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Review

Jellyfish blooms in China: Dominant species, causes and consequences

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ABSTRACT

Three jellyfish species, *Aurelia aurita*, *Cyanea nozakii* and *Nemopilema nomurai*, form large blooms in Chinese seas. We report on the distribution and increasing incidence of jellyfish blooms and their consequences in Chinese coastal seas and analyze their relationship to anthropogenically derived changes to the environment in order to determine the possible causes. *A. aurita*, *C. nozakii* and *N. nomurai* form blooms in the temperate Chinese seas including the northern East China Sea, Yellow Sea and Bohai Sea. *N. nomurai* forms offshore blooms while the other two species bloom mainly in inshore areas. Eutrophication, overfishing, habitat modification for aquaculture and climate change are all possible contributory factors facilitating plausible mechanisms for the proliferation of jellyfish blooms. In the absence of improvement in coastal marine ecosystem health, jellyfish blooms could be sustained and may even spread from the locations in which they now occur.

1. Introduction

Over the last decade, a significant increase in jellyfish blooms has been observed worldwide in marine ecosystems and are becoming seen as an indicator of a state shift in pelagic ecosystems (Arai, 2001; Graham et al., 2001; Mills, 2001; Purcell, 2005; Purcell et al., 2007; Uye, 2008; Zhang et al., 2009; Richardson et al., 2009). Distinguished from the natural phenomena of jellyfish aggregation, jellyfish blooms in pelagic ecosystems are regarded as a response to anthropogenic disturbance and climate change and can cause numerous deleterious consequences for industry and the community, such as, reduced fishery production from the competition for food with fish, stinging of swimmers by venomous species and clogging coastal power plant cooling water intakes (Purcell et al., 2007; Richardson et al., 2009).

Mounting evidence indicates that the environmental changes caused by intensive human activity (e.g., eutrophication, overfishing, translocations, habitat modification, etc.) and climate change are all contributors to jellyfish blooms (Arai, 2001; Purcell, 2005; Graham and Bayha, 2007; Purcell et al., 2007; Uye, 2008; Richardson et al., 2009). The marine environment of China has deteriorated significantly over recent decades, particularly in coastal areas, due to the impact of rapid economic development, increased population and the associated consequences of habitat loss, eutrophication, pollution and overfishing (Zhang et al., 1999; Tang et al., 2003; Jin, 2004; Liu and Diamond, 2005). For example, the population living in the coastal regions of China increased to 529 million in 2000 from 243 million in 1952 (National Census Reports of China, 2000). In recent years, the warning signs of ecological deterioration, such as algal blooms, fishery collapse, hypoxia and now jellyfish blooms have increased significantly in Chinese seas (Li et al., 2002; Tang et al., 2003, 2006; Liu et al., 2009; Zhang et al., 2009).

The consequences of jellyfish blooms have concerned scientists and environmental managers due to the increasing incidence of blooms in the late of 1990s and their significant impact in Chinese seas (Table 1). For example, the decline of fisheries in the East China Sea and Yellow Sea were associated with the increase of jellyfish blooms (Cheng et al., 2004; Ge and He, 2004; Ding and Cheng, 2007). In the autumn of 2003, a bloom of the jellyfish *Nemopilema nomurai* occurred in the East China Sea with an average biomass of 1555 kg/ha and the maximum biomass of 15,000 kg/ha, consequently, the CPUE of the commercial fishery for *Pseudosciaena polyactis* declined 20% during the period of the bloom (Ding and Cheng, 2005, 2007). Another example is the bloom of jellyfish *Cyanea nozakii* in Liaodong Bay of Bohai Sea in 2004, which was regarded as the main cause for the approximately 80% decline of edible jellyfish *Rhopilema esculentum* and the direct economic losses were approximately US$70 million (Ge and He, 2004). Moreover, venomous jellyfish can produce skin erythema, swelling, burning and vesicles, and at times, severe dermonecrotic, cardio- and neurotoxic effects, which are occasionally fatal for some patients (Mariottini et al., 2008). The published hospital reports showed that over 2000 cases of jellyfish stings occurred in the popular coastal areas of China since 1983, including 13 fatal cases (Table 2). However, the real numbers could be higher than these considering the limited available information. About 80% of stinging cases occurred in the last

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Table 1
Published accounts of jellyfish blooms in Chinese seas and their negative impacts on human enterprises.

Species	Year	Location	Direct consequences	Source
Aurelia aurita	2004; 2008	Qinhuangdao, Hebei province	Over 4000 tons of *A. aurita* were cleaned up in July 2008	Liu (2008)
A. aurita	2007	Yantai, Shandong province	Interference with aquaculture	Su (2007)
A. aurita	2008	Weihai, Shandong province	20–50 tons of *A. aurita* were cleaned up each day	Chinese Huaneng Group (personal communication)
A. aurita	2009	Qingdao, Shandong province	Over 10 tons of *A. aurita* were cleaned up for two days	Lu (2009)
Cyanea sp.; *Nemopilema nomurai*	1999	Middle South Zhejiang province	Interference with fisheries	Dong (2000)
Cyanea nozakii	2004	Liaodong Bay	Sharp decline of edible jellyfish *Rhopilema esculentum*	Ge and He (2004)
Cyanea sp.	2003; 2004	Yangtze Estuary	Comprised 85.47% of the total catch of fisheries in November 2003 and 98.44% in May 2004	Xian et al. (2005)
Nemopilema nomurai	2003–2005	East China sea	Mean biomass in monitoring sites 608–7144 kg/h	Ding and Cheng (2007)
N. nomurai	2005; 2007	Huludao, Liaoning province	Interference with fisheries	Hua (2007)

Table 2
Published hospital-based records of jellyfish stingings in Chinese seas.

Location	Period	Number of cases	Number of severe cases	Number of deaths	Source
Qinhuangdao, Hebei province	1983–1987; 1995–2000	583	7	2	Li (1988), Wang (2002) and Xu et al. (2007)
Huludao, Liaoning province	2006	2	1	0	Yu et al. (2007)
Dalian, Liaoning province	2001–2004; 2007	241	11	1	Li and Sun (2003), Zhang et al. (2005), Chen et al. (2006), Wang et al. (2008) and Wang (2009)
Weihai, Shandong province	1994–2000; 2007	1274	58	10	Cao and Shao (2001), Liu et al. (2002), Wang and Wang (2002), Jiang et al. (2008b) and Zhang and Yang (2008)
Yantai, Shandong province	2002	1	1	0	Zhang et al. (2002)
Qingdao, Shandong province	2001–2003; 2005–2006	93	3	0	Yang and Qian (2003), Chou and Bian (2005) and Li (2007)
Zhejiang province	1998–2004	32	2	0	Xu (2005)
Fujian province	2001; 2006	106	No data	0	Chen et al. (2003) and Wu et al. (2007)
Guangdong province	2004	35	No data	0	Lin et al. (2005)
Sanya, Hainan Island	1984–1993; 2001–2005	133	6	0	Li and Chen (1994) and Cui and Xu (2008)

decade and this underlines the increasingly urgent need to study the causes of jellyfish blooms. The species *N. nomurai*, *C. nozakii*, *A. aurita*, *Physalia physalis*, *Pelagia noctiluca* and *R. esculentum* were the most common jellyfish responsible for stinging cases.

The current information indicates that jellyfish blooms are becoming an annual event in the Bohai Sea, Yellow Sea and northern East China Sea (Table 1). However, it is not known whether these recent increases in jellyfish blooms will be sustained in future, and it is also difficult to attribute which if any of the large range of human induced environmental impacts is responsible for jellyfish blooms. In this study, we focus on three dominant scyphozoan species; *A. aurita*, *C. nozakii* and *N. nomurai*, which were responsible for most cases of jellyfish blooms in Chinese seas (Table 1). We discuss the distribution of blooms of each species along with the consequences and likely causes with the purpose of classifying their hazards and relating these to management policy.

2. Dominant bloom forming jellyfish species in Chinese seas

2.1. *A. aurita* (Linnaeus, 1758)

A. aurita is distributed worldwide in coastal waters and is associated with a wide range of water temperatures (0–36 °C) and salinities (3–36‰) (Arai, 1997; Martin, 1999). The cases of *A. aurita* blooms have been reported in many coastal areas, including the Baltic region, Japan, Korea, India and Australia (Mills, 2001). In Chinese seas, the aggregation and blooms of *A. aurita* were mainly observed in harbors and inshore areas in the temperate region including Yellow Sea and Bohai Sea (Fig. 1; Table 1).

Aggregations of *A. aurita* can clog the cooling water intakes at coastal power plants and block fishing nets. Observations from previous studies indicate that July and August are the most prevalent months for *A. aurita* blooms along the coast of northern China and the blooms mainly occurred in Hebei province (Qinhuangdao) and Shandong province (Yantai, Weihai and Qingdao) which are popular tourist coasts (Fig. 1; Table 1) and coastal aquaculture regions. For example, in July 2008, over 4000 tons of *A. aurita* were cleaned up from the clogged intake screens in coastal power plant of Qinhuangdao (Liu, 2008, Fig. 1; Table 1). In August 2008, 20–50 tons of *A. aurita* were cleaned up from the clogged intake screens in the coastal power plant of Weihai (Fig. 1; Table 1). From July 7 to July 8 in 2009, over 10 tons of *A. aurita* were cleaned up from the clogged intake screens in the coastal power plant of Qingdao (Lu, 2009, Figs. 1 and 2a; Table 1).

A. aurita was thought to be relative harmless to human in previous studies (Cleland and Southcott, 1965). However, Burnett et al. (1988) reported the significant stinging cases caused by *A. aurita* in the Gulf of Mexico. Toxinological studies conducted by Radwan et al. (2001) and Segura-Puertas et al. (2002) demonstrated

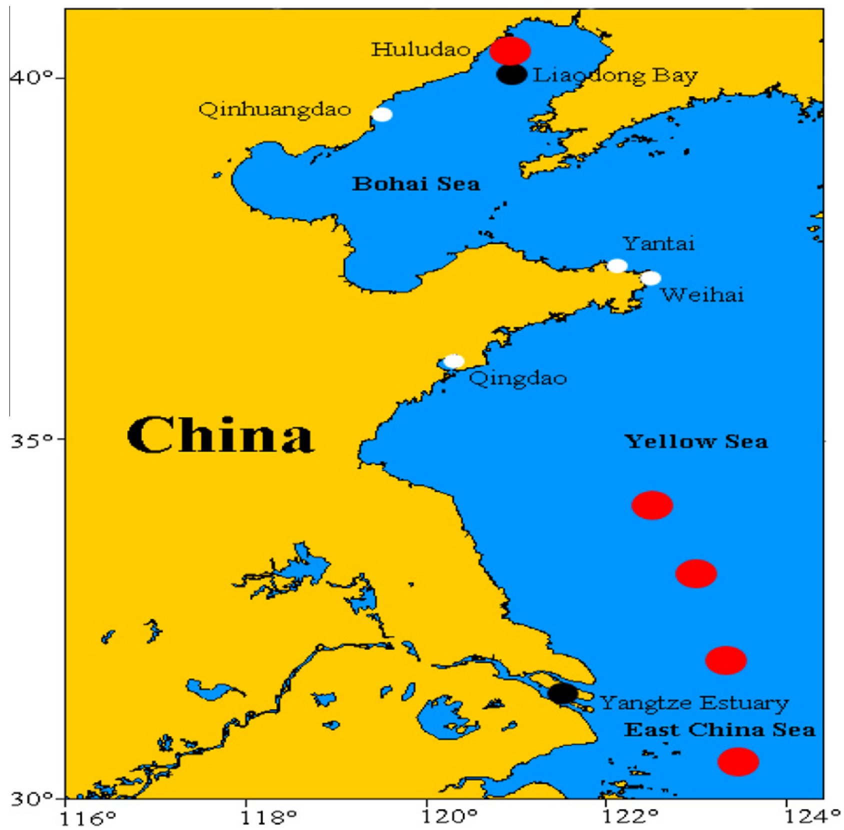

Fig. 1. Distribution of blooms of the three dominant jellyfish species in Chinese seas (white dot: *Aurelia aurita*; black dot: *Cyanea* sp.; red dot: *Nemopilema nomurai*. Data source from Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that *A. aurita* can be venomous to humans and elicit localized skin eruptions. In China, Cao and Shao (2001) also reported 136 patients stung by *A. aurita* in the coast of Shandong province, in which 18 patients showed severe clinical symptoms (Table 2).

There have been very few studies on the cause of *A. aurita* blooms in China. However, previous case studies in other countries indicated that coastal eutrophication could be an important contributor to the *A. aurita* blooms (Arai, 2001; Mills, 2001). The increased nutrients in coastal waters can significantly increase phytoplankton biomass which could support the food source of jellyfish (e.g., zooplankton). Moreover, the greater tolerance of polyps and medusae to low-oxygen waters gives them an advantage to live in eutrophicated waters compared with fish (Decker et al., 2004; Shoji et al., 2009a). In addition, increased substrate suitable for jellyfish larval settlement has resulted from aquaculture development in coastal waters and this was regarded as an important factor causing *A. aurita* blooms in Taiwan by Lo et al. (2008). Lo et al. suggested that aquaculture rafts enhanced jellyfish populations by providing substrates and shading for the larval settlement and polyp colony formation.

2.2. Cyanea

There are four species of jellyfish in the genus of *Cyanea* in Chinese waters including *C. nozakii*, *C. capillata*, *C. ferruginea* and *C. purpurea* (Gao et al., 2002; Fig. 2c). *C. nozakii* is distributed widely along the coast of China and their abundance has showed an obvious increase since the end of the 20th century and cases of blooms have been reported (Dong et al., 2006). Some studies showed that *C. nozakii* is a relative warm-temperature and high-salinity species that occurs in peak biomass when the sea surface temperature reaches between 23 and 26.8 °C (Zhou and Huang, 1956; Lu et al., 2003; Ding and Cheng, 2007).

Cyanea sp. can split and ruin fishing nets, prey on and kill juvenile of fish, crabs and mollusks and produce toxins that are poisonous to people and marine animals (Zhou and Huang, 1956; Peng and Zhang, 1999; Zhong et al., 2003). *C. nozakii* blooms were observed in the northern East China Sea, Yellow Sea and the Bohai Sea (Fig. 1; Table 1) causing significant impact on fishery production. As a result, Peng and Zhang (1999) found that fish were replaced by *C. nozakii* in the fishery catch in the major fishing grounds (Lvsi fishing ground, Dasha fishing ground and Yangtze Estuary fishing ground) in the East China Sea. For example, in 2003, the jellyfish production accounted for 70% of the total fishery catch and reached up to 1000–2000 kg per day in the Zhoushan fishing ground (Shengsi Island) (Chen et al., 2007). In the Yangtze Estuary, similar results were observed (Xian et al., 2005; Table 1), the proportion of *Cyanea* sp. reached 85.5% and 98.4% of the total fishery catch in November 2003 and May 2004, respectively. Moreover, in Liaodong Bay of the Bohai Sea, a *C. nozakii* bloom was regarded as the main cause for the approximate 80% decline of the edible jellyfish *R. esculentum* (Ge and He, 2004). For example, the production of *R. esculentum* was 37,700 tons in 1998 in Liaodong Bay but declined to 695 tons in 2004. However the numbers of *C. nozakii* increased to average value of 4000–6000 ind./km^2 near the sea of Jinzhou city in Liaodong Bay based on the survey made by Jinzhou City Oceanic and Fishery Administration in 2004 (Zhang et al., 2005). The cause of *Cyanea* blooms in the Chinese seas is still a puzzle, but overfishing, eutrophication and increased seawater temperature and salinity were regarded as potentially important factors (Ge and He, 2004; Xian et al., 2005). Moreover, *Cyanea* sp. has a broad diet, for example, *Cyanea* sp. has the ability to catch and digest relatively large prey such as *A. aurita* through some

Fig. 2. The consequences of blooms of the three dominant jellyfish species in Chinese seas (a: *A. aurita* clogging power plant cooling water intakes in Qingdao coast in July, 2009; b: *A. aurita* blooming in Yantai harbor in August, 2009; c: the hair jelly *Cyanea* sp., which can split and ruin fishing nets, prey on and kill juvenile of fish, crabs and mollusks and produce venoms that are poisonous to people and marine animals; d: clearing the beach of *N. nomurai* in Weihai international bathing beach to prevent stinging cases).

digestion process (Hansson, 1997). Therefore, the *A. aurita* blooms may potentially enhance the food source of *Cyanea* sp.

Contact with the tentacles of the genus *Cyanea* may produce a burning feeling that develops into a severe pain and a mix of toxins has been found in the species of this genus (e.g., *C. capillata* and *C. lamarckii*) (Tibballs, 2006; Helmholz et al., 2007). However, no death has been attributed to these species. In Chinese waters few studies have identified the species responsible for jellyfish stings based on the patient's description of jellyfish morphological characteristics or by knowledge of the dominant jellyfish found in the area at that time (Table 2). However, we infer that considerable patients were stung by *Cyanea* sp. because they were abundant and widely distributed in Chinese coastal areas (Gao et al., 2002).

2.3. *N. nomurai* (Kishinouye, 1922)

N. nomurai is one of the largest jellyfish in the world capable of growing to a bell diameter of 2 m and a weight of 200 kg (Omori and Kitamura, 2004; Fig. 2d). *N. nomurai* is mostly distributed in the east asian marginal seas including Bohai Sea, Yellow Sea, Northern East China Sea and the seas of Korea and Japan (Kawahara et al., 2006). The increase of *N. nomurai* can damage fishing nets, severely sting fishermen and damage fishery production (Cheng et al., 2004; Uye, 2008; Yoon et al., 2008). In the East Asian Margin Seas, blooms of the giant jellyfish *N. nomurai* have been regarded as an enormous threat to the fisheries stock through competition for planktonic food and predation on eggs or larvae of fish (Cheng et al., 2004; Uye, 2008). Massive blooms of the giant jellyfish *N. nomurai* were reported in the northern part of East China Sea and Yellow Sea in 2003 and Liaodong Bay in 2005 and 2007 (Fig. 1; Table 1) (Cheng et al., 2004; Ding and Cheng, 2007).

The annual fish catch in the northern part of East China Sea and Yellow Sea declined 64% while the annual catch of *N. nomurai* increased 250% from 2000 to 2003 (Cheng et al., 2004). Yan et al. (2004) analyzed the dynamics of macro-jellyfish resources and their relationship with fish catch based on surveys conducted in the northern East China Sea and southern Yellow Sea during 1990–2003. They found the biomass of *N. nomurai* and *Cyanea* sp. in recent years was much greater than in the early 1990s consistent with the decrease of fishery resource.

The giant jellyfish *N. nomurai* was also responsible for most severe or fatal cases of jellyfish stings in Chinese sea (Zhang et al., 1993; Xu et al., 2007; Jiang et al., 2008b). In total 13 fatal cases of jellyfish *N. nomurai* stings were reported in medical journals (Table 2). Kawahara et al. (2006) reported a patient exposed to *N. nomurai* tentacles induced only cutaneous symptoms rather than severe systemic disorders, but other studies found the venom extract of *N. nomurai* showed selective toxicity on cardiac tissue (Kim et al., 2006; Kang et al., 2009).

Previous studies indicated that the changes in water temperature and salinity caused by hydrodynamic conditions in the East China Sea can significantly impact the distribution and abundance of *N. nomurai* (Ding and Cheng, 2007). *N. nomurai* is a relatively low-temperature and high-salinity species (Gao et al., 2002; Ding and Cheng, 2007). In the East China Sea, the water temperature and salinity can be impacted significantly by the Yangtze Diluted Water (YD) forming a low salinity water mass, the East China Sea Warm Water Mass (EW) with high water temperature and salinity and the Yellow Sea Cold Water Mass (YC) with low water temperature and moderate salinity. During a survey in 2003–2005, Ding and Cheng (2007) found the abundance of *N. nomurai* showed high values in 2003 when strong YC occurred and low values in 2005 when strong YD occurred. However, the cause of the *N. nomurai* bloom is still a puzzle to scientists. Unfortunately, nothing is known about the appearance and location of the polyps or ephrae of *N. nomurai* in Chinese seas. Nor is their any knowledge about the ecology of the medusa and the polyp phases of the life cycle in Chinese seas.

3. Scyphozoan jellyfish biodiversity and distribution in Chinese seas

There are 35 species of scyphomedusae belonging to 20 genera in 16 families that have been recorded in Chinese seas, of these seven species belonging to Coronate, eight to Semaeostomeae and 20 to Rhizostomeae respectively (Hong and Lin, 2010; Table 3). Stauromedusae, once considered as an order in the Class Scyphozoa, was not included in the inventory because recent morphological and molecular studies suggested they should be considered as a Class Staurozoa (Marques and Collins, 2004). *Stomolophus meleagris* was also not included in the inventory because recent molecular analysis showed that *S. meleagris* and *N. nomurai* should be the same species (Zhang et al., 2009). There are four species of scyphomedusae occurred in the Bohai Sea, six species in the Yellow sea, 25 species in the East China Sea and 23 species in the South China Sea (Table 3). Among them, *C. nozqkii* and *R. esculentum* are commonplace along the entire shoreline of Chinese seas. *N. nomurai* and *A. aurita* occurred mostly in northern Chinese seas included Bohai Sea, Yellow Sea and East China Sea. Based on their geography and ecological characters, the scyphomedusae species in Chinese seas could be dived into five groups included inshore warm-temperature groups, inshore warm-water groups, widespread tropical groups, deep-water oceanic groups and widely distributed groups (Hong and Lin, 2010; Table 3).

Although only a few scyphozoan jellyfish species have been reported to form conspicuous blooms in Chinese seas, the other scyphozoan jellyfish species should not be neglected. Therefore, we compared the scyphomedusae biodiversity in Chinese Seas with reports of scyphomedusae species that bloomed in other seas (Table 3). Ten scyphozoan species were recorded to bloom in other seas. For example, The edible jellyfish *R. esculentum*, *Rhopilema hispidum*, *Lobonema smithi* and *Lobonemoides gracilis* have been fished commercially in southeast Asia and occurred locally blooms during a particular period in most years (Omori and Nakano, 2001; Hamner and Dawson, 2009). The coronate medusae *Periphylla periphylla* has maintained a very high density for more than a decade in certain Norwegian fjords (Sørnes et al., 2007). *P. noctiluca* formed periodic blooms in the Mediterranean and Adriatic seas that have attracted public notoriety through stinging swimmers (Purcell, 2005). The edible jellyfish blooms seemed to be not a big problem because they were fished commercially and are now overexploited; however, the other potential bloom-forming species might be troublesome if they bloomed in Chinese waters due to their negative effects on human enterprises.

Table 3
Biodiversity and distribution of scyphomedusae in Chinese seas and comparison of reports of blooms in Chinese seas with other seas.

Species	Geographical distribution of the Scyphomedusae in Chinese Seas[a]				Bloom or Not in Chinese Seas	Bloom or Not in other seas[b]
	Bohai Sea	Yellow Sea	East China Sea	South China Sea		
Coronatae						
Atolla wyvillei Haeckel			+	+	No data	No data
Atorella arcturi Bigelow				+	No data	No data
Atorella subglobosa Vanhoffen				+	No data	No data
Atorella vanhoeffeni Bigelow				+	No data	No data
Linuche draco Haeckel				+	No data	No data
Nausithoe punctata Kolliker			+	+	No data	Does not bloom
Periphylla periphylla Peron et Lesueur			+		No data	Very high density achieved only in fjords
Semaeostomeae						
Cyanea capillata Linnaeus		+			No data	Blooms
Cyanea ferruginea Eschscholtz		+	+		No data	No data
Cyanea nozqkii Kishinouye	+	+	+	+	Blooms	No data
Cyanea purpurea Kishinouye			+		No data	No data
Chrysaora helvola Brandt			+	+	No data	No data
Pelagia noctiluca Forskal			+	+	No data	Blooms
Sanderia malayensis Goette			+	+	No data	No data
Aurelia aurita Linnaeus	+	+	+		Blooms	Blooms
Rhizostomeae						
Cassiopea andromeda Forskal			+	+	No data	No data
Acromitus flagellatus Maas			+	+	No data	Blooms in harbors, shrimp ponds
Acromitus hardenbergi Stiasny				+	No data	No data
Acromitus rabanchatu Aunandale				+	No data	No data
Acromitus tankahkeei Light			+		No data	No data
Catostylus townsendi Maas			+		No data	Blooms
Cephea conifera Haeckel			+		No data	No data
Netrostoma setouchianum Kishinouye			+		No data	No data
Netrostoma coerulescnsens Maas			+		No data	No data
Lobonema smithi Mayer			+	+	No data	Blooms
Lobonemoides gracilis Light			+	+	No data	Blooms
Lychnorhiza arubae Stiasny				+	No data	No data
Lychnorhiza malayensis Stiasny				+	No data	No data
Mastigias papua Lesson			+	+	No data	Does not bloom
Mastigias ocellatus Modeer			+	+	No data	No data
Nemopilema nomurai Kishinouye	+	+	+		Blooms	Blooms
Rhopilema esculentum Kishinouye	+	+	+	+	Blooms now overexploited	No data
Rhopilema hispidum Vanhoffen			+	+	No data	Blooms
Rhopilema rhopalophorum Haeckel			+		No data	No data
Thysanostoma flagellatun Haeckel				+	No data	No data

[a] Cited from Hong and Lin (2010).
[b] Cited from Hamner and Dawson (2009).

4. The possible causes for increases in jellyfish in Chinese seas

4.1. Eutrophication

Eutrophication is considered to be one of important factors contributing to increased jellyfish abundance and blooms (Mills, 2001; Diaz and Rosenberg, 2008). The excessive nutrients led to a high biomass of phytoplankton which can support polyp and medusa stage jellyfish. Eutrophication in Chinese seas is a significant environmental problem characterized by high N:P ratios (Zhang et al., 1999). The pollution monitoring data collected for the each of Chinese seas during 2000–2008 by the State of Ocean Administration (SOA, 2009), is shown in Fig. 3. The water quality in the East China Sea showed the highest nutrient concentrations with 22–30% severely polluted area (IV Level) in contrast to the other sea area (Fig. 3). However, 4–21% of Yellow sea, 3–25% of Bohai Sea and 5–25% of South China Sea still presented the level IV eutrophication (Fig. 3). Consequently, red tides have become a significant annual ecological hazard in Chinese seas, particularly in the East China Sea where there is a very high frequency of red tides (SOA, 2009). The dinoflagellate species *Prorocentrum donghaiense* was responsible for the most red tide cases in the East China Sea (Xu et al., 2010). The increased abundance of dinoflagellates as well the hypoxic conditions caused by red tide bloom events could create conditions which favor the growth of jellyfish (Purcell et al., 2007).

4.2. Overfishing

The relationships between the gelatinous medusae and fish are complex due to varying interactions at different stages of their life cycle. For example, the medusae may predate on pelagic eggs and larvae of fish, but fish also predate on gelatinous species. Meanwhile, the medusae compete with some small planktivorous fish for the same zooplankton prey (Purcell and Arai, 2001; Richardson et al., 2009). Therefore, some studies suggested that overfishing might help facilitate the jellyfish outbreaks (Purcell et al., 2007; Lynam et al., 2005, 2006; Richardson et al., 2009). Changes in marine fishery catches in Chinese coastal regions over the last two decades are shown in Fig. 4. It has been estimated that the maximum sustainable yield (MSY) was 1.03×10^6 tons in Bohai and Yellow Sea fisheries, $2.79–4.00 \times 10^6$ tons in the East China Sea fisheries and $2.24–2.60 \times 10^6$ tons in South China Sea fisheries (Yang, 2000; Zheng, 2007). Comparing the annual marine catches (Fig. 4) with the estimated MSY, we found that the marine fishery resources have been intensively exploited in different parts of China with catches exceeding MSY in the Bohai Sea since 1998, in the Yellow Sea since 1992, in the East China Sea since 1995 and in the South

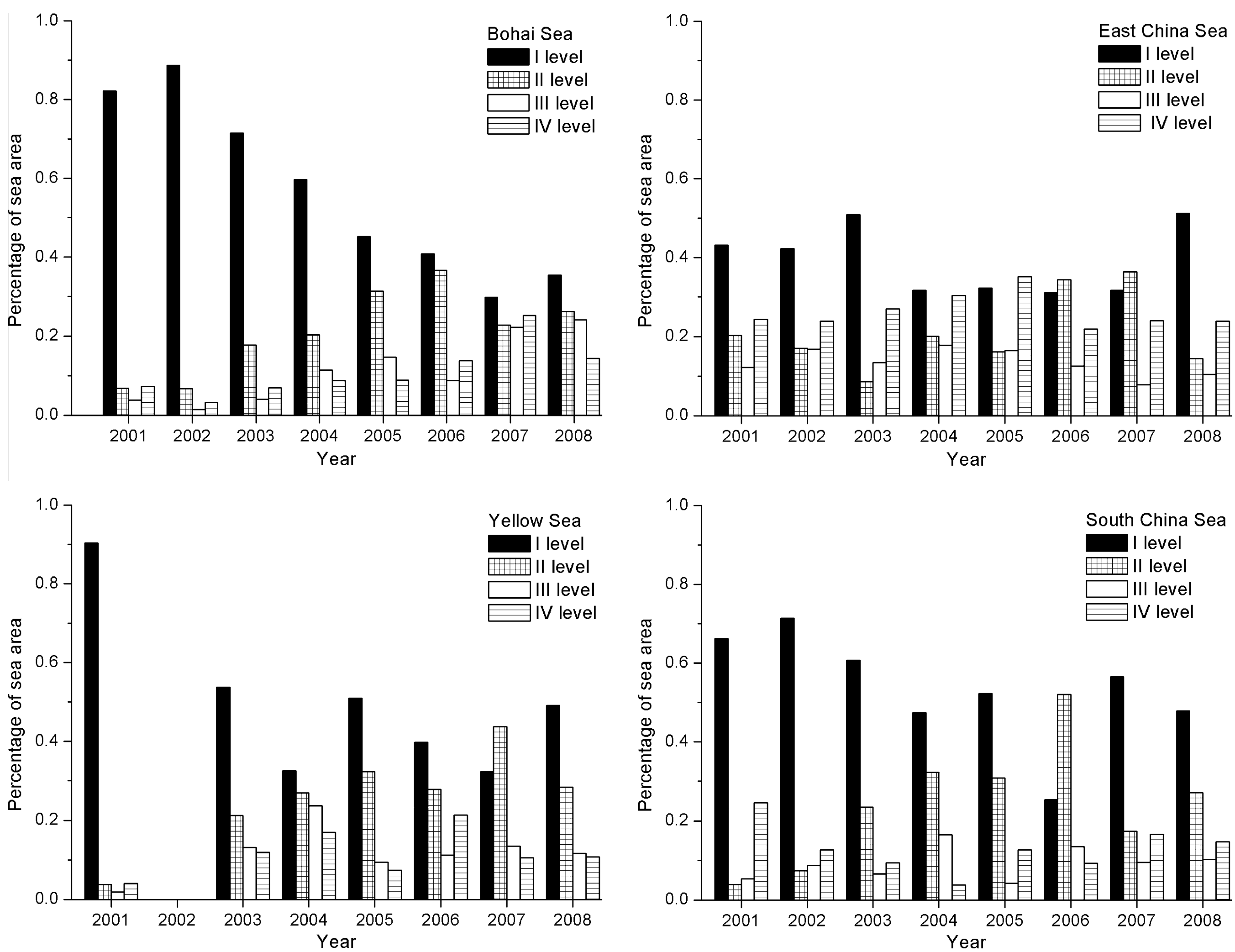

Fig. 3. The comparison of nutrient levels in Chinese seas during 2000–2008 (I level: DIN < 14 μM; PO4–P < 0.5 μM; II level: 14 μM < DIN < 21 μM; 0.5 μM < PO4–P < 1 μM; III level: 21 μM < DIN < 28 μM; 0.5 μM < PO4–P < 1 μM; IV level: 28 μM<DIN; 1 μM<PO4–P; data source: SOA, 2009).

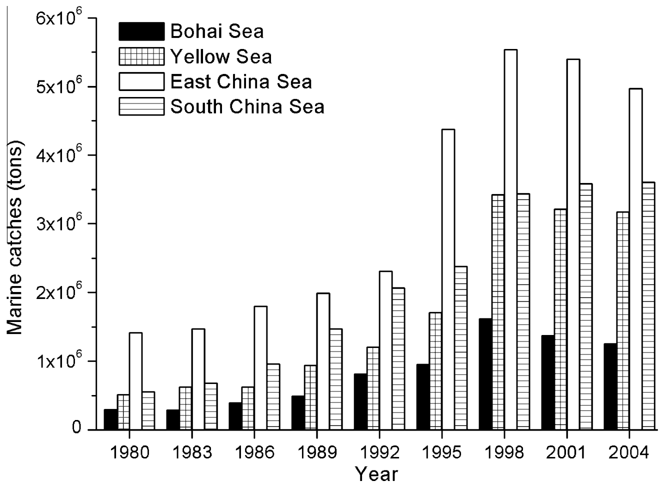

Fig. 4. The marine fisheries catches from Chinese seas during 1980–2004 (data source: SOA, 2008).

China Sea since 1998. However, there have been substantial decreases in the marine catches in the Bohai Sea, Yellow Sea and East China Sea since 1998 (Fig. 4). Only landings in the South China Sea have continued to increase since 1998 (Fig. 4). Moreover, the community structure of fishery resources have changed in Chinese Seas due to the overfishing. The dominant species within the fishery resources shifted from economically important high-value demersal species to the low-value small pelagic species in the Bohai Sea, Yellow Sea, East China Sea and South China Sea (Tang et al., 2003; Jin, 2004; Chen et al., 2008). Japanese anchovy *Engraulis japonicus* is a small planktivorous pelagic and the most abundant fish species in the Yellow Sea and Bohai Sea (Tang et al., 2003), but it has shown a sharp decline following the introduction of pair-trawler fishing in 1989 (Jin et al., 2001; Tang et al., 2003; Zhao et al., 2003; Fig. 5). During the 1980s and the beginning of the 1990s, the stock size of Japanese anchovy ranged from 2 to 4 million tons in the Yellow Sea. However the stock size undergone a rapid decline to only 0.18 million tons in 2002 (Zhao et al., 2003; Fig. 5). The advent of jellyfish outbreaks has followed the collapse of the Japanese anchovy stocks in the Yellow Sea and Bohai Sea since the mid-1990s. *E. japonicus* is a major zooplankton feeder in the Yellow Sea ecosystem which mainly prey on copepods and their eggs and larval (Meng, 2003; Zhao et al., 2003). Previous studies showed that the Japanese anchovy might compete for the same zooplankton prey with moon jellyfish *A. aurita* or the giant jellyfish *N. nomurai* (Uye, 2008; Shoji et al., 2009b). Therefore, the large jellyfish species population increases might have been at least in part due to a decline in competition for food resources from the Japanese anchovy. Ecological modeling to compare alternative hypotheses may be the best approach to understanding the role of jellyfish in large fished ecosystems and the factors leading to jellyfish blooming (Purcell, 2009; Pauly et al., 2009). For example, Jiang et al. (2008a) developed a mass balance (Ecopath) model to investigate the impact and control mechanism of large jellyfish blooms on trophic structure and energy flows in the East China Sea. Their results showed strong interactions between large jellyfish, Stromateoidae and small pelagic fish.

4.3. Habitat modification

The increased availability of hard substrate habitats caused by human activities may benefit jellyfish populations, for example, the novel habitats from aquaculture (e.g., live and dead shellfish, rafts, calcareous debris and farm materials) potentially provide more hard substrate for benthic polyp proliferation (Holst and Jarms, 2007; Purcell, 2007; Richardson, 2009; Lo et al., 2008). The intensity of aquaculture use along the Chinese coastline was estimated using the ratio of mariculture area per unit area of coastline (Fig. 6). The results showed the mariculture density in the Bohai Sea (220 ha/km) and the Yellow Sea (140 ha/km) was significantly enhanced (by 100–120% between 1998 and 2006) and much higher than that in the East China Sea and South China Sea (ca. 30 ha/km) (Fig. 6). Our results indicate that the *A. aurita* and perhaps also *C. nozakii* blooms appeared more in the Yellow Sea and the Bohai Sea than further south and that also they bloomed in inshore areas (Fig. 1 and Table 1). Thus, we suggest that the expansion of intensive use of coastal areas for aquaculture may have provided a large scale availability of new habitat for the proliferation of jellyfish and that further study on this aspect needs to be carried out as a matter of high priority.

4.4. Climate change

Global warming might also lead to increasing populations of jellyfish because it could affect the distribution, growth and ephyrae production of medusae (Richardson et al., 2009). Response of

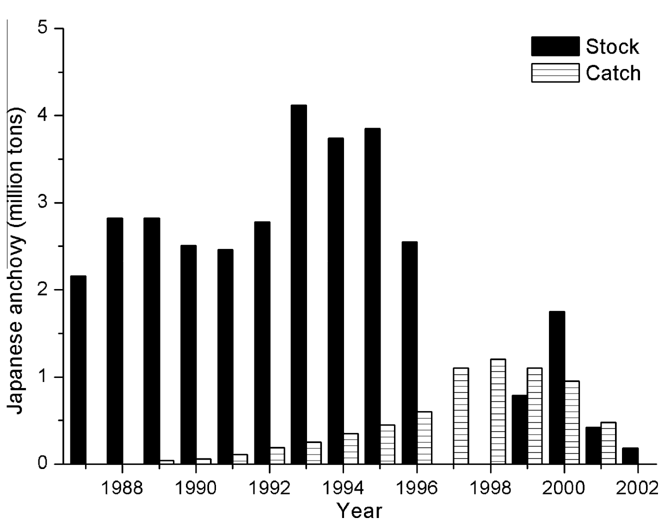

Fig. 5. The Japanese anchovy stock and annual landings of anchovy from the Yellow Sea during 1984–2002 (data source: Zhao et al., 2003).

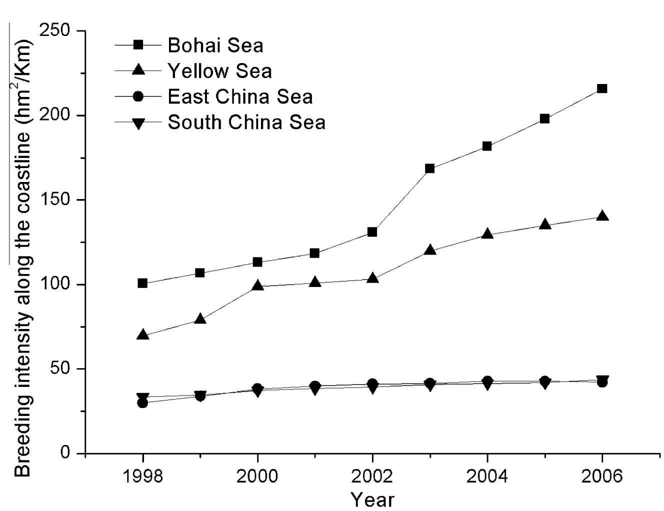

Fig. 6. Intensity of aquaculture use along the coastlines of China seas during 1998–2006 (data source: SOA, 2008).

scyphozoan medusae population in Chinese seas to the global warming trend can not be inferred due to the lack of long-term observation data on the jellyfish. However, the significant warming trend in Chinese seas, based on sea surface temperature (SST) records, is well documented (Fang et al., 2002; Lin et al., 2005; Ning et al., 2009; Tang et al., 2009). For example, the annual mean SST increased by 0.48 °C between 1965 and 1997 in the Bohai Sea, 1.7 °C between 1976 and 2004 in the Yellow Sea and 2.26 °C between 1976 and 2004 in the northern South China Sea (Fang et al., 2002; Lin et al., 2005; Ning et al., 2009). While in the northern East China Sea the average SST is about 0.46 °C and 0.53 °C higher respectively in summer and in winter during the period of 1977–1996 than that of 1957–1976 (Tang et al., 2009). Comparing the warming trend in different parts of Chinese seas, no significant difference has been shown that might be responsible for the spatial distribution of jellyfish blooms. Nevertheless, we could not exclude the likely links between climate change and jellyfish outbreaks given that 18 out of 24 temperate jellyfish species have been reported to increase in warm waters (Purcell et al., 2007).

4.5. Concluding remarks on possible causes

Our results suggest that almost all reported jellyfish blooms occurred in the northern Chinese seas included Bohai Sea, Yellow Sea and northern East China Sea, while they were infrequently found in the South China Sea. From the discussion above, no significant difference has been shown in the eutrophication status or the warming trend between northern Chinese seas and South China Sea. However, differences occurred in the mariculture density and the intensity of exploitation of small pelagic species between northern Chinese seas and South China Sea and this might have contributed to differences in the spatial distribution of jellyfish blooms.

5. Could jellyfish blooms lead to new jellyfish products?

Jellyfish blooms are likely to have been caused by multiple interacting factors. Reducing nutrient pollution, overfishing and man made juvenile habitat (coastal aquaculture infrastructure) would be positive steps to reducing the incidence of jellyfish blooms along with a host of other environmental maladies. However, the ecosystem response to reducing these impacts will be slow and each of these measures comes with a significant economic cost at least in the short to medium term and as such, seems unlikely to happen. One response to increasing jellyfish blooms could be developing new jellyfish products for food and medicine. Particularly in Asian markets, jellyfish is popular seafood with a long history and good market values. For example, the economic value of jellyfish production in 2005 was estimated at US$121 million (FAO, 2007). However, the fluctuation in abundance of the valuable edible species *R. esculentum* may affect the potential to sustain this. *R. esculentum* has high economic and nutritional value in Asian fishery markets (Hsieh et al., 2001), but its production in Yellow Sea and Bohai Sea has declined significantly over the last decade (Ge and He, 2004; Zhang et al., 2005). The production in 1998 was 40,000 tons but declined to only 695 tons in Liaodong Bay of Bohai Sea from 1998 to 2004 (Zhang et al., 2005). In 2005 and 2006, stock enhancement of *R. esculentum* was conducted in Liaodong Bay of Bohai Sea by rearing and releasing juvenile jellyfish into the sea as a strategy to saving the fishery for this valuable jellyfish species (Dong et al., 2008). The increased blooms of *C. nozakii* jellyfish were regarded as the main cause for the about 80% decline of edible jellyfish *R. esculentum* in Liaodong Bay (Ge and He, 2004; Dong et al., 2006).

So the obvious question is: are the blooming jellyfish species suitable to develop new seafood products? Fishermen in Dongshan Island successfully processed *C. nozakii* into jellyfish food in 1985. From 1986 to 1994, the jellyfish food made from *C. nozakii* was 10^4 tons per year in Zhangzhou city (Lu et al., 2003). However as a result of low quality and unpleasant taste, jellyfish products made from *C. nozakii* had approximately 100 fold lower values compared to the average price of *R. esculentum* (Zhong et al., 2003). The same predicament also occurred in *N. nomurai*, unfavorable taste made it cheap and unpopular (Hong and Zhang, 1982). In contrast to the sharp decline of the valuable species *R. esculentum*, the three dominant bloom forming jellyfish species are increasing gradually in the north East China Sea, Yellow Sea and Bohai Sea each year (Cheng et al., 2004; Xian et al., 2005), however, based on the above cases, we have to doubt whether jellyfish products based on these species is economically viable.

6. Conclusion

This study showed that the bloom forming jellyfish *A. aurita*, *C. nozakii* and *N. nomurai* are distributed in the temperate Chinese seas including the northern East China Sea, Yellow Sea and the Bohai Sea. In contrast to *N. nomurai*, the blooms of *A. aurita* and *C. nozakii* occurred mainly in inshore areas. Prominent environmental problems (e.g., eutrophication, overfishing, habitat modification and climate change) in the Chinese seas have created a suite of altered environmental conditions which favor the proliferation of jellyfish. This suggests that increased jellyfish blooms could be sustained in the future in the China as has been predicted in other parts of the world (Purcell et al., 2007; Richardson et al., 2009). Much more research is needed to be able to determine the key factors responsible for increasing jellyfish blooms by targeted studies on the biology, ecology and habitat use of individual species at each stage of their life cycle and by determining their responses to localized environmental conditions in different parts of the coastal seas of eastern and north-eastern China. It seems unlikely that these bloom forming jellyfish will be useful as seafood due to their low quality and unpleasant taste. Therefore, some management actions and bioremediation countermeasures (Guan et al., 2007) should be conducted to prevent large-scale alteration of pelagic ecosystems from dominance by fish to dominance by jellyfish in near future (Richardson et al., 2009; Uye, 2010).

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