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Initial occurrence, ontogenic distribution-shifts and advection of *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in Liaodong Bay, China, from 2005–2015

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ABSTRACT: Large aggregations of *Nemopilema nomurai* have occurred in the northern East China Sea, Yellow Sea and East Sea/Japan Sea since the end of the 20th century, and the Changjiang River mouth and its adjacent sea have been suspected as the source of these jellyfish blooms. Bohai Sea, China, located in the northwestern Yellow Sea, has had similar blooms that have had a major impact on local and regional fisheries, and as a consequence ecological studies were initiated in 2005 to further understand the ecology and dynamics of this jellyfish. In this paper, we present results of the spatiotemporal pattern of distribution and abundance of *N. nomurai* in Liaodong Bay (LDB) and the southern waters of Liaodong peninsula. These waters exhibit decreasing temperature and increasing salinity with depth. Warm and less saline waters are found in the river mouths, and relatively colder, more saline waters in the central part of LDB. The first appearance of *N. nomurai* metaephyrae or juveniles in LDB occurs in the northern inner coastal areas every year, clearly indicating that LDB is a habitat for *N. nomurai* polyps. As the season progresses, the jellyfish grow and mature, and their area of distribution expands to the whole LDB, or they are advected to the southern Liaodong peninsula. This is interpreted as a horizontal advection that facilitates completion of the entire *N. nomurai* life cycle in this area.

KEY WORDS: *Nemopilema nomurai* · Distribution · Advection · Breeding place · Jellyfish blooms · Liaodong Bay

INTRODUCTION

Nemopilema nomurai is one of the largest jellyfish species, attaining a bell diameter of ca. 2 m and a wet weight of ca. 200 kg. It is the dominant jellyfish in the waters of China, Korea and Japan from late spring to autumn. Previous reports on its occurrence indicated that the main habitat of this species was in the northern parts of the East China Sea (ECS), Yellow Sea (YS), Bohai Sea (BS) and the East Sea/Japan Sea (ES/JS) (Omori & Kitamura 2004, Yasuda 2004, Kawahara et al. 2006, Yoon et al. 2014). High densities of *N. nomurai* have been reported in these waters annually since the mid-1990s (Kawahara et al. 2006, Uye 2008, Li et al. 2009, Xu et al. 2013, Yoon et al. 2014). Such blooms of *N. nomurai* in the East Asian Marginal Seas (EAMS) have caused severe damage to local fisheries and to the economy and management of coastal power plants. In Korean waters, the fisheries

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damage accounted for US $68.2 to 204.6 million yr^{-1} (Kim et al. 2012).

It is well recognized that jellyfish play an important role in marine ecosystems, from being predators of zooplankton, fish eggs and larvae, to being prey for many fish species (Lucas et al. 1997, Hansson et al. 2005, Lynam et al. 2005, Møller & Riisgård 2007, Kimmel et al. 2012). They also play a role in nutrient cycling and provisioning of habitats for juvenile fishes (Lebrato et al. 2012, McNamara et al. 2013, Doyle et al. 2014). Therefore an increase in jellyfish populations could not only cause significant damage to the fishery industry but also profound changes to the environmental ecosystem (Nagai 2003, Uye & Ueta 2004, Kawahara et al. 2006, Uye 2008, 2011, 2014).

Recently, there has been increased focus on determining the origins of *N. nomurai* blooms. Toyokawa et al. (2012) and S. Sun et al. (2015) collected ephyrae in the northwestern ECS and YS in May 2011 and 2013, respectively. These investigations clearly indicated that the area off Changjiang River was one of the sources of *N. nomurai* polyps. Yoon et al. (2014) reported occurrence of small juveniles in areas off Gunsan, east YS, in 2004 and 2008, whereas no similar reports were made in Japanese waters, implying that the settlement of new polyp populations in ES/JS was unsuccessful (Uye 2008). Both field surveys (Kawahara et al. 2006, Uye 2008, Yoon et al. 2008, Iguchi et al. 2010, Randriarilala et al. 2014, Kitajima et al. 2015, S. Sun et al. 2015) and physical modeling of *N. nomurai*'s spatiotemporal distribution suggest that the medusae are released from benthic polyps between April and June in the area off Changjiang River, China, transported by the Yellow Sea Warm Current to the northern YS, by Changjiang Diluted Water to the Eastern ECS (Luo et al. 2012), and by the Tsushima Current to the ES/JS from their native habitat or nursery grounds (i.e. the Korean Peninsula, YS and ECS) (Moon et al. 2010).

Recently, based on a comparison of the spatiotemporal variation in abundance between Liaodong Bay (LDB) (Wang et al. 2013) and eastern YS, Yoon et al. (2014) suspected that BS may be another source of *N. nomurai*. However, apart from Wang et al. (2013), no reports have been made about *N. nomurai* in LDB. Here, we gathered and analyzed all available data from monitoring programs in LDB to determine if (1) LDB is truly one of the breeding places of *N. nomurai*, (2) *N. nomurai* advects from the shallow northern to the deep southern LDB as the individuals grow, and (3) the *N. nomurai* population completes its whole life cycle in LDB.

MATERIALS AND METHODS

Data sources

Jellyfish distribution and abundance was estimated from data collected from 3 jellyfish monitoring programs in LDB (Fig. 1): The Monitoring Program for the Giant Jellyfish in the Northern Part of LDB (MJ), the Offshore Fishery Resources Monitoring Program (OFM), and the Fishing Dynamic Information Acquisition (FDIA) data collection network.

During the MJ, jellyfish monitoring cruises were carried out at 18 sites in the northern part of LDB within the 10 m isobaths, 5 times yr^{-1} from May to July 2005 to 2015 (Fig. 1). These surveys focused on *Rhopilema esculentum* and *Nemopilema nomurai*; of these, the former is considered a highly valuable edible jellyfish, and the latter considered edible but of low quality and causative of fisheries damage in LDB. From this monitoring program, only data of *N. nomurai* were retrieved and analyzed. Sites 1 to 11 were within the 5 m isobaths, and Sites 12 to 18 were within the 5 to 10 m isobaths. As the jellyfish grew, drift nets of different mesh sizes (1, 3 and 10 cm for small, large juvenile and adult, respectively) were used. They were placed across the current flow with a system of floats and sinkers. The length of each net was 30 to 60 m with a height of 8 to 12 m. Each vessel loaded between 10 and 30 nets, depending on the power of the vessel.

The OFM program has been operating since 2008, with bottom trawls occurring in June, August, September and October in the entire LDB to monitor the fishery resources. Among these 4 survey periods, jellyfish were sampled at Sites 18 to 37 in August 2008, 2011, 2013 and 2014. The sweep width of trawl nets is 10 m with 2 cm net mesh, and the towing speed is approximately 2.5 knots h^{-1}.

The FDIA is a fishermen-based data collection network, established in 2009. From this database, we gathered and analyzed information from 150 vessels fishing for *N. nomurai* in LDB for sale to the food industry. Data included catch output per net, time and place, and approximate bell size from August to November 2013 to 2015. We calculated catch output as catch per unit effort (CPUE) using:

$$\mathrm{CPUE} = 1 / n\sum(C_i / f_i) \quad (1)$$

where C_i = catch output (kg), f_i = fishing effort (kW) and n = number of vessels.

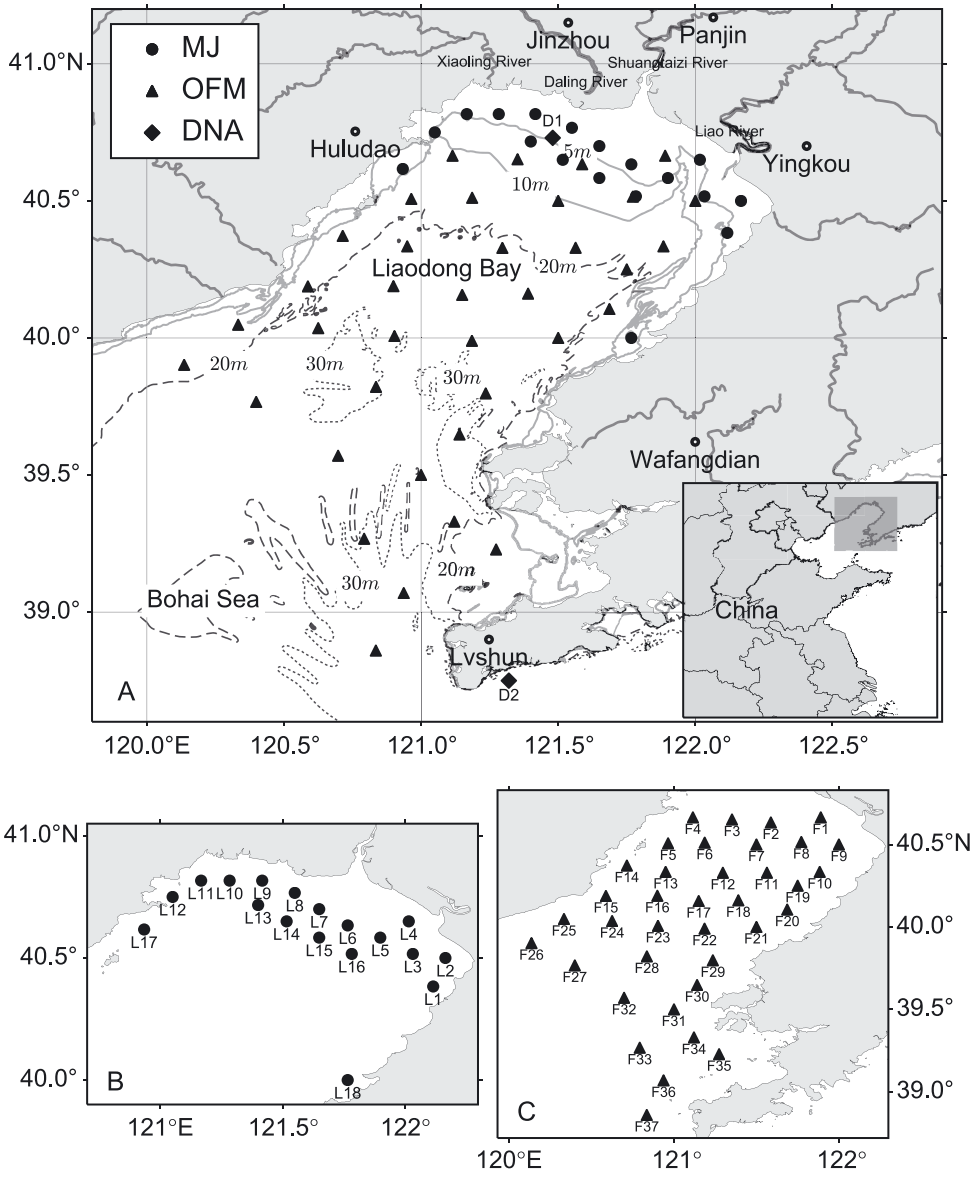

Fig. 1. (A) Monitoring area for *Nemopilema nomurai* in Liaodong Bay (LDB), Bohai Sea, China, depicting jellyfish monitoring surveys. Survey sites were located at 5, 10, 20 and 30 m isobaths (gray, dashed and dotted lines). D1 and D2 are sites where DNA samples were collected. (B) Survey area of the Monitoring Program on the Giant Jellyfish in the Northern Part of LDB (MJ) using drift nets. Sites L1 to L11 were within the 5 m isobath, and L12 to L18 at 5 to 10 m. (C) Survey area of the Offshore Fishery Resources Monitoring Program (OFM) using trawl nets

Measurement and analytical methods

Sea surface and bottom temperature and salinity were measured at every site in August 2013 and August 2014 with an AAQ1183 multi-parameter controller (ALEC); only sea surface temperature and salinity were measured from May to July 2005 to 2015 with a YSI 30 (YSI). We estimated jellyfish abundance in catch (ind. net^{-1} h^{-1}). For field measurements of diameter, we adopted the standard bell diameter (BD): distance from lappet to lappet of opposite sides for advanced metaephyra, and distance from one edge to the other edge of the bell for juvenile and medusa. The distribution maps of temperature, salinity and jellyfish catch were made with Surfer v.8.0® and ArcGIS v.9.3. Correlation analysis for temperature, salinity and jellyfish catch was done with StatsModels v.0.8.0, and cross-examined with R v.3.3.1. The regression relationship between wet weight and bell diameter was calculated with ordinary least squares (OLS).

RESULTS

Temperature and salinity associated with jellyfish abundance and distribution

Water depth throughout the study area varied between 2.2 and 45.6 m. Temperature and salinity for all cruises from May 2005 to August 2015 ranged between 14.8 and 28.4°C and 24.4 and 33.2 psu, respectively.

In August, the surface temperature was higher in the area where the water depth was shallow, and vice versa for salinity. Surface temperature in August decreased with depth in 2011 ($r = -0.818$, $p < 0.01$), 2013 ($r = -0.507$, $p < 0.01$) and 2014 ($r = -0.616$, $p < 0.01$). Salinity, however, increased with depth (2008: $r = 0.709$, $p < 0.01$; 2011: $r = 0.766$, $p < 0.01$; 2013: $r = 0.73$, $p < 0.01$; 2014: $r = 0.78$, $p < 0.01$). The results of salinity measurements showed that the inner sites of the studied area were more influenced by river flows compared to those in the central LDB at 10 to 20 m isobaths.

Warm and less saline waters were found in the river mouths, and relatively colder and more saline waters in the central part of LDB, around the 10 to 20 m isobaths. Differences in surface temperature and salinity, respectively, between these 2 areas were: 0.9°C and 6.1 psu in 2008, 2°C and 2.9 psu in 2011, 1.6°C and 8.3 psu in 2013, and 2°C and 2.6 psu in 2014, indicating less horizontal variation in temperature than in salinity. For bottom waters, the difference was similar or slightly greater: from 1.2°C in 2013 to 2.5°C in 2014 for temperature, and from 2.5 psu in 2014 to 6.2 psu in 2013 for salinity (Fig. 2). The inter-annual variation in temperature and salinity in the northern LDB was not significantly different across the years of 2005 to 2015. No sign of increasing temperature was observed. However, salinities showed a sharp decrease from 2010 to 2012, and stayed low between 2012 and 2014 (Fig. 3).

Occurrence and population characteristics of *Nemopilema nomurai*

Two *N. nomurai* advanced metaephyrae were caught for the first time in the innermost area of northern LDB (Site L9; Figs. 1 & 4) on 21 May 2005. Water depth at that station was ca. 3.5 m, surface water temperature 14.8 to 15.6°C, salinity 30.8 psu and pH 7.96 to 8.04. The BDs of the specimens were 1.6 and 1.8 cm, respectively. We identified the advanced metaephyrae as *N. nomurai* with the following mor-

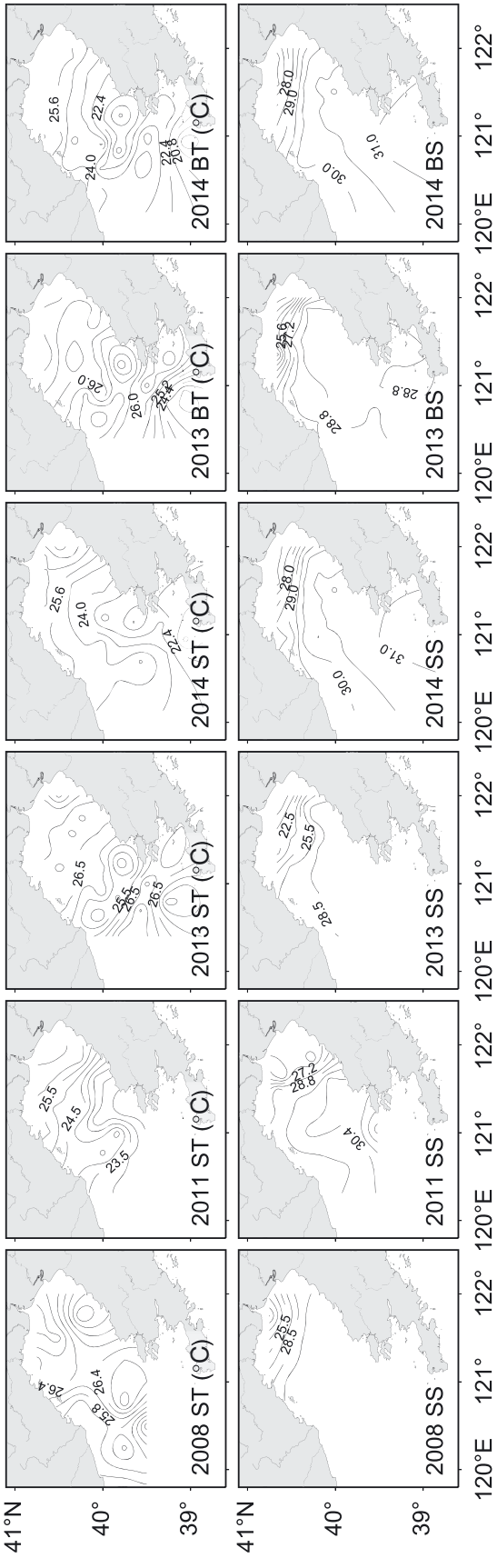

Fig. 2. Horizontal variation in temperature and salinity during August 2008 to 2014 in Liaodong Bay. ST: surface temperature; BT: bottom temperature; SS: surface salinity; BS: bottom salinity

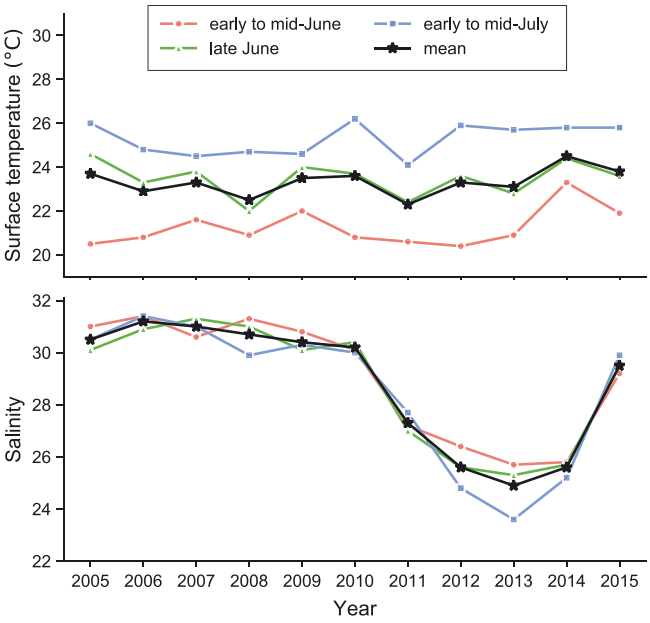

Fig. 3. Inter-annual variation in surface temperature and salinity in the northern part of Liaodong Bay from early to mid-June to early to mid-July 2005 to 2015

phological characteristics: the subgenital pits were large, 2 vertical lines of gastric cirrum were apparent in the stomach cavity, the shape of the central mouth was crossed by a small open window, and a germinated filamentous subsidiary organ developed at the junction point of the wings (Fig. 4).

Similar surveys were undertaken in the following years (2009 and 2010), but failed to catch *N. nomurai* specimens at the very early developmental stage. Small young medusae of *N. nomurai* (average BD: 6 to 12 cm; range: 3 to 20 cm) appeared in early to mid-June (Fig. 5B). The lowest catch was in 2005 (0.15 ind. net^{-1} h^{-1}), and the highest in 2011 (85.24 ind. net^{-1} h^{-1}). We noted that the catch was more pronounced at or near the river mouths, at the 5 m isobaths of the Xiaoling, Shuangtaizi and Liao rivers (Fig. 1). The highest catch, recorded in mid-June 2011, was 533 ind. net^{-1} h^{-1} at the mouth of Shuangtaizi River, followed by 400 ind. net^{-1} h^{-1} in early June 2008 from the area of the Shuangtaizi and Liao River mouths.

Young *N. nomurai* medusae of larger size (18 to 27 cm) appeared to be scattered throughout the northern part of LDB in late June (Fig. 5C). The catch was still high at the 5 and 10 m isobaths of the Shuangtaizi River mouth. The average catch was lowest in 2014 (0.58 ind. net^{-1} h^{-1}) and highest in 2010 (115.44 ind. net^{-1} h^{-1}). We noted that compared to those of early and mid-June (Fig. 5B), catches increased and area of occurrence expanded in 2005–2007 and 2009–2010, whereas in 2008 and 2011–2015 there were decreased catches and reduced areas of occurrence.

Adults were found in early to mid-July (Fig. 5D). Catches of *N. nomurai* varied from 0.16 ind. net^{-1} h^{-1} in 2014 to 10.00 ind. net^{-1} h^{-1} in 2007. The BD was 50 to 65 cm and some individuals reached 1 m in BD. The catches were high at the stations in the 5 to 10 m isobaths (Fig. 5D). Areas of high catch varied from the river mouths (as observed in 2011) to the whole northern LDB (as in 2008). In northeast and northwest LDB, jellyfish were rare or absent. Compared to those in late June (Fig. 5C), the catches were fewer, area of occurrence reduced and areas of high catch moved toward the 5 to 10 m isobaths. The year 2015 was exceptional in that the catches were increased and area of occurrence was expanded. Few large adult medusae (50 to 130 cm) of *N. nomurai* were found within the 10 m isobaths in late July (Fig. 5E). The catch (1.18 ind. net^{-1} h^{-1}) was low compared to

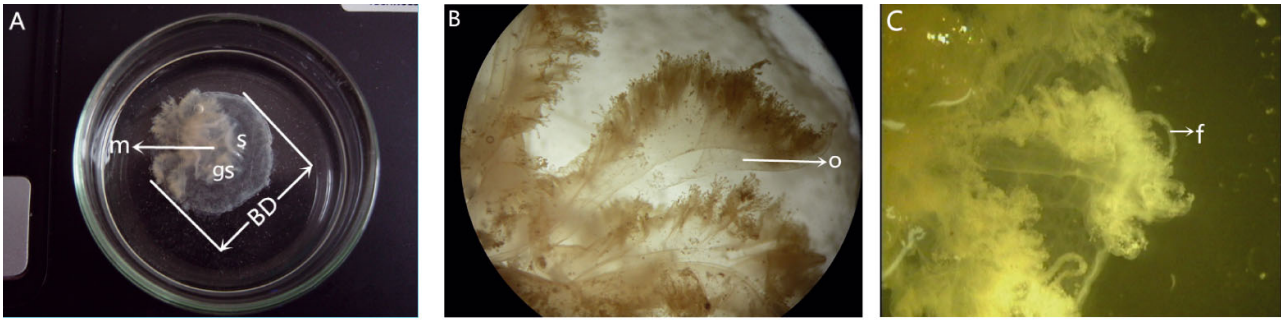

Fig. 4. Specimens of advanced metaephyrae of *Nemopilema nomurai* collected for the first time in the innermost coastal area of northern Liaodong Bay on 21 May 2005. (A) General morphology of the specimen (BD: distance from lappet tip to lappet tip; m: central mouth; gs: gastric cirrum; s: stomach cavity). (B) oral arm (o), (C) filamentous subsidiary organ of specimen (f). Specimen in (A) is 1.6 cm and that in (C) 1.8 cm in BD

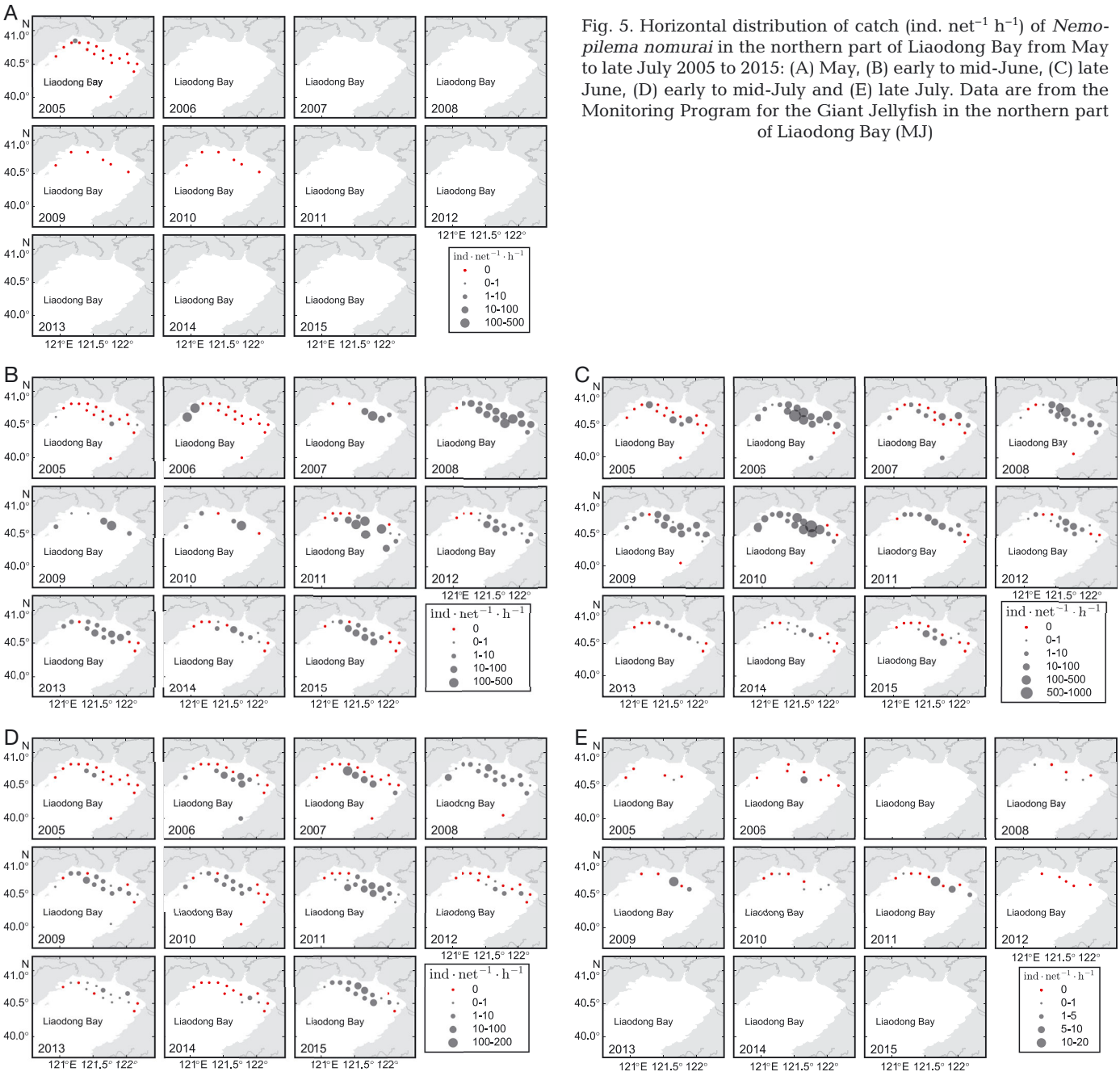

Fig. 5. Horizontal distribution of catch (ind. net^{-1} h^{-1}) of *Nemopilema nomurai* in the northern part of Liaodong Bay from May to late July 2005 to 2015: (A) May, (B) early to mid-June, (C) late June, (D) early to mid-July and (E) late July. Data are from the Monitoring Program for the Giant Jellyfish in the northern part of Liaodong Bay (MJ)

that of early to mid-July (4.02 ind. net^{-1} h^{-1}) (Fig. 5D) and area of occurrence was significantly reduced.

Catches of *N. nomurai* varied yearly (Fig. 6) and reinforced the idea of a distribution shift from shallow inshore to deeper offshore waters in LDB (Fig. 5). Many *N. nomurai* juvenile medusae were found in the inshore waters of LDB in June, concentrated around the 5 m isobath in coastal estuaries of the Shuangtaizi River. In July, the catch decreased markedly with medusae increasing to adult size, and surveys of the whole LDB in August showed that areas of high catch were either aggregated in the northern coastal area (in 2008 and 2011) or dispersed throughout the entire LDB (in 2013 and 2014; Fig. 7). This might imply that after June the higher density area advected to deep offshore waters. The BD of *N. nomurai* caught in August ranged from 50 to 130 cm, with average size varying from 56.6 ± 16.7 cm in 2014 to 83.5 ± 37.9 cm in 2008. We noted that *N. nomurai* were caught invariably at the 10 to 30 m isobaths

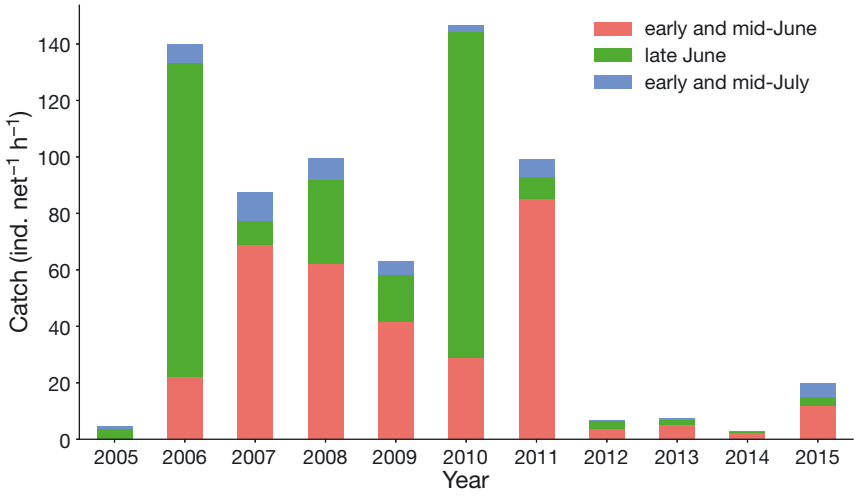

Fig. 6. Variation of the catches of *Nemopilema nomurai* among years and 3 sampling periods in the offshore waters of northern Liaodong Bay

regardless of the site location, especially in the area of the 10 to 20 m isobaths in the central part of LDB. In addition, the average wet weight (5060.51 kg net^{-1} h^{-1}) and catch (429.2 ind. net^{-1} h^{-1}) of jellyfish in 2013 were the highest, but the average BD was not the smallest (Fig. 7).

The relationship between the bell diameter of the individual jellyfish (BD_t) and wet weight (W_t) using drift net data (from MJ) and bottom trawl data (from OFM) can be described with the following equation: $W_t = 0.0003448BD_t^{2.442}$ (where t = time), R = 0.95, $F = 1384 > F_{0.005}(1,120) = 8.18$ (Fig. 8).

Distribution of *N. nomurai* revealed by commercial fishing

Fishing for *N. nomurai* in Liaoning Province mainly occurred in the waters of Yingkou, Huludao, Wafangdian and Lvshun. Fishing season varied with location. In the former 3 cities of the northern and inner LDB, the season was from early August to late September. The average output was 341.63 ± 76.06 kg kW^{-1} d^{-1} and 297.35 ± 68.12 kg kW^{-1} d^{-1}, respectively for August and September in the waters of Yingkou city, LDB. Fishing season in Lvshun, which is in the

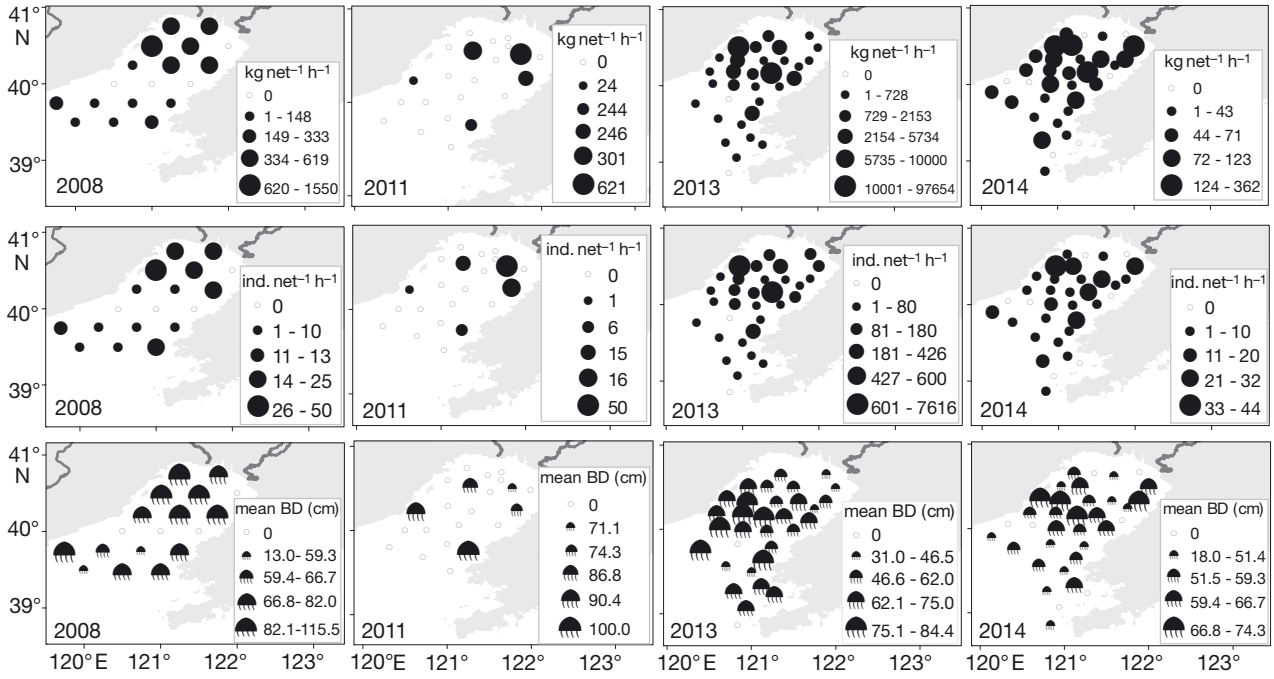

Fig. 7. Horizontal distribution of wet weight density (kg net^{-1} h^{-1}; top row), catch density (ind. net^{-1} h^{-1}, middle row) and average bell diameter (BD, cm; bottom row) of *Nemopilema nomurai* during August of 2008, 2011, 2013 and 2014 in Liaodong Bay. Data are from the Offshore Fishery Resources Monitoring Program (OFM)

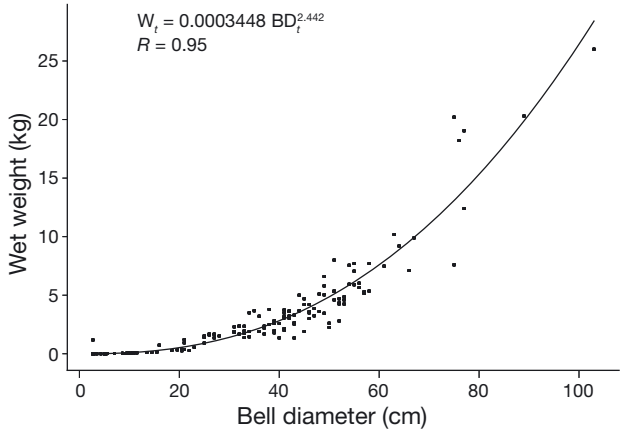

Fig. 8. Relationship between bell diameter and wet weight of *Nemopilema nomurai*

southern outer and deeper LDB was from late August to mid-November, and the output varied from 76.15 ± 31.08 kg kW^{-1} d^{-1} in late August to 716.24 ± 59.98 kg kW^{-1} d^{-1} in October (Fig. 9). This difference in fishing season in LDB implied that catchable, larger *N. nomurai* moved to the southern deeper LDB, and that this might be closely related to the horizontal distribution and depth preference of adult *N. nomurai*.

Our results on the catch of *N. nomurai* in LDB showed high catches in years with low to average temperature and high salinity. Statistical tests showed a significant positive relationship between catch and salinity ($r = 0.604$, $p < 0.05$), but no significant relationship between catch and temperature ($r = -0.513$, $p > 0.05$; Fig. 10).

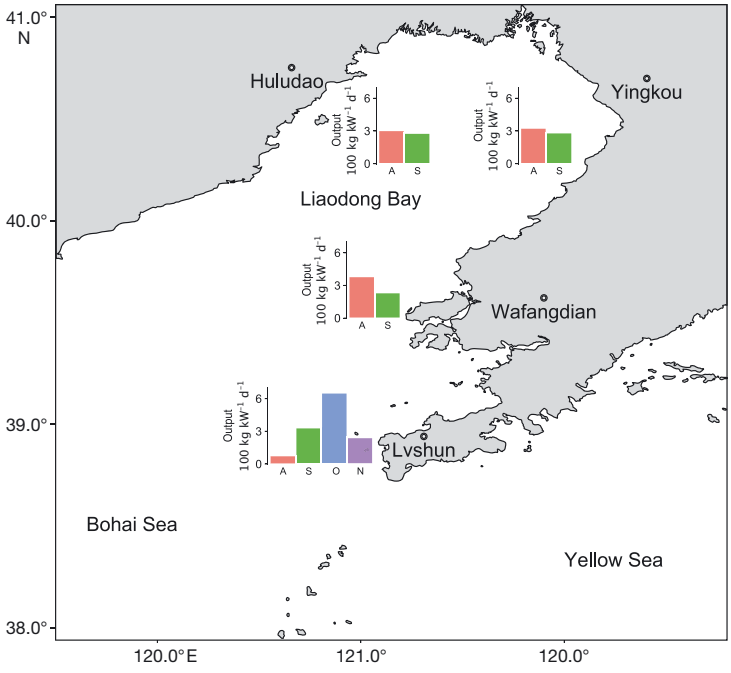

Fig. 9. Fishing season (A: Aug; S: Sep; O: Oct; N: Nov) and output (100 kg kW^{-1} d^{-1}) of *Nemopilema nomurai* in Liaodong Bay and in the waters off Lvshun in 2014. Data are from the Fishing Dynamic Information Acquisition (FDIA) data collection network

DISCUSSION

Occurrence and distribution of *Nemopilema nomurai* in LDB

Temperature and salinity have a significant influence on the abundance and distribution of jellyfish (Purcell et al. 1999, Purcell 2005, Doyle et al. 2007, Lynam et al. 2011) as they do on the growth and development of the giant jellyfish. The catch and abundance data showed that juveniles were found in areas of low salinity and high temperature, i.e. shallow coastal areas (20.4 to 24.4°C and 24.7 to 31.6 psu), and as they grew in July and August, they advected into the central and southern LDB where the waters were colder and more saline. This would indicate that advection plays an important role in the distribution of *N. nomurai*. Indeed, Zhao et al. (1995) and Wei et al. (2001) showed water movement patterns in the BS and LDB (Fig. 11) and emphasized the Estuary Low Salinity Waters (ELSW) composed of freshwater from 4 rivers (Fig. 1), the clockwise gyre and multiple local eddies in summer, and the tidal residual currents between east and southeast (Fig. 11). This water movement, which is strongly affected by wind, hydrography and river runoff (Zhao et al. 1995), should entrain *N. nomurai* juveniles of the northern innermost LDB toward the southern outer LDB, and *N. nomurai* should grow during this advection, reaching adult size at the central and southern LDB. We noted that catches were low in the years of low salinity in the northern LDB (2012 to 2015; Fig. 10). This might imply that an abrupt change in salinity in that area killed *N. nomurai* polyps or pushed young medusae to move to the central and southern LDB earlier than they normally would. However, the salinity that we measured in that area (>24 psu) was not in the range that would be lethal to any developmental stages of *N. nomurai* (salinity inducing death for polyps of *N. nomurai* is <17.5 psu; Dong et al. 2013). As the catches in early to late June between 2005 and 2015 were high in the northernmost area of LDB, and in July the catch decreased mark-

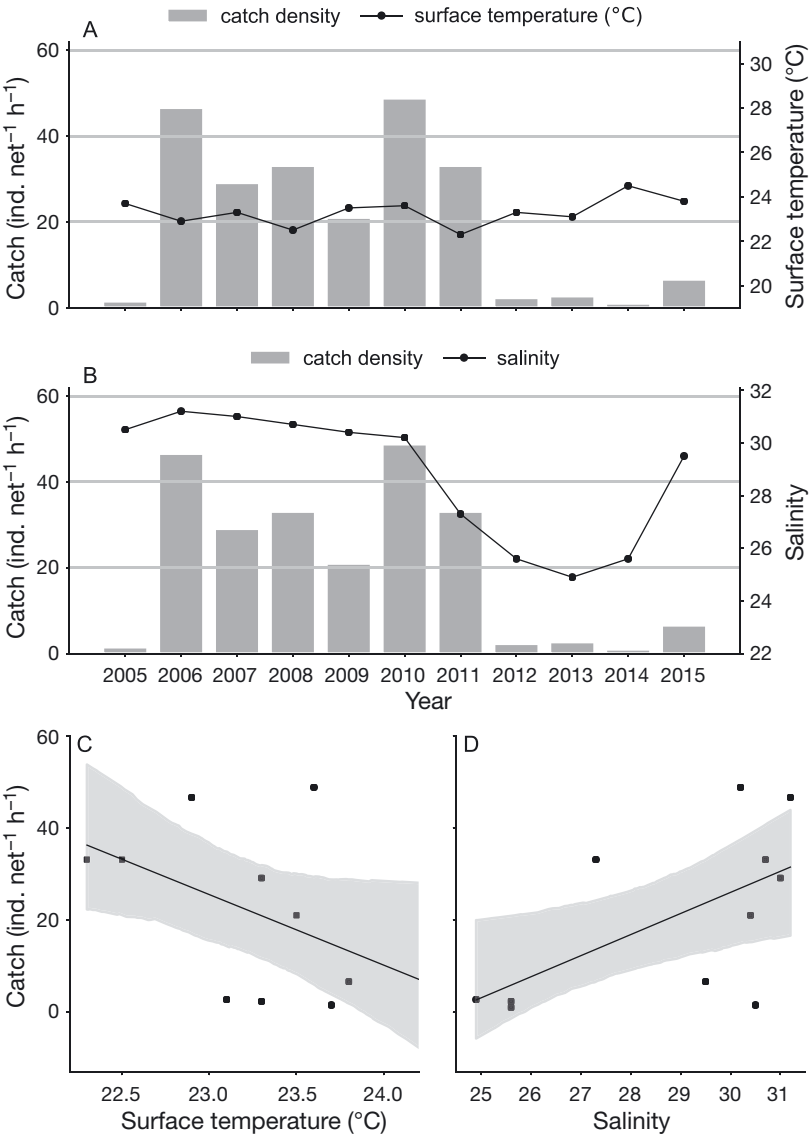

Fig. 10. Relationship of mean catch of *Nemopilema nomurai* with (A,C) sea surface temperature and (B,D) salinity in the northern part of Liaodong Bay, with 95% confidence intervals displayed in (C) and (D). Data are averages of June and July from the Monitoring Program for the Giant Jellyfish in the northern part of LDB

edly in the northern LDB with medusae size increasing (Figs. 5 & 6), we speculate that juveniles and young medusae left the northern LDB early and advected toward the central and southern LDB. In this horizontal advection, ELSW of northern LDB (which is less saline) should be of greater importance than temperature, as was shown by the statistical test results. Previous studies reported no clear relationship between *N. nomurai* and temperature (Zhang et al. 2012), but a positive relationship between Changjing Diluted Water and *N. nomurai* abundance (Yoon et al. 2008).

Initial occurrence and source of bloom

In our surveys from May 2005, 2 advanced metaephyrae were caught for the first time in the shallow estuarine waters of Xiaoling River and Daling River (Fig. 1). This was the first recorded occurrence of advanced metaephyrae in the BS. In early to mid-June 2008 to 2011, young *N. nomurai* medusae of 3 to 20 cm BD were collected in the shallow estuarine waters of Shuangtaizi River, also in the northern part of LDB (Wang et al. 2013). Similar observations have repeatedly been made over the past 11 yr. This indicates that LDB is one of the sources of the polyps that asexually release ephyrae of *N. nomurai* in the EAMS.

In laboratory-rearing experiments, Kawahara et al. (2006) found that newly liberated ephyrae grew to metaephyrae (BD: 8 to 14 mm) by 20 d post-liberation. Using this growth rate, we assume that our advanced metaephyrae collected in the northern LDB on 21 May 2005 (14.8 to 15.6°C) were liberated in late April to early May. Taking into account the physical regime of that area (semidiurnal tide and alternating tidal current in the river mouth of northern LDB) and truly planktonic behavior of metaephyrae and young medusae, we are certain that the river mouth of northern LDB is one of the principal sources of *N. nomurai*.

Dong et al. (2013, 2015) and M. Sun et al. (2015) showed that a salinity range of 20 to 27.5 psu was most appropriate for *N. nomurai* survival and somatic growth of polyps, and asexual production of podocysts. These results reinforce the conclusion that *N. nomurai* reproduces in LDB, and imply again that salinity might be the determining factor of the *N. nomurai* blooms. However, temperature is unlikely to be a key factor. In fact, the northern part of LDB was covered by ice every winter, and surprisingly a high proportion of polyps overwintered and strobilated the next spring (result from field hanging polyps experiment; J. Dong unpubl. data). Based on our related results on

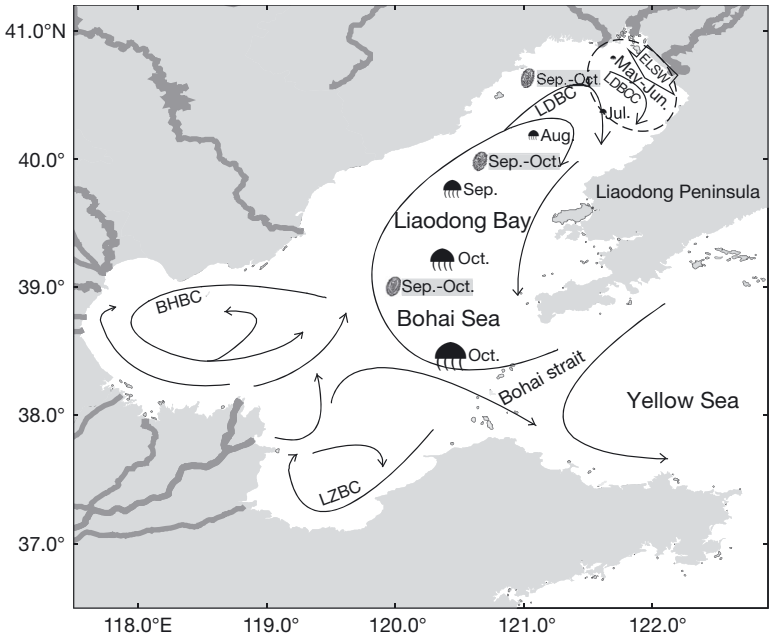

Fig. 11. Current patterns in Bohai Sea (modified from Zhao et al. 1995) influencing advective transport of *Nemopilema nomurai* medusa from their presumed polyp habit (indicated by dashed circle) to deeper waters of Liaodong Bay. Size of medusa followed by month corresponds to catches of adult *N. nomurai*; planulae are shown with month range. LDBCC: Liaodong Bay Coastal Current; LDBC: Liaodong Bay Circulation current; BHBC: Bohai Bay Circulation current; LZBC: Laizhou Bay Circulation current; ELSW: Estuary Low Salinity Waters

this subject, we can conclude that LDB is one of the sources of *N. nomurai* blooms.

We also examined the first appearance of *N. nomurai* in other locations (Table 1). Ephyrae of *N. nomurai* were collected in the northwestern ECS and southwestern YS (Toyokawa et al. 2012). S. Sun et al. (2015) collected 58 early pelagic larvae and juveniles in southern YS and northern ECS. Among them, the ephyrae and metaephyrae were all found off the Changjiang River Mouth. Zhang (2008) reported collection of small juvenile medusae in southern YS. Li et al. (2009) also reported that juveniles and young *N. nomurai* medusae were present in the northern ECS. Altogether, these field monitoring data showed that the first appearance of *N. nomurai* was from the area off the Changjiang River in May and early June.

The time of the first occurrence of *N. nomurai* in LDB (21 May; BD: 10 to 20 mm) was delayed compared to the southern YS (6 May; BD: 5 mm) and northern ECS (4 May; BD: 10 to 25 mm) (Table 1). The temperature at which liberation should occur must be similar for all presumed polyp habitats of *N. nomurai* (LDB, southern YS and northern ECS). Our results showed that the temperature at which metaephyrae occurred in the northern part of LDB was between 14.8 and 15.6°C, which is in line with the temperature of polyp strobilation and ephyra liberation (<15°C; Kawahara et al. 2013). From the 'field hanging polyps experiment' (J. Dong unpubl. data), we noted that the rate of strobilation was ca. 34% when the temperature reached 13.58°C in April 2016. It is reasonable then to surmise that at temperature ca. 14°C or less,

Table 1. Literature reporting first occurrence of ephyrae, metaephyrae and young medusae of *Nemopilema nomurai*. CDD: Central disc diameter; nwECS: northwestern East China Sea; sYS: southern Yellow Sea; YS: Yellow Sea; nLDB: northern Liaodong Bay; eYS: eastern Yellow Sea; Ksw: Korea southern waters; swJI: southwest Jeju Island; eES/JS: eastern East Sea/Japan Sea

Time	Sea area	Stage	Bell diameter (mm)	Reference
22 and 26 May 2011	nwECS, YS	Ephyra	1–2 (CDD)	Toyokawa et al. (2012)
4 May 2013	nwECS	Metaephyra	10–25	S. Sun et al. (2015)
6 May 2013	sYS	Ephyra	5	S. Sun et al. (2015)
21 May 2005	nLDB	Advanced metaephyra	10–20	Present study
Early June, 2008–2011	nLDB	Juvenile medusa	30–200	Wang et al. (2013)
31 May to 6 June 2013	sYS	Juvenile medusa	50–140	S. Sun et al. (2015)
Mid-June 2008	nwECS	Young medusa	100–510	Li et al. (2009)
Early May 2007	sYS	Juvenile medusa	50–100	Zhang (2008)
Late June 2007	sYS	Young medusa	60–400	Zhang (2008)
Mid-May 2008	Gunsan, eYS	Young medusa	<100	Yoon et al. (2014)
Early June 2004	Gunsan, eYS	Juvenile medusa	20–80	Kawahara et al. (2006)
May 2012	eES/JS	Young medusa	Not mentioned	Yoon et al. (2014)
May 2010	swJI	Young medusa	Not mentioned	Yoon et al. (2014)
June 2009	Ksw	Young medusa	Not mentioned	Yoon et al. (2014)

ephyrae liberation occurs in the northern LDB. Our results agree with that of S. Sun et al. (2015), who showed ca. 12 to 18°C for ephyrae liberation. Kawahara et al. (2006) had suggested that ephyrae liberation took place in April, May and June.

In summary, we found that (1) the occurrence season of *N. nomurai* in LDB was late May, a little later than that of the area off Changjiang River (April/May), (2) the temperature at which ephyrae liberated was similar, (3) LDB was the source of the *N. nomurai* blooms, as off the Changjiang River mouth and (4) considering the weak ability of young medusae to move, the long distance between the 2 locations, and the current patterns in the northern ECS, YS and BS, ephyrae, juveniles and young medusae were likely to come from polyps liberated by strobilation near their respective native places. We conclude that blooms of *N. nomurai* are from more than one source in the EAMS, and that the initial occurrence pattern should have multiple origins in terms of succession in seeding and nursery grounds in EAMS. Therefore, our aim to determine the initial occurrence and source of bloom has been achieved.

Advection of jellyfish in LDB

Our finding regarding the occurrence and distribution of *N. nomurai* in LDB clearly showed that (1) the occurrence and area of appearance in the shallow coastal area decreased as summer approached, (2) this decrease coincided with a corresponding increase in the deep central area and (3) individual size increased along with the change of occurrence and area of appearance. This indicates that the horizontal advection of the *N. nomurai* population was taking place in the LDB, as a result of water mass circulation (Zhao et al. 1995, Wei et al. 2001) (Fig. 11). Hence our aim to determine if *N. nomurai* advects from the shallow northern to the deep southern LDB has been fulfilled.

Molecular data (J. Dong & Y. Li unpubl. data) showed that the nucleotide divergence in mtDNA COI sequence was only 0 to 0.9% (>99% similarity) between *N. nomurai* individuals (n = 55) from the northern part of LDB (Site D1) and the southern waters of Lvshun (Site D2; Fig. 1). Thus, molecular data also proved that the population of *N. nomurai* that reached the southern part of LDB came from the northern part of LDB, and that it was driven by the clockwise current from north to south. This is in agreement with the results of Dong et al. (2016), that no geographically structured pattern could be found for *N. nomurai* collected in Chinese coastal waters, including the BS and YS. Consequently, it is possible that a small number of *N. nomurai* that initially appeared in the northern part of LDB passed through the Bohai Strait, reached YS, and mingled with *N. nomurai* coming from the southern YS and northwestern ECS, as Yoon et al. (2014) speculated.

Life cycle of *N. nomurai* in LDB

The life cycle of *N. nomurai* is characterized by alternation between a sexually reproducing medusae stage and an asexually reproducing polyp stage (Kawahara et al. 2006, Dong et al. 2012, 2013). Polyps have the capacity to rapidly increase the population size by asexually producing podocysts. Further, asexual production of many ephyrae (strobilation) by polyps increases the medusa population. LDB is located in the northeast BS, and experiences 4 distinctive seasons. We presumed that ephyrae are likely produced in mid-spring. We collected metaephyrae in late spring, young medusae from late spring to early summer, and adults in summer and autumn. We observed that *N. nomurai* reached the mature stage and became ready to spawn in early to mid-autumn. In late autumn, a high proportion of the population was observed in the inner and outer LDB as shrinking individuals. Afterward, population size decreased, umbrella size continuously and gradually diminished, and medusae died—probably due to the low temperature and/or individual senescence. This strongly suggests that *N. nomurai* can successfully complete their whole life cycle in LDB and the southern waters of Liaodong peninsula, which fulfills the final aim of this paper.

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