13 to 31.4 psu, respectively, and bottom temperature

and salinity varied from 12.7 to 17°C and from 29.5 to 33.1 (Table 2). According to our unpublished data, in situ results of experiments on observing the process of strobilation, by hanging a plastic plate with attached artificially cultured scyphistoma of *N. nomurai* in the seawater during winter and spring in Jiaozhou Bay, Qingdao (36.07°N, 120.32°E), showed that the ephyrae were liberated at 10–18°C (also indicated by Feng et al., 2015). Therefore, the surface and bottom temperatures where ephyrae first occurred are completely compatible with the findings of these experiments. The temperature range where the earliest ephyrae occurred also supported the idea that the time when temperature reaches 15°C is a critical step that enables polyps to induce strobilation and then release ephyra to grow, thus modulating the highest cumulative rate of strobilation for *N. nomurai* (Kawahara et al., 2013; Xu et al., 2013).

The place where the early larvae of *N. nomurai* occurred in 2013 coincides with the first place where the occurrence of wild ephyrae of *N. nomurai* was found by Toyokawa (2012). He reported one ephyra and four ephyrae of *N. nomurai* with 1–2-mm diameter at (32°12.3'N, 123°12'E) and (34°05.8'N, 121°50.0'E), respectively, in the northwestern ECS on 22 and 26 May 2011. These two sites are close to the area (31.50–33.00°N and 122.00–122.75°E) where early planktonic larvae of this species occurred in this study.

**Fig. 4** Distribution and biomass ( $\text{kg km}^{-2}$ ) of *Nemopilema nomurai* in the Yellow Sea and East China Sea in 2012 and 2013 (plus indicates the stations where no *N. nomurai* presented)

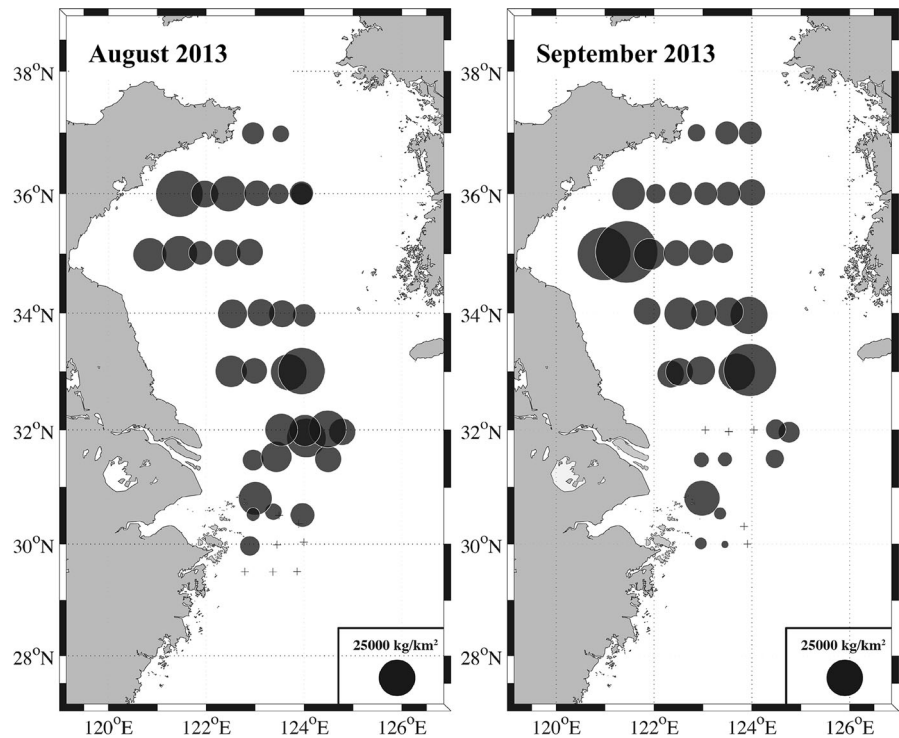


The first appearance places of *N. nomurai* were also found in other places, e.g., the southwestern Cheju Island in May 2010 and the eastern coastal sea of

Korea in May 2012 (Yoon et al., 2014). Kawahara et al. (2006) documented that several tens of juvenile medusae (extended bell diameter: 2–8 cm) were



Fig. 4 continued



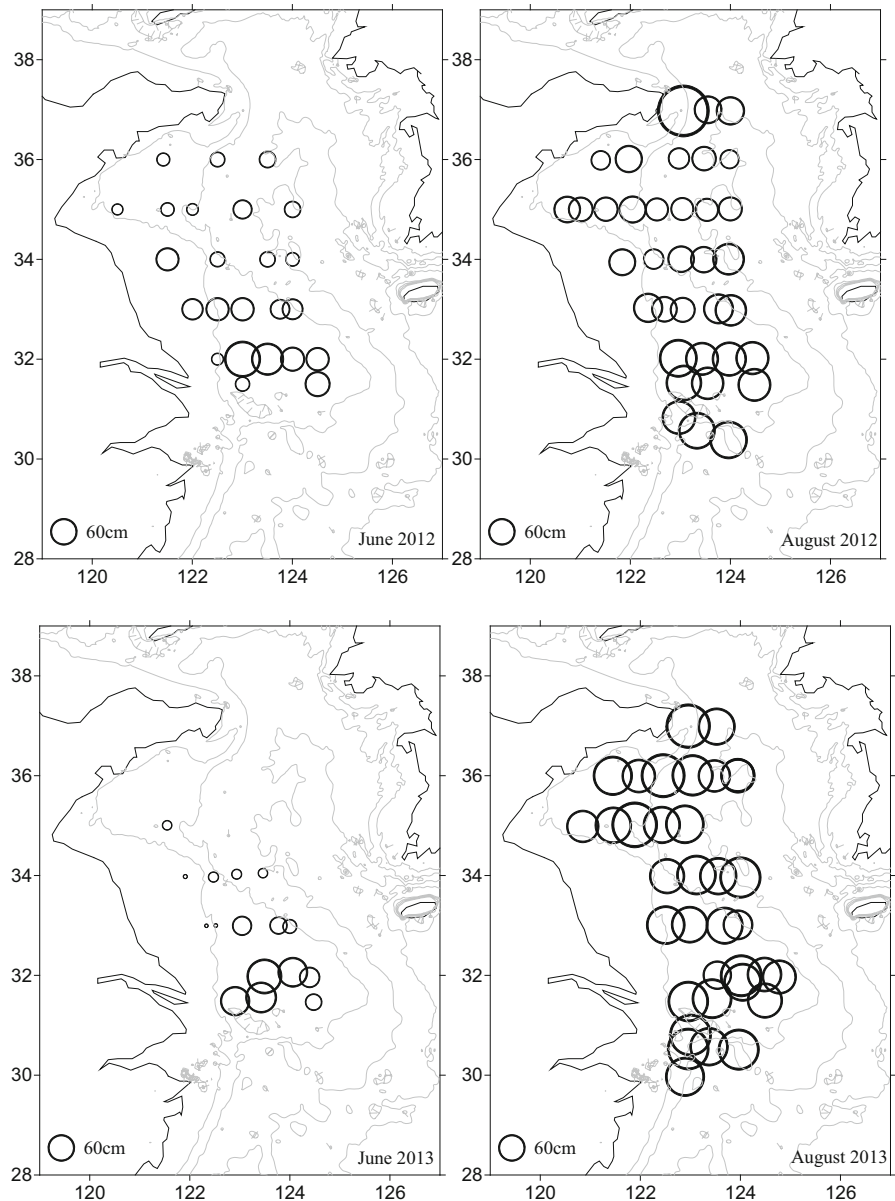
collected in early June 2004 in a set-net near Gunsan, west Korea, and also several young medusa (BD < 10 cm) were found in the coastal area off Gunsan in May 2008 (Yoon et al., 2014). Wang et al. (2013) investigated the *N. nomurai* medusae (BD: ca. 10 cm) occurring in Liaodong Bay, Bohai Sea in early June from 2008 to 2011. We strongly suggest these populations are not the same cohort as the earlier occurring population off the Changjiang River, taking account of the time and location of occurrence, and the currents in the southern YS (Fig. 2). Hence, juvenile medusae off the Changjiang River mouth are likely to have come from ephyrae liberated earlier from the strobila in the locality, while the other places where juvenile medusae occurred would have come from strobilae liberated later at or near their native place.

Therefore, in the YS and the ECS, it is off the Changjiang River where the pelagic stages of *N. nomurai* first occur, and appear to be one of the major population sources of *N. nomurai*. Aim 1 of the study (Introduction), to test whether that the ephyra of *N. nomurai* occurs first offshore of the Changjiang River estuary in May, is thus achieved, and the hypothesis is supported.

#### Population dynamics and distribution pattern

Our findings now allow us to describe the population dynamics, from the initial occurrence, the increase and the decay as well as BD, of the planktonic stages of *N. nomurai* in the YS and northern ECS. The temporal change in population dynamics and distribution pattern of *N. nomurai* in 2012 and 2013 in YS and Northern ECS was almost the same as those in 2006–2007 (Zhang et al., 2012). The data for 2006, 2007, 2012, and 2013 are also consistent with those for the years 2009 and 2011, although in these years the process of population development was recorded in less detail. Based on the distribution of *N. nomurai* mentioned above from 2006 to 2013 in the YS and ECS, and from monitoring information on the coast of Bohai Sea (X. Zheng, Fisheries Research Institute of Hebei, China, Personal Communication), the documentation about the Liaodong Bay, Bohai Sea (e.g., Wang et al., 2013), and the records about the first occurrence of *N. nomurai*, we show a sketch map which summarizes our conclusions on variations of the distribution pattern in Bohai Sea, YS, and northern ECS (Fig. 7).

**Fig. 5** The distribution of average bell diameter of *Nemopilema nomurai* in the Yellow Sea and East China Sea in 2012 and 2013



A few ephyrae, metephyrae, and juvenile medusae of this species first appear in China and Korea coastal sea areas in May and June. They first appear offshore of the Changjiang River, and then are found successively in other northern sea areas: southwest of Cheju Island, the eastern coastal sea of Korea, the offshore of Gunsan, Korea, and finally Liaodong Bay, Bohai Sea, China. The distribution pattern of *N. nomurai* expanded progressively to about 31.5–36°N in the southern YS in June (there were no medusae found in the northern YS), along with the growth in BD, then

spread northward to the whole YS, southward to 30°N in August, before shrinking to the northern YS in October, until they died and disappeared in the late autumn and winter. The medusa life span is thus less than 1 year. Similarly, the life cycle of *N. nomurai* northwest of Japan and in the Sea of Japan, where medusae first appear near Tsushima Island (between Kyushu and Korea) in late July, then the leading edge of this medusa bloom is thought to be transported northeast by the Tsushima Current into the Sea of Japan, successively from the end of August, until the

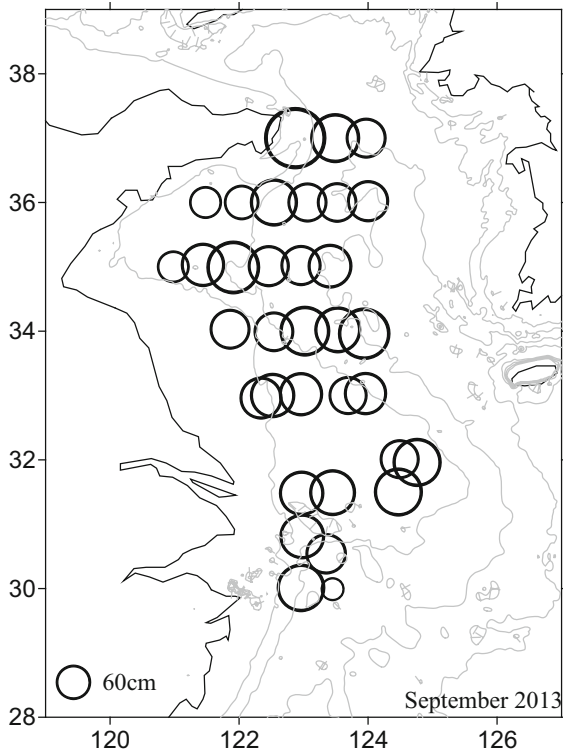


Fig. 5 continued

medusae die in December due to low temperatures and/or genetically determined senescence (Kawahara et al., 2006; Uye, 2008).

In brief, based on the consistent population dynamics of distribution in recent years, aim 2 of the study to investigate the population dynamics is achieved, and the hypothesis that there is marked seasonal variation in the process of population

increase and decay in spring and summer among different years is seriously countered.

Mechanism of distribution patterns

Since we have found seasonal variation patterns of *N. nomurai* to be consistent for different years, we suggest that some intrinsic and extrinsic factors may be causing this coherence. At first, from our results, a few ephyrae, metephyrae, and juvenile medusae of this species occurred offshore of the Changjiang River and the adjacent waters, and then the newly liberated ephyrae, metephyrae, and other stages appeared progressively later in other northern sea areas. This may also explain why medusae of *N. nomurai* were mostly smaller in the north of their range in the YS and ECS than in the south of their range, not only in June, but also extending into early August (Fig. 5). Because currents in the southern YS rotate mainly counter-clockwise in summer (Fig. 2, Su, 1998), they cannot transport ephyrae or young medusae to the northern areas (The coastal current from south to north at offshore of the Subei Shoal would not be strong enough to be significant). Therefore, we suggest that at least most of the smaller medusae in the northern areas of the ECS/YS are produced locally (i.e., in the northern parts of the ECS/YS) and are not the result of advection from the south. This means that the distribution pattern of medusae in June is mainly caused by local succession, rather than by advection.

Along with the increasing BD, the distribution pattern in June spreads northward to the whole YS (resulting from local succession), and southward to 30°N in August, which may be driven by the current

Table 3 Biomass and abundance of *Nemopilema nomurai*, and temperature and salinity in 2012 and 2013 in the YS and ECS

	2012						2013					
	June		August		October		June		August		September	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
B	9513	18,998	26,699	34,867	78.2	153.8	391.6	1360	11,389	14,635	16,026	37,822
A	2051	3274	3794	7499	5.7	9.9	154.6	341.2	689	1058	1395	3513
St	22.21	2.14	26.95	0.90	21.02	1.68	22.39	1.87	27.05	1.68	25.17	1.52
Bt	15.05	4.69	14.55	5.96	17.22	6.24	15.10	4.74	16.91	6.32	17.43	6.65
Ss	29.10	4.27	30.05	3.67	31.16	2.00	30.90	2.66	31.29	1.68	31.36	1.68
Bs	32.78	1.17	33.76	1.88	32.27	1.15	33.39	1.27	32.79	1.21	32.65	1.25

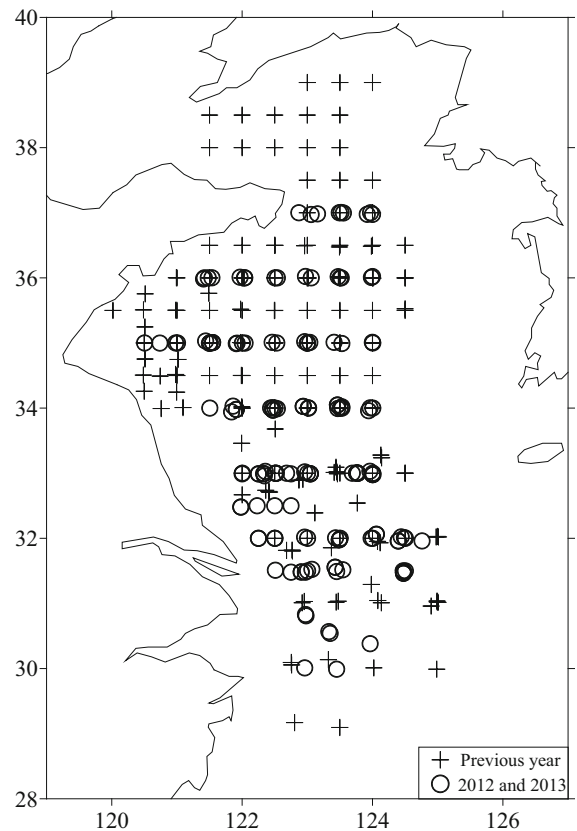
B biomass (kg/km<sup>2</sup>), A abundance (ind/km<sup>2</sup>), St surface temperature (°C), Bt bottom temperature (°C), Ss surface salinity, Bs bottom salinity

from northwest to southeast (30–32°N, Fig. 2). When the season moves to autumn (October), not only may the medusae in the Northern ECS be transported by the Yellow Sea Warm Current (northwestward from the center of the southern YS) to the northern YS, but may be transported also by Changjiang Diluted Water (CDW) to the Eastern ECS, and some may also be transported northeast by the Tsushima Current into the Sea of Japan. Furthermore, mature medusae die after sexual reproduction, and hence we suggest that these three mechanisms (advection away by the YSWC; advection away by the CDW; and death after sexual reproduction) result in the population decrease observed in Northern ECS in autumn.

However, comparing the distribution pattern of *N. nomurai* surveyed in 2012 with that in 2013 (Figs. 4, 5), there existed differences in quantities and extent, e.g., the distribution range was larger and the medusae appeared earlier in northern areas in June 2012 than they did in 2013, even though the annual cycles of development and distribution were basically similar. We suggested that the differences in hydrological characteristics in these 2 years (see the detail in Wei et al., 2015) may be related to the distribution patterns. Wei et al. thought that the CDW extended to 35°N, the utmost northern edge that it could reach, and stronger Kuroshio intrusion onto the continental shelf in 2012, while the CDW spread at the surface to the east of Cheju Island, and Kuroshio water intruded northward and was confined to 31°N. As for what the mechanism is between them, the stronger Kuroshio water may bring water with favorable temperature, nutrients, algae constituents, and zooplankton, which would benefit the survival rate of *N. nomurai* ephyrae, although further investigation of this idea will require more experimental and long-time series data.

#### Inter-annual variation of abundance and biomass

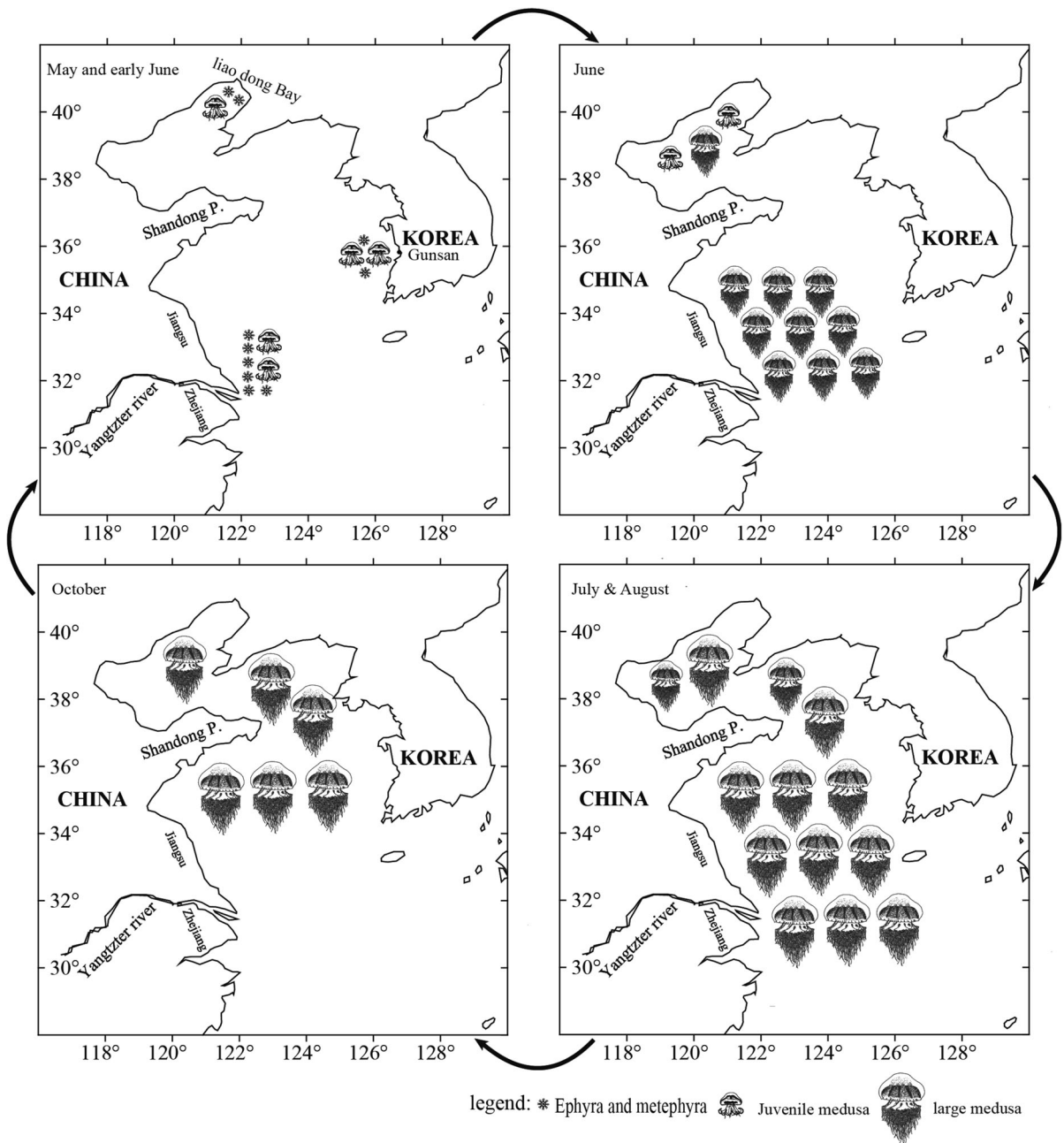
The abundance and biomass of *N. nomurai* were all generally much higher in 2012 than that in 2013 (Fig. 4; Table 3). Compared to the abundance of this species here in other years (Table 4), 2012 was a jellyfish bloom year, while 2013 was a mid-bloom year. Comparing environmental conditions in summertime between 2012 and 2013 (Wei et al., 2015), the summer of 2012 was unusual in many observed aspects. There is evidence that a much stronger Kuroshio intruded onto the continental shelf in 2012



**Fig. 6** Stations at which *Nemopilema nomurai* was observed in spring–summer in the Yellow Sea and East China Sea in 2006–2013

than in 2013. In addition, maybe because the CDW exceptionally extended to 35°N, the average temperature in June was almost the same between these 2 years, while the average salinity in June 2012 was pronouncedly lower by 1.8 (surface) and by 0.6 (bottom) than that in 2013 (ANOVA,  $P < 0.01$ ). We suggest that the lower salinity in June may have been helpful for the jellyfish bloom in 2012. This suggestion is supported by our experiment in the laboratory that showed low salinity gave better survival of scyphistoma and medusa, but more investigations in future years are needed to refine these ideas.

Table 4 roughly shows inter-annual variation in abundance of *N. nomurai* in the southern YS based on our own data in the same area in August and early September, 2006–2013, among which, data from (2006–2009 and 2012–2013) were obtained by the same bottom trawl method, while data from 2011 were obtained by surface observation (methods introduced



**Fig. 7** Proposed annual variation in the distribution of *Nemopilema nomurai* in ECS/YS: increase and decrease in biomass

by Wang et al., 2012). For consistent and visualized analysis, we converted bottom trawl and surface observed data into each other by the correction factor (we compared these two methods in the August 2006 and June 2012 surveys), and we found that the abundance data from surface observations were generally ten times as big as the data from the bottom

trawls). These rough results were almost in agreement with the bloom description of this species in recent years in the YS and ECS, i.e., jellyfish years (2002–2007, 2009), and non-jellyfish years (2008, 2010, and 2011) (Xu et al., 2013; Fisheries Research Agency, Japan: [http://jsnfri.fra.affrc.go.jp/Kurage/kurage\\_top.html](http://jsnfri.fra.affrc.go.jp/Kurage/kurage_top.html)). Although Xu et al. (2013)

**Table 4** Annual variation of abundance of *Nemopilema nomurai* in the southern Yellow Sea

Year	2006	2007	2008	2009	2010	2011	2012	2013
Bottom trawl (ind/km <sup>2</sup> )	2045*	2580*	765*	4951*	No data	34	3674	837*
Surface observation (ind/100 m <sup>2</sup> )	2.05	2.58	0.77	4.95		0.034*	3.67	0.84

“\*” means the average real data obtained by the corresponding methods, otherwise data corrected by conversion (see text for conversion method)

suggested that the long-term increases in *N. nomurai* outbreaks and the recent absence may be driven by anthropogenic factors and climate change, we still need more data and analysis to find the relationship between the biomass/abundance and the different factors concerned, e.g., the environmental parameters, the food density, and so on.

#### Validation of distribution bound of *N. nomurai*

Not only the appearance data in 2012 and 2013, we also analysed the occurrence data in previous year (from 2006 to 2011, Table 1). The results from the stations at which *N. nomurai* presented from 2006 to 2013 show that almost all *N. nomurai* occurred north of 30°N except for at two stations in 2009. The current system can partly explain this phenomenon, from the distribution pattern of average northerly residual currents during spring–summer (April–September) in the ECS (Fig. 2), and despite the weak south-eastward current running along the 50 m isobath off the Changjiang River. The main direction of the whole current system i.e., Taiwan Current and other branches of the Kuroshio Current are all northeasterly, which may prevent *N. nomurai* spreading southward from north of 30°N. A small quantity of medusae was observed at two stations south of 30°N in 2009. Because the survey included observations begun just after Typhoon Morisot, the individuals captured at ca. 29°N might have been entrained southward by the typhoon.

In addition, predation by other organisms may be another reason why *N. nomurai* is found only north of 30°N. Latitudinal patterns of distribution have been observed for *N. nomurai* and *Cyanea* spp. (mainly *Cyanea nozakii*) in the YS and ECS (Zhang et al., 2012), and the boundary for which is generally 30–31°N. *Cyanea* spp. are considered to be warm-water species, and our experiments and previous studies indicate that it feeds ferociously on other

jellyfish e.g., *Aurelia aurita* and smaller *N. nomurai* (Hansson, 1997), thus they may decimate *N. nomurai* by predation. Therefore, aim 3 of the study has been achieved, and the hypothesis was nearly always supported that the southern distribution limit of the pelagic stages of *N. nomurai* in the ECS is 30°N.

In summary, by focusing on observations of the conspicuous stages of *N. nomurai* in the field, we have contributed to elucidating its life cycle and population dynamics in the YS and ECS.

**Acknowledgments** We thank Dr. H. Wei for contributing CTD data. We are grateful to the captain and crew of the RV “Beidou” and two fishery boats for their efforts in the field and to the people who provided support in our sampling. We also would thank the three anonymous reviewers for their help in improving this manuscript. Funding was provided by the national key fundamental developing projects No. 2011CB403601, the Strategic Priority Research Program of the Chinese Academy of Sciences XDA11020305, and NSFC Project (41230963) to S. Sun.

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