# Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters

## Masato Kawahara[1,*], Shin-ichi Uye[1], Kohzoh Ohtsu[2], Hitoshi Iizumi[3]

[1]**Graduate School of Biosphere Sciences, Hiroshima University, 4-4 Kagamiyama 1 Chome, Higashi-Hiroshima 739-8528, Japan**

[2]**Oki Marine Biological Station, Department of Biological Science, Shimane University, 194 Kamo, Okinoshima-cho, Oki 685-0024, Japan**

[3]**Japan Sea National Fisheries Research Institute, 5939-22 Suido-cho 1 Chome, Niigata City, Niigata 951-8121, Japan**

ABSTRACT: A population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) occurred in the Sea of Japan in 2002 and 2003, causing severe damage to fisheries. There was a further population explosion in 2004, but on a much smaller scale. In both years, young medusae began to appear in the Tsushima and Korea Strait in July and August, followed by a northward expatriation in the Tsushima Current to the northern Sea of Japan. We obtained scyphistomae of this species by artificial fertilization, and reared them to the young medusa stage in the laboratory. Asexual reproduction of scyphistomae occurred by means of podocyst formation. A thermal increase from 13 to 23°C induced strobilation, followed by liberation of 3 to 7 ephyrae from a strobila. The ephyrae developed to metephyrae having a complex canal system and characteristically possessing long reddish purple filiform appendages. By 40 d post-liberation, the metephyrae had grown to medusae in which the central mouth had closed and been replaced by numerous mouthlets on both oral wings and scapulets. The results from both laboratory-rearing experiments and field investigations were combined to construct the seasonal life cycle and geographical distribution of *N. nomurai* in eastern Asian waters. Possible causes for the mass occurrence of *N. nomurai*, which has tended to be more frequent in the last decade, are discussed.

KEY WORDS: *Nemopilema nomurai* · Rhizostomeae · Mass occurrence · Geographical distribution · Fishery impacts · Life cycle · Sea of Japan

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## INTRODUCTION

*Nemopilema nomurai* (Cnidaria: Scyphozoa: Rhizostomeae) is one of the largest of all jellyfish species, attaining a bell diameter of ca. 2 m and a wet weight of ca. 200 kg (Kishinouye 1922, Omori & Kitamura 2004). *N. nomurai* was first described by Kishinouye (1922) as a new species and genus based on specimens collected in the Sea of Japan. Uchida (1954) later regarded *Nemopilema* as a junior synonym of *Stomolophus* without any plausible reason and referred to this species as *S. nomurai.* Many subsequent Japanese researchers (Shimomura 1959, Yamada 1997) adopted this species name. Furthermore, Kramp (1961) and Hon et al. (1978) regarded this species as a synonym of *S. meleagris*. However, *N. nomurai* is very different from *S. meleagris* in morphology, size and geographic range. Omori & Kitamura (2004) recently revised the taxonomy of 3 rhizostome species from Japanese waters and concluded that this species should be reassigned to the genus *Nemopilema.*

Little is known about the biology and ecology of *Nemopilema nomurai*. Previous reports on its occurrence (Hon et al. 1978, Zhang & Li 1988, Cheng et al. 2004, Omori & Kitamura 2004) indicate that the main habitat of this species is in the northern parts of the East China Sea, Yellow Sea and Bohai Sea. This species is also carried by the Tsushima Current to the Sea of Japan, usually in small numbers, but very rarely in extreme abundances (e.g. thousands of

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medusae entrapped per set-net $d^{-1}$) sufficient to seriously damage local fisheries. To our knowledge, such mass occurrences of *N. nomurai* took place in 1920, 1958, 1995 and 2002 (Kishinouye 1922, Nishimura 1959, 1961, Shimomura 1959, Yasuda 2004). The blooms of 2002 and 2003 represent the first time such abundances occurred in 2 consecutive years. *N. nomurai* also bloomed in 2004, but the bloom was not as extensive as during the 2 preceding years. Population explosions of *N. nomurai* appear to have become more frequent and larger in extent over the last decade. A similar phenomenon has also been observed in Korean coastal waters (Dr. Y. S. Kang, National Fisheries Research and Development Institute, pers. comm.). This suggests that environmental and/or ecological changes, resulting from a variety of factors, may be enhancing the jellyfish populations in coastal waters of East Asia, as has already been demonstrated in the Bering Sea (Brodeur et al. 1999, 2002), northern Gulf of Mexico (Graham 2001, Graham et al. 2003) and the Black Sea (Purcell et al. 2001, Shiganova et al. 2001). Furthermore, there have been some earlier reports about invasions by rhizostome species, *Rhopilema nomadica* (Galil et al. 1990, Lotan et al. 1992, Kideys & Gücü 1995, Silfen et al. 2003) and *Phyllorhiza punctata* (Graham et al. 2003). These cases indicate that *N. nomurai* may have the potential to invade and colonise the Sea of Japan.

In order to clarify the causes for the observed mass occurrences of *Nemopilema nomurai*, it is necessary to understand its life cycle, geographic origins and transportation routes. We succeeded in obtaining fertilized eggs of this species, and followed the development from scyphistoma to young medusa in the laboratory for the first time. In this paper, we report on the mass occurrences of medusae in 2003 and 2004, and describe the morphological and ecological characteristics of various life stages. Based on field and laboratory studies, we construct the seasonal life cycle and geographical range of *N. nomurai*, and speculate on the possible causes for the unusual mass occurrences.

## MATERIALS AND METHODS

**Mass occurrences in 2003 and 2004.** We collected information on the occurrence of *Nemopilema nomurai* by: (1) actual visits to the sites and personal interviews with local fishermen and (2) telephone and Email communications with local diving shops and fisheries cooperatives. Having become aware of

the mass occurrence of *N. nomurai*, the Japan Sea National Fisheries Research Institute undertook a rapid-response survey from late August 2003, by requesting fisheries offices of 18 prefectures to report the incidents (e.g. dates, locations, type of fishing nets and approximate numbers of medusae caught per net). From the compiled information for 2003 and 2004 (www.jsnf.affrc.go.jp/), we calculated the average number of medusae entrapped per set-net $d^{-1}$ for every half-month period for 5 representative prefectures (i.e. Shimane, Kyoto, Niigata, Aomori and Miyagi; see Fig. 1 for locations). These prefectures usually collected information about the incidents from 10 to 30 set-net owners.

**Artificial fertilization.** We collected mature *Nemopilema nomurai* during the period between 23 October and 7 November 2003, in Kamo Inlet, a small inlet at Oki Island (Fig. 1). Gonadal fragments (ca. 500 g) were cut off and transported to a laboratory at the Oki Marine Biological Station, Shimane University. Small pieces of ovary and testis (ca. 10 g) from 3 to 5 specimens were placed together in a plastic colander (20 cm in diameter) set up in a plastic funnel, through which the seawater was gently running from a hose to a plankton net with 30 μm mesh. Fertilized eggs and planulae were collected in the cod-end of the plankton net. The planulae were isolated with a Pasteur pipette under a dissecting microscope and transferred to styrene vessels containing 300 ml filtered seawater of
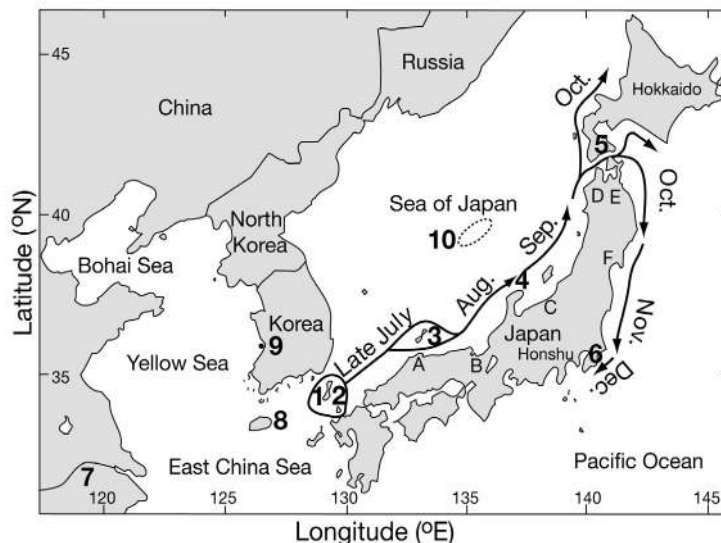


Fig. 1. *Nemopilema nomurai*. Monthly geographical expansion of the occurrence of *N. nomurai* along the coast of Japan in 2003, based on various information sources (see 'Materials and methods' and 'Results'). 1: Tsushima Island; 2: Iki Island; 3: Oki Island; 4: Noto Peninsula; 5: Tsugaru Strait; 6: Boso Peninsula; 7: Changjiang (Yangtze) River; 8: Cheju Island; 9: Gunsan; 10: Yamato Bank; A: Shimane prefecture (pref); B: Kyoto pref; C: Niigata pref; D: West Aomori pref; E: East Aomori pref; F: Miyagi pref

33 psu. These procedures were undertaken at ambient temperatures ranging from 18 to 22°C.

**Laboratory rearing.** Scyphistomae settling on the bottom of the vessels were fed with copepod nauplii isolated from natural zooplankton samples at least once a day. Scyphistomae (7 d old) were transported to the laboratory of Hiroshima University, Higashi-Hiroshima, by filling the styrene containers with seawater to make them airtight. After removing the lid, the containers were placed on the bottom of glass aquaria containing 10 l of seawater in a temperature control room (18°C, 12:12 h light:dark photoperiodicity), so that most of the scyphistomae were in a suspended position. At 2 to 3 d intervals newly hatched *Artemia* nauplii (Vinh Chau, Vietnam) were given as food, and dead *Artemia* were removed with a pipette. After the scyphistomae were kept for 6 mo, they were separated into 2 groups and exposed to 13 and 9°C, respectively, for 1 mo before being returned to 18°C for possible induction of strobilation. Since nothing happened, they were kept at 18°C for 1 mo further and again exposed to 13°C for 1 mo before delivering a stronger thermal stimulus, i.e. elevating the temperature to 23°C, to induce strobilation. Shortly thereafter, strobilation began. Ephyrae were reared to young medusae in containers of various volumes from 0.5 to 20 l at temperatures ranging from 22 to 28°C, with newly hatched *Artemia* nauplii being used as food at least twice daily. Half of the rearing water was replaced with fresh seawater at 2 d intervals. The wet weight of each life stage was measured by an electric balance, and selected specimens were preserved in 5% formalin-seawater solution.

## RESULTS

### Mass occurrences in 2003 and 2004

*Nemopilema nomurai* first appeared in southern Japan (Tsushima Island) in late July 2003. Local fishermen observed that <10 d$^{-1}$ medusae began to enter their set-nets. Continuous reports on the mass occurrence of *N. nomurai* were received from coastal areas all around the Sea of Japan soon after this first sighting (Fig. 1). The medusae at the leading edge of this bloom were transported by the Tsushima Current to near the Noto Peninsula by the end of August. In September, they reached northern Honshu. In October, the population split into 2 groups, one drifting northward along the west coast of Hokkaido and the other passing through the Tsugaru Strait to the Pacific Ocean. The latter was transported by a northerly coastal current along northern Honshu as far south as the Boso Peninsula, until the medusae died in December.
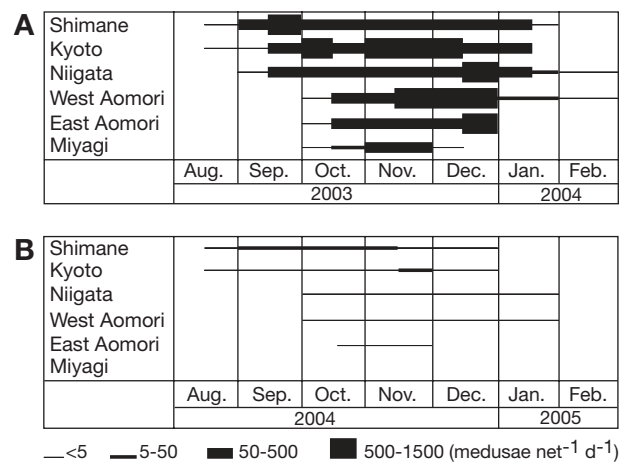


Fig. 2. *Nemopilema nomurai*. Daily average number of jellyfish caught per set-net in Shimane, Kyoto, Niigata, Aomori (west and east) and Miyagi prefectures in (A) 2003/2004 and (B) 2004/2005. See Fig. 1 for prefecture locations

Temporal changes in average daily medusa abundance caught per set-net in Shimane, Kyoto, Niigata, Aomori (both Sea of Japan and Pacific sides) and Miyagi prefectures in 2003 and 2004 are shown in Fig. 2. At each location, the main bloom population arrived about 1 mo after the first occurrence of the medusae. Entrapment of >50 medusae per set-net d$^{-1}$ continued for 4 to 5 mo in Shimane, Kyoto and Niigata, for 3 mo in Aomori and for 1 mo in Miyagi.

Along the entire coast of the Sea of Japan and on the Pacific side of northern Honshu, the aggregation of *Nemopilema nomurai* caused severe damage not only to set-net but also to seine-net, gill-net and trawl fisheries, which continued until the medusae died off by midwinter. The problems included: (1) clogging and bursting of the nets, (2) lower catches of finfish, (3) high mortality of finfish by nematocyst venom, and lower commercial value, (4) increased labour to remove medusae from the nets, (5) higher risk of capsizing trawl boats, (6) painful stings caused by medusae etc. One of the most severe incidents was reported by Niu Fisheries Cooperative on the west coast of the Noto Peninsula: several thousand medusae were trapped almost daily in a set-net during October (Fig. 3; Y. Taniguchi pers. comm.). Many set-net fishermen were forced to remove their nets even during the regular fishing season. The nuisance to fisheries created by *N. nomurai* has been reported from at least 17 prefectures (www.jsnf.affrc.go.jp/). Although no information is available on the total loss for all prefectures, the loss (e.g. decrease in fish catch, damage to nets, etc.) in Aomori prefecture alone was 2.3 billion Japanese yen (ca. 20 million US$)

In 2004, fishermen and researchers were on the alert for a possible repeat of the event. Indeed, *Nemopilema nomurai* began to occur in the Tsushima and Korea
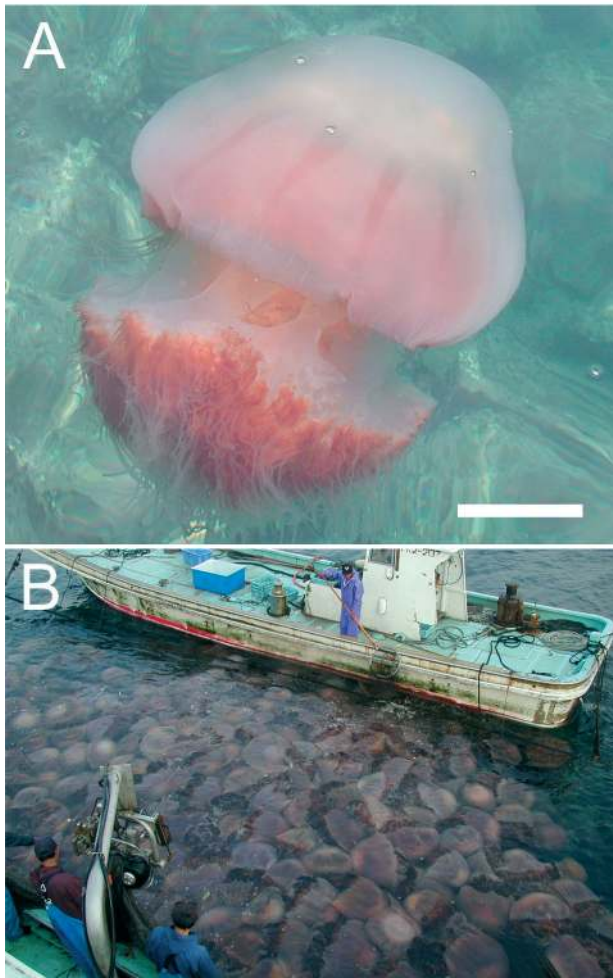
Fig. 3. *Nemopilema nomurai.* (A) Immature medusa at Tsushima Island in August 2003. (B) Mass occurrence of mature medusae in a set-net on the western coast of the Noto Peninsula (courtesy of Mr. Y. Taniguchi, Niu Fisheries Cooperative). Scale bar = 10 cm (A)

Strait in August, and followed a distributional pattern similar to that of the previous year. However, the bloom in 2004 was 2 to 3 orders of magnitude less intense than that of the previous year, since the maximum average number of jellyfish trapped was ca. 50 medusae per set-net d$^{-1}$ (Fig. 2). Prior to transportation to the Sea of Japan, new information on the occurrence of *N. nomurai* was obtained. Several tens of juvenile *N. nomurai* medusae (extended bell diameter: 2 to 8 cm) were collected in early June in a set-net near Gunsan, west Korea (Y. S. Kang pers. comm.), and a total of ca. 700 kg of medusae (extended bell diameter: ca. 50 to 100 cm) was caught in the middle of July by a trawl-net (net opening: $5 \times 5$ m) at a station (31° 45′ N, 124° 50′ E) southwest of Cheju Island, Korea (K. Nishiuchi, Seikai National Fisheries Research Institute, pers. comm.; see Fig. 1 for locations).

## Life cycle

### Gonad maturation

*Nemopilema nomurai* caught in August around Tsushima and Iki Islands (mean extended diameter: 53 cm, mean wet weight: 7.6 kg, n = 21) had a translucently whitish body, with pinkish or reddish scapulets and oral arms (Fig. 3), and transparent immature gonads. The medusae caught on the coast of south-western Honshu in mid-September (no size and weight data) still appeared to be immature, due to their transparent gonads. However, those sampled at Oki Island in October (mean extended diameter: 110 cm, mean wet weight: 66.0 kg, n = 4) had colored gonads (male testis: milky white; female ovary: dark brown) (Fig. 4A). Of 20 medusae sampled for artificial fertilization, 13 individuals were males and 7 were females. All males had sperm follicles containing mobile spermatozoa (Fig. 4B), indicating that they were fully mature. The ovaries of females contained different-sized oocytes, ranging from 30 to 80 μm in diameter. The oocytes of 60 to 80 μm diameter had a clear germinal vesicle (Fig. 4C), indicating that oogenesis stopped at the Prophase I stage of meiosis. Neither fertilized eggs nor planulae were found in or on the ovary, which indicates that fertilization takes place in the water. In December, medusae of *N. nomurai* attained maximum size (mean extended diameter: 123 cm, mean wet weight: 96.3 kg, n = 4), and the gonads of 20 medusae examined looked the same as in October.

### Fertilization and planula

Fertilized eggs and planulae were taken 2 to 4 d after the start of incubation in the artificial fertilization apparatus. The fertilized eggs were ca. 60 to 80 μm in diameter, with a transparent perivitelline space of ca. 8 μm (Fig. 4D). The first and second polar bodies, which were discharged into the perivitelline space, were clearly visible. The fertilized eggs developed into planula larvae about 24 h after fertilization at 20°C. Planulae were ca. 170 μm long and ca. 130 μm wide, whitish in color and covered with cilia or flagella of 10 μm length over the body surface (Fig. 4E). They swam for 4 to 8 d until settlement occurred on the bottom of the styrene vessels. We placed bivalve shells, slide glasses and ceramic plates in the styrene vessels to evaluate substrate preference, but very few planulae settled on these materials. However, many planulae attached to the air–water interface and underwent morphogenesis there.
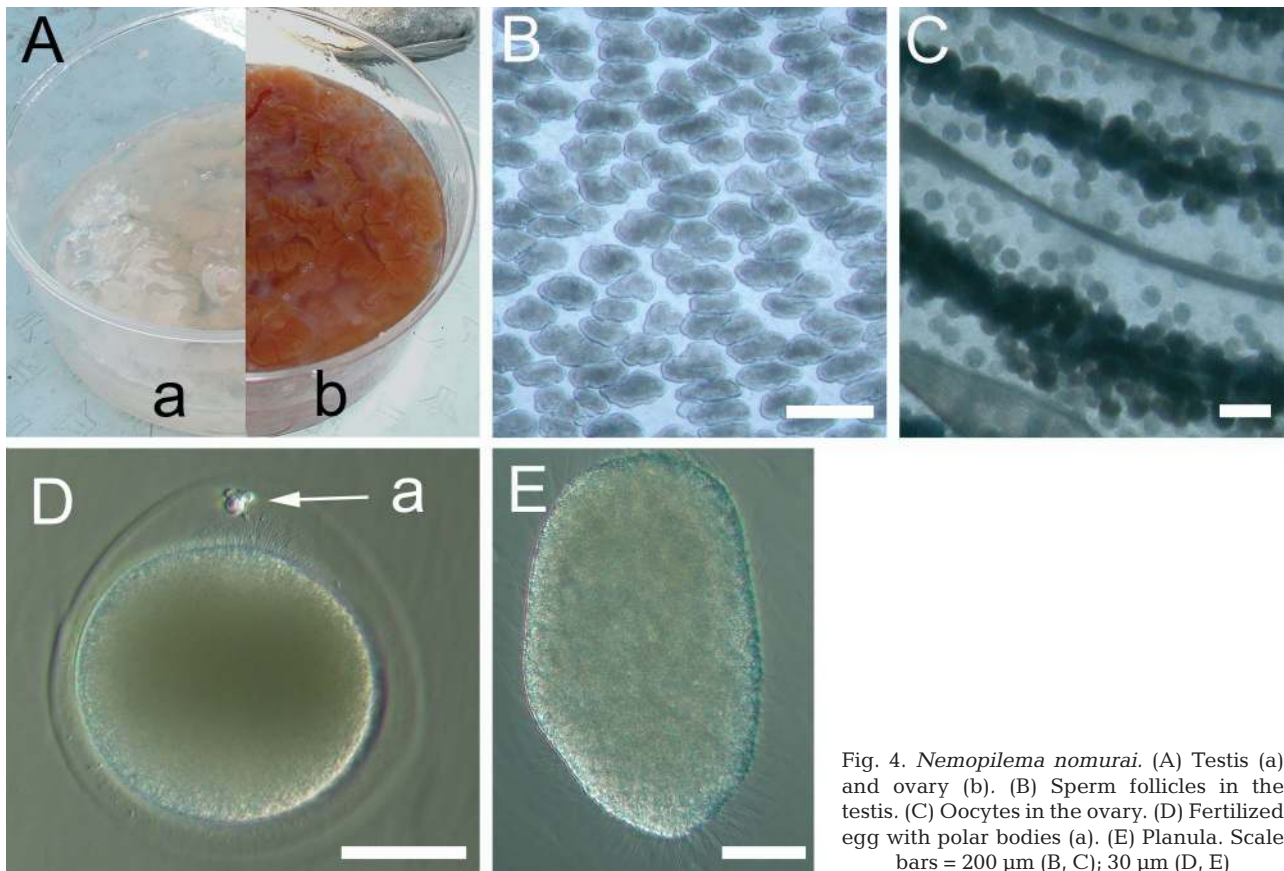
Fig. 4. *Nemopilema nomurai.* (A) Testis (a) and ovary (b). (B) Sperm follicles in the testis. (C) Oocytes in the ovary. (D) Fertilized egg with polar bodies (a). (E) Planula. Scale bars = 200 µm (B, C); 30 µm (D, E)

### Scyphistoma

Newly settled scyphistomae were translucently whitish, goblet-shaped, and had 4 tentacles. The calyx was 250 to 300 µm in diameter. The dome-shaped manubrium was one-third of the scyphistoma height. Immediately after settlement, they were able to ingest copepod nauplii of ca. 40 µm body length using their tentacles.

Young scyphistomae developed to an intermediate stage with 8 tentacles 6 to 10 d after settlement. The calyx diameter was ca. 500 µm. They were able to ingest newly hatched *Artemia* nauplii of ca. 300 µm body length.

The fully developed scyphistoma stage, with 16 tentacles, was attained 10 to 20 d after settlement. The calyx diameter was 800 to 1100 µm. A stolon protruded from the bottom of the calyx and attached to the substrate ca. 10 to 300 µm away from the base of the scyphistoma. The scyphistoma body mass gradually moved to the new attachment site, leaving a podocyst behind at the former position. The podocyst was whitish in color and ca. 300 µm in diameter (Fig. 5A). From the podocyst, a new scyphistoma was formed. Asexual reproduction by means of podocyst formation was continuous until strobilation. The duration of the formation of a new podocyst varied greatly, from 7 d to 3 mo. Fig. 5A shows a scyphistoma colony from a single original (or founder) scyphistoma, formed over 6 mo at 18°C. From a single founder, we observed the generation of as many as 18 podocysts, from which 6 scyphistomae were newly formed. The scyphistomae survived at 9°C for at least 1 mo.

### Strobila

Within 24 h of a temperature increase from 13 to 23°C, strobilation was induced; the calyx became elongated and segmented. The regression of tentacles started about 30 h after the beginning of strobilation; following the start of regression, rhopalia with statoliths became apparent. Both ephyral lappets and manubrium elongated, and simultaneously the tentacles of the basal scyphistoma regressed. Nascent ephyrae pulsated rhythmically, and the tip of the manubrium turned brown in color 48 h after strobilation began (Fig. 5B). Fully developed strobilae, 2.2 to 2.8 mm long from the base of the scyphistoma to the top of the ephyral mouth, liberated ephyrae one by one into the water within 7 d after strobilation. The numbers of ephyrae formed by a strobila varied from 3 to 7 (mean: 4.6, n = 16).
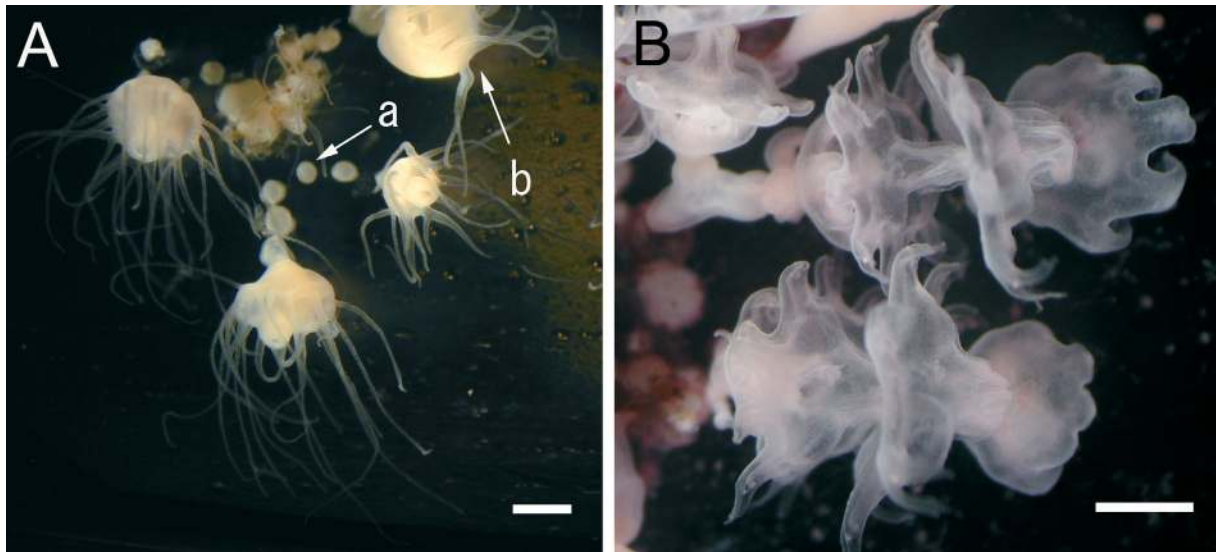
Fig. 5. *Nemopilema nomurai*. (A) A colony of scyphistomae and podocysts (a) formed from a founder scyphistoma (b). (B) 48 h old strobilae. Scale bars = 1 mm

### Ephyra

Newly liberated ephyrae were 2.2 to 3.8 mm wide from lappet tip to lappet tip (Fig. 6A). There were 8 pairs of lappets and 8 rhopalia. The rhopalar clefts were usually U-shaped and reached more than one-third of the distance along the marginal lobe. The distal end of each lappet branched into 2 to 6 pointed tips. Nematocyst batteries were present, particularly in the centre and along radial canals of the exumbrella. The ephyra was able to ingest *Artemia* nauplii immediately after liberation.

As the ephyrae grew to ca. 8 mm wide from lappet tip to lappet tip (i.e. 5 d post-liberation), 8 pairs of secondary lappets developed, extending approximately to one-third of the length of the primary lappets at the mid-point of each cleft (Fig. 6B). The 4 oral arms changed to become J-shaped in lateral view, and each branched into 2 terminally. At the same time, the subgenital cavity and the primitive scapulets appeared (Fig. 6C).

### Metephyra

The ephyrae grew to metephyrae, reaching a width of 8 to 14 mm from lappet tip to lappet tip ca. 10 d post-liberation (Fig. 6D). The secondary lappets extended outwards to the primary lappets, making the bell margin polygonal. A ring canal appeared along the bell margin and connected with the 16 radial canals. The oral arms were clearly divided into 8, and each arm branched into 2 wings at the tip. The distal half of each scapulet branched into 2 wings, and on the upper side of each one, a mouth connected to the scapulet canal opened (Fig. 6E). Nematocyst batteries were scattered over the entire exumbrella.

In advanced metephyrae (up to 14 to 18 mm wide, ca. 20 d post-liberation, Fig. 6F), 16 centripetal canals extended from the mid-point of the adjacent radial canals on the ring canal (Fig. 6D). The margins of the oral arms and scapulets formed thin membranes, which were folded alternately and complexly as frills carrying numerous cirri (Fig. 6G). Each cirrus bore a small terminal knob armed with nematocysts. The central mouth was still open. At the junction point of the wings where the mouth membranes coalesced, a primary appendage occurred (Fig. 6H). The appendage was: (1) reddish purple, (2) filiform and of 200 to 400 µm width, (3) hollow inside, (4) armed with 1 to 5 nematocyst batteries of 140 to 160 µm diameter length per mm (Fig. 6I), (5) non-contractile, (6) lacking in predation capacity and (7) elongate, extending about 10 times longer than the body length.

Secondary appendages occurred on the distal ends of each wing (Fig. 6H), followed by the formation of tertiary appendages when new wings were formed about 30 d post-liberation. Almost at the same time, numerous appendages occurred on the inner oral arms, and the mouth membranes coalesced to form many mouthlets. The radial canals branched out to form many short canals anastomosing like the mesh of a net.

### Young medusa

As the central mouth closed, the metephyra passed into the medusa stage, where they measured 40 to 110 mm in bell diameter 40 to 50 d post-liberation
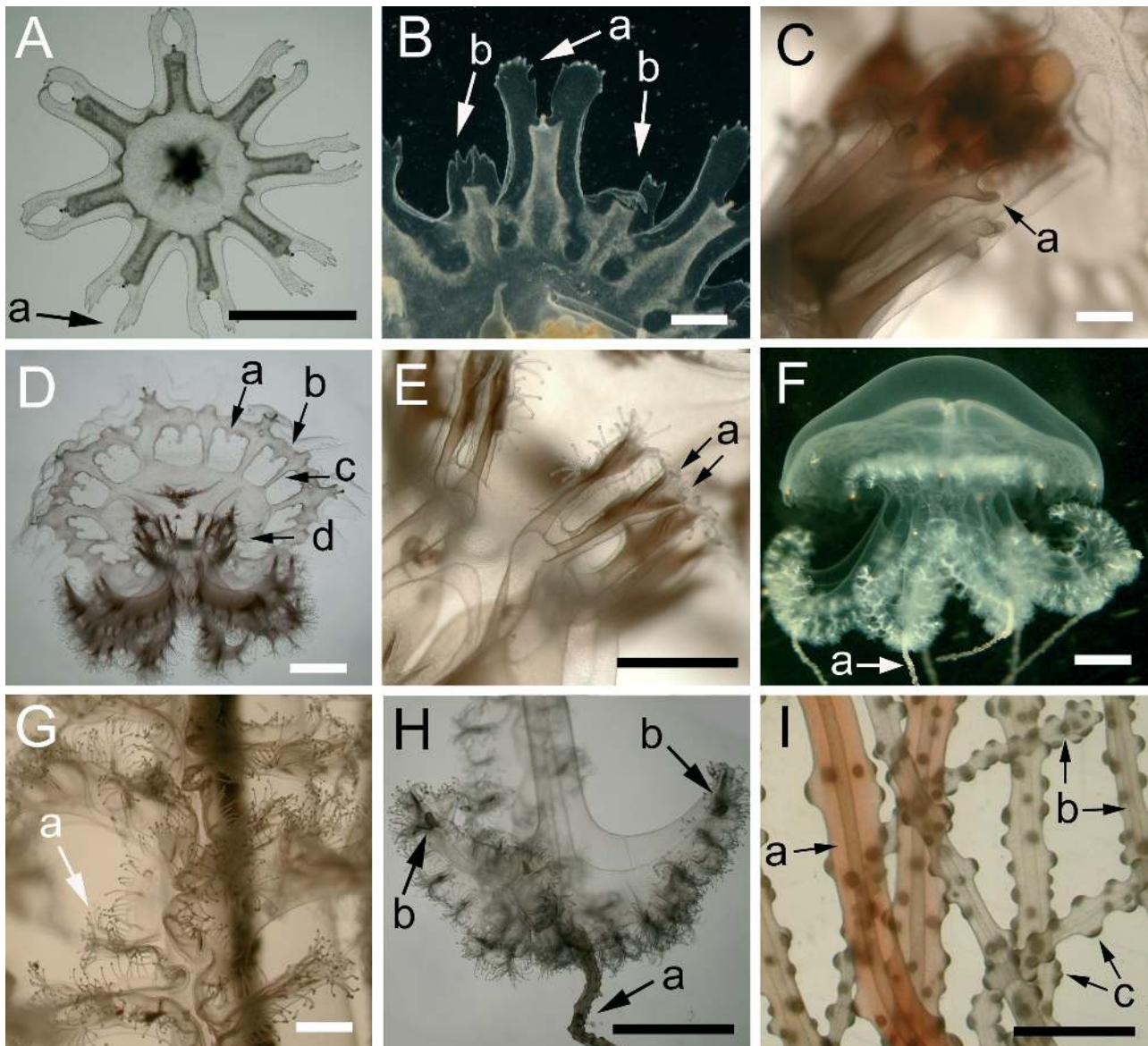
Fig. 6. *Nemopilema nomurai.* (A) Newly liberated ephyra with pointed lappet tips (a). (B) Advanced ephyra with primary (a) and secondary (b) lappets. (C) Advanced ephyra with primitive scapulets (a). (D) Metephyra with centripetal canals (a) extending from the mid-point of the adjacent radial canals (b) on the ring canal (c) and scapulets (d). (E) Metephyra with scapulets with branched wings (a). (F) Advanced metephyra with primary appendages (a). (G) Mouth membrane of metephyra, with cirri (a). (H) Oral wings of metephyra, with primary (a) and secondary appendages (b). (I) Primary (a) and secondary appendages (b) of metephyra, with nematocyst batteries (c). Scale bars = 1 mm (A, I); 500 µm (B, C, G); 2 mm (D, E, H); 4 mm (F)

(Fig. 7A). The lappet tips were light brown in color. The mouth membranes on the oral wings and scapulets coalesced between the mouth canal and distal end of mouthlets. The coalesced parts were gradually penetrated to open as windows with a diameter of 100 to 500 µm (Fig. 7B). With the formation of the windows and appendages, the mouth canals became narrower and many mouthlets were formed. Numerous appendages occurred on the oral wings and scapulets. The anastomosing canal network was connected with

the gastric cavity only by radial canals (Fig. 7C), a characteristic feature in the suborder Daktyliophorae (Russell 1970, Mianzan & Cornelius 1999).

## Growth

Mean wet weight of a 20 d old metephyra (mean extended diameter: 26 mm, n = 11) was 1.5 g and that of a 48 d old medusa (mean extended diameter: 71 mm,
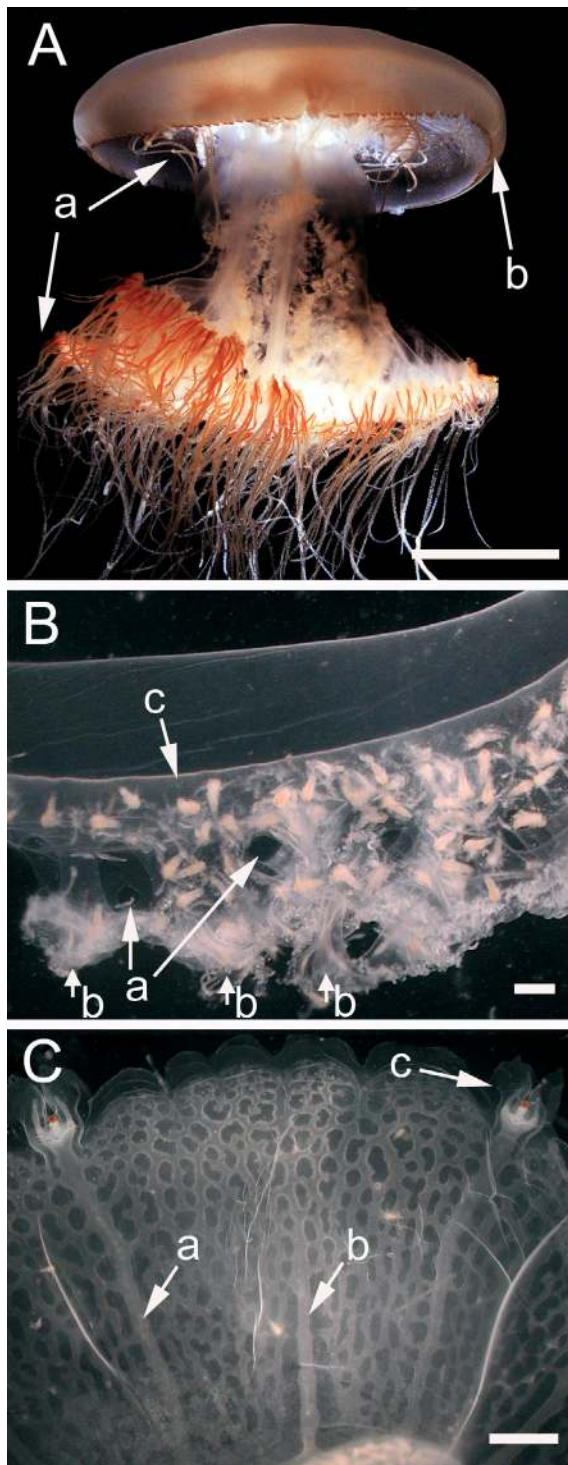
Fig. 7. *Nemopilema nomurai.* (A) 40 to 50 d old medusa with appendages (a) and light brown coloured lappets (b) (courtesy of Mr. T. Murakami, Kamo Municipal Aquarium). (B) Oral wing of young medusa, with window-like openings (a) and mouthlets (b). Ingested *Artemia* nauplii being transported from mouthlets to stomach cavity through the mouth canal (c). (C) Canal system of young medusa, with rhopalar canal (a), inter-rhopalar canal (b) and rhopalium (c). Scale bars = 50 mm (A); 300 μm (B); 4 mm (C)
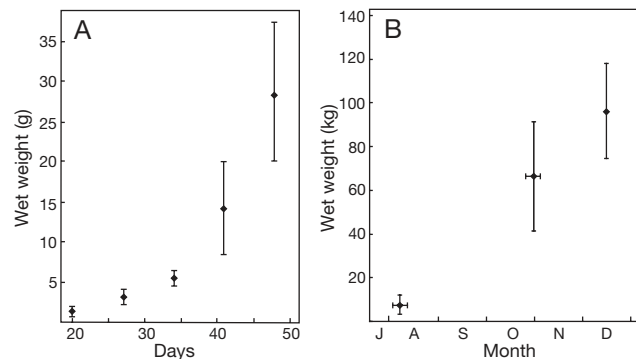


Fig. 8. *Nemopilema nomurai.* Growth in the (A) laboratory and (B) field. Vertical lines denote standard deviation, and horizontal lines, sampling period

n = 8) was 29.0 g, showing an exponential growth rate (Fig. 8A). The daily specific growth rate during the above-mentioned period was 0.11 d$^{-1}$.

The actual measurements of wet weight of wild medusae were sporadic and confined to early August at Tsushima and Iki Islands (mean wet weight: 7.6 kg, n = 21), late October at Oki Island (66.0 kg, n = 3) and mid-December at Oki Island (96.3 kg, n = 4) (Fig. 8B). The specific growth rate between August and December was estimated to be 0.02 d$^{-1}$.

## DISCUSSION

### Mass occurrence

The temporal shift in the geographical distribution of the *Nemopilema nomurai* aggregation in 2003 and 2004 was almost the same as in the past, i.e. in 1958, 1995 and 2002 (Nishimura 1959, 1961, Shimomura 1959, Yasuda 2004). Nevertheless, it is unprecedented that the remarkable bloom of *N. nomurai* appeared 3 yr in a row. In the above-mentioned years, the medusae first began to occur in the Tsushima and Korea Strait in mid-summer and then spread into the northern Sea of Japan. Shimomura (1959) investigated the geographical distribution of *N. nomurai* extensively over a wide area of the Sea of Japan in September and October 1958, and found very dense populations (e.g. a medusa every few meters) in the frontal eddies formed by the third branch of the Tsushima Current (Naganuma 1973) in the central Sea of Japan near the Yamato Bank (see Fig. 1 for location). This means that after passage through the Tsushima and Korea Strait, the medusae are transported not only by the first, or the most nearshore, branch of the Tsushima Current, but also to offshore waters by the second and third branches. Although our survey in 2003 and 2004 was primarily confined to coastal waters, offshore popula-

tions may have been transported to nearshore areas by the wind-driven surface current, as the northwest monsoon prevailed in fall and winter. Congregations of nearshore and offshore populations caused massive aggregations of medusae in set-nets along the coast of the Sea of Japan during these seasons. The majority of medusae died off by mid-winter, probably due to low water temperatures (i.e. ca. 10°C), starvation (Lucas & Lawes 1998), or simply genetically determined senescence (Möller 1980, Lucas 2001). A very small number of medusae survived until March.

### Life cycle and morphological specificity

From our laboratory-rearing experiments, the life cycle of *Nemopilema nomurai* was elucidated and is schematically shown in Fig. 9. Its life cycle is essentially the same as that reported for several other rhizostome species (Paspaleff 1938, Calder 1973, 1982, Ding & Chen 1981, Lotan et al. 1992). The scyphistomae of

*N. nomurai* underwent ongoing asexual reproduction for >1.5 yr in our laboratory. Our experiments also revealed that thermal elevation, although unnaturally sudden (i.e. a 10°C rise over a few hours), is one of the triggers inducing strobilation, as already reported for rhizostome species such as *Cephea cephea* (Sugiura 1966), *Rhopilema esculentum* (Chen & Ding 1983) and *R. nomadica* (Lotan et al. 1994). More detailed studies of temperature effects, mimicking the seasonal thermal increase in nature, are needed to estimate the time of strobilation in the field.

Some morphological and ecological characteristics of *Nemopilema nomurai* have been compared with closely associated species belonging to the superfamily Scapulatae (Russell 1970, Mianzan & Cornelius 1999), which includes the genera *Nemopilema*, *Rhizostoma*, *Rhopilema* and *Stomolophus* (Table 1). Their scyphistoma morphology and methods of asexual reproduction are the same. However, asexual reproduction in *Rhizostoma pulmo* occurs by polyp budding, stolon budding and planuloid formation, as well as by
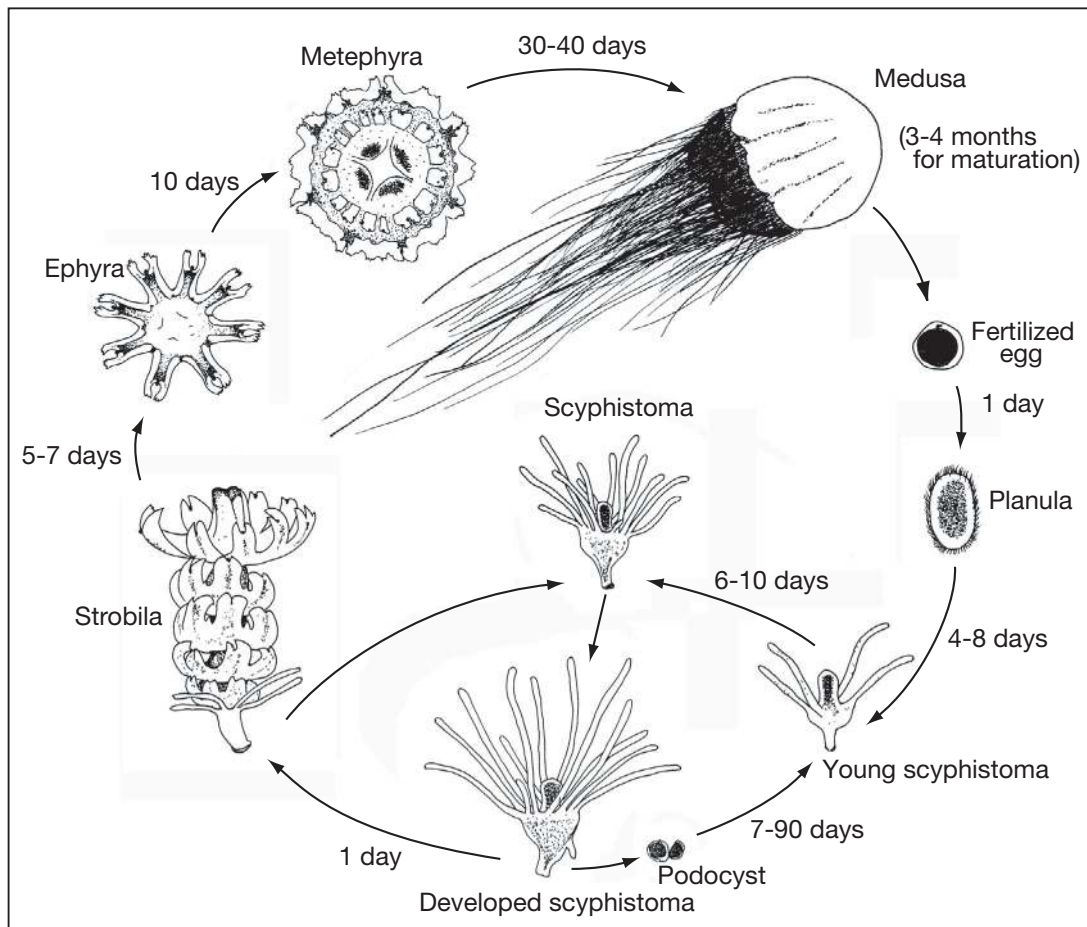


Fig. 9. *Nemopilema nomurai.* Composite image of the life cycle of *N. nomurai*, based on laboratory and field surveys. Inter-stage durations are also shown

Table 1. Life cycles and morphology of 6 species of rhizostome Scyphozoa

| Species | No. of tentacles in scyphistoma | Form of asexual reproduction | No. of ephyrae per strobila | Morphology of ephyral lappet | Shape of appendage | Source |
|---|---|---|---|---|---|---|
| *Nemopilema nomurai* | 16 | Podocyst | 3–7 | Branched into 2–6 small tips | Filiform | Present study |
| *Rhizostoma pulmo* | 16 | Podocyst, planuloid, polyp bud, stolon bud | Several | Almost round | Club-shaped, triangular in cross section | Paspaleff (1938), Russell (1970) |
| *Rhopilema esculentum* | 16 | Podocyst | 6–17 | Branched into 4–6 small tips | Circular cone | Ding & Chen (1981) |
| *Rhopilema nomadica* | 16 | Podocyst | 5–6 | Almost round | Filiform | Galil & Ferguson (1990), Lotan et al. (1992) |
| *Rhopilema verrilli* | 16 | Podocyst | 1 (occasionally several) | Almost round | Circular cone | Calder (1973), Kramp (1961) |
| *Stomolophus meleagris* | 16 | Podocyst | 1–3 | Almost round | Absent | Calder (1982), Mianzan & Cornelius (1999) |

podocysts. The numbers of ephyrae budding from a strobila vary among species, with *Rhopilema verrilli* usually liberating 1 (i.e. monodisk strobilation) and the others usually liberating >2 (i.e. polydisk strobilation). Two groups can be recognised based on the morphology of the ephyral lappets: one group (comprising *N. nomurai* and *Rhopilema esculentum*) has 2 to 6 branched tips and another group (comprising *Rhizostoma pulmo*, *Rhopilema nomadica*, *R. verrilli* and *Stomolophus meleagris*) has almost round tips. This means that the ephyrae of *N. nomurai* and *R. esculentum*, which usually co-occur in Chinese coastal waters (Hon et al. 1978, Chen & Lu 1991), cannot be morphologically distinguished based on this character. However, their metephyrae and young medusae can be differentiated by the shape of the appendages; *N. nomurai*, like *R. nomadica*, bears numerous long and filiform appendages, while *R. esculentum*, like *R. verrilli* and *R. pulmo*, bears fusiform appendages (Kramp 1961, Russell 1970, Omori & Kitamura 2004). *S. meleagris* has no appendages (Mianzan & Cornelius 1999).

## Seasonal life cycle and geographical distribution in East Asian waters

As shown in Fig. 1, the distribution of *Nemopilema nomurai* is clearly confined to the Tsushima Current and regions influenced by it, such as the Pacific side of Honshu, where the medusae are like live drifting bottles. In the Sea of Japan, young *N. nomurai* with bell diameters <30 cm have never been reported; *N. nomurai* with bell diameters >30 cm began to appear from late July. The locations where scyphistomae exist and where ephyrae and medusae originate are unknown, but it is speculated that they are from coastal areas along China and the western Korean Peninsula (i.e. the Bohai, Yellow and northern East China Seas), because mature medusae are often found in great numbers and are commercially harvested in these areas (Hon et al. 1978, Omori 1978, Zhang & Li 1988, Cheng et al. 2004, Omori & Kitamura 2004).

The results of our laboratory and field surveys are combined to construct the seasonal life cycle and associated geographical distribution of *Nemopilema nomurai* in East Asian waters. The growth rate of laboratory-reared *N. nomurai* fed on *Artemia* nauplii was 0.11 d$^{-1}$, although an even higher growth rate might be expected if medusae were reared in more spacious aquaria. Extrapolating this growth rate to the field population of medusae weighing 7.6 kg, which is the mean wet weight in early August, an estimated 99 d would be required to attain this size following the liberation of the ephyra. Thus, we estimate that the liberation of ephyrae occurred in early May. Taking variable environmental conditions in the field into account, we speculate that strobilation and ephyral liberation may take place in April, May and June, when water temperature increases from ca. 10 to 20°C, coinciding with the rise that triggered strobilation in the laboratory, as depicted in Fig. 10. This speculation is also supported by findings of juvenile medusae (we examined their morphology and confirmed that they are *N. nomurai*) in early June 2004, in Gunsan, west Korea, where ephyrae might be liberated in late April and early May based on our estimate of the growth.

Only a few reports are available on the occurrence of *Nemopilema nomurai* in June and July. A local set-net fisherman at Cheju Island informed us during an interview that *N. nomurai*, measuring 20 to 30 cm in bell diameter, began to appear in 2003 during June. Another
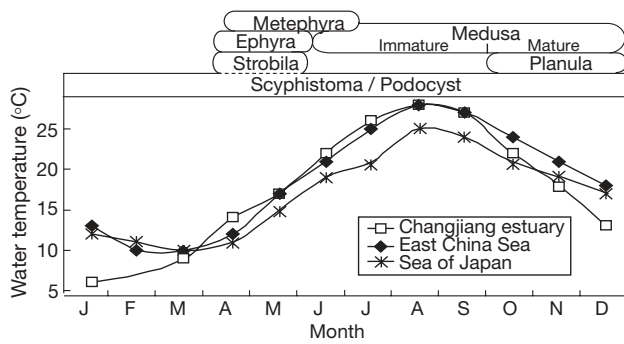
Fig. 10. *Nemopilema nomurai.* Estimated seasonal life cycle in East Asian waters. Monthly average surface water temperatures in the Changjiang estuary (122°N, 31°E), East China Sea (125°N, 31°E) and southern Sea of Japan (134°N, 36°E) in 2003 are also shown (satellite images provided by the Japan Meteorological Agency)

report concerns the catch of a large number of 50 to 100 cm diameter medusae by RV 'Youkou Maru' (Seikai National Fisheries Research Institute) southwest of Cheju Island in mid-July 2004. June and July coincide with the rainy season in temperate East Asia. An increased freshwater discharge from the Changjiang (Yangtze) River forms a low salinity water mass in the southern Yellow Sea and northern East China Sea, which extends north-eastwards toward Cheju Island (our Fig. 11, Chang & Isobe 2003). It is highly likely that larval and young medusae originating from the coastal waters of China and Korea are trapped in
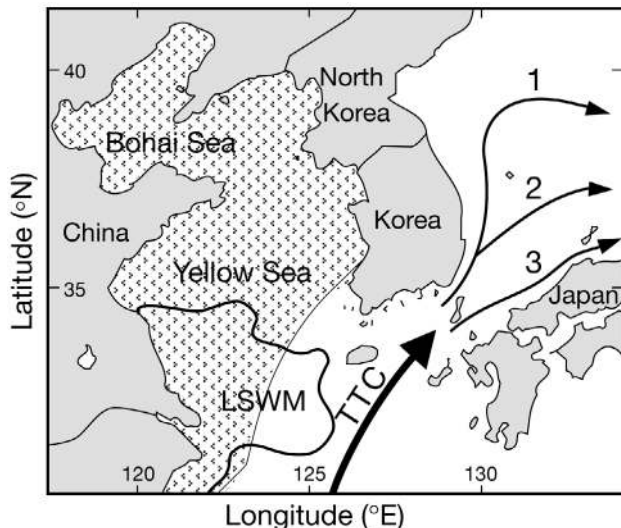


Fig. 11. Schematic representation of hydrographical features in early summer in East Asian waters, which may play a role in the transportation of *Nemopilema nomurai* medusae from their expected seeding place (dotted area) to the Sea of Japan. LSWM: low salinity (<30 psu) water mass (from Chang & Isobe 2003); TTC: Taiwan-Tsushima Current (from Isobe 1999); 1, 2, 3: first, second and third branch of the Tsushima Current (from Naganuma 1973)

this water mass and then entrained by the southerly Taiwan-Tsushima Current (Isobe 1999), as schematically shown in Fig. 11. The main population of *N. nomurai* resides in the Bohai, Yellow and northern East China Seas, while a sub-population extending from the main habitat is transported into the Sea of Japan.

Medusae grow at relatively higher rates in summer, when water temperatures rise to >25°C, and at much lower rates in fall. The medusae were mature by October. So far, we have observed no evidence of natural spawning and/or sperm release of *Nemopilema nomurai* in the field, even in aggregated conditions in the set-nets. In the main habitat, we presume that maturation and sexual reproduction occur in the fall. Resulting planulae settle on suitable substrates and give rise to scyphistomae, which undergo quasi-perennial asexual reproduction, making this area a seedbed (Figs. 10 & 11).

## Possible causes of mass occurrences and future prospects

Why blooms of expatriated medusae occurred and why the blooms were infrequent in the past (once every several decades), but have become more frequent in the last decade, are still open questions. Tanaka & Suzuki (2005) found that blooms occurred 3 to 4 yr after heavy flooding in the Changjiang River plain, but gave no plausible explanation for a link between heavy rain and jellyfish blooms 3 to 4 yr later. It has been argued that environmental changes, such as increased eutrophication, habitat modification, over-fishing and global warming, may be responsible for the enhancement of jellyfish populations (Arai 2001, Graham 2001, Parsons & Lalli 2002, Uye & Ueta 2004). Indeed, such environmental changes are significant in Chinese coastal waters (Zhang et al. 1999, Anderson et al. 2002, Li et al. 2002). Hence, we speculate that both recent ecosystem change and annual hydrographical conditions (e.g. Changjiang River discharge, expansion of low salinity water mass, strength of the Taiwan–Tsushima Current) in and near the main habitat of *Nemopilema nomurai* may be responsible for the frequent bloom occurrence in the Sea of Japan.

There have been some earlier reports about invasions by rhizostome species; *Rhopilema nomadica*, native to the Indo-Pacific region, has invaded the Mediterranean Sea (Galil et al. 1990, Lotan et al. 1992, Kideys & Gücü 1995, Silfen et al. 2003), and *Phyllorhiza punctata*, native to Australian waters, has been introduced to the Atlantic (Graham et al. 2003). Given the opportunistic nature of jellyfishes, *Nemopilema nomurai* has the potential to be successful as an invader in the Sea of Japan. In our experiments, the scyphistomae of *N. nomurai* were kept at 9°C for 1 mo. Under such conditions, tentacle movements became slower and rates of

feeding and podocyst formation decreased, but the jellyfish nevertheless survived. Thus, we conclude that the scyphistomae of *N. nomurai* are capable of withstanding the winter season in the southern Sea of Japan, as the annual lowest temperature here is ca. 10°C (Fig. 10). Podocysts are essentially dormant stages (Calder 1974, Black 1981), and may be the key to winter survival in much colder waters, such as the Changjiang estuary (5°C, Fig. 10) and the northern Sea of Japan. Once unfavorable conditions such as low temperatures pass, podocysts 'excyst' and form scyphistomae, which re-establish the population. However, we have no indication whether the invasion is permanent or whether *N. nomurai* undergoes a complete life cycle in the Sea of Japan. If the sessile life stages become established in the Sea of Japan, the bloom of *N. nomurai* will be an annual event and fisheries might suffer disaster. The risk of this is now considered high.

We have described herein the life cycle and morphological and ecological characteristics of various life stages of *Nemopilema nomurai*. Such information is essential if the causes of blooms of the species and the impacts these have on both fisheries and food-web dynamics are to be understood. Given the environmental changes occurring in the coastal waters of East Asia, a potential threat exists that population explosions of jellyfishes may increase. Fundamental knowledge provided here may be useful in future investigations of *N. nomurai*, as well as in studies of other jellyfish species (*Aurelia aurita*, *Chrysaora melanaster*, *Cyanea nozakii*, etc.) that tend to explode in abundance periodically in this area.

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