Artificial reefs for sea cucumber aquaculture confirmed as settlement substrates of the moon jellyfish *Aurelia coerulea*

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**Abstract** In coastal areas with a high intensity of human activities, expansion of artificial structures may enhance *Aurelia* spp. blooms because these constructions may provide additional substrates for the settlement and proliferation of the polyps. In the present study, the possible occurrence and distribution of *Aurelia coerulea* ephryae and polyps were investigated in sea cucumber (*Apostichopus japonicus*) culture ponds that contain huge amounts of artificial structures. Our results showed that *A. coerulea* ephryae were widely distributed in the *A. japonicus* culture ponds along the Bohai and Yellow Seas. Furthermore, underwater photography revealed that polyps of *A. coerulea* mainly occurred on the undersides of the artificial reefs made by plastic sunshade nets, tiles and substrate cages. The artificial reefs may decrease the time *A. coerulea* planulae spend settling, provide more hidden, calm and shady places for the settlement and proliferation of *A. coerulea* planulae, and thus were suitable substrates for the moon jellyfish *A. coerulea*. Our study suggests that the *A. japonicus* culture ponds may act as nursery grounds for the jellyfish *A. coerulea* and may potentially enhance the blooms of this species in the coastal waters along the Bohai and Yellow Seas.

**Keywords** Jellyfish blooms · Ephyrae · Polyps · Sea cucumber · *Aurelia coerulea*

**Introduction**

Blooms of the moon jellyfish *Aurelia* spp. have occurred in harbours, lakes and coastal waters worldwide, including those in East Asia, Europe and the USA, and are regarded as a nuisance to coastal fisheries, aquaculture, power plants and tourism (Lucas, 2001; Hamner & Dawson, 2009; Baxter et al., 2011; Uye, 2011; Purcell et al., 2013; Dong et al., 2014). Mass aggregations of *A. coerulea* von Lendenfeld, 1884 medusae have been reported in the harbours and coastal waters of the Bohai and Yellow Seas (i.e. Dong et al., 2012, 2014; Wang & Sun, 2015). Multiple environmental factors such as overfishing, coastal eutrophication, global warming, translocation...
and habitat modification can affect the population dynamics of *Aurelia* spp. across different stages of their life cycle and thus have been proposed as possible causes of jellyfish blooms (Richardson et al., 2009; Dong et al., 2010; Purcell, 2012; Duarte et al., 2012).

*Aurelia* spp. has a complex life cycle, alternating between the asexual polyp stage and the sexual medusa stage. Compared to the medusa stage, information on the polyps of *Aurelia* spp. in situ is relatively scarce due to their small size and the difficulty of seeing them underwater. Published studies show that colonies of *Aurelia* spp. polyps are mainly distributed on artificial constructions off the coasts of Japan, the UK, France and the Mediterranean (Miyake et al., 2002; Ishii & Katsukoshi, 2010; Duarte et al., 2012; Malej et al., 2012; Marques et al., 2015; Vodopivec et al., 2017). Recently, the results from Makabe et al. (2014) confirmed that the installation of a floating pier in a fishing port contributed to the remarkable growth of *Aurelia aurita* (Linnaeus, 1758) ephyrae in the Inland Sea of Japan. Therefore, the expansion of artificial structures in coastal waters might be an important driver of the increase in *Aurelia* spp. populations due to the resultant increase in the availability of suitable benthic habitats for polyp proliferation (Duarte et al., 2012; Purcell, 2012; Makabe et al., 2014).

As an important human activity in coastal areas, aquaculture makes great contributions to economic development and food provisioning. However, negative interactions between jellyfish and aquaculture species have been reported in Europe, Australia and North America (Willcox et al., 2008; Rodger et al., 2011; Purcell et al., 2013). For example, ephyrae and small medusae of *Aurelia aurita* are thought to cause mortalities of marine-farmed salmonids in European waters (Baxter et al., 2011; Purcell et al., 2013). Moreover, aquaculture activities may have potentially contributed to the increase in the jellyfish population, because aquaculture facilities may provide additional suitable substrates for the settlement and proliferation of benthic polyps (Lo et al., 2008; Purcell et al., 2013).

The provinces of Shandong, Hebei and Liaoning along the coasts of the Bohai and Yellow Seas are major areas for aquaculture of the sea cucumber *Apostichopus japonicus* (Selenka, 1867); they comprise approximately 214,000 ha of coastal area in total (China Fishery Statistical Yearbook, 2016). The expansion of *A. japonicus* culture ponds in the coastal area may provide a more suitable benthic habitat for jellyfish polyps because artificial structures are widely used in these ponds (Yang et al., 2015). For example, artificial reefs made of tiles, bricks, lantern nets and plastic are widely used to protect farmed sea cucumbers in culture ponds from predators (Chen, 2004). In addition, some concrete dams may also provide substrate for the settlement of *A. coerulea* planulae. We infer that jellyfish planula larvae can enter into the *A. japonicus* culture ponds through tides or pumps and settle in the artificial structures because adult medusae of *Aurelia* frequently occur near the *A. japonicus* culture ponds during the summer.

The mass occurrence of *A. coerulea* ephyrae in a coastal aquaculture pond (Shidao) in northern China was first recorded in April 2015. The mean density of ephyrae in the reddish colour zone of the aquaculture pond was estimated to be $7.38 \times 10^6$ individuals/m$^3$ (Dong et al., 2017). We hypothesised that the increased artificial structures in the *A. japonicus* culture ponds might provide a suitable surface for the settlement and proliferation of *A. coerulea* polyps. In addition, it is unclear if blooms of *A. coerulea* ephyrae are an occasional or common appearance in the *A. japonicus* culture ponds along the Bohai and Yellow Seas. Therefore, the aims of our study are (1) to investigate the occurrence and distribution of the *A. coerulea* ephyrae in the *A. japonicus* culture ponds along the Bohai and Yellow Seas; and (2) to investigate the possible occurrences and distribution of *A. coerulea* polyps and reveal the possible origin of the *A. coerulea* blooms in the coastal waters.

**Materials and methods**

**Study area**

This study was conducted in the aquaculture ponds located on the coasts of the Bohai and Yellow Seas in April 2016, where a high density of *A. coerulea* medusae has commonly occurred in recent years (Dong et al., 2014). These ponds are mainly used for aquaculture of the sea cucumber, *A. japonicus*. The majority of the ponds are shallow, with a typical depth of 1.5–2 m, and range in area from approximately 2–6 ha (Han et al., 2016). Water exchange between the coastal ponds and coastal waters is accomplished by
tides or pumps. The water inlets and outlets are covered with nylon fishing nets (maximum mesh size 10 mm) to prevent the entrance of potential predators and the escape of farmed sea cucumbers. Artificial reefs are considered an essential element in sea cucumber culture ponds because they can provide protection from predation, food resources and a habit for aestivation and hibernation (Xu et al., 2017). Many materials have been widely used to build artificial reefs for *A. japonicus* aquaculture in China, including tile, brick, stone, lantern nets and plastic (Chen, 2004). Four sampling sites on the coast of the Bohai and Yellow Seas were selected for our survey: Qingdao, Rongcheng, Dongying and Leting (Fig. 1). At each site, one survey district, including approximately 60–100 ponds, was investigated at a time (Fig. 1).

**Distribution of ephyrae**

Quantitative collections of ephyrae were conducted in April 2016. At each pond, four surface water samples were collected using a 1 L Teflon bottle sampler, one sample from each of the four corners in each square pond. The water sample was filtered through a 160-μm mesh filter. Ephyrae were immediately picked and preserved in 4% buffered formaldehyde–seawater solution. In the laboratory, the ephyrae were identified according to morphological characteristics described

![Fig. 1](http://www.adobe.com/)  
*Fig. 1* Survey sites in coastal aquaculture ponds along the Bohai and Yellow Seas. Abbreviation IDs for geographic regions: *LT* Leting, *DY* Dongying, *RC* Rongcheng, *QD* Qingdao. The figure was generated by Adobe Photoshop CS2 software (http://www.adobe.com/), based on data from Google Earth (v.7.1)
in previous studies (Straehler-Pohl & Jarms, 2010; Dong et al., 2017). The number of ephyrae sampled at each site was counted and recorded. The densities of A. coerulea ephyrae in each sample were then calculated. Morphometric identification of the ephyrae was conducted using a stereo microscope (Olympus, SZX10) fitted with a digital camera (Optec, TP510). The dam foundation construction materials of each pond were also recorded. Three types of dam construction materials (rocks, concrete and mud) were distinguished during the field survey.

At each site, surface seawater samples were collected in ephyrae-blooming ponds and ponds without ephyrae. To determine chlorophyll a and nutrient concentrations, surface water samples were taken using a 1 l Niskin bottle. Chlorophyll a concentrations were determined using a UV–VIS spectrophotometer (TU-1810, Beijing Purkinje General Instrument Co., Ltd., China) after filtration on GF/F membranes (Whatman) (Lorenzen, 1967). Nutrient concentrations, including dissolved inorganic nitrogen (DIN: NO$_3^-$, NO$_2^-$, NH$_4^+$), dissolved organic nitrogen (DON), dissolved inorganic phosphate (DIP) and dissolved silicate (DSi), were analysed using Flow Injection Analysis (AA3, Bran + Luebbe, Germany). The data quality was ensured through careful standardisation, procedural blank measurements, appropriate sample numbers and analytical replicates. Environmental parameters, including seawater temperature and salinity, were measured with a YSI-600 multiparameter water quality sonde (YSI, Yellow Springs, OH).

Distribution of polyps

To investigate the possible occurrence and distribution of A. coerulea polyps in the A. japonica culture ponds, one ephyrae-blooming pond from each site was selected and surveyed using an underwater camera in April 2016 (Table 1). The videos were taken using a diver-held digital video camera (Canon, G7X) within a Nauticam waterproof housing (Nauticam, NA-G7X). Previous studies have shown that Aurelia polyps were mainly distributed on the undersides of hard structures (Durate et al., 2012). Therefore, artificial constructions made of concrete or rocks and artificial reefs made of tiles, bricks, lantern nets and plastic in the A. japonicus culture ponds were selected and surveyed. In addition, colonies of polyps with the substrates were sampled and maintained in an incubator (BSG-800, Boxun, Shanghai) at a constant temperature of 8°C. Strobilation was induced by raising the temperature to 13°C. The ephyrae released were identified as A. coerulea based on morphological characteristics (Straehler-Pohl & Jarms, 2010; Dong et al., 2017). Therefore, we treated all the scyphozoan polyps as A. coerulea polyps in our study.

Four types of substrate used in the A. japonica culture ponds were recorded in the present study: triangle tile, cage substrate, hollow bricks and plastic sunshade net. In the ephyrae-blooming pond of Rongcheng, 12 tiles were randomly selected and surveyed. In the ephyrae-blooming ponds of Leting, Dongying and Qingdao, roughly 50 m transects of cage substrate or plastic sunshade net were randomly selected and surveyed. The densities of A. coerulea polyps were difficult to precisely determine due to the huge differences in shape and structure of the artificial reefs used in the A. japonicus culture ponds. Therefore, we determined the percentage cover of A. coerulea polyps across different artificial structures using the methods described by Toyokawa et al. (2011). In brief, the colonies of polyps were photographed using the underwater camera and carefully examined using Adobe Premiere Pro (Adobe Corporation, USA) to identify polyp colonies and other fouling organisms. The percent coverage of polyp colonies and other fouling organisms were determined for the whole substrate by eye and quantified up to 100% using intervals of 5% (Toyokawa et al., 2011).

| Pond       | Latitude  | Longitude | Dam construction | Artificial reef       |
|------------|-----------|-----------|-------------------|-----------------------|
| Leting     | 118°40.9’E | 39°8.3’N  | Mud               | Plastic sunshade net  |
| Dongying   | 118°59.2’E | 37°58.0’N | Concrete           | Plastic sunshade net  |
| Rongcheng  | 122°30.7’E | 36°55.2’N | Mud               | Triangle tile         |
| Qingdao    | 120°15.4’E | 36°12.1’N | rocks             | Cage substrate        |
Data analysis

A one-factor ANOVA was used to examine the differences in the density of A. coerulea ephyrae among dam types and sites, the percentage coverage of polyps among the substrate types, and the nutrients and Chl-a concentrations among sites. One-way ANOVA was also used to compare the nutrients and Chl-a concentrations between the ephyrae-blooming and no-ephyrae ponds. Fisher’s least significant difference (LSD) method was performed to determine whether the differences in the density of A. coerulea ephyrae and the distribution of dissolved nutrients and Chl-a concentrations among sites was significant at $P < 0.05$. The relationships between the abundance of A. coerulea ephyrae in the ephyrae-blooming ponds and their environmental variables including nutrients and Chl-a concentrations were determined using Pearson’s rank correlation. All statistical analyses were performed using SPSS Statistics, version 19 (IBM, Armonk, NY, USA).

Results

Distribution of ephyrae

In total, 327 A. japonicus culture ponds were surveyed and sampled in April 2016. During the sampling time, the seawater temperature across the four sites ranged between 15.6 and 17.6°C. The salinity across the four sites was between 32.5 and 37.5. The A. japonica culture ponds surveyed commonly had a dam foundation built with rocks (Fig. 2A), concrete (Fig. 2B) or mud (Fig. 2C). Scyphozoan ephyrae were found in the A. japonicus culture ponds at all four study sites. All sampled ephyrae were identified as A. coerulea based on morphological characteristics (Straehler-Pohl & Jarms, 2010; Dong et al., 2017). Furthermore, an obvious reddish colour caused by blooms of A. coerulea ephyrae, similar to “red tides”, was also observed in the surface water of the A. japonicus culture ponds.

The mean abundances of A. coerulea ephyrae in the A. japonica culture ponds of Leting, Dongying, Rongcheng and Qingdao were $1.03 \times 10^5 \pm 3.47 \times 10^5$, $0.26 \times 10^5 \pm 0.73 \times 10^5$, $2.17 \times 10^5 \pm 7.20 \times 10^5$ and $0.31 \times 10^5 \pm 2.60 \times 10^5$ individuals/m$^3$, respectively (Fig. 3). The highest abundances of A. coerulea ephyrae in the A. japonica culture ponds of Leting, Dongying, Rongcheng and Qingdao were $5.70 \times 10^6$, $2.19 \times 10^6$, $2.27 \times 10^6$ and $3.46 \times 10^6$ individuals/m$^3$, respectively. There were 5, 5 and 1 pond(s) in Leting, Dongying and Rongcheng, respectively, that had an extremely high density above $1 \times 10^9$ individuals/m$^3$. The proportions of the ponds in which A. coerulea ephyrae were found in Leting, Dongying, Rongcheng and Qingdao were 0.524, 0.486, 0.452 and 0.145, respectively.

Among the ponds surveyed in our present study, 1.23% of the ponds were constructed using natural rocks, 15.34% were constructed using concrete and 83.44% were constructed using mud. There was no significant difference in the abundance of A. coerulea ephyrae among the three pond types ($P = 0.633$). The abundances of ephyrae in the ponds constructed with concrete, rocks and mud were $0.47 \times 10^5 \pm 2.29 \times 10^5$ individuals/m$^3$, $0.80 \times 10^5 \pm 1.36 \times 10^5$ individuals/m$^3$ and $1.12 \times 10^5 \pm 4.70 \times 10^5$ individuals/m$^3$, respectively.

Variations of dissolved nutrients (DIN, DON, DIP and DSI) and Chl-a concentrations between the ephyrae-blooming and no-ephyrae ponds at each of the four sites are shown in Fig. 4. Results showed that the distribution of dissolved nutrients and Chl-a were irregular between the ephyrae-blooming and no-ephyrae ponds. The DIN concentrations were between 3 and 18 μM in both the ephyrae-blooming and no-ephyrae ponds (Fig. 4A). The DON concentrations were 43–53 μM in the ephyrae-blooming ponds and 29–89 μM in the no-ephyrae ponds (Fig. 4B). The DIP concentrations were 0.15–1.20 μM in the ephyrae-blooming ponds and 0.12–0.42 μM in the no-ephyrae ponds (Fig. 4C). The DSI concentrations were 0.90–5.51 μM in the ephyrae-blooming pond and 1.60–5.46 μM in the no-ephyrae ponds (Fig. 4D). The Chl-a concentrations were between 0.18 ± 0.09 μg/L and 4.85 ± 0.25 μM in the ephyrae-blooming ponds and between 0.23 ± 0.20 μM and 0.91 ± 0.09 μM in the no-ephyrae ponds (Fig. 4E).

The correlation analysis revealed that the abundance of A. coerulea ephyrae in the ephyrae-blooming ponds was significantly positively correlated with DIP concentrations ($r = 0.952$; $P = 0.024$) and Chl-a concentrations ($r = 0.931$; $P = 0.035$). There were significant differences in nutrient and Chl-a concentrations in the ephyrae-blooming ponds among the four sites, with the exception of DON concentrations ($P = 0.425$). The concentrations of...
DIP and Chl-a in the ephyrae-blooming ponds of Leting were significantly higher than those from other regions \((P = 0.000)\). The abundances of *A. coerulea* ephyrae in the ephyrae-blooming ponds of Leting were also higher than those from other regions.

**Distribution of polyps**

The different types of artificial construction found in the ponds are shown in Fig. 2. The structures of the dams and artificial reefs used in the *A. japonicus* ponds varied in the ephyrae-blooming ponds across the four sites. There were four main types of artificial reefs constructed in the *A. japonicus* culture ponds: plastic sunshade net (Fig. 2D), triangle tile (Fig. 2E), cage substrate (Fig. 2F) and hollow brick. Plastic sunshade nets and metal supporting structures were found in the ephyrae-blooming pond in Leting. The artificial construction in the ephyrae-blooming pond in Dongying included a dam and hollow bricks made with concrete and plastic sunshade nets. Triangle tiles made of clay were used in the ephyrae-blooming pond in Rongcheng. In the ephyrae-blooming pond of Qingdao, the dam was made with rocks, and substrate cages were used. No statistically significant difference in the percentage coverage of *A. coerulea* polyps on the
different substrate types was found in this study ($P = 0.352$).

The dam and plastic sunshade nets were selected to investigate the occurrence and distribution of scyphozoan polyps in the *A. japonicus* culture pond in Leting. No polyps were found on the concrete dam. *A. coerulnea* polyps were distributed across the underside of the black plastic nets (Fig. 2G). The mean percentage coverage of *A. coerulnea* polyps was $37 \pm 25\%$ (Fig. 5). Tubeworm, the dominant fouling organism, co-occurred across the underside of the plastic sunshade nets. The mean percentage coverage of other fouling organisms was $62 \pm 10\%$ (Fig. 5).

The dam, plastic sunshade nets and hollow bricks were selected to investigate the occurrence and distribution of polyps in the *A. japonicus* culture ponds in Dongying. No polyps were found in the concrete dam or hollow bricks. *A. coerulnea* polyps were distributed across the underside of the plastic sunshade nets (Fig. 2G). The mean percentage coverage of *A. coerulnea* polyps was $43 \pm 25\%$ (Fig. 5). Tubeworm, the dominant fouling organism, co-occurred across the underside of the plastic sunshade nets. The mean percentage coverage of other fouling organisms was $41 \pm 32\%$ (Fig. 5).

Twelve triangle tiles were selected to investigate the occurrence of polyps in the *A. japonicus* culture ponds in Rongcheng. Polyps were distributed across the underside of the tiles, with no polyps found on the outer sides of the tiles (Fig. 2H). The mean percentage coverage of *A. coerulnea* polyps was $34 \pm 28\%$ (Fig. 5). The mean percentage coverage of other fouling organisms was $55 \pm 26\%$ (Fig. 5).

Substrate cages and the rock dam were selected to survey the distribution of polyps in the *A. japonicus* culture ponds in Qingdao. No polyps were found on the dam made of rocks. The outer sides of the substrate cages were covered with macro algae. *A. coerulnea* polyps were found on the inner sides of the substrate cages (Fig. 2I). The mean percentage coverage of *A. coerulnea* polyps was $46 \pm 16\%$ (Fig. 5). Ascidians, the dominant fouling organisms, co-occurred on the underside of the substrate cages. The mean percentage coverage of other fouling organisms was $18 \pm 9\%$ (Fig. 5).

**Discussion**

Blooms of *A. coerulnea* medusae are frequently reported in the harbours and coastal waters of the Bohai and Yellow Seas (Dong et al., 2010, 2012; Wang & Sun, 2015). However, the occurrences and distributions of the early life stages of *A. coerulnea*, including ephyrae and polyps, in Chinese coastal waters are largely unknown. Previous surveys show that newly released ephyrae of the *Aurelia* spp. are mainly distributed in coastal waters near artificial constructions (i.e. fishing ports, power station, floating piers) (Toyokawa et al., 2011; Bonnet et al., 2012; Makabe et al., 2014; Wang & Sun, 2015). Therefore, the huge number of aquaculture ponds constructed at the coastal areas of the Bohai and Yellow Seas are potential occurrence areas for *A. coerulnea*. Our present study revealed that *A. coerulnea* ephyrae are widely distributed in *A. japonicus* culture ponds along the Bohai and Yellow Seas. The high density of *A. coerulnea* ephyrae in the *Apostichopus japonicus* culture ponds suggests that the polyps of *A. coerulnea* might be distributed in these ponds. Our study was the first to confirm that artificial reefs made with plastic sunshade nets, tiles and substrate cages were used as settlement substrate by *A. coerulnea* polyps. *A. coerulnea* polyps were mainly distributed across the undersides of the plastic sunshade nets, tiles and substrate cages.

Similar results revealed by other field surveys also showed that *Aurelia* spp. polyps were primarily located on the undersides of artificial structures in the coastal waters of Japan, the UK, and the Mediterranean Sea (Miyake et al., 2002; Purcell et al., 2009;...
Duarte et al., 2012; Malej et al., 2012; Marques et al., 2015). For example, *Aurelia aurita* polyps were found across the undersides of floating piers and buoys in Kagoshima Bay, Japan (Miyake et al., 2002). Polyps of *Aurelia* spp. were distributed across the undersides of marine floats in Cornet Bay Marina (Purcell et al., 2009). Polyps of *A. labiata* Chamisso and Eysenhardt, 1821 were distributed across the undersides of marine floats in Kagoshima Bay, Japan (Miyake et al., 2002). Polyps of *Aurelia* spp. were attached to the undersides of oyster
shells growing on dock pillars in the northern Adriatic (Malej et al., 2012). Polyps of *Aurelia* sp. settled mainly on artificial hard substrates including metal, concrete and plastics (Marques et al., 2015).

Previous studies indicate that jellyfish planulae have different substrate choices and settlement preferences between natural and artificial materials (Holst & Jarms, 2007; Hoover & Purcell, 2009; Duarte et al., 2012). For example, *Aurelia aurita* planulae prefer to settle on plastic rather than shells (Holst & Jarms, 2007). The planulae and polyps of *A. labiata* preferred plastics to rubber and treated wood when choosing a habitat from man-made surfaces (Hoover & Purcell, 2009). Therefore, the artificial reefs made by plastic nets and plastic substrate cages were suitable substrates for the settlement of *A. coerulea* planulae. There have been no other reports of clay tiles as a settlement preference. However, based on this field survey, we infer that *A. coerulea* planulae also have high settlement rates on these tiles.

*Aurelia* spp. planulae have a pelagic larval lifespan of less than 1 week before they settle on suitable substrate, during which time there are risks of predation, offshore transport away from suitable substrata and exposure to extreme environmental conditions (Brewer, 1978; Lucas et al., 2012; Conley & Uye, 2015). Therefore, reduction of the time planulae spend seeking suitable substrate may increase the survivorship of *A. coerulea* planulae. The bottoms of the Bohai and Yellow Seas are composed mainly of sand, mud and mixed sediment and are not suitable for the settlement of *A. coerulea* planula larvae (Chen & Zhu, 2012; Duarte et al., 2012). The artificial reefs used in the *A. japonicus* culture ponds may reduce the distances between suitable settlement sites for planula larvae and increase the successful settlement of *A. coerulea* polyps.

Artificial reefs in *A. japonicus* culture ponds provide many hidden places for *A. japonicus*, protecting them from predation and providing food sources and habitat for aestivation and hibernation (Xu et al., 2017). Artificial reefs made of various materials also provide a large shaded surface that *A. coerulea* planulae prefer (Holst & Jarms, 2007; Hoover & Purcell, 2009; Duarte et al., 2012). Previous studies suggest that *Aurelia* spp. polyps distributed at shallow depths are exposed to extensive competition with other fouling organisms for space (Watanabe & Ishii, 2001; Ishii et al., 2008; Feng et al., 2017). Our results revealed less coverage of other sessile organisms across the undersides of artificial reefs made of substrate cages or plastic sunshade nets, thus decreasing competition for space with *A. coerulea* polyps. Furthermore, artificial reefs may provide a suitable environment that excludes some predators and competitors of polyps. Previous studies have shown that nudibranchs, gastropods and crustaceans were the main predators of *Aurelia* spp. polyps (Hoover et al., 2012; Takao et al., 2014). The settlement areas of *A. coerulea* on the artificial reefs were relatively well concealed, possibly preventing some predators (e.g. crustacean species) from accessing the undersides of these artificial reefs. A long-term monitoring of the presence of predators of polyps in different months would help to address this hypothesis.

*A. japonicus* culture ponds have a relatively enclosed surrounding environment. Artificial constructions in the ponds also restrict water flow, which may benefit the settlement of *A. coerulea* planulae. The *Aurelia* spp. planula larvae were thought to be weak swimmers, with a reported swimming speed of 1–2 mm S\(^{-1}\) (Conley & Uye, 2015). Therefore, physical factors (i.e. water flow) may have strong effects on the settlement of *A. coerulea* planula larvae, although the extent of these effects is unknown. However, it is certain that the dams and artificial reefs can protect *A. coerulea* polyps from being washed away from the attached substrate.

Coastal eutrophication was indicated as an important contributor to the *A. aurita* blooms in other
countries (Arai, 2001; Richardson et al., 2009; Purcell, 2012). Increased nutrient concentrations in coastal waters can significantly increase phytoplankton biomass, which could support the food sources of jellyfish (e.g. zooplankton) (Lo et al., 2008; Richardson et al., 2009; Purcell, 2012). Our results showed that the highest abundance of A. coerulea in the ephyrae-blooming ponds of Leting was related to the increased nutrient concentrations (e.g. DIN and DIP concentrations). Meanwhile, the Chl-a concentration, an indicator of phytoplankton biomass and abundance, was also highest in the ephyrae-blooming ponds of Leting. In addition, temporal variations in nutrient concentrations frequently occur in A. japonicus culture ponds which show high average annual nutrients levels (Wang et al., 2012; Zhang et al., 2013). For example, the results of Zhang et al. (2013) show that the average concentrations of DIN, DIP and DSi in the Zhuanghe aquaculture ponds were 17.36, 0.4 and 19.76 µM, respectively. Therefore, due to the limited nutrient concentration data available in our study, the possible contributions of eutrophication to ephyrae blooms cannot be excluded.

Blooms of the moon jellyfish Aurelia spp. are negative influences on the aquaculture industry in many areas (Purcell et al., 2016). For example, A. aurita have caused severe gill problems in marine-farmed Atlantic salmon Salmo salar (Baxter et al., 2011). A. aurita mediated pathological gill damage in Atlantic salmon on the northwest coast of Ireland, resulting in mortality (Mitchell et al., 2011). The extent of possible damage to sea cucumbers caused by A. coerulea blooms is not known. However, fishermen have noted stings on sea cucumbers by A. coerulea ephyrae. In addition, decomposing A. coerulea may cause bottom water hypoxia that is a threat to the sea cucumber A. japonicus. Future studies are needed to assess the possible influences of A. coerulea blooms in the sea cucumber culture ponds.

Artificial reefs are considered an essential element in A. japonicus culture ponds. The wide occurrence of A. coerulea ephyrae in these coastal ponds and the high numbers of aquaculture ponds located on the coastal areas along the Bohai and Yellow Seas suggest that A. coerulea ephyrae in the A. japonicus culture ponds may be an important seed source of A. coerulea in the nearby coastal waters. The water inlets and outlets are covered with nylon fishing nets to prevent the entrance of potential predators and the escape of farmed sea cucumbers; however, they cannot prevent the exchange of A. coerulea planulae and ephyrae between the A. japonicus culture ponds and coastal waters. It is likely that A. coerulea ephyrae flow out to the coastal waters with the tidal currents. Therefore, A. coerulea ephyrae in coastal aquaculture ponds may contribute to A. coerulea blooms in the coastal waters of the Bohai and Yellow Seas.

In summary, we examined the relationship between the mass occurrences of A. coerulea and the extensive use of aquaculture facilities in the A. japonicus culture ponds along the Bohai and Yellow Seas. Our results showed that A. coerulea ephyrae were widely distributed in the A. japonicus culture ponds along the Bohai and Yellow Seas. We confirmed that the polyps of A. coerulea were mainly settled on the undersides of artificial reefs made of plastic sunshade nets, tiles and substrate cages. These artificial reefs provided more hidden, calm and shady places for the settlement and proliferation of polyps. Therefore, our study suggests that the A. japonicus culture ponds may act as nursery grounds for A. coerulea and may potentially enhance the blooms of A. coerulea in the coastal waters along the Bohai and Yellow Seas.

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