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Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian Marginal Seas

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Abstract: The rhizostome jellyfish *Nemopilema nomurai*, which is endemic to the East Asian Marginal Seas (i.e. the Bohai, Yellow, East China and Japan Seas), is unique both by its enormous body size (ca. 2 m maximum bell diameter and 200 kg wet weight) and propensity for occasional population explosionss. Massive blooms of this species have historically been reported only once per ca. 40 years (i.e. in 1920, 1958 and 1995), but have become increasingly frequent recently (i.e. in 2002, 2003, 2005 and 2006). Both accumulated knowledge on the spatiotemporal distributions and physical modeling of the water circulation show that the medusae are released from benthic polyps during April–June in the Yellow Sea and East China Sea, and transported by the Tsushima Current to the Japan Sea. The bloom in 2005 might be the largest ever in history; as many as $3–5\times10^8$ medusae passed through the Tsushima Strait daily during the summer and there were more than 100,000 complaints from commercial fishermen. The recent blooms of *N. nomurai* may have been caused by environmental changes, such as increased water temperature, eutrophication, coastal modification, and over-fishing in Chinese coastal waters. Frequent jellyfish blooms can apparently be a threat to the fisheries sustainability of the East Asian Marginal Seas, one of the world's most productive fisheries grounds.

Key words: Bloom, East Asian Marginal Seas, giant jellyfish, nuisance to fisheries

1. Introduction: brief history of mass occurrences of jellyfish in Japan

In Japanese coastal waters, like many other coastal waters, the moon jellyfish *Aurelia aurita* Linnaeus 1758 (see Dawson & Martin 2001, Dawson 2003, for sibling species of the genus *Aurelia*) is the most common and abundant scyphozoan species. The seasonal aggregation of its medusa stage has been a well-known phenomenon even before modern times. The oldest Japanese history book, the Kojiki published in 712 AD, described that in the beginning of the Japanese islands were like aggregated medusae on the sea surface. Until recently, jellyfish have received little scientific attention, particularly concerning their roles in marine ecosystems. There is great concern that the occurrence of jellyfish aggregations has intensified or that the jellyfish biomass has increased in the last few decades, since the effects of jellyfish on fisheries and coastal power plant operations have become seriously in many cases (Purcell et al. in press). The first noticeable increase in the *A. aurita* population took place in Tokyo Bay during the 1960s, when the bay was heavily eutrophicated by increased industrial and civil sewage discharge (Unoki & Kishino 1977). At the same time, aggregated medusae often clogged the cooling water intakes of coastal power plants (Kuwabara et al. 1969). The *A. aurita* medusa population has since become one of the predominant zooplankton components in Tokyo Bay (Omori et al. 1995, Toyokawa et al. 2000, Ishii 2001). After the 1980s, the *A. aurita* population significantly increased in the Inland Sea of Japan (Seto Inland Sea), due probably to a combination of factors such as increases in water temperature, food supply and marine construction, as well as decreased zooplanktivorous fish stocks (Uye & Ueta 2004). The largest recorded bloom occurred during the summer of 2000, with estimated biomass of ca. 9.4×10^4 tons of *A. aurita* medusa wet weight (WW) extending along approximately 100 km of coastline in the Uwa Sea, western Shikoku (Uye et al. 2003).

From the turn of this century, the population of the giant jellyfish, *Nemopilema nomurai* Kishinouye 1922, began to explode in the Japan Sea. This species is one of the largest jellyfish in the world, attaining a bell diameter of ca. 2 m and a body weight of ca. 200 kg WW (Kishinouye 1922, Omori & Kitamura 2004). The medusae are transported

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from the main habitat, i.e. the Bohai, Yellow and East China Seas, by the Tsushima Current to the Japan Sea, usually in small numbers, but sometimes in extreme abundances sufficient to seriously damage local fisheries. Such a mass occurrence took place in 1920, 1958 and 1995, about once per 40 years (Kishinouye 1922, Shimomura 1959, Yasuda 2004). Since 2002, however, damaging blooms have occurred almost every year.

In this article, I summarize the current knowledge of the ecological characteristics of *N. nomurai* and the known impact of this species to fisheries and marine food chain dynamics.

2. Life cycle and transportation route of *N. nomurai*

In the fall of 2003, we collected *N. nomurai* medusae with fully mature gonads, obtained its scyphistomae (polyps) by artificial fertilization, and reared the budded ephyrae to the young medusa stage (Kawahara et al. 2006). This rearing experiment enabled us to reconstruct the life cycle of this species as depicted in Fig. 1. At 20°C, the fertilized eggs develop into planula larvae ca. 1 day after fertilization. After swimming for 4 to 8 days, they settle onto hard substrates and metamorphose into scyphistomae. Developed scyphistomae with 16 tentacles asexually reproduce by podocyst formation. An incubation of the scyphistomae at 23°C from pre-incubation at 13°C induces strobilation, followed by liberation of 3 to 7 ephyrae from each strobila. After releasing ephyrae, the basal part of the strobila develops into a normal scyphistoma to resume asexual reproduction; the life span of the benthic scyphistoma stage may be several years.

Field collections plus laboratory rearing enabled a description of the annual population dynamics of *N. nomurai*. Based on seasonal temperatures in the area where the medusae originate, the above results suggest that ephyrae are released into the plankton in early summer. In the laboratory at 23°C and with abundant food, the new ephyrae grow through metephyrae to young medusae of ca. 10 cm bell diameter in approximately 50 days following liberation. In the southern Japan Sea, the medusae reach ca. 0.5 m bell diameter in summer and larger than 1 m by fall. After gonad maturation and subsequent sexual reproduction, they die during winter due to low temperatures and/or genetically determined senescence. The medusa life span is less than one year.

In addition to Chinese literature on the occurrence of *N. nomurai* medusae (cf. Hon et al. 1978, Zhang & Li 1988, Cheng et al. 2004), recent information on the occurrence of larval/young medusae (Kawahara et al. 2006, Uye unpublished) and on the probable transportation routes of medusae as estimated by a numerical model of water circulation (Reizen & Isobe 2006) demonstrate that the large bay area surrounded by the Korean Peninsula and the mainland of China (i.e. the Bohai, Yellow and East China Seas) is the geographical origin or the main habitat of *N. nomurai* (Fig. 2). However, its scyphistomae have not yet been found in the field. The ephyrae may be released into the plankton from the benthic scyphistomae during April–June (Kawahara et al. 2006). Due to heavy rainfall in June and July in temperate East Asia, the Chanjiang (Yangtzu) low salinity water mass (LSWM) is formed in the Yellow Sea and northern East China Sea, with its front extending to near Cheju Island (Chang & Isobe 2003). The larval/young medusae are entrained offshore by this LSWM, and are then transported by the southerly Taiwan-Tsushima Current (Isobe 1999). Hence, the medusae first begin to appear in the Tsushima Strait in July/August, and spread into the northern Japan Sea. In October, they pass through the

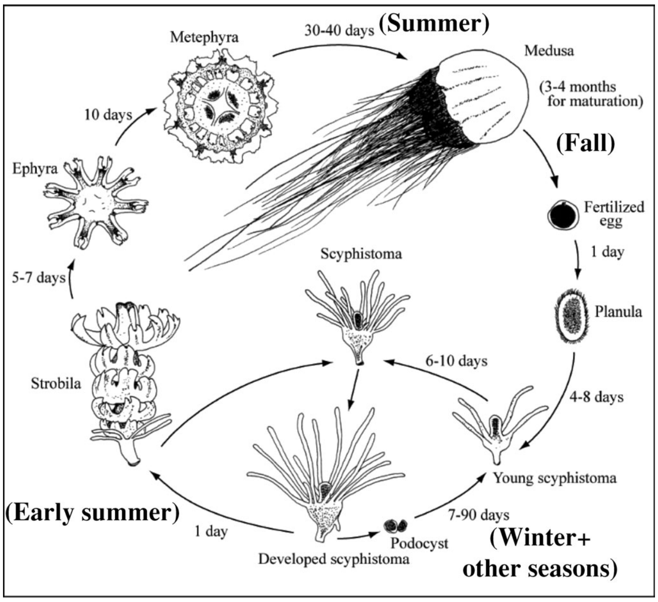

Fig. 1. Composite image of the life cycle of *Nemopilema nomurai* (after Kawahara et al. 2006).

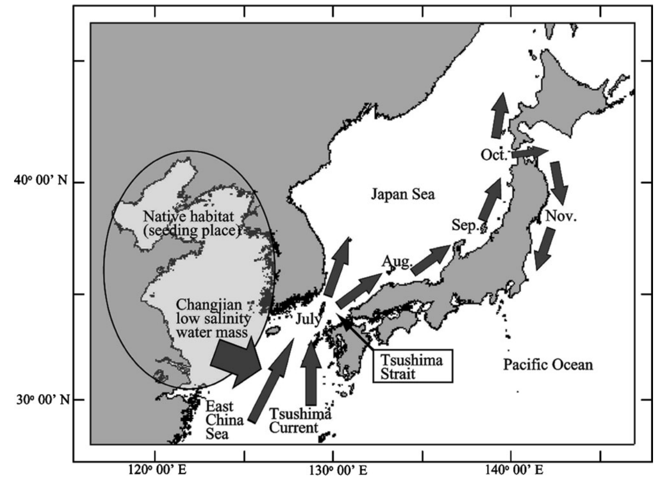

Fig. 2. Schematic representation of hydrographic features which may transport *Nemopilema nomurai* medusae from their native habitat or the nursery ground in Chinese coastal waters to the Japan Sea until they die in winter (see text for detail).

Tsugaru Strait to the Pacific Ocean, and are transported by a coastal current as far south as the Boso Peninsula, until they die during the winter months (Fig. 2). Hence, the medusae entrained into the Tsushima Current are expatriated from their home waters.

3. Bloom of *N. nomurai* in 2005

The year of 2005 saw perhaps the largest bloom of *N. nomurai* in history. In late July of 2005, a cruise conducted by the T&R/V *Toyoshio Maru* (Hiroshima University) found many medusae occurring over an extensive area around Tsushima Island. During sighting from the ship deck, we encountered as many as 23 medusae aggregated near the sea surface in a 15 m×15 m sighting field on the morning of July 21. During the daytime on July 22, their vertical distribution was investigated at a station west of Tsushima Island (34°16′N, 129°10′E, depth: 65 m) by towing a net (mouth diameter: 1.5 m, length: 10 m, mesh opening: 1 cm) horizontally for 15 min at 10, 30 and 50 m depths. The medusae (average body weight: ca. 3.0 kg WW) occurred throughout the water column, most abundantly at 30 m depth, with an average abundance of 2.5 medusae $1000\,m^{-3}$ (Fig. 3). Multiplying this density with the average flow rate of the Tsushima Current (i.e. 2.7 Sv., Takikawa et al. 2005) gives a transportation rate of 5.8×10^8 medusae per day, although it may be overestimated few medusae occurred in the eastern extremity of the Tsushima Current. A reasonable estimate is that the daily passage through the Tsushima Strait ranged from 3×10^8 to 5×10^8 medusae. A similar level of transport might continue until the end of August, and thereafter the number gradually diminished to almost nil in late October, judging from monitoring of medusae trapped in set-nets in Tsushima (Y. Sakumoto, a set-net fisherman, personal comm.).

Along with the transportation of the leading edge of the bloom population, the damage to set-net fisheries also shifted northward along the Japan Sea coast. The damage

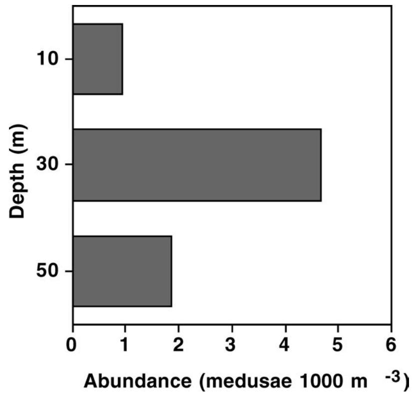

Fig. 3. Vertical distribution of *Nemopilema nomurai* medusae at a station west of Tsushima Island in late July, 2005.

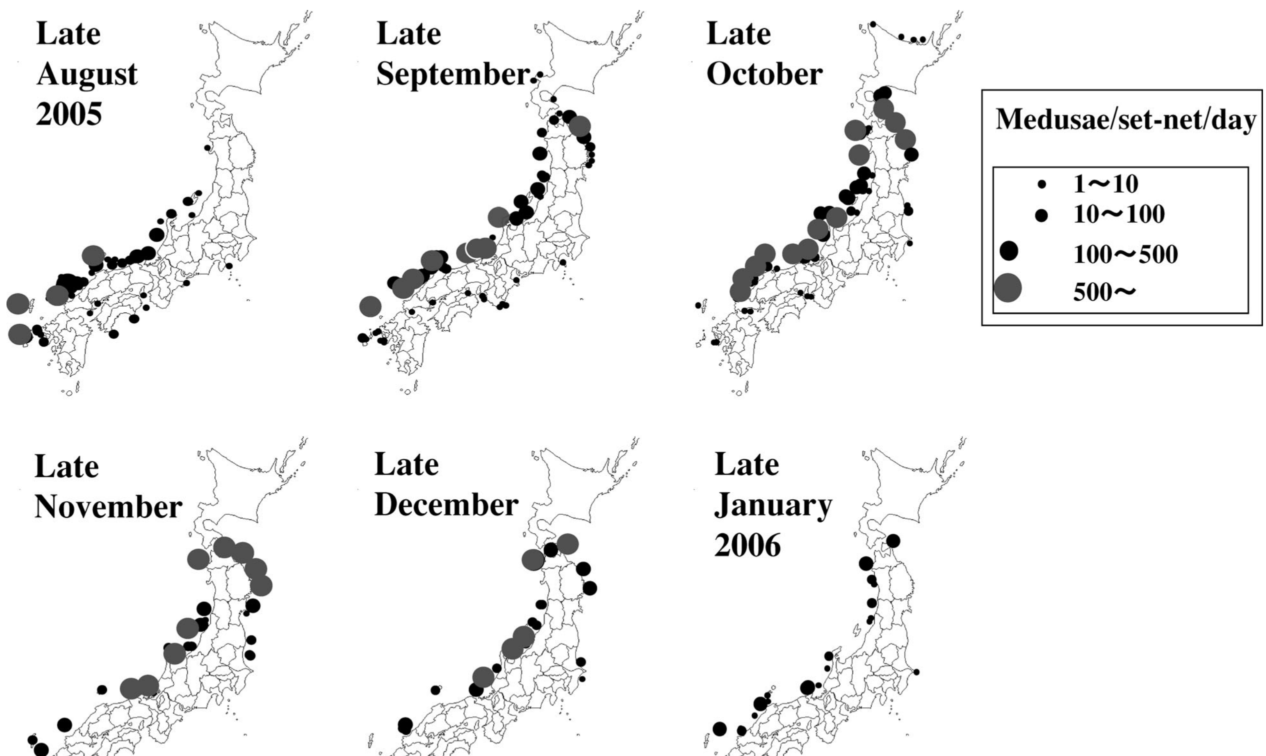

Fig. 4. Seasonal geographical shift of the *Nemopilema nomurai* bloom population based on medusa numbers trapped in set-nets (drawn by Fisheries Agency, Japan, based on data compiled by the Japan Sea National Fisheries Research Institute).

Fig. 5. Fishermen fighting with *Nemopilema nomurai* medusae entrapped in a set-net off the coast of Kuji, Iwate Prefecture, in December, 2005.

was most serious and wide spread in late October and lessened gradually until the medusae died (Fig. 4). Fishermen were exhausted from constantly having to remove the medusae to avoid bursting their nets (Fig. 5). The bloom in 2005 was characterized by: 1) extraordinary abundance of the medusae, 2) relatively smaller medusae with more water-content as well as more fragile bodies, 3) the first occurrence of the bloom near Tsushima Island (i.e. in early July) being approximately one month earlier than usual, 4) a significant number of medusae being transported into the Okhotsk Sea as far as Shiretoko Peninsula, Hokkaido, and a significant number of medusae being transported by the Kuroshio to waters along the coast of the south-west Pacific side of Japan including the Inland Sea of Japan.

Therefore, the occurrence of *N. nomurai* medusae was widespread over almost the entire Japanese coast. At the same time, damages to fisheries operations spread widely throughout the nation, culminating in >100,000 complaints from fishermen (Fishery Agency, Japan).

4. Causes of the bloom of *N. nomurai*

The recent more frequent occurrences of *N. nomurai* blooms may be attributable to environmental changes in Chinese coastal waters, but it is difficult to specify which factors are really responsible for the increase in the *N. nomurai* population. As has already been argued in previous studies (Arai 2001, Graham 2001, Parsons & Lalli 2002, Uye & Ueta 2004, Purcell 2005, Lynam et al. 2006), the following factors, which are in evidence in Chinese coastal waters, are thought to be among the causes.

1) Over-fishing

The stock sizes of fishes, which are predators of, as well as competitors with, jellyfish for zooplankton prey, are declining in Chinese waters. For example, the catch per unit effort in the Bohai Sea declined by ca. 95% during the period from 1959 to 1998 (Tang et al. 2003). Further, Korean fish catch statistics show that the annual fish catch in the Yellow Sea declined from ca. 13×10^4 tons in the mid-1980s to $<5\times10^4$ tons in 2004 (Fig. 6). Such excess removal of fish populations may result in opening an ecological niche for jellyfish to invade.

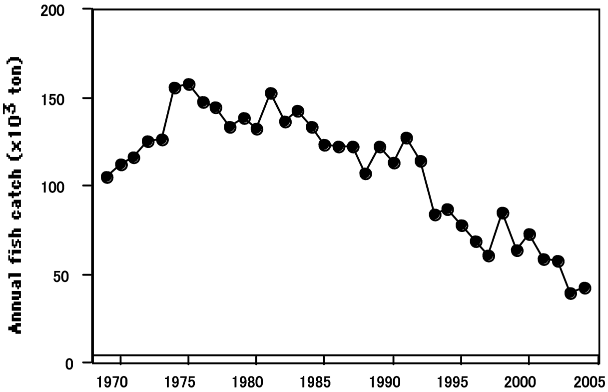

Fig. 6. Change in annual fish catch in the Yellow Sea by Korean fishing vessels (from National Fisheries Research and Development Institute, Korea).

2) Global warming

Due to recent global warming, the Yellow Sea surface temperature has increased by 1.7°C from 1976 to 2000 (Fig. 7, Lin et al. 2005). Since scyphistoma asexual reproduction, in general, accelerates at higher temperatures, such a warming tendency may lead to higher birth rates of medusae.

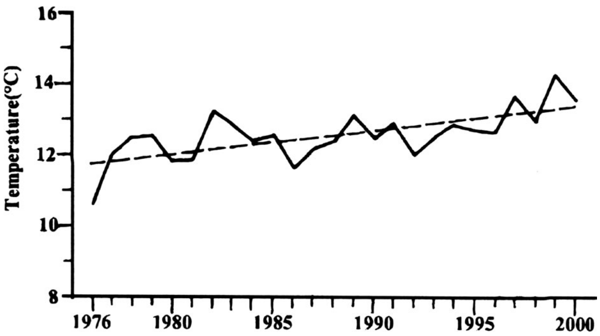

Fig. 7. Change in annual average surface temperature in the Yellow Sea. The dotted line denotes a fitted regression line (after Lin et al. 2005).

3) Eutrophication

Because of increased anthropogenic activity in China, particularly in the coastal zone, nutrient loading from land is increasing, as evidenced by dissolved inorganic nitrogen concentration in Changjiang River water (Fig. 8, Yan et al. 2003). The input of nutrients may boost phytoplankton production in coastal waters, which may further enhance zooplankton production to supply more food to jellyfish.

4) Marine construction

Marine construction activities such as harbor and waterfront constructions are substantially increasing in China.

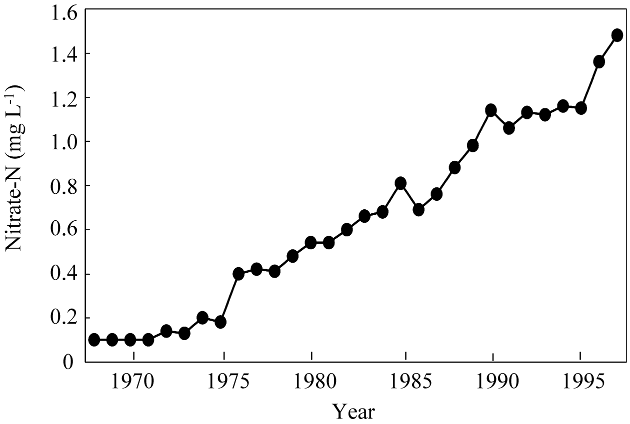

Fig. 8. Change in annual average dissolved nitrate concentration in the Chanjiang estuary (modified from Yan et al. 2003).

Such coastline modifications may provide an increased area for scyphistomae to attach, although the actual attachment sites of scyphistomae of *N. nomurai* have yet to be found.

5. Food, growth, respiration and food requirement of *N. nomurai*

N. nomurai medusae have two elaborate feeding apparatuses, i.e. scapulets and branched oral arms underneath the bell. The food organisms near the upper portion of the bell are entrained into the flow generated by pulsation toward the lower bell portion and are then transported posteriorly through the scapulets and oral arms. They are captured by numerous mouthlets, surrounded by cirri with nematocysts at their distal end, found on the scapulates and oral arms. Since the diameter of the mouthlets is ca. 1 mm and constant throughout the medusa stage, their food is confined to micro- and mesozooplankton. The gastric pouch contents were examined from specimens (body weight: 30–120 kgWW) caught near Oki Island, Shimane Prefecture, in November 2005. They contained many copepod carcasses (mainly hard-shelled *Oncaea* and *Corycaeus*) and gastropod shells (Fig. 9). Fish eggs and larvae are also consumed as food, although our observation revealed that *N. nomurai* medusae (weight: ca. 10 gWW) do not consume eggs of the red sea bream (*Pagrus major*) but only hatched larvae (Uye & Kawahara unpublished).

The growth rates of *N. nomurai* medusae were determined for laboratory-reared larval and field-collected juvenile/adult specimens (Kawahara et al. 2006). In the laboratory, 20-day old medusae of average weight of 1.5 gWW grew to 29 gWW over 28 days, giving a specific growth rate of 0.11 d^{-1} for this period. The medusae caught in August (average: 7.6 kgWW) grew to 96.3 kgWW in December, indicating that the growth rate is 0.02 d^{-1} during the summer and fall.

The respiration rates of *N. nomurai* were measured on board the T&R/V *Toshoshio Maru* during July 2005 for individuals weighing from 0.8 to 8.0 kgWW. Their weight

Fig. 9. Copepods and gastropods remained in the gastric pouch of a *Nemopilema nomurai* medusa caught near Oki Island, Shimane Prefecture, in November, 2005.

Table 1. Estimated feeding and clearance rates of a *Nemopilema nomurai* medusa in early summer, mid-summer and fall, at various combinations of body weights and the specific growth rates (see text for other assumptions).

Seasons	Early summer	Mid-summer	Fall
Body weight (kg WW)	3	30	80
Specific growth rate (d^{-1})	0.10	0.03	0.01
Feeding rate (g C medusa^{-1} d^{-1})	0.98	6.38	14.4
Clearance rate (m^3 medusa^{-1} d^{-1})	98	638	1440

specific respiration rates were constant irrespective of medusa weight, i.e. 12 mL O_2 kg^{-1} of WW h^{-1} (Uye & Kawahara unpublished).

Based on the above-mentioned physio-ecological parameters, an attempt was made to roughly estimate the food requirements of a medusa in the early summer, mid-summer and fall. In these calculations, the following assumptions are made: 1) the medusa body weight is 3, 30 and 80 kgWW, and the specific growth rate is 0.10, 0.03 and 0.01 d^{-1} in early summer, mid-summer and fall, respectively, 2) the carbon content of *N. nomurai* medusae is 0.13% of wet weight, similar to *Aurelia aurita* (Uye & Shimauchi 2005), and 3) the respiratory quotient and assimilation efficiency are 0.85 and 0.80, respectively (Schneider 1989).

Results of these calculations are shown in Table 1. Medusae in each season are required to ingest 0.98, 6.38 and 14.4 g C d^{-1}, respectively, to meet their metabolic and somatic growth demands. If the ambient mesozooplankton biomass is 10 mg C m^{-3}, a value similar to that found in a previous survey in the central part of the East China Sea (Uye unpublished), a medusa would capture all the prey in 98, 638 and 1440 m^3 per day, respectively, to achieve the above ingestion rates. Under the bloom conditions encountered near Tsushima Island in late July, 2005 (i.e. medusa weight: 3.0 kgWW, density: 2.5 medusae $1000\,m^{-3}$), the medusa population might have ingested approximately 24% of the total mesozooplankton biomass per day, a significant predation pressure.

6. Threat to fisheries sustainability

The East Asian Marginal Seas (i.e. the Bohai, Yellow, East China and Japan Seas) are the world's most productive fisheries grounds (total fish catch in 2003: ca. 9.0×10^6 ton, or 11% of the world marine fish catch, Fisheries Center, University of British Colombia, Canada). However, the annual fish catch in this area has been declining steeply since the 1990s, as is exemplified by the Japanese fish catch statistics for both the East China Sea and Japan Sea (Fig. 10). As demonstrated above, the predation pressure by the *N. nomurai* population on the micro- and mesozooplankton community is potentially very high under bloom conditions. At the same time, the recruitment of fish populations may also be affected since their eggs and larvae are preyed upon by the medusae. Hence, it is theoretically possible that the more jellyfish prevail, the more fish would be eradicated and thus the harder it would be for fish populations to recover. Such an ecosystem shift from dominance by fish to dominance by jellyfish may proceed in a spiral fasion and has been termed "jellyfish spiral" (Uye 2005). In this sense, the East Asian Marginal Seas are likely to fall into a jellyfish spiral.

Although the year to year changes in annual fish catch (Fig. 10) do not always show a significant decline in the years during and immediately after the years of mass occurrence of *N. nomurai* (i.e. 1995, 2002 and 2003), repeated occurrences of the bloom are apparently a sign of the deterioration of the traditionally productive ecosystem of the East Asian Marginal Seas. As a consequence of their high abundance and feeding rates, this species can be considered a threat to the fisheries sustainability of this area.

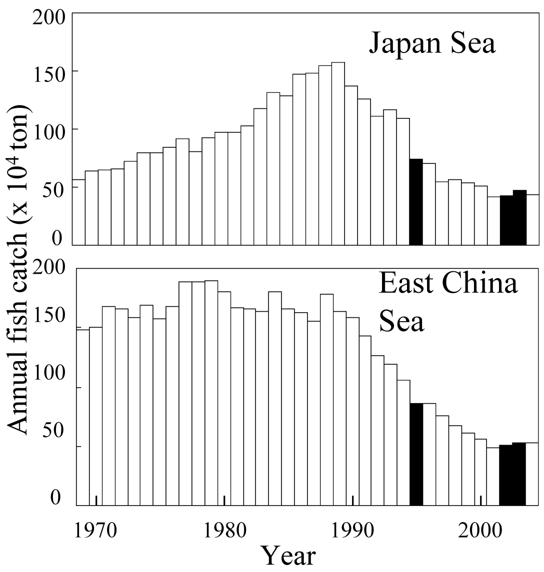

Fig. 10. Change in annual fish catch in the East China Sea and the Japan Sea by Japanese fishing vessels (after Ministry of Agriculture, Forestry and Fisheries, Japan). *Nemopilema nomurai* medusa bloom years (1995, 2002 and 2003) are shown by dark columns.

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