

# Intraguild predation by polyps of three scyphozoan jellyfish: *Nemopilema nomurai*, *Aurelia coerulea*, and *Rhopilema esculentum*\*

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**Abstract** Jellyfish blooms occur worldwide and have resulted in serious problems in tourism, fisheries, coastal industries, and the marine ecosystem. The life cycle of scyphozoan jellyfish consists of a pelagic medusa stage and a benthic polyp stage. Success of asexual reproduction of the polyps determines directly the number of medusae; thus, the polyp stage is the key to understanding the population dynamics of medusae. *Nemopilema nomurai*, *Aurelia coerulea*, and *Rhopilema esculentum* are three scyphozoan jellyfish commonly inhabit in Chinese coastal waters. Polyps of *A. coerulea* are easily visible, while those of *N. nomurai* and *R. esculentum* remain yet to be found in the wild. However, distribution of the medusa indicates that the polyps of all three species may occur together. To evaluate the distribution pattern of polyps of the three species and explore intraguild predation by the polyps, we conducted a laboratory experiment that considered the attachment sequence and size relationship of calyx diameter of the polyps. We found that the polyps of *A. coerulea* preyed on polyps of the other two species in all treatments, except when polyps of *R. esculentum* were bigger than those of *A. coerulea*. The polyps of *R. esculentum* preyed on the polyps of *N. nomurai* only when polyps of *R. esculentum* attached first and were bigger than those of *N. nomurai*. Colonies of *N. nomurai* polyps were rarely found in the places inhabited by *A. coerulea* polyps. In addition, *A. coerulea* polyps are known to inhabit at depths of less than 20 m in coastal sea, thus, we speculate that *N. nomurai* polyp colonies might occur at depths of more than 20 m. Therefore, our finding that polyps of *A. coerulea* aggressively preyed on polyps of other species may help understand other such systems of jellyfish bloom in the world.

**Keyword:** jellyfish bloom; polyps; intraguild predation; nature habitats

## 1 INTRODUCTION

In recent decades, jellyfish blooms are reported frequently from many coastal waters (Purcell et al., 2007; Pauly et al., 2009; Uye, 2014). Massive blooms of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomea) have been observed in the Bohai Sea, Yellow Sea, and East China Sea every year since 2002, except for 2008, 2010, and 2011 (Dong et al., 2010; Kawahara et al., 2013; Sun et al., 2015b).

The moon jellyfish *Aurelia aurita* sp. l. (Linnaeus) is a species of worldwide distribution in inner neritic waters between 70°N and 40°S (Lucas, 2001). The

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species found in China is *A. coerulea* (Feng et al., 2017), and it mainly occurs along the tourist coasts and coastal aquaculture regions (Dong et al., 2010). Blooms of these two species have had negative impacts on tourism, fisheries, coastal industries, and the marine ecosystem (Purcell et al., 2007; Uye, 2008). Blooming is thought to be related to climate change, overfishing, eutrophication, hypoxia, agriculture, and increasing amounts of anthropogenic hard substrate (Purcell et al., 2007; Purcell, 2012; Sun et al., 2015a). Another species common to China is the edible jellyfish, *Rhopilema esculentum* (Scyphozoa: Rhizostomea). It is one of the most important fishery species in China (Dong et al., 2014), and it inhabits a wide range in the Bohai Sea, Yellow Sea, East China Sea, and northern South China Sea (You et al., 2007).

The life cycle of the scyphozoan jellyfish consists of a pelagic sexual medusa stage and a benthic asexual polyp stage. Sexual fertilization occurs in the female or in the open seawater (Dong et al., 2008; Schiariti et al., 2012) and fertilized eggs develop into free-swimming planulae, which settle on hard substrate and metamorphose into sessile polyps (Van Walraven et al., 2016). The polyps are perennials (Lucas, 2001), and asexual strobilation of the sessile polyps directly determines the population dynamics of the medusa. Therefore, increasing attention is being paid to the important benthic polyp stage (Kawahara et al., 2006; Hoover and Purcell, 2009; Feng et al., 2015a; Lee et al., 2017). However, the polyps of many species of jellyfish have never been found in the wild (Ceh and Riascos, 2017; Feng et al., 2017), and they are known only from experiments using sexual and asexual propagation.

Considering the overlap of spatial distribution of the medusa stage of the three scyphozoan jellyfish species common to Chinese coastal seas, it is possible that the polyps of each species develop near each other. The polyps of *A. aurita* can reproduce by budding, fission, or podocysts (Thein et al., 2012), and the polyps of *N. nomurai* and *R. esculentum* reproduce mainly by podocysts (Dong et al., 2013; Feng et al., 2015b), which produce colonies of millions of individuals that extend the spatial distribution of the polyps. After settlement, the polyps are surprising mobile, using stolons to ‘walk’ around different surfaces or detaching and floating to new locations (Hoover and Purcell, 2009). As a result, it is likely that the polyps of different species encounter each other.

The polyps of *Aurelia* sp. 1. have been found on natural substrates, such as bare rock, shells, amphipod and polychaete tubes, ascidians, and macroalgae and on artificial substrates, such as glass, ceramic, or plastic pieces in the sea (Lucas, 2001). The medusae of *N. nomurai* also breed and form polyps along coastal waters, but the polyps of *N. nomurai* have not yet been found in the field (Toyokawa et al., 2012). However, Feng et al. (2015a) suggested that the Changjiang River estuary and northern Liaodong Bay might be their nursery ground. Confirming the nursery ground of *N. nomurai* remains one of the most important topics of the Chinese National Basic Research Project (Sun et al., 2015a). The polyps of *R. esculentum* have not been found in the field, despite numerous field surveys along Chinese coastal waters (Dong et al., 2013). Why the habitat of polyps of these two species remains unknown is still a puzzle (Feng et al., 2017).

To better understand the dynamics of jellyfish blooms, it is essential to understand the intraguild predation relationship of polyps of the most common scyphozoan jellyfish species in the Bohai Sea, Yellow Sea, and East China Sea; determine their distribution patterns; and identify possible natural habitats that may host wild polyps of *N. nomurai* and *R. esculentum*. To our knowledge, no previous studies have focused on the intraguild predation relationship of the polyp stage of these jellyfish species at the individual level.

## 2 MATERIAL AND METHOD

### 2.1 Material

Mature medusae of *N. nomurai* (6 females, 4 males) were captured by hand nets in Jiaozhou Bay in September 2013 and then transferred to a 30-m<sup>3</sup> pond for fertilization in the laboratory of the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. The rearing temperature and salinity were maintained at 20±0.5°C and 30±0.5, respectively. After planulae were detected, parent medusae were removed and polyethylene corrugated plates were placed in the pond for attachment. Polyps of *N. nomurai* (abbreviated to NP hereafter) with two to four tentacles formed on the plates within a week and developed fully to polyps with 16 tentacles one month later. Polyps of *A. coerulea* (abbreviated to AP hereafter) were also cultured at the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. Polyethylene corrugated plates were used for attachment of planulae produced by mature medusae

**Table 1** Intraguild predation results of all treatments

Experiment treatment number	Attached first	Larger polyps	Size parameter ( $\mu\text{m}$ )			Smaller polyps	Size parameter ( $\mu\text{m}$ )			Intraguild predation frequency (the former preyed on the latter)		
			Min	Max	Mean $\pm$ SD		Min	Max	Mean $\pm$ SD	AP $\rightarrow$ NP	NP $\rightarrow$ AP	Coexist
1	NP	NP	370	430	393.8 $\pm$ 14.4	AP	360	395	374.7 $\pm$ 9.9	28	0	2
2	NP	AP	365	1150	673.3 $\pm$ 172.3	NP	180	415	336.2 $\pm$ 60.9	30	0	0
3	AP	NP	365	430	400 $\pm$ 17.7	AP	360	405	382 $\pm$ 14	30	0	0
4	AP	AP	360	1050	606 $\pm$ 148.9	NP	195	430	318 $\pm$ 62.3	30	0	0
			Min	Max	Mean $\pm$ SD		Min	Max	Mean $\pm$ SD	AP $\rightarrow$ RP	RP $\rightarrow$ AP	Coexist
5	RP	RP	513	795	681.4 $\pm$ 73.3	AP	446	786	590 $\pm$ 78.2	1	0	29
6	RP	AP	605	1094	858.8 $\pm$ 104.3	RP	488	787	651.7 $\pm$ 89.1	30	0	0
7	AP	RP	530	785	671.3 $\pm$ 79.1	AP	440	720	583.2 $\pm$ 78.9	0	0	30
8	AP	AP	702	1020	853.4 $\pm$ 69.5	RP	627	792	730.8 $\pm$ 45	30	0	0
			Min	Max	Mean $\pm$ SD		Min	Max	Mean $\pm$ SD	RP $\rightarrow$ NP	NP $\rightarrow$ RP	Coexist
9	NP	NP	453	590	539.3 $\pm$ 43.2	RP	441	562	495.4 $\pm$ 34.8	0	0	30
10	NP	RP	445	626	534.2 $\pm$ 51.1	NP	378	584	476.5 $\pm$ 55.8	2	0	28
11	RP	NP	457	592	529.4 $\pm$ 45.6	RP	441	584	488.3 $\pm$ 40	0	0	30
12	RP	RP	443	593	519.6 $\pm$ 44.5	NP	255	493	360.2 $\pm$ 70.3	30	0	0

NP: polyps of *N. nomurai*; AP: polyps of *A. coerulea*; RP: polyps of *R. esculentum*.

of *A. coerulea* collected from nearby Jiaozhou Bay in May 2014. Fully developed polyps of *A. coerulea* were formed after a month at 20 $\pm$ 0.5 $^{\circ}$ C and 30 $\pm$ 0.5 in sand-filtered seawater. Polyps of *R. esculentum* (abbreviated to RP hereafter) were bred at Yancheng Jinyang Aquatic Products Breeding Company in Jiangsu, China, in June 2014. Polyps of the three species were fed with newly hatched *Artemia* nauplii for 1–2 h every 3 d, and freshly sand-filtered seawater was used for replacement every 2 d before the experiment. The cultivation temperature and salinity were maintained at 18 $\pm$ 0.5 $^{\circ}$ C and 30 $\pm$ 0.5, respectively.

## 2.2 Method

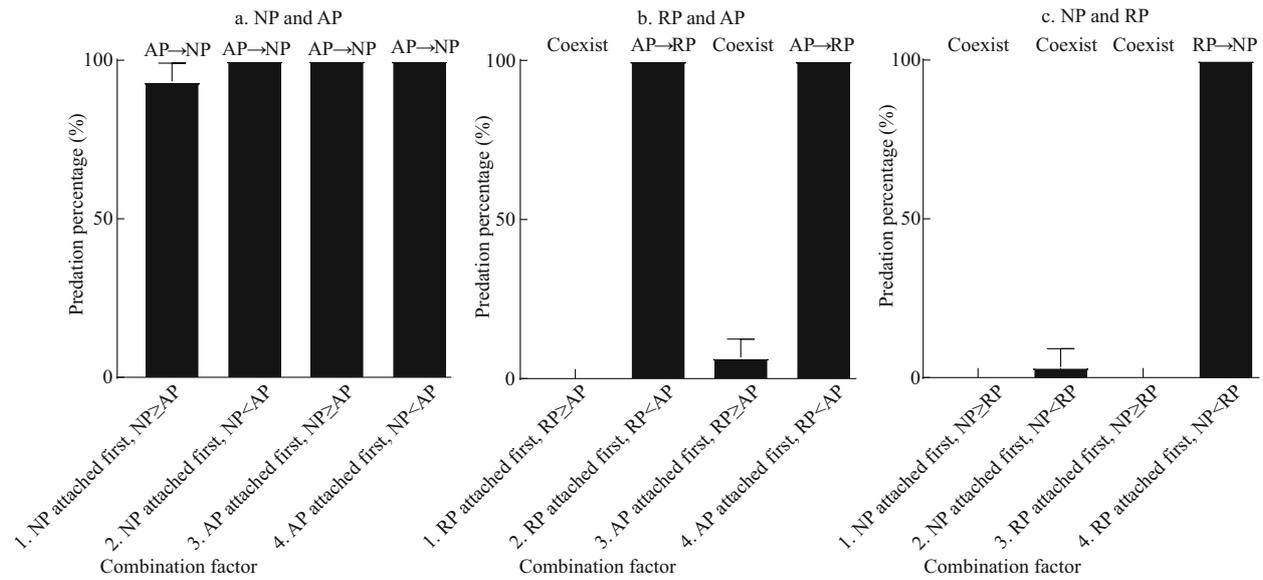
In the field, the medusae of the three species become mature at different periods of time (Wang, 2013; Dong et al., 2014; Sun et al., 2015b), indicating that the attachment sequence of the polyps would differ among different species. After formation, the body size of the polyps also differs among different species. To approximately simulate the encounter situation of the polyps of the three species in the field, polyps of each species were allowed to attach first, then they were fed polyps of another species. Additionally, the polyp size of the first species, relative to the second species, was experimentally manipulated.

Fully developed polyps with 16 tentacles were used in the experiment. For each case, the polyps of

one species were detached carefully from the root of the pedal disc with a dissecting needle under a dissecting microscope. Ten undamaged polyps were transferred to one well of a six-well cell culture plate containing 15-mL of freshly filtered seawater. After 2-d of acclimation without food in an incubator (18 $^{\circ}$ C), all polyps were able to reattach. Ten polyps of another species, also detached carefully from the settle plates, then were collected into a capillary pipette and released within the tentacles of each polyp of the former species. The calyx diameter of all polyps was measured with the ocular micrometer, and the predation reactions of each polyp and its final state after 5 d were observed. Because the calyces of the polyps were not uniformly circular, the approximate diameter was calculated by the average of maximum and minimum diameters. Twelve situations were tested, with three replicates containing 30 pairs of polyps in total per situation (Table 1). For every replicate, the predation percentage was recorded as follows:

$$\text{Predation percentage} = \frac{\text{Number of polyp pairs for which predation occurred}}{\text{Total number of polyp pairs}} \times 100\%.$$

The experiment was conducted in a temperature controlled room (18 $\pm$ 0.5 $^{\circ}$ C). The seawater in the culture plates was cautiously replaced with freshly filtered seawater of the same temperature and salinity daily. The experiment began on September 23, 2014 and lasted for 50 d.



**Fig.1 Mean predation percentage of polyps (mean±SD) for two attachment sequences and two size relationships of calyx diameter**

a. polyps of *N. nomurai* and *A. coerulea*; b. polyps of *R. esculentum* and *A. coerulea*; c. polyps of *N. nomurai* and *R. esculentum*. The former preyed on the latter.

**Table 2 Summary of variables not in the results of the binary logistic regression equation**

$H_{01}$	AP preyed on NP or not	Score	df	Sig.
Step 0	Variable			
	Attachment sequence	2.034	1	0.154
	Size relationship	2.034	1	0.154
	Overall statistics	4.068	2	0.131
$H_{02}$	AP preyed on RP or not	Score	df	Sig.
Step 0	Variable			
	Attachment sequence	0.033	1	0.855
	Size relationship	116.066	1	0.000*
	Overall statistics	116.099	2	0.000*
$H_{03}$	RP preyed on NP or not	Score	df	Sig.
Step 0	Variable			
	Attachment sequence	33.409	1	0.000*
	Size relationship	43.636	1	0.000*
	Overall statistics	77.045	2	0.000*

Significant difference results were marked \* at the significant level of 0.05.

**2.3 Overview of the sea area**

The sea surface temperature and average salinity of the Bohai Sea, Yellow Sea, and East China Sea ranges from -1.5 to 29.7°C and 30 to 34, respectively. The major ocean currents include the Kuroshio, Yellow Sea Warm Current, Yellow Sea Cold Water Mass, Bohai Sea circulation, and longshore current. The area is characterized by a monsoon climate, which mainly includes a warm temperate monsoon and a subtropical monsoon climate. The most remarkable feature of the topography is the wide stretch of continental shelf, which tilts from northwest to

southeast (Su, 2005). The seafloor mainly consist of argillaceous sediment in the nearshore area and arenaceous sediment in the central and offshore areas (Liu, 1992).

**2.4 Statistical analysis**

Binary logistic regression using SPSS 23.0 was used to test the following three null hypotheses, and GraphPad Prism 8 was used to plot the results:

$H_{01}$ : whether or not AP preyed on NP was not related to attachment sequence and size relationship;

$H_{02}$ : whether or not AP preyed on RP was not related to attachment sequence and size relationship;

$H_{03}$ : whether or not RP preyed on NP was not related to attachment sequence and size relationship.

**3 RESULT**

Neither asexual reproduction nor cyst formation was observed in any treatment during 5 d under the given experimental condition. Polyps of *A. coerulea* preyed on polyps of *N. nomurai* in all treatments containing this pair (Fig.1a) and digested them into white flocculent residues, some of which were released from the *A. coerulea* mouth, within 24 h. The calyx diameter of polyps of *N. nomurai* and *A. coerulea* were 180–430 μm and 360–1150 μm, respectively. AP predation on NP did not differ significantly with attachment sequence or size relationship (Table 2); thus,  $H_{01}$  was not refused.

Polyps of *A. coerulea* preyed on polyps of *R. esculentum* when polyps of *A. coerulea* were larger than polyps of *R. esculentum* and digested them into white flocculent residues within 24 h, regardless of which polyp species attached first. However, the two species could coexist when the polyps of *A. coerulea* were smaller than the polyps of *R. esculentum* for more than 5 d (Fig. 1b). The calyx diameter of polyps of *R. esculentum* and *A. coerulea* were 488–795  $\mu\text{m}$  and 440–1 094  $\mu\text{m}$ , respectively. AP predation on RP differed depending on calyx size (Table 2), and therefore,  $H_{02}$  was rejected. Further analysis of the variables revealed that the predation reaction difference was caused by the calyx size relationship of RP and AP (Table 2).

The polyps of *R. esculentum* preyed on polyps of *N. nomurai* only when RP attached first and the calyx diameter of RP was larger than that of NP. Under these conditions, RP digested NP into white flocculent residues within 24 h. When these conditions were not present, polyps of the two species could coexist for more than 5 d (Fig. 1c). The calyx diameter of polyps of *N. nomurai* and *R. esculentum* were 255–592  $\mu\text{m}$  and 441–626  $\mu\text{m}$ , respectively. RP predation on NP differed depending on conditions (Table 2), thus  $H_{03}$  was rejected. Further analysis of the variables revealed that the predation reaction difference was caused by both the attachment sequence and the calyx size relationship of NP and AP (Table 2).

#### 4 DISCUSSION

In this study, the polyps of *A. coerulea* preyed on the polyps of *N. nomurai*. When AP attached first, NP were captured by the tentacles of AP and placed in the mouth of the polyps within a few hours. When NP attached first, polyps of both species exhibited the capture reaction of the tentacles, but ultimately AP were able to turn upside down, swallow NP, and digest them into white flocculent residues within 24 h. The calyx diameter size relationship of AP and NP did not significantly affect the predation reaction. This finding is not unique among cnidarians, as Kaliszewicz (2013) concluded that larger size did not guarantee competitive superiority among hydras, which are also sessile sit-and-wait predators. Our data showed that the newly formed polyps of *N. nomurai* were preyed upon by the polyps of *A. coerulea*, even when the *A. coerulea* polyps were present for only a short time. Even when the colony of polyps of *N. nomurai* formed first, the newly formed *A. coerulea* polyps preyed on them and took over the living space. These results

indicate that colonies of *N. nomurai* polyps could not survive in locations inhabited by *A. coerulea*.

The polyps of *A. coerulea* are distributed widely in coastal waters (Malej et al., 2012). Our scuba diving group found *A. coerulea* polyps along the coast of Shandong Province (Qingdao), Liaoning Province (Dalian), and Hebei Province (Qinghuangdao), and this distribution might explain why it is so difficult to find *N. nomurai* polyps in the field. Russell (1970) reported that *A. aurita* polyps were not found deeper than 20 m, and a variety of in situ experiments carried out at depths between 0.3 m and 25 m reported the same finding (Brewer, 1978; Hernroth and Gröndahl, 1985; Keen, 1987; Feng et al., 2017). Relative to the medusae of *A. aurita*, which occur mainly in nearshore waters (Dong et al., 2012; Wan and Zhang, 2012) and are rare in deep waters (Zhang et al., 2012), *N. nomurai* is a deep sea species that shows diurnal vertical movement and migration between depths of over 100 m and the surface (Honda et al., 2009). Consequently, we speculate that the polyps of *N. nomurai* might be located in their natural habitat at a depth >20 m in Chinese coastal waters or in locations where polyps of *A. coerulea* are not present. Similarly, Ceh and Riascos (2017) proposed that the polyps of the scyphozoan jellyfish *Chrysaora plocamiai*, whose natural habitat remains unknown, might be located up to 20-m deep based on the results of planulae settlement preference for substrate color.

The results of our experiment showed that polyps of *A. coerulea* preyed on polyps of *R. esculentum* when the calyx diameter size of the former was larger than that of the latter. However, AP could not prey on RP when the calyx diameter of AP was smaller than that of RP; slight damage to the tentacles of RP was detected, but both polyp types survived and coexisted for more than 5 d. Similarly, Li et al. (2012) and Chi et al. (2013) reported that AP and RP could coexist for 24 h. Our results suggest that the ability of AP to prey on RP is determined by the calyx size relationship between the two polyp types, but overall AP is competitively superior to RP, even though colonies of the two species can coexist to some extent.

Polyps of *R. esculentum* and *N. nomurai* coexisted for more than 5 d in most cases, except when *R. esculentum* polyps attached first and when the calyx diameter was larger than that of *N. nomurai*. This result indicates that the polyps of *R. esculentum* are slightly more competitive than those of *N. nomurai*. It might be attributed to the same class and order (Scyphozoan: Rhizostomea) they shared

and similar morphological characteristics (Liu et al., 2009).

The polyps of *A. coerulea* aggressively outcompeted polyps of other species, and this pattern might be true in other coastal areas of the world, especially in areas where blooms of different species of jellyfish co-occur. Intraguild predation by the polyps might be useful for the study of searching for polyps of other species in other areas as well.

## 5 CONCLUSION

In this study, *A. coerulea* and *R. esculentum* polyps were able to coexist to some extents, and the same was true for *R. esculentum* and *N. nomurai* polyps. However, it was almost impossible for *N. nomurai* polyps to settle and form colonies in locations inhabited by *A. coerulea*. Considering the wide distribution of polyps of *A. coerulea* along Chinese coastal seas at a depth of less than 20 m, we propose that *N. nomurai* polyps might be located in the natural habitat at a depth of more than 20 m. Future studies should search for the polyps of *N. nomurai* at greater depths and confirm the location of nursery grounds. The results of this study offer valuable insights into competition between polyps of different co-occurring species of jellyfish that likely will be applicable to other locales.

## 6 DATA AVAILABILITY STATEMENT

All data generated and/or analyzed during this study are available upon request by contacting with the corresponding author.

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