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# Controls of *Aurelia coerulea* and *Nemopilema nomurai* (Cnidaria: Scyphozoa) blooms in the coastal sea of China: Strategies and measures

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Outbreaks of scyphozoan *Aurelia coerulea* and *Nemopilema nomurai* in the coastal sea of China are managed in recent years because they have severely jeopardized local socioeconomic development and ecological health. In this study, we propose specific strategies to control these blooms based on the different physio-ecological characteristics of their polyps, which can produce medusae by strobilation. High densities of *A. coerulea* polyps can survive chronically on the surfaces of some artificial constructions submerged in harbors or bays, China. Through buddings, they can resist the invasion of biofouling organisms and proliferate on the surfaces of some fouling organisms (e.g., ascidians, and bryozoans). However, *N. nomurai* polyps have not been recorded in natural environment. The *in situ* experiments found that polyps on settling plates fail to survive *via* podocysts due to severe biofouling invasion and post-strobilated degeneration in late spring and summer. As a result, the population size following is strongly dependent on the sexual recruitment of medusae during late summer and autumn. Therefore, we suggest that the reasonable governance strategy is to manage polyp populations together with biofouling organisms for *A. coerulea* blooms, however, with a focus on the medusa stage (particularly young medusae) to decrease the sexual reproduction in *N. nomurai* blooms. Accordingly, massive occurrences of *A. coerulea* in Qingdao Middle Port, China were alleviated by eliminating polyps and biofouling organisms on the undersurfaces of floating docks and then brushing the surfaces with modified alloprene paints. Some applicable control measures, including resource utilization of *N. nomurai* medusae and more severe and earlier summer fishing moratoriums, were used to possibly help restrain outbreaks of *N. nomurai* in Chinese coastal waters.

## KEYWORDS

jellyfish blooms, control, biofouling organisms, polyps, medusae

## Introduction

In recent decades, frequent jellyfish blooms around the globe have had detrimental ecological and socioeconomic nuisance such as stinging bathers, clogging the cooling water intakes of coastal power plants, disturbing normal fishery production, as well as threatening fishery resources (Purcell et al., 2007; Graham et al., 2014). Jellyfish blooms have been frequently claimed to result from anthropogenic disturbances to the coastal environment including climate change, eutrophication, overfishing, development of aquaculture, and habitat modification (Richardson et al., 2009; Purcell, 2012; Duarte et al., 2013; Bayha and Graham, 2014), although robust evidence supporting these assertions is lacking (Pitt et al., 2018). The Chinese coastal waters are also one of the jellyfish blooming hotspots, where the outbreaks of *Aurelia coerulea* von Lendenfeld, 1884 (Scorrano et al., 2017) and *Nemopilema nomurai* Kishinouye, 1922 (Omori and Kitamura, 2004) have

frequently appeared in the last two decades (Dong et al., 2010; Sun et al., 2015).

*A. coerulea* occurs mainly in neritic regions, such as harbors and bays, along the Chinese coast (Wang et al., 2012; Zheng et al., 2014; Dong et al., 2015). Frequent outbreaks of *A. coerulea* had damaged the normal operation of coastal infrastructures and the development of shallow sea aquaculture. In July 2014, a massive aggregation of *A. coerulea* clogged the cooling water intake of the Hong Yanhe nuclear power plant, Liaoning (Figure 1), causing the outage of two reactors (Li et al., 2017). The biomass of medusae salvaged around the cooling water intake was >10 tons in just 1 week (Li et al., 2017). The clogging cases of the cooling water intakes resulting from medusa aggregations also frequently occurred in several coal-fired power plants located in Qingdao and Qin Huangdao, China (Dong et al., 2010). For example, a serious clog appearing in the Qingdao power plant threatened the normal power supply of partial areas in July 2009 (Ren, 2009). Recently, outbreaks of *A.*

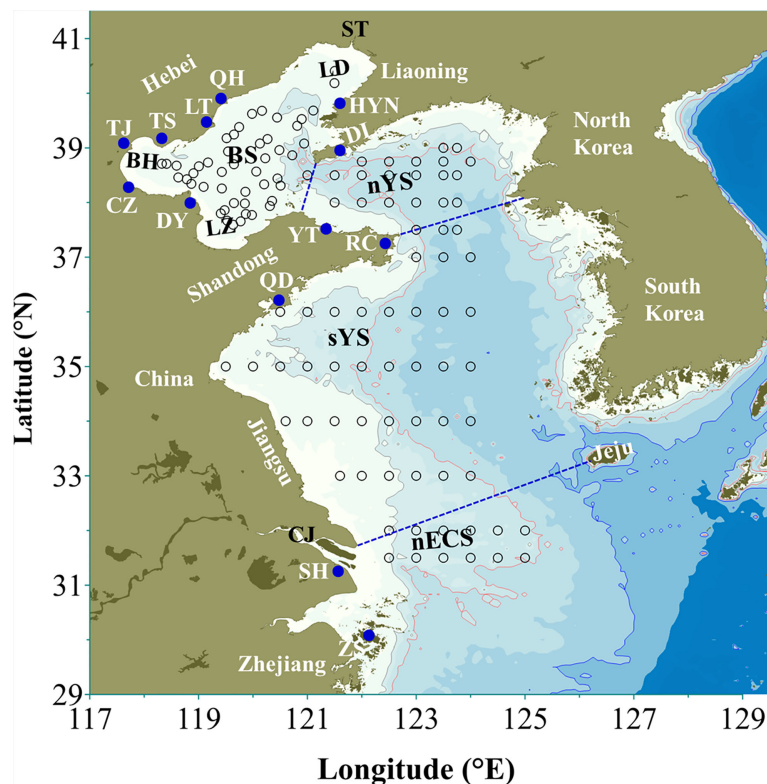


FIGURE 1

Map of Bohai, Yellow, and northern East China seas. BS: Bohai Sea, nYS: northern Yellow Sea, sYS: southern Yellow Sea, nECS: northern East China Sea, LD: Liaodong Bay, BH: Bohai Bay, LZ: Laizhou Bay, ST: Shuang Taizi River, CJ: Changjiang River, QH: Qin Huangdao, HYN: Hong Yanhe nuclear power plant, LT: Laoting, TS: Tangshan, DL: Dalian, TJ: Tianjin, CZ: Cangzhou, DY: Dongying, YT: Yantai, RC: Rongcheng, QD: Qingdao, SH: Shanghai, ZS: Zhoushan. The blue dots represented the locations of some coastal cities in China mentioned in the study. The black circles denoted the investigation stations of large jellyfish in Bohai, Yellow and northern East China seas in recent years cited from Zhang et al., 2012; Sun et al., 2015 and Wang et al., 2020b.

*coerulea* have also occurred in many artificial sea cucumber culture ponds along the Bohai and Yellow seas (e.g., in Laoting, Dongying, and Rongcheng, Figure 1), which have been regarded as the cause of sea cucumber vomiting because ephyrae could sting them (Dong Z. et al., 2018; Dong, 2019). In addition, *A. coerulea* blooms might also affect the community structure of zooplankton. In the northern Jiaozhou Bay, *A. coerulea* medusae frequently appeared in great numbers in June and July (Wan and Zhang, 2012) when the abundance of total zooplankton (except *Noctiluca scintillans*), in particular, copepods significantly decreased in 2009, a year with a large bloom of *A. coerulea*, in comparison with 2008 and 2010, which were non-blooming years (Wang et al., 2020a).

*N. nomurai* is considered as a long-distance transport species (Takao and Uye, 2018), distributed in East Asian marginal seas (Uye, 2011; Yoon et al., 2014; Sun et al., 2015; Dong J. et al., 2018; Kitajima et al., 2020). Its blooms (medusa abundance  $\geq 1$  ind·100m<sup>-2</sup>) occurred in 5 out of 10 years from 2000 to 2009 in the southern Yellow Sea (sYS) and northern East China Sea (nECS), but have been relatively modest from 2010 to 2019 (Sun et al., 2015; Zhao et al., 2016; Sun and Zhang, 2017). The bloom only appeared in 2012, and no blooms (medusa abundance  $< 1$  ind·100m<sup>-2</sup>) occurred in the other years. However, the published total hospital-based records of *N. nomurai* stings have increased more than threefold since 2012 in Qingdao, Weihai, and Qin Huangdao (>7331 cases) in comparison with that before 2007 (about 1950 cases) (Dong et al., 2010; Niu and Wang, 2014; Wen et al., 2014; Huo et al., 2017). In Liaodong Bay, Bohai Sea, *N. nomurai* also seriously threatened the Hong Yanhe nuclear power plant, with the maximal catches of medusae near its cooling water intakes reaching 986–1160 kg·h<sup>-1</sup> per net in August 2015 (Zhang et al., 2019). Similar to reports from Japanese and Korean waters (Kawahara et al., 2006; Yoon et al., 2008; Uye, 2011), the outbreaks of *N. nomurai* have also negatively affected fishery production in the coastal sea of China by clogging and destroying nets, decreasing fish catches, increasing the amount of labor required to select fish, and stinging fishermen (Cheng et al., 2004; Zheng et al., 2014). In addition, frequent *N. nomurai* blooms might influence phytoplankton and micro-zooplankton communities as well as fishery stocks. For example, in June 2012 (a blooming year with medusa abundance  $\geq 1$  ind·100m<sup>-2</sup>), in the southern sYS, the size compositions of ciliates, the dominant group of micro-zooplankton, tended to be smaller at the mature stage (i.e., the period that *N. nomurai* biomass increased to more than 10 t·km<sup>-2</sup>) than at the developing stage (i.e., the period that *N. nomurai* biomass was less than 10 t·km<sup>-2</sup>) of *N. nomurai* blooms, while the phytoplankton compositions shifted to be fewer diatoms and cryptophytes but more dinoflagellates (Xiao et al., 2019). In *N. nomurai*-dense regions of the nECS, the number of fish species and catch per unit effort (CPUE) declined in summer 2003 (a blooming year with medusa abundance  $\geq 1$

ind·100m<sup>-2</sup>) compared to 1999–2001 (non-blooming years with medusa abundance  $< 1$  ind·100m<sup>-2</sup>) (Ding and Cheng, 2005).

In order to reduce economic losses and harm to humans, jellyfish blooms have been actively addressed in many areas in recent years. The early warning measures had been widely reported to indirectly relieve the adverse effects of jellyfish blooms. For example, in the Mediterranean coast, the Medjellyrisk Project created a western and central Mediterranean Basin forecasting platform to foresee the probability of a jellyfish bloom arising based on stranded and near-to-coast jellyfish presence data from Spain, Italy, Tunisia, and Malta in combination with Species Distribution Model (Canepa et al., 2016). It was accessible through a free downloadable mobile app (Medjelly) and the project's webpage, which could help warn beach users of the risk of stings. On the Great Barrier Reef, Australia, blooms of Irukandji jellyfish were forecast based on wind conditions, which largely coincide with relaxation of the prevailing southeasterly trade winds (Gershwin et al., 2014). To alleviate the damages of *N. nomurai* blooms to Japanese fishery production, Uye (2014) developed a method of forecasting the annual blooming intensity of *N. nomurai* in Japan based on on-deck sighting surveys from ferries en route from the sYS and nECS to the Sea of Japan in July. This blooming forecast effectively helps fishermen prepare for possible jellyfish encounters well in advance (Uye, 2014).

Comparatively speaking, jellyfish blooms have also been directly controlled by some affected enterprises. For instance, to address the threat of large jellyfish aggregations (e.g., *Chrysaora hysoscella*) on salmon aquaculture, the bubble curtains were made by releasing compressed air from a perforated tube at depth, forming a plume of bubbles that entrain the water to create a vertical current as the jellyfish barriers in Ireland (Haberlin et al., 2021). To prevent clogging caused by jellyfish aggregations in cooling water intakes, some local power plants in Japan have built structures such as arresting barriers, channel networks, jellyfish conveyers, and crushers to intercept and channel the influx of massive medusae and facilitate the removal of the entrapped medusae (Kazunari, 2014). For the sake of reducing economic losses from *A. coerulea* blooms in Korean coastal areas, waterjets and scrapers have been used to remove *A. coerulea* polyps since 2012. This approach decreased the appearance of medusae in Lake Shihwa for 3 consecutive years (Yoon et al., 2018). To reduce the bycatches of *N. nomurai* in the Japanese fishery production, various jellyfish excluders such as a bottom trawl fishing gear with an intercepting net and a vent in its main net have been applied (Matsushita et al., 2005; Okino et al., 2009). In particular, during the months of the densest *N. nomurai* aggregations (October–December) in 2009, some modified set nets, consisting of leading nets with an enlarged mesh size, bypass nets, and a partition net, were also introduced to effectively remove entrapped *N. nomurai* medusae (usually less than a hundred medusae were trapped per

net per day) in fish catches (Uye, 2014). On the whole, various control methods have been used to reduce the impacts of jellyfish blooms. But most of them adopted a strategy of disposing of easily-visible medusae, and few were involved in the other stages of jellyfish life cycle with interspecific specificity. In the coastal sea of China, the management of *A. coerulea* and *N. nomurai* blooms has also been carried out accompanied by recent studies on the blooming mechanisms to improve the ecological environment inshore and alleviate the economic losses resulting from such blooms. In this review, we suggest specific control strategies based on the different physiological characteristics of their polyps in the life cycles and discuss some current control measures in China.

## Specific control strategies

The controls of jellyfish blooms first need to take into account the jellyfish-centered mechanisms of the outbreaks. The life cycle of scyphozoans is characterized by generational alternation, involving a sexually reproducing medusa and an asexually reproducing benthic polyp (Lucas et al., 2012). The polyp is the key stage that could produce medusae through strobilation to realize the transformation from benthic to pelagic living (Lucas et al., 2012). *A. coerulea* polyps are found most often on the surfaces of some artificial substrates (e.g., floating docks, concrete platforms) submerged in the harbors and bays along the Chinese coasts (Dong Z. et al., 2018; Feng et al., 2021), as is the case in other regions (Miyake et al., 2002; Ishii and Katsukoshi, 2010; Makabe et al., 2014; Yoon et al., 2018). However, *N. nomurai* polyps have not yet been recorded, although the areas around estuaries, such as the Changjiang estuary and innermost estuaries of northern Liaodong Bay, are considered to be the major habitats of *N. nomurai* polyps according to the recorded appearances of early pelagic *N. nomurai* larvae (i.e., ephyrae, metephyrae and juvenile medusae; Toyokawa et al., 2012; Yoon et al., 2014; Sun et al., 2015; Dong J. et al., 2018).

On the other hand, *A. coerulea* and *N. nomurai* polyps show different asexual reproduction modes and ecophysiological responses to environmental changes including temperature, food supply, and biofouling invasion in the natural environment (Han and Uye, 2010; Wang et al., 2015; Feng et al., 2015a; Feng et al., 2018a), despite both generally having to grow and settle on the surfaces of hard substrates (Kawahara et al., 2006; Lucas et al., 2012). *A. coerulea* polyps have multiple asexual modes for propagation (Schiariti et al., 2015). They are able to produce podocysts under starvation conditions (Thein et al., 2012; Wang et al., 2015), and multiply rapidly via various buddings at warm temperatures ( $\geq 18^{\circ}\text{C}$ ) and abundant food supply (Han and Uye, 2010). However, polyps of *N. nomurai* only proliferate asexually through podocysts (Kawahara et al.,

2006; Feng et al., 2015a; Feng et al., 2015b). Under identical temperature and food conditions, polyps with multiple asexual modes could proliferate to higher densities compared with mono-mode polyps (Schiariti et al., 2014). Moreover, through buddings, *A. coerulea* polyps on the substrates can expand to spaces not occupied by neighboring biofouling organisms (Figure 2A) and even proliferate on the surfaces of some fouling organisms against their invasion (Feng et al., 2017; Feng et al., 2018a). For example, on the undersurface of a floating dock “Haiou” in Jiaozhou Bay, China, *A. coerulea* polyps were found to grow on the surfaces of many ascidians, bryozoans, and mussels (e.g., *Styela clava*, *Watersipora subtorquata*, and *Mytilus galloprovincialis*) besides on the areas without macro-fouling organisms (Figures 2B–E) like some other *Aurelia* spp. (Willcox et al., 2008; Di Camillo et al., 2010; Rekestad et al., 2021). However, *in situ* *N. nomurai* polyps on the plastic plates cultivated in Jiaozhou Bay were gradually covered by some neighboring fouling organisms (Figure 2F, Feng et al., 2017; Feng et al., 2018a). Ultimately, they could not survive in the combination of severe biofouling invasion and post-strobilated degeneration in late spring and summer (Feng et al., 2017; Feng et al., 2018a; Feng et al., 2020). Thus, the polyp population following strongly depended on the sexual recruitment of medusae in late summer and autumn (Feng et al., 2018a; Feng et al., 2018b). These different ecophysiological characteristics indicate that the focus of *A. coerulea* bloom control should be on polyps and biofouling organisms, whereas the focus of *N. nomurai* bloom control should be on medusae (particularly young medusae) to decrease the sexual reproduction rate.

## Control case of *A. coerulea* blooms in Qingdao middle port harbor

The coastal industries, such as nuclear power plants, in China, have generally addressed local population explosions of *A. coerulea* by establishing a series of barrier nets and capturing medusae. Recently, the control of *A. coerulea* blooms by managing *A. coerulea* polyps and biofouling organisms was successfully conducted in Qingdao Middle Port harbor, China (Figures 3A, B; Feng et al., 2021), where *A. coerulea* frequently appeared in large numbers from June to July in recent decade (Wang et al., 2012). In 2014, dense *A. coerulea* polyp colonies were found inhabiting the undersides of some docks at a depth of about 1.8m in Qingdao Middle Port (Feng et al., 2021), indicating that these docks are one of the sources of medusa blooms there.

On the undersurfaces of these floating docks, *A. coerulea* polyps settled on some areas without macro-fouling organisms as well as on the body surfaces of some fouling organisms (e.g., ascidians, bryozoans, and mussels) (Feng et al., 2021). Two docks (I, II) were the main polyp hotspots, where the average

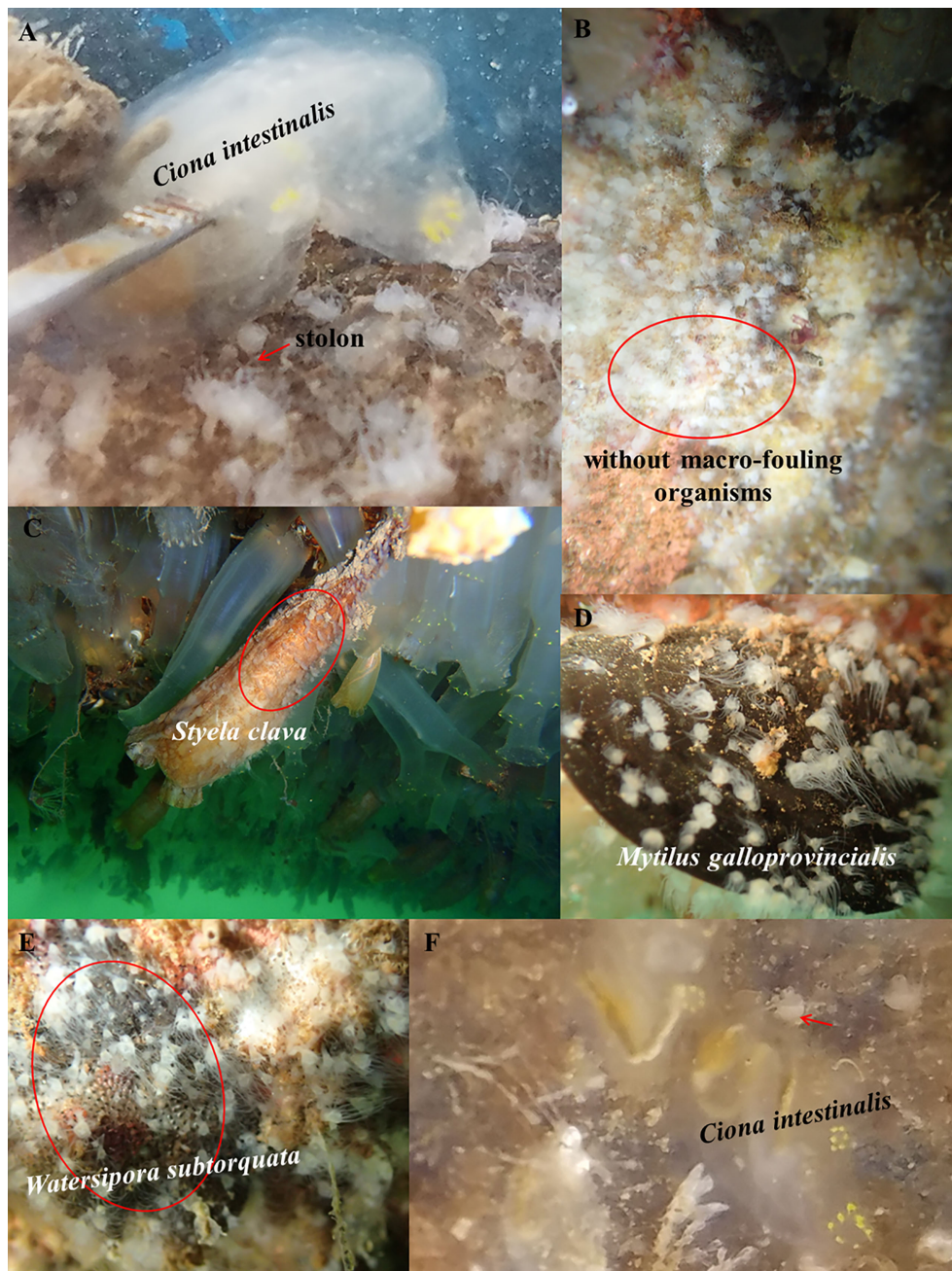


FIGURE 2

*Aurelia coerulea* and *Nemopilema nomurai* polyps in the field. (A) An *A. coerulea* polyp on a plate hanging in Jiaozhou Bay, China extending to the unoccupied area by an ascidian *Ciona intestinalis* via a stolon (red arrow) for proliferation. (B) *A. coerulea* polyps settled on some areas without macro-fouling organisms (red circles) on the undersurface of the dock "Haiou" in Jiaozhou Bay, China. (C-E) Many *A. coerulea* polyps growing on the surfaces of an ascidian *Styela clava* (C), a mussel *Mytilus galloprovincialis* (D), and a bryozoan *Watersipora subtorquata* colony (E) on the undersurface of the dock "Haiou" in Jiaozhou Bay, China. (F) *A. coerulea* polyp (red arrow) on a plate hanging in Jiaozhou Bay, China being invaded by an ascidian *C. intestinalis*. These pictures were photographed with an Olympus waterproof camera.

density of polyps reached  $2634.63 \pm 490.20 \text{ ind}\cdot\text{m}^{-2}$  in June 2014 (Feng et al., 2021; Figure 3B). Thus, both docks were selected for the control of *A. coerulea* blooms in the harbor. Docks I and II were transferred to a nearby shipyard in early April 2015 and

2016, respectively, to avoid the release of massive *A. coerulea* ephyrae. *A. coerulea* polyps and biofouling organisms on the undersurfaces of both docks were scraped away completely. Then the modified paint manufactured by the Yantai federal

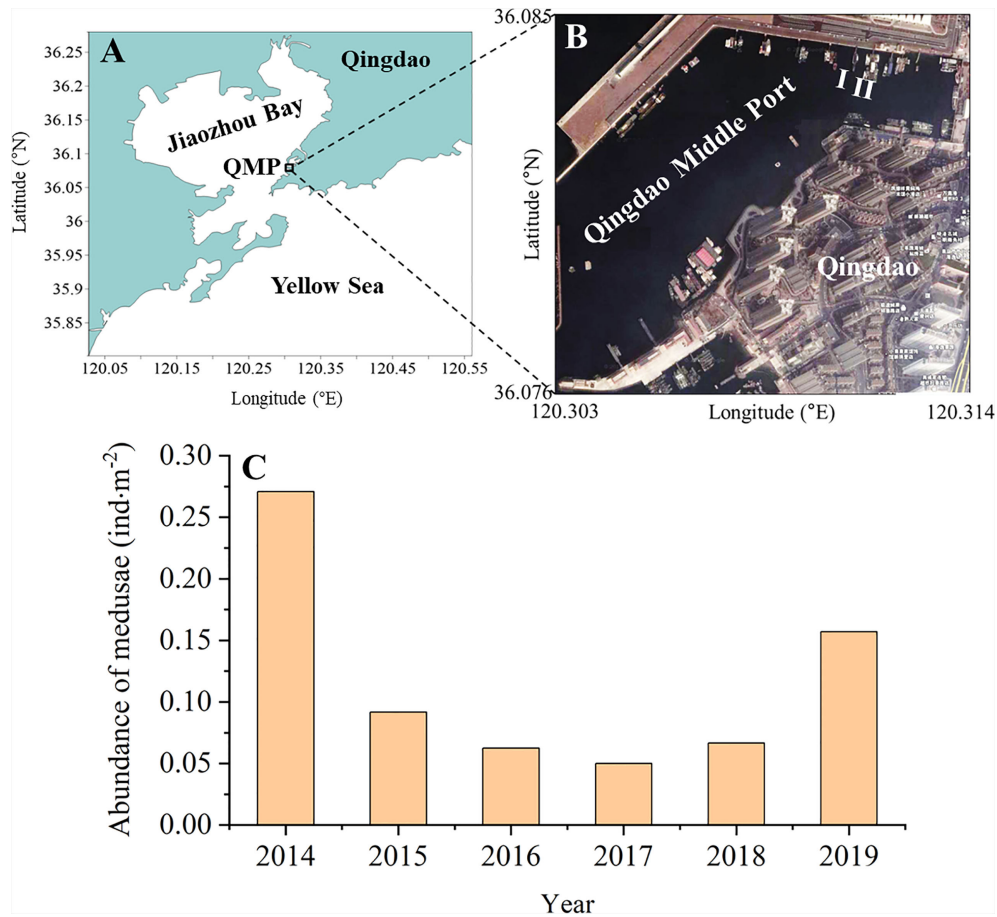


FIGURE 3

Control of *Aurelia coerulea* blooms in the Qingdao Middle Port, China (A, B) and changes in the abundance of medusae near the seawater surface in June from 2014 to 2019 (C). Because trawling was banned in the Qingdao Middle Port, the abundance of *A. coerulea* medusae was monitored through on-deck sighting surveys on the floating docks in the middle of June (the blooming period of medusae) as per the methods described in previous reports (Uye, 2014; Yoon et al., 2014). The number of medusae on both sides of docks was roughly counted by the naked eye from 9:00 to 15:00 in a day. The sighting width of the sea surface was estimated as 4m by a trigonometric function. The abundance of *A. coerulea* medusae was calculated from the total number of medusae observed on docks divided by the total sighting area of the sea surface. QMP: Qingdao Middle Port.

chemical company, China, consisting of alloprene, plasticizer, cuprous oxide, and pigment, was brushed on the undersurface of the dock I in three layers at a thickness of 50–75  $\mu\text{m}$  (Feng et al., 2021). Dock II was left untreated as a control group. After being sun-dried, both docks were then returned to their original positions in July 2015 and 2016, respectively (Feng et al., 2021).

From June 2015 to June 2018, the abundance of *A. coerulea* medusae observed near the seawater surface in the Qingdao Middle Port declined dramatically by 66–81% compared with 2014, reaching its lowest value in 2017 (Feng et al., 2021; Figure 3C). In June 2019, the medusa abundance was only 42% less than that in 2014. Only a few biofilms developed on the undersurface of Dock I 1 month later (Figure 4A); after 2 years, a few macro-fouling organisms were found. They mainly

included barnacles, mussels, and ascidians with densities of  $238.10 \pm 64.70 \text{ ind}\cdot\text{m}^{-2}$ ,  $92.00 \pm 75.94 \text{ ind}\cdot\text{m}^{-2}$ , and  $33.55 \pm 27.61 \text{ ind}\cdot\text{m}^{-2}$ , respectively (Feng et al., 2021; Figure 4B). *A. coerulea* polyps occurred at a very low density of  $1.08 \pm 3.02 \text{ ind}\cdot\text{m}^{-2}$  in the third year post-treatment, when ascidians and mussels were the dominating biofouling organisms (densities of  $155.84 \pm 87.35 \text{ ind}\cdot\text{m}^{-2}$  and  $309.52 \pm 120.85 \text{ ind}\cdot\text{m}^{-2}$ , respectively; Figure 4C). In contrast, many biofouling organisms were found on the undersurface of Dock II 1 year later, with ascidians, oysters, and mussels being the main taxa (densities of  $179.30 \pm 127.07 \text{ ind}\cdot\text{m}^{-2}$ ,  $106.06 \pm 83.33 \text{ ind}\cdot\text{m}^{-2}$ , and  $55.56 \pm 50.44 \text{ ind}\cdot\text{m}^{-2}$ , respectively; Figure 4D). After 2 years, numerous *A. coerulea* polyps were discovered in September, the density of which had exceeded the initial level ( $3512.31 \pm 2229.78 \text{ ind}\cdot\text{m}^{-2}$ ) (Feng et al., 2021). The dominating biofouling organisms were ascidians,

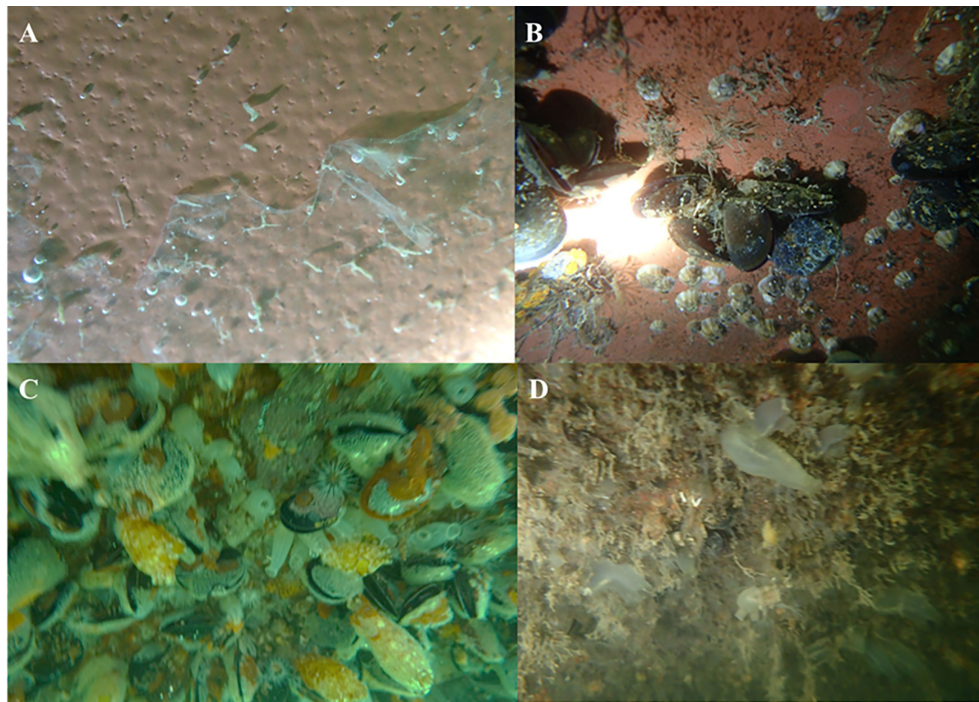


FIGURE 4

Resettlement photographs of the main fouling organisms including ascidians, mussels, barnacles, etc. on the undersurfaces of Docks I and II over 3 years following their initial removal. (A) Some thin biofilms appeared on the undersurface of Dock I 1 month later. (B) A few macro-fouling organisms, such as *Mytilus galloprovincialis* and *Balanus* spp., appeared on the undersurface of Dock I after 2 years. (C) A large number of macro-fouling organisms including *M. galloprovincialis*, *Styela* spp., etc. settled on the undersurface of Dock I in the third year. (D) Many macro-fouling organisms (e.g., *Ciona intestinalis*) resettled on the undersurface of Dock II 1 year later. To monitor the resettlement of *A. coerulea* polyps and other macro-fouling organisms on the undersurfaces of Docks I and II, 10–15 quadrats, each with an area of 600 cm<sup>2</sup>, on the undersurface of the dock were chosen randomly and photographed via scuba diving using an Olympus waterproof camera in September. The number of *A. coerulea* polyps and other macro-fouling organisms in each quadrat image was counted. Their density on the undersurface of the dock was calculated from the average of the corresponding number divided by the area of each quadrat.

barnacles, and mussels, with densities of  $284.10 \pm 170.09 \text{ ind}\cdot\text{m}^{-2}$ ,  $252.53 \pm 257.32 \text{ ind}\cdot\text{m}^{-2}$ , and  $150.25 \pm 201.47 \text{ ind}\cdot\text{m}^{-2}$ , respectively. Thus, applying modified alloprene paint to the undersurface of Dock I effectively inhibited the resettlement of *A. coerulea* polyps on there in comparison with Dock II during 3 years. It follows that the long-term control of *A. coerulea* blooms in the harbor, where polyps massively inhabit the surfaces of movable floating docks, may be accomplished by regular maintenance of these structures using modified alloprene paint.

In addition, *A. coerulea* polyps are also capable of settling in large numbers on the permanent infrastructures submerged in the sea, such as bridge piers and fixed platforms (Ishii and Katsukoshi, 2010; Yoon et al., 2018). For these immovable constructions, physical methods of eliminating polyps, such as waterjets or mechanical scraping, could be adopted (Yoon et al., 2018; Feng et al., 2021), although their inhibition on the resettlement of *A. coerulea* polyps on substrate surfaces may be less effective than antifouling paint (Feng et al., 2021). Compared to capturing medusae and establishing a series of arresting nets to solve *A. coerulea* blooms, methods of

eliminating polyps have a lower cost (Yoon et al., 2018), and have the potential to prevent the formation of *A. coerulea* blooms at their source and decrease the risks of outbreaks in affected areas ahead of time.

## Applicable measures to suppress *N. nomurai* blooms

### Resource utilization of *N. nomurai* medusae

In China, the edible species *Rhopilema esculentum* is popular seafood with a long history and good market value, which has been an important Chinese jellyfish fishery (Dong et al., 2009). In recent decades, as the production of *R. esculentum* sharply declined (Dong et al., 2014; Li et al., 2014) and *N. nomurai* frequently bloomed in the coastal sea of China (Sun and Zhang, 2017; Dong J. et al., 2018), the Chinese fishermen have started to

massively capture *N. nomurai* medusae in the nearshore waters of many coastal cities, where jellyfish manufacturing districts have been established to process them into new edible jellyfish products alternative to *R. esculentum* for improving the local fishery economy. For example, in Huangshan village, Qingdao, massive *N. nomurai* medusae were captured nearby by a kind of specialized jellyfish net with a mesh size of about 18cm from July to October. Then they were made into various jellyfish products (e.g., salted jellyfish, instant jellyfish, and other dishes). Thus, the market share of *N. nomurai* has exceeded 95% of all jellyfish production in some cities, such as Qingdao and Tangshan (Zheng et al., 2014). According to statistics, the annual catch of *N. nomurai* has increased continuously in the Bohai and Yellow seas from 2009 to 2013 (Figure 5A; Li et al., 2014). In particular, in Tangshan, Hebei Province, China (Figure 1), since 2009, *N. nomurai* catches have been more than twice annually compared with those in 2008 (Figure 5B, Zheng et al., 2014). This resource utilization of *N. nomurai* medusae can conduce to decreasing the number of medusae and their sexual reproduction in the adjacent seas, which may be one of the potential reasons for the decline in *N. nomurai* blooms in the 2010s as compared with that in the 2000s. Thus, the long-term persistence of this measure might reduce the possibility of *N. nomurai* blooms in the coastal seas of China.

## More severe and earlier summer fishing moratorium

In the marine ecosystem, jellyfish and fish were generally adversaries (Uye, 2011). *N. nomurai* could compete with fish for copepods (Uye, 2008). They also ingest fish eggs and larvae from species such as *Paralichthys olivaceus* and *Sebastes schlegeli* (Liu et al., 2016). In addition, some fish (e.g., *Thamnaconus septentrionalis* and *Pampus argenteus*) also prey on *N. nomurai* (Ding and Cheng, 2005; Tong et al., 2013; Liu et al., 2014). Thus, changes in the governance of fishery resources also affect the abundance of *N. nomurai* in the Bohai Sea, Yellow Sea, and nECS. To maintain fish stocks and enhance fishery production, a summer fishing moratorium came into effect in 1995. Its duration was gradually prolonged in different regions over the last two decades. For example, in the 27–35°N areas of Chinese coastal seas, which include the major birthplaces and high-density areas (31.5–35°N) of *N. nomurai* in the sYS and nECS (Zhang et al., 2012; Sun et al., 2015; Zuo et al., 2016), the summer fish moratorium extended from July 1 to August 31 in 1995, then from June 16 to September 15 in 1998, and from June 1 to September 16 in 2009 (Chen and Bao, 2010). In Bohai Sea, the summer fish moratorium also changed from June 16 to September 1 in 2004 into from June 1 to September 1 in 2009 (Hu, 2020). Since 2017, the longest summer fishing moratorium was imposed with tougher enforcement from May 1 to September 16 in the 26.5–35°N areas and from May 1 to September 1 in the north of 35°N,

respectively (Yan et al., 2019a; Hu, 2020). The advancement of the moratorium onset time to May 1 might play an important role in regulating both the biomass of *N. nomurai* and the fishery resource. When the fishing ban is implemented later than early June, the overfishing of adult and juvenile fish (e.g., *P. argenteus*, *Larimichthys polyactis*, and *Trichiurus lepturus*; Chen and Bao, 2010; Wang, 2012) might create more suitable conditions in spring (e.g., abundant zooplankton bait and reduced fish predation rate) for the development of early pelagic *N. nomurai* larvae, which are weakly competitive compared with medusae. Therefore, these larvae can grow well into medusae within 1 month (Kawahara et al., 2006; Sun et al., 2015). When the fishing ban began to be implemented more rigorously and forcefully in early May 2017, these conditions favorable to early pelagic *N. nomurai* larvae may reduce as the annual fish catches decreased (Figure 6) and fishery resources were forecast to improve during the summer fishing moratorium (Yan et al., 2019a; Yan et al., 2019b; Xu et al., 2022). Thus this might contribute to the weakening of outbreaks of *N. nomurai* in these years.

## Other experimental control measures

Some additional physical and chemical measures have been examined experimentally in the laboratory to solve the problems of jellyfish blooms along the Chinese coasts. Liu et al. (2017) designed a monolithic trawl net 5m long with a mouth of 2m×2m, at the bottom of which a circular steel ring 50cm in diameter with 16 crossed steel wires inside was installed. The medusae are captured and crushed while the net is towed at sea. However, this equipment awaits further testing in terms of its feasibility and efficiency in destroying medusae. Some drugs, such as “tea saponin”, comprising saponins extracted from plants, have been reported to be capable of killing the polyps, ephyrae, or medusae of jellyfish at low concentrations (Dong et al., 2017; Liu et al., 2017). However, because of their lethal effects on many microorganisms, algae, and zooplankton (Liu et al., 2017), the method that treats jellyfish blooms by using a large amount of the drugs, might produce serious secondary damage to the marine ecosystem. Therefore, these drugs have limitations concerning field application.

## Prospects

It is a general perception that coastal anthropogenic stressors (e.g., climate change, eutrophication, increase of man-made structures, and overfishing) are responsible for jellyfish blooms (Richardson et al., 2009; Purcell, 2012; Uye, 2014). However, the particular causes of medusa outbreaks differ among species (Pitt et al., 2018). For example, the frequent outbreaks of *A. coerulea* are closely associated with the increase of artificial substrates in



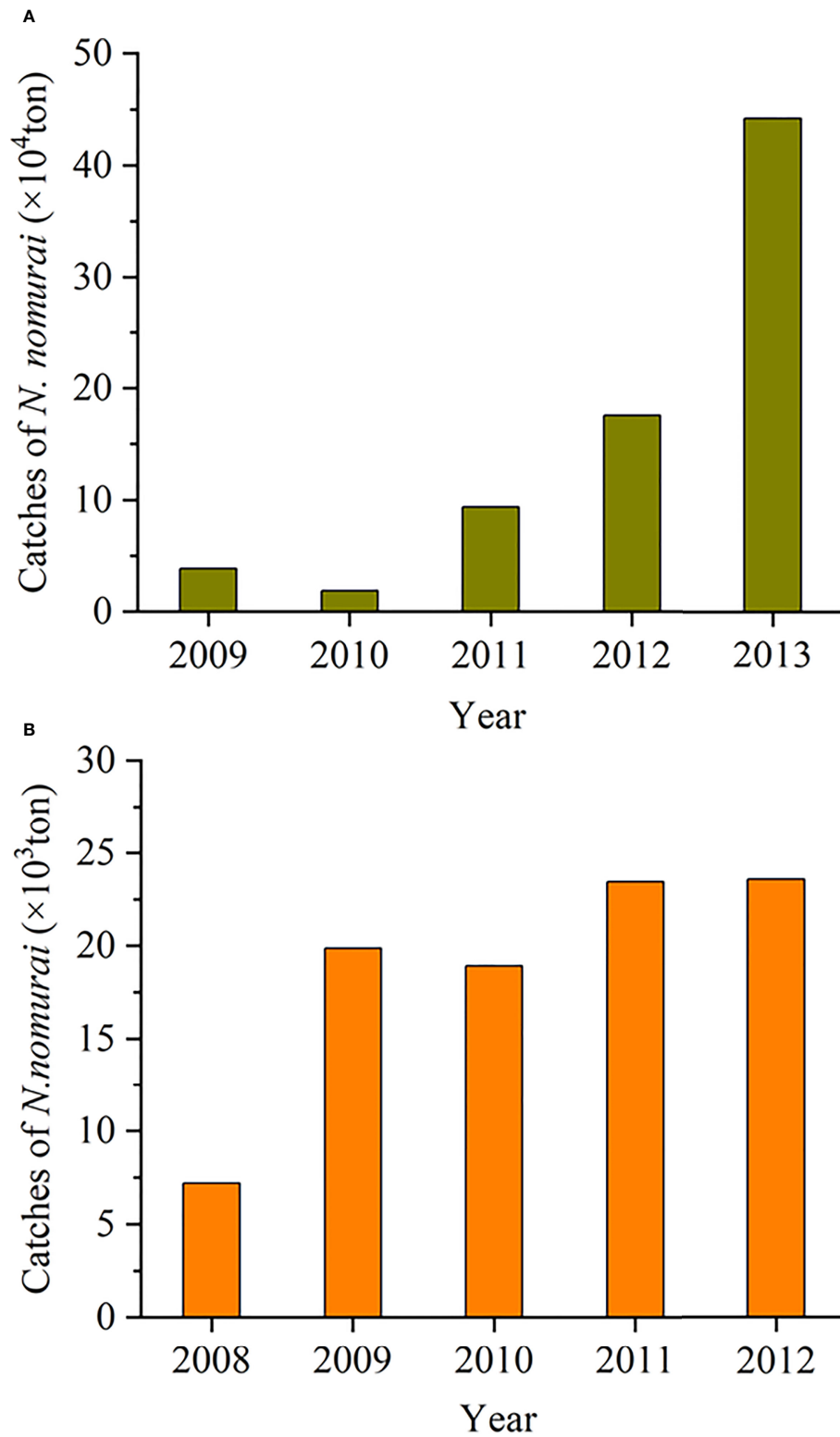


FIGURE 5

Changes in the annual catches of *Nemopilema nomurai* in the Bohai and Yellow seas from 2009 to 2013 (A) and in Tangshan, Hebei Province, China from 2008 to 2012 (B). The data are from Report on China's marine fishing situation, [Li et al., 2014](#), and [Zheng et al., 2014](#). The location of Tangshan is marked in Figure 1.

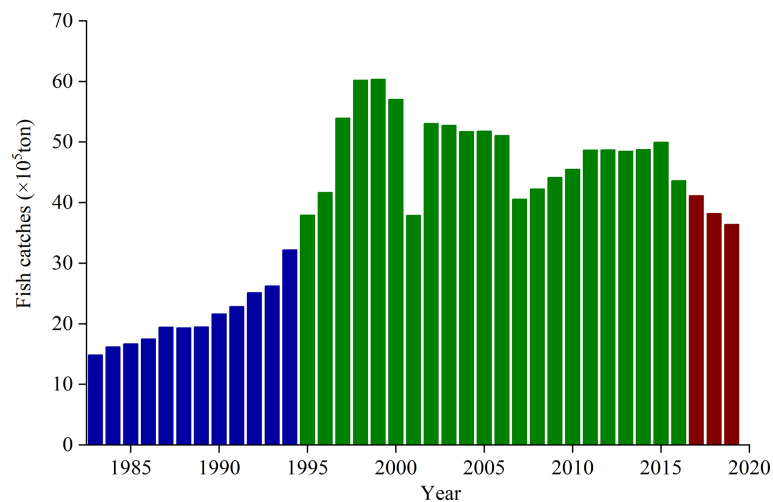


FIGURE 6

Changes in annual fish catches in Bohai, Yellow, and northern East China seas. The data are from Chinese fishery statistics, which were collected from Liaoning, Hebei, Tianjin, Shandong, Jiangsu, Shanghai, and Zhejiang. The blue column reflects the annual fish catches before the summer fishing moratorium was established. The green column represents the annual fish catches from 1995 to 2016, when the summer fishing moratorium started after early June. The red column represents the annual fish catches after 2017, when the fishing ban was enforced more rigorously and forcefully on May 1.

the coastal sea of China (Feng et al., 2017; Dong Z. et al., 2018; Feng et al., 2021). Therefore, to decrease *A. coerulea* blooms, government administration policies relevant to inshore artificial constructions need to be formulated. For example, agencies that manage marine development should require the regular application of antifouling paint to the undersurfaces of floating constructions and the elimination of *A. coerulea* polyps on the surfaces of fixed platforms in the harbors. In contrast, the control of *N. nomurai* blooms may require an expansion of medusa utilization as a food source or as other beneficial products and strict enforcement of the current summer fishing moratorium. Thus, for the health of the marine ecosystem in China, reasonable management of these two jellyfish blooms will require a long-term commitment and perseverance.

## Author contributions

SF carried out the field investigation, and data analysis, and drafted the manuscript. SS, CL, and FZ contributed to the project administration, conceptualization, and paper editing. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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