Contribution to the Theme Section 'Jellyfish bloom research: advances and challenges'

Strobilation of three scyphozoans (*Aurelia coelurea*, *Nemopilema nomurai*, and *Rhopilema esculentum*) in the field at Jiaozhou Bay, China

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ABSTRACT: Studies of strobilation of scyphozoan polyp populations in the field are essential for determination of the natural seasonal period of ephyra release and for predicting the size of medusa populations, but they have rarely been conducted. We set up experimental polyp colonies of 3 scyphozoans (*Aurelia coerulea*, *Nemopilema nomurai*, *Rhopilema esculentum*) on settling plates in Jiaozhou Bay, China, and monitored them at 2–7 d intervals for 8 mo (December 2012 to August 2013). Polyps of *A. coerulea* survived, even proliferating by budding during the entire period, while those of *N. nomurai* and *R. esculentum* experienced high mortality and died out after strobilation. Strobilation in all 3 species occurred from late winter to early summer, but the exact timing, duration, frequency, strobilation percentage, and disc numbers strobila^{-1} differed by species. *A. coerulea* started strobilation earliest, on 25 February (temperature: 3.9°C), and persisted for 105 d until 9 June (18.1°C). *N. nomurai* strobilated from 28 March to 9 June (6.4–18.1°C), with some performing a second, less conspicuous strobilation from 6 May to 9 June (12.0–18.1°C). *R. esculentum* strobilated last, from 15 April to 8 July (9.0–21.5°C). Greater polyp population resilience in *A. coerulea* over *N. nomurai* and *R. esculentum* can be attributed, at least in part, to persistent propagation by budding, which may facilitate the annually recurring medusa blooms of *A. coerulea* observed in the region. The latter 2 species may give rise to medusa blooms only when their vulnerable polyps have survived well. Due to the later strobilation, *R. esculentum* ephyrae may be susceptible to competition for food with and predation by post-ephyra stages of *A. coerulea* and *N. nomurai*.

KEY WORDS: Polyp · Ephyra · Survivorship · Artificial substrate · Jellyfish bloom

INTRODUCTION

Jellyfish blooms have raised worldwide concern in recent years owing to their deleterious ecological and socioeconomic impacts (Purcell et al. 2007, Condon et al. 2012, Graham et al. 2014, Pitt & Lucas 2014). Possible causes of jellyfish blooms may be both envi-ronmental and anthropogenic. The latter includes climate change, overfishing, eutrophication, development of aquaculture, and habitat modification (Purcell et al. 2007, Purcell 2012, Duarte et al. 2013, Bayha & Graham 2014). That jellyfish populations have recently increased on a global scale remains to be fully substantiated (Condon et al. 2013), yet

regional cases of definite increase have been documented (Brotz et al. 2012, Boero et al. 2016). The East Asian Marginal Seas (i.e. the Bohai, Yellow, East China, and Japan Seas) are among these hot spots for jellyfish blooms, in particular blooms of large scyphozoan species such as *Aurelia coerulea* (previously designated as *Aurelia* sp. 1; Dawson 2003, Scorrano et al. 2017), *Nemopilema nomurai*, and *Rhopilema esculentum* (Uye 2011, 2014, Dong et al. 2014).

A. coerulea is distributed primarily in temperate Asian waters, including Chinese coastal waters (Ki et al. 2008, Z. Dong et al. 2015). It has bloomed most intensely and more frequently in inlets and bays, such as Jiaozhou Bay in China (S. Wang et al. 2012), Gamak Bay, Masan Bay, and Shiwha Lake in Korea (Hong et al. 2013), and Tokyo Bay and the Inland Sea of Japan (Toyokawa et al. 2000, Ishii 2001, Uye & Ueta 2004). Dense aggregations have disrupted power plant operations, including those at nuclear power stations, by clogging cooling water intakes (Purcell et al. 2007, Graham et al. 2014). More than 4000 t of medusae were cleaned from the clogged intake screens at a nuclear plant in Qinhuangdao, China, in July 2008 (Dong et al. 2010), and there has been increased frequency of shut downs at Korean nuclear power plants (Korean Nuclear Power Plant Operational Performance Information System, http://opis.kins.re.kr/).

N. nomurai is extensively distributed across the East Asian Marginal Seas (Kawahara et al. 2006, B. Wang et al. 2012, Zhang et al. 2012, Yoon et al. 2014), but its strobilation occurs in the coastal Bohai, Yellow, and northern East China Seas (Uye 2014, S. Sun et al. 2015). Its population blooms have become increasingly prominent since 2002 (Ding & Cheng 2005, 2007, Uye 2014, S. Sun et al. 2015), causing serious damage to local fisheries (Kim et al. 2012, Graham et al. 2014), although it is now commercially exploited in China (Dong et al. 2010, Brotz 2016).

R. esculentum is a popular 'edible jellyfish' (Hsieh et al. 2001), and it has been the most heavily harvested among the world's jellyfish species (Brotz 2016). In Chinese coastal waters, it occurs most densely near estuaries (Dai et al. 2004, Jiang et al. 2007, B. Wang et al. 2010, 2012). To compensate for wide stock fluctuations, as well as for decreased catches, stock enhancement projects were started in 1984, and the catch increased by nearly 10-fold (to 0.42 million t) by 1999. However, catches again declined to 0.22 million t in 2010 (Dong et al. 2014). In the coastal waters of western Korea (J. Chae pers. comm.) and in the Ariake Sea, western Kyusha, Japan (Fujii et al. 2014, Malej et al. 2014), intensive blooms of this species have been occurring in recent years.

In order to clarify the mechanisms causing medusa blooms, it is essential to study the ecophysiology of polyps (scyphistomae), as these determine the timing and magnitude of medusa occurrence. Polyps proliferate asexually by various modes: budding, podocyst formation, and release of ephyrae (Kawahara et al. 2006, Lucas et al. 2012, Schiariti et al. 2014). Ephyrae are often released by strobilation in multiple numbers polyp^{-1} (Chen & Ding 1983, Purcell et al. 2012, Uye 2014). Therefore, strobilation is a key process determining the medusa population numbers. The majority of previous studies on factors affecting strobilation have been performed in the laboratory, exploring the critical inducing factors and determining the optimal environmental conditions, including temperature, salinity, light, and food supply (reviewed by Lucas et al. 2012, Purcell et al. 2012). Among those, temperature has been regarded as the principal determinant of strobilation (Chen & Ding 1983, Y. Wang et al. 2012, Kawahara et al. 2013, Fuchs et al. 2014, Feng et al. 2015a,b). However, laboratory results have limitations for accurately predicting the timing of strobilation in the field, where multiple abiotic and biotic factors have effects. Hence, field investigations are of great significance. Previous studies in actual polyp habitats have been primarily confined to the genus *Aurelia*, since its polyps are easily spotted on the undersurface of artificial constructions (Willcox et al. 2008, Purcell et al. 2009, Ishii & Katsukoshi 2010, Toyokawa et al. 2011, Makabe et al. 2014). Polyps of other scyphozoans, however, have been discovered in the field for very few species (Brewer & Feingold 1991, Toyokawa 2011).

Jiaozhou Bay, a semi-enclosed eutrophic bay on the coast of the Yellow Sea, probably harbors *A. coerulea*, *N. nomurai*, and *R. esculentum* (S. Wang et al. 2012), although our SCUBA surveys have discovered polyp colonies only of *A. coerulea* on ascidians and mussel and oyster shells attached to the undersides of wharfs (unpublished). In this study, we established experimental polyp populations of all 3 species on settling plates. We suspended those in Jiaozhou Bay and monitored them in order to clarify their species-specific behaviors, including their releases of ephyrae by strobilation.

MATERIALS AND METHODS

Preparation of polyps

Mature medusae of 3 scyphozoan species were captured in Jiaozhou Bay, on 3 August 2012 for *Aure-*
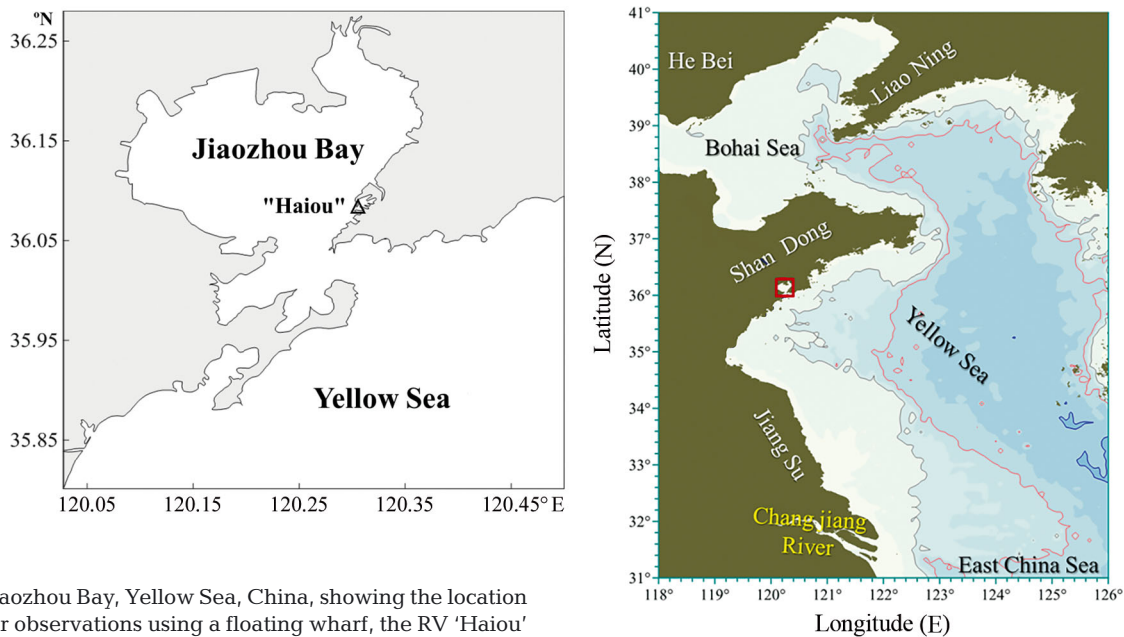
Fig. 1. Jiaozhou Bay, Yellow Sea, China, showing the location (▲) of our observations using a floating wharf, the RV 'Haiou'

lia coerulea and on 28 September 2012 for *Nemopilema nomurai* and *Rhopilema esculentum*. Specimens were immediately transferred to the Institute of Oceanology, Chinese Academy of Science, Qingdao, and 6 females and 4 males of each species were introduced into each of 30 m^3 indoor concrete tanks (5 × 4 × 1.5 m) containing filtered seawater (smallest filter meshes were 1 mm) pumped up from the nearby coast (average salinity ca. 30.5). Sufficient numbers of planulae were produced within 1 wk, when the average water temperature was ca. 25°C for *A. coerulea* and 21°C for *N. nomurai* and *R. esculentum*. Medusae were then removed from the tank, and 10 polyethylene plates (30 × 20 cm) were suspended for 1 wk, so that many 2- to 4-tentacle polyps developed on the plates.

Thereafter, water in the tank was renewed with filtered ambient seawater every day, and polyps were fed with newly hatched *Artemia* sp. nauplii every 4 d until mid-December, when temperature decreased to ca. 5°C. By that time, the majority of polyps had developed to the 16-tentacle stage.

In situ experiment

In mid-December, the polyethylene plates with polyps were cut into pieces (8 × 4 cm), and some polyps were removed with a needle in order to make 1 side of each plate carry a similar number of 16-tentacle polyps having similar body sizes. Numbers per plate were 35, 10, and 30 polyps for *A. coerulea*, *N.*

nomurai, and *R. esculentum*, respectively. Twelve such plates were prepared for each species and placed in plastic containers (80 × 100 × 50 cm) filled with filtered ambient seawater at 5°C for 1 wk starting 17 December. Wild zooplankton collected by a plankton net (mesh size: 0.17 mm) in Jiaozhou Bay was provided as food for the polyps twice during that week. The seawater was replaced on the days following feeding.

On 24 December 2012, the polyp plates were transported to our study site in Jiaozhou Bay, Qingdao (depth range: 4.5–6.0 m, Fig. 1), where a floating wharf (the 'Haiou,' a former research vessel of the Institute of Oceanology, length: 50 m, width: 8 m) was installed for the field experiment. Each plate with polyps hanging down was tied to a plastic disc with 3 cotton strings and suspended in a plastic cylinder (diameter: 10 cm, height: 8 cm) with 63 holes of 1.5 cm diameter. Groups of 3 cylinders were secured with stainless steel wires to an iron grating (60 × 50 cm), which was suspended with a rope from the floating pier (Fig. 2). For each species, a total of 12 plates were submerged, with 3 plates (1 grating) at each of 4 depths: 1, 2, 3, and 4 m below the sea surface.

Monitoring was undertaken weekly by pulling the grating up gently to the deck of the wharf and placing it in a plastic container (80 × 100 × 50 cm) filled with ambient seawater. Each plate was removed from the cylinder and placed in a glass dish (diameter: 20 cm, depth: 7 cm) filled with seawater. After the polyp numbers were counted under a dissecting
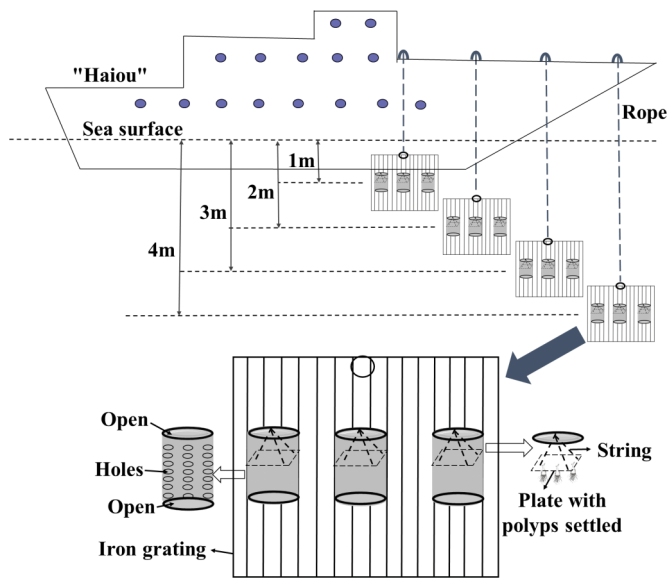
Fig. 2. Set-up of the experiment in Jiaozhou Bay, China. A plate with polyps hanging down was tied to a plastic disc and suspended in a plastic cylinder (diameter: 10 cm, height: 8 cm) with holes. Three cylinders were secured to each of 4 iron gratings (60 × 50 cm), which were suspended with ropes at each of 4 depths from the floating pier (the RV 'Haiou')

microscope, the plates were put back into their cylinders, and the grating was returned to its assigned depth. After signs of strobilation were detected, each plastic cylinder was enclosed with a 100-μm mesh cloth to collect released ephyrae. More intensive monitoring was then conducted at 2–3 d intervals until strobilation was finished. With the aid of a dissecting microscope, we enumerated strobilating polyps (strobilae), disc numbers strobila^{-1}, and released ephyrae. In addition, to determine the strobilation time in detail, we recorded both nascent strobilae, those that displayed the calyx elongated and segmented and the tentacles regressed, and fully-developed strobilae, those with fully developed ephyrae pulsating rhythmically. The time for the above observations was usually less than 5 min plate^{-1}. On each monitoring occasion until 21 August 2013, a vertical profile of temperature and salinity was measured with a CTD meter (AAQ1183-1F, Alec Electronics).

Calculation and statistical analysis

The null hypothesis that strobilation did not significantly differ among depths and species was tested. The following parameters were determined repeatedly with time for 12 plates of each species (3 plates at each

Table 1. Summary of 2-way repeated measures ANOVA results testing the significant difference among depths and species in biological parameters, i.e. percentage of polyps relative to the initial polyp number, strobilation percentage, number of discs strobila^{-1}, and number of ephyrae released by *Aurelia coerulea*, *Nemopilema nomurai*, and *Rhopilema esculentum*

Parameters	Effects	df	F	p
Percentage of polyps	*Treatment effects*			
	Depth	3	0.189	0.903
	Species	2	49.18	<0.001
	Depth×Species	6	0.873	0.529
	Error	24		
	Time effects			
	Time	35	12.647	<0.001
	Time×Depth	105	1.679	<0.001
	Time×Species	70	6.007	<0.001
	Time×Depth×Species	210	1.568	<0.001
	Error	840		
Strobilation percentage	*Treatment effects*			
	Depth	3	2.221	0.112
	Species	2	5.088	0.014
	Depth×Species	6	1.886	0.125
	Error	24		
	Time effects			
	Time	34	8.64	<0.001
	Time×Depth	102	1.505	0.002
	Time×Species	68	6.474	<0.001
	Time×Depth×Species	204	1.089	0.212
	Error	816		
Discs strobila^{-1}	*Treatment effects*			
	Depth	3	0.781	0.516
	Species	2	24.872	<0.001
	Depth×Species	6	0.446	0.84
	Error	24		
	Time effects			
	Time	20	25.136	<0.001
	Time×Depth	60	0.83	0.813
	Time×Species	40	13.042	<0.001
	Time×Depth×Species	120	0.857	0.846
	Error	480		
Number of ephyrae released	*Treatment effects*			
	Depth	3	1.539	0.230
	Species	2	9.103	0.001
	Depth×Species	6	0.448	0.839
	Error	24		
	Time effects			
	Time	34	9.363	<0.001
	Time×Depth	102	0.964	0.581
	Time×Species	68	8.501	<0.001
	Time×Depth×Species	204	0.814	0.964
	Error	816		

of 4 depths): (1) percentage of 16-tentacle polyps relative to the initial polyp number, (2) strobilation percentage, (3) number of discs strobila^{-1}, and (4) number of ephyrae released. Two-way repeated measures ANOVA was used to examine the difference in these parameters among depths, species, and their combina-
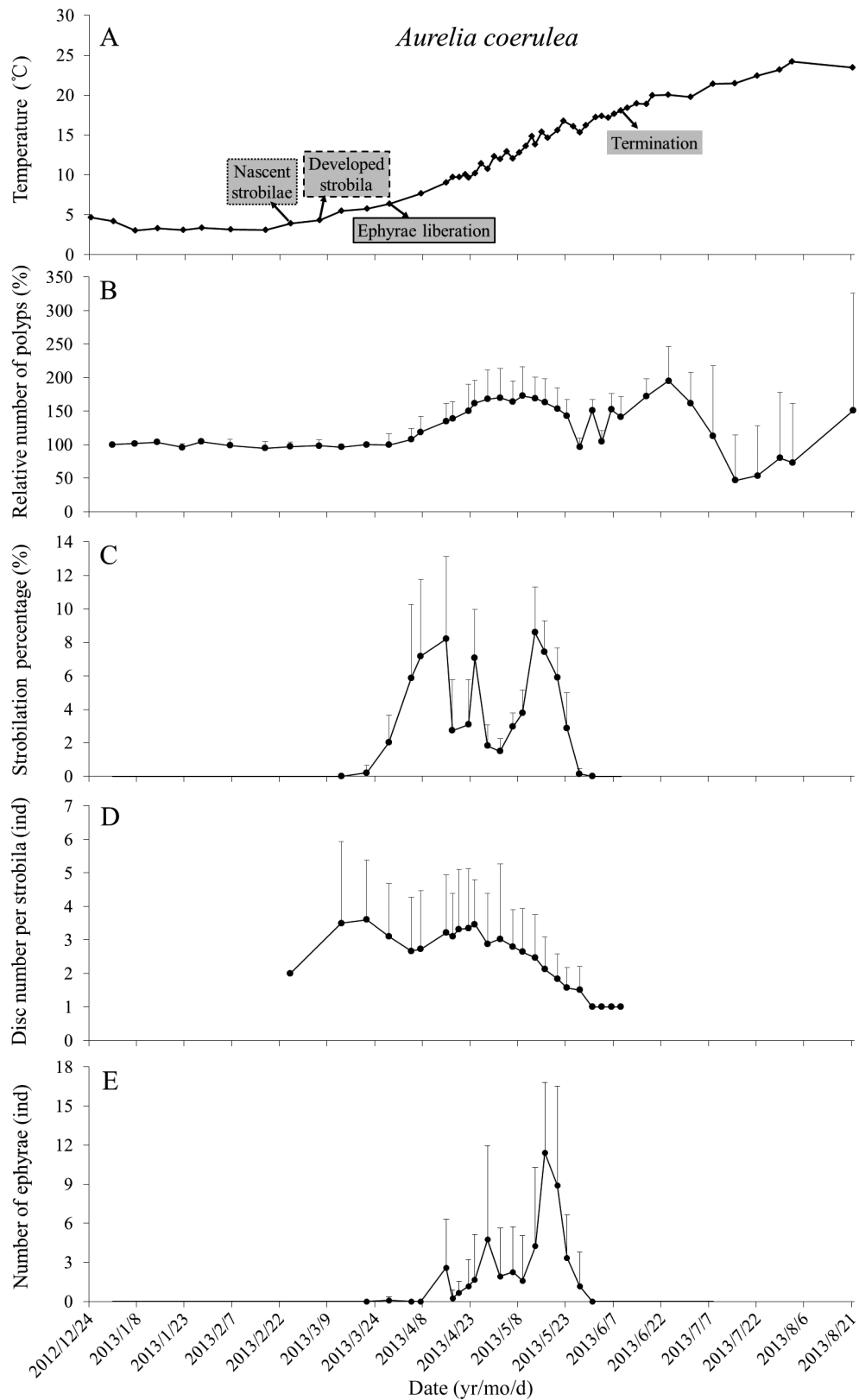
Fig. 3. Time sequence of strobilation of *Aurelia coerulea* observed from December 2012 to August 2013 in Jiaozhou Bay, China. (A) Water-column average temperature with notes on major events, (B) number of surviving 16-tentacle polyps relative to the initial polyp number, (C) strobilation percentage, (D) number of discs strobila^{-1}, and (E) number of ephyrae liberated per plate. Error bars are SD

tions. Percentages were arcsine square root transformed before statistical analysis. For each parameter, the ANOVA results were chosen after Greenhouse-Geisser correction since the data violated the assumption of sphericity according to Mauchly's test of sphericity. As there was no significant difference among depths, but there was a significant difference among species (Table 1), data from 12 plates were pooled to determine their average on each date for each species.

RESULTS

Environmental parameters

From the start of the field experiment on 24 December 2012, the water temperature was vertically homogenous until June, and thereafter it was weakly stratified. The water-column average temperature declined from 4.7°C to the annual minimum of 3.0°C on 7 January, and then it continuously increased to 24.2°C toward the end of the observations (Fig. 3A). The vertical differences in temperature were less than 1°C, except for 2 August, when it was 1.3°C. The salinity was also vertically homogenous, with average salinity fluctuating in a narrow range between 30.4 and 31.0 until 22 July, when it abruptly dropped to the minimum (27.5), followed by a gradual increase toward the end of survey. Only during this recovery period was salinity stratification prominent (maximum vertical difference: 1.5).

Polyp population dynamics and strobilation

Aurelia coerulea

The number of original polyps of *A. coerulea* stayed very stable until 28 March, when the numbers of polyps with 16 tentacles increased prominently from recruitment of new polyps by budding. A first peak (173% of the original polyp numbers) occurred on 9 May. Their numbers then dropped temporarily but peaked again (195%) on 24 June. Similar oscillations followed until the end of experiment (Fig. 3B).

Nascent strobilae were first recorded on 25 February (temperature: 3.9°C), and fully developed strobilae were first seen on 13 March, followed by release of the first ephyra on 28 March (6.4°C, Fig. 3A). Three peaks of strobilation percentage were observed on 15 April, 24 April, and 13 May (Fig. 3C). Polyps apparently never strobilated a second time.

Although enumeration was not possible, some of the daughter polyps also strobilated late in the strobilation period. Strobilation terminated altogether by 9 June (18.1°C).

The number of discs (= ephyrae) strobila^{-1} ranged from 1 to 12. The average (± SD) disc number was relatively high (3.2 ± 0.3) until the end of April, declining thereafter to 1 (Fig. 3D). The total number of ephyrae liberated from each plate was 46.0 ± 16.1 (mean ± SD). There were 3 peaks of ephyra release, each following a strobilation percentage peak, with gradual elevation with increasing temperature. The most prominent peak was recorded on 16 May (11.4 ± 5.4), when the temperature was 14.7°C.

Nemopilema nomurai

Unlike *A. coerulea*, *N. nomurai* polyps never multiplied on the plates submerged in Jiaozhou Bay. Although only a few individuals (≤3 polyps plate^{-1}) produced podocysts in the latter part of the experiment (after mid-May), the polyps from those podocysts eventually died (see 'Discussion'). The numbers of polyps steadily declined until 25 May (mortality: 34%), and thereafter the numbers declined rapidly to 0 on 8 July (Fig. 4B). The first appearance of nascent strobilae was recorded on 28 March (temperature: 6.4°C), the first fully developed strobilae were seen on 15 April, and the liberation of ephyrae started on 17 April (13.9°C; Fig. 4A). Small numbers of polyps, with 4–8 tentacles after strobilation, had elongated and segmented stalks, and their tentacles regressed to prepare for the next strobilation. A second set of nascent strobilae was noted on 6 May (12.0°C), followed by the fully-grown strobilae on 10 May and release of ephyrae on 12 May (14.9°C). Strobilation ceased on 9 June (18.1°C; Fig. 4A).

The percent of polyps in first strobilation showed a prominent, unimodal peak on 28 April (mean ± SD: 48.7 ± 15.4%). The second strobilation was much less extensive, and very variable among plates, with the highest value of 8.3 ± 9.1% recorded on 20 May (Fig. 4C). Disc numbers of the first strobilation varied from 1 to 4, and they were initially only 1 or 2 during the second strobilation. The mean disc numbers gradually increased to 2.4 ± 1.2 strobila^{-1} on 22 April and then rapidly dropped (Fig. 4D). The average total numbers of ephyrae released from each plate were 15.1 ± 7.4 and 1.8 ± 1.6 from the first and second strobilations, respectively. The number of ephyrae released peaked on 2 May at 2.4 ± 1.7, when the temperature was 12.0°C (Fig. 4E).
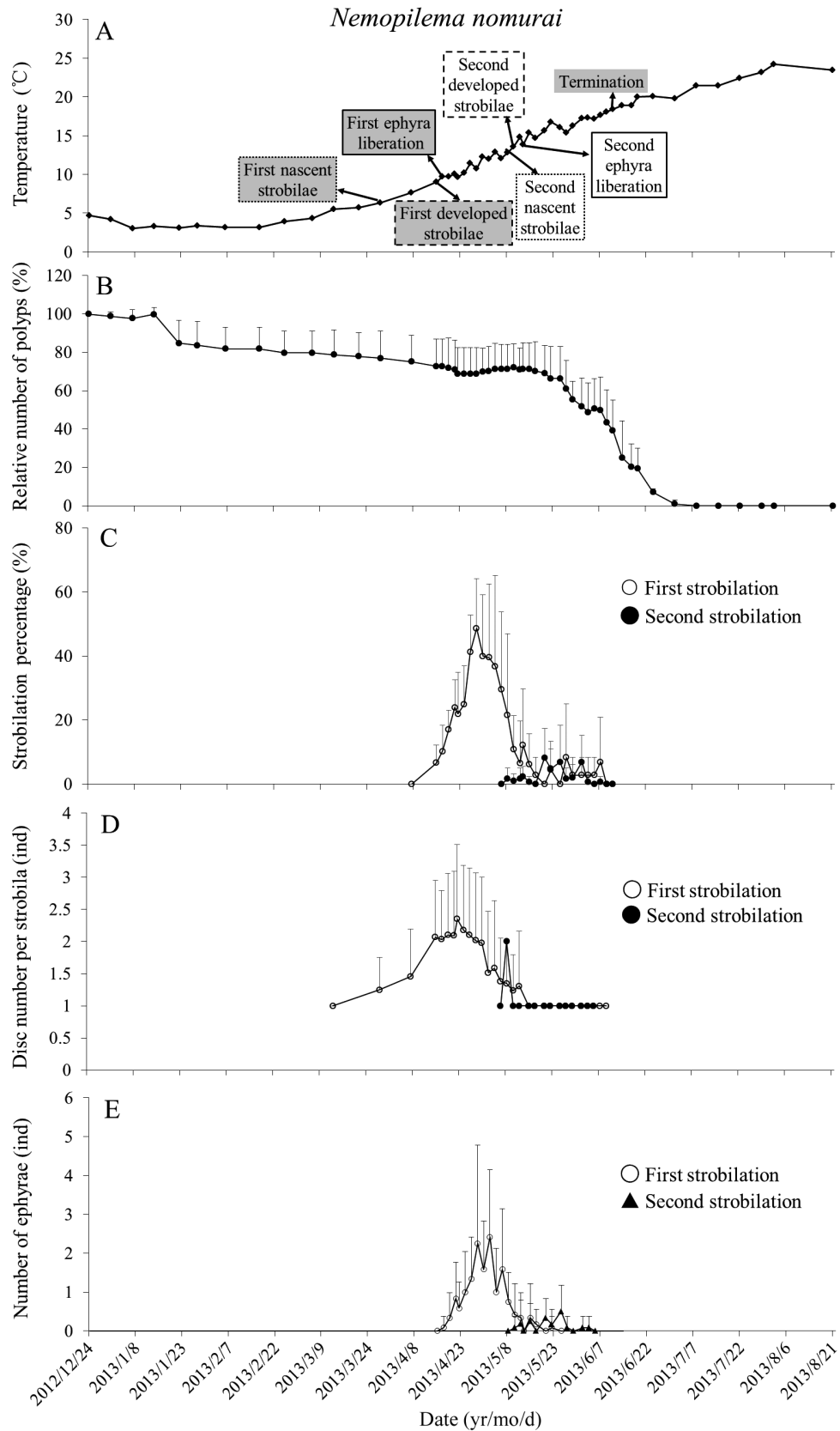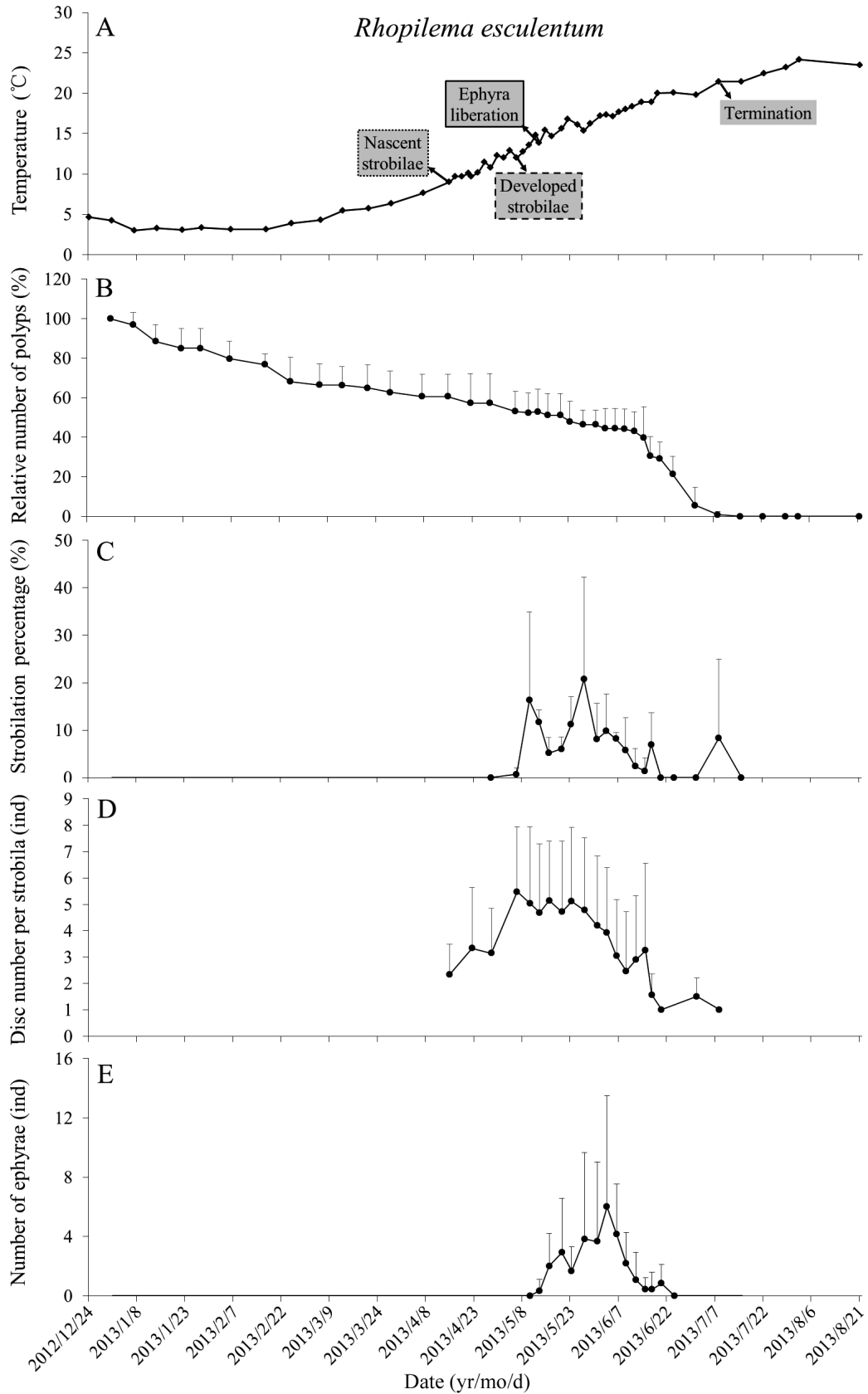
Fig. 4. As in Fig. 3, but for *Nemopilema nomurai*

Fig. 5. As in Fig. 3, but for *Rhopilema esculentum*

Rhopilema esculentum

The survivorship of *R. esculentum* polyps had a similar pattern to that of *N. nomurai*; it fell to 40% by 12 June and then rapidly declined to 0 on 15 July (Fig. 5B), although they produced a small number of podocyts before extinction, as did *N. nomurai*. The first nascent strobilae appeared on 15 April, when the temperature in Jiaozhou Bay was 9.0°C. They developed fully by 6 May and were liberated on 13 May, at 13.9°C. The strobilation percentage was higher in the former period, from 13–27 May, with a maximum of 20.7 ± 21.5% (mean ± SD), compared to the latter period (Fig. 5C). Strobilation continued, though tapering off, until 8 July (temperature: 21.5°C).

Although the disc numbers varied from 1 to 12 strobila^{-1}, the average (± SD) number peaked on 6 May at 5.5 ± 2.5 strobila^{-1}, and gradually decreased thereafter (Fig. 5D). The number of released ephyrae was highest (6.0 ± 7.5) on 3 June, when temperature was 17.4°C (Fig. 5E); the average of total ephyrae plate^{-1} was 29.5 ± 24.1.

DISCUSSION

Different polyp resiliency

The temperature and salinity to which 3 fully-developed polyps placed in Jiaozhou Bay were exposed fluctuated within their preferred environment threshold (Chen & Ding 1983, Lu et al. 1997, Willcox et al. 2007, J. Dong et al. 2015, M. Sun et al. 2015), indicating that the physicochemical environment *in situ* was appropriate for their long-term survival and strobilation. The survivorship or resiliency of the polyp populations differed significantly among the 3 scyphozoan species (Table 1). This may be primarily attributed to different modes of asexual reproduction, i.e. budding by *Aurelia coerulea* and podocyst production by *Nemopilema nomurai* and *Rhopilema esculentum*. During the course of our experiment, fouling organisms such as ascidians and bryozoans increasingly attached to the polyp settling plates, starting in May and attaining their maximum coverage area in June and July, when the highest mortality occurred for *N. nomurai* and *R. esculentum* (Figs. 4B & 5B). Against the biofouling invasion, *A. coerulea* polyps were capable of extending stolons into empty areas on the plates, extending even over ascidians and bryozoans to generate new polyps. In contrast, as the attachment sites of *N. nomurai* and *R. esculentum* polyps were gradually invaded, they lost vitality and disintegrated. The stocks on the plates were finally eliminated by settling animals (Feng et al. 2017). Furthermore, the nudibranch *Sakuraeolis enosimensi* occurred sporadically after April (Feng et al. 2017), and it may have preyed on polyps (Hernroth & Gröndahl 1985, Gröndahl & Hernroth 1987, Hoover et al. 2012, Takao et al. 2014). Greater asexual reproduction of *A. coerulea* by stolon extension and budding could compensate for the biofouling and predation mortality, thus avoiding substantial population destruction (Fig. 3B). Although chitin-covered podocysts of *N. nomurai* and *R. esculentum* could prevent predation loss (Arai 2009, Ikeda et al. 2011), newly excysted polyps were susceptible to both predation and biofouling (Feng et al. 2017). In the final part of the experiment, when temperatures warmed to ≥20°C, biofouling on the settling plates was reduced, and *A. coerulea* polyps multiplied rapidly, reaching a stock size 1.5-fold larger than the initial one. By that time, the *N. nomurai* and *R. esculentum* polyps were completely wiped out, and biofouling had taken up all of their plates.

The post-settlement mortality of polyps, outcompeted by other sessile animals or eaten by predators, is common (Watanabe & Ishii 2001, Colin & Kremer 2002, Lucas et al. 2012). It may constitute a population bottleneck in the life cycles of scyphozoans. Greater resiliency may enable *A. coerulea* polyps to sustain greater benthic populations, which would facilitate recurrent, even annual, blooms of its medusae. In contrast, high mortality of *N. nomurai* and *R. esculentum* polyps may often leave too few to establish a significant bloom. They may only give rise to medusa blooms when polyps can survive well. Although the actual specific polyp habitats of these species remain unidentified, the polyps may need refuges from the settlement of biofouling animals for abundant survival, sites such as inside dead bivalve shells, where polyps of *Cyanea* sp. and *Chrysaora pacifica* have been found (Brewer & Feingold 1991, Toyokawa 2011). To better understand the mechanisms for occasional population explosions of *N. nomurai* and *R. esculentum*, more extensive surveys are needed on their natural polyp habitats and their survival in those. In addition, there are certainly year-to-year variations in initial polyp population size after recruitment of settled planulae from the sexual reproduction of adult medusae (Ohtsu et al. 2007). Excystment from dormant podocysts (Kawahara et al. 2013) may also be significant.

Species-specific strobilation

Previous laboratory studies have indicated that ex-posure to lower temperatures for definite periods is a prerequisite for strobilation, and the threshold tem-perature, below which the strobilation is induced, is surprisingly uniform, i.e. approximately 18°C, for *A. coerulea* (Kakinuma 1962, Han & Uye 2010), *N. nomurai* (Kawahara et al. 2013, Feng et al. 2015a,b), and *R. esculentum* (Chen & Ding 1983). In *N. nomu-rai*, more detailed studies on thermal effects on stro-bilation are available. Kawahara et al. (2013) found that the polyps kept at temperatures ≥19°C did not strobilate at all, but those held at temperatures ≤15°C did. The time required for 50% of them to strobilate was ca. 50 d at both 15 and 11°C, ca. 150 d at 8°C, and further prolonged at lower temperatures. In ad-dition, Feng et al. (2015a) found that polyps that had been exposed to 5°C for a longer time (117 d), stro-bilated more quickly than those chilled for shorter times (40 d), upon placement in an identical warming sequence: 0.5°C increase d^{-1}. These observations in-dicate that seasonal cooling may trigger physiologi-cal changes of polyps preparing them for strobilation, and the subsequent seasonal warming may acceler-ate this mode of reproduction.

The 3 sympatric scyphozoans on our gratings sus-pended in Jiaozhou Bay had different schedules of strobilation, from the first occurrence of nascent stro-bilae to the completion of ephyra liberation (Table 1). Those differences corresponded with different tem-perature ranges: 5–18, 9–18, and 12–21°C for *A. coe-rulea*, *N. nomurai*, and *R. esculentum*, respectively. Apparently there are species-specific differences in the thermal thresholds for strobilation. Strobilating polyps of both *N. nomurai* and *R. esculentum* were founder polyps derived from settled planulae, whereas those of *A. coerulea* contained considerable numbers of daughter polyps, particularly in the later period. Strobilation by 1 or several asexual generations of polyps over a wide temperature range is apparently beneficial for *A. coerulea*, allowing release of more ephyrae.

In this experiment, the strobilation of *A. coerulea* and *R. esculentum* occurred only once, although the latter has been shown in the laboratory to be capable of strobilating 5 times at least during short intervals: 3–14 d at temperatures warming from 18 to 27°C under abundant food supply (Chen & Ding 1983). To our knowledge, preparation for a second strobilation after the first has not been reported for *A. coerulea*. In Jiaozhou Bay, a small number of our post-strobila *N. nomurai* performed a second strobilation after ca.

3 wk, although those were much less extensive than their first. This might be attributed to sufficient energy reserves contained in some of the strobilated polyps. Failure of the second strobilation by *R. esculentum* implies either insufficient energy reserves or the loss of suitable polyps by competition and predation of other settling animals. The nutritional conditions might also affect the numbers of discs strobila^{-1}. Their means (± SD) during the early strobilation periods (3.2 ± 0.1, 1.8 ± 0.5, and 4.3 ± 0.1 for *A. coerulea*, *N. nomurai*, and *R. esculentum*, respectively) were about half of the numbers produced by well-fed polyps in the lab-oratory (Chen & Ding 1983, Kawahara et al. 2006, Feng et al. 2015a, Wang & Li 2015). This suggests that the food supply in this eutrophic embayment was insufficient for the polyp populations to attain their potentials for ephyra production.

Interspecific competition for medusa bloom formation

In Jiaozhou Bay, *A. coerulea*, *N. nomurai*, and *R. esculentum* are sympatric, and their medusae often occur massively in coastal waters of the Bohai and Yellow Seas (B. Wang et al. 2012, 2013, Zheng et al. 2014). The time sequence of strobilation observed for these species in Jiaozhou Bay may also be applicable to those wider areas, as demonstrated in previous surveys on the umbrella diameters of field popula-tions, which were notably larger in early June for *A. coerulea* (5–15 cm) and *N. nomurai* (5–45 cm) than for *R. esculentum* (1–3 cm) (B. Wang et al. 2010, 2012, 2013, Wang & Sun 2015, S. Sun et al. 2015), implying that the former 2 species get earlier starts on their pelagic life phase, based on a similar growth rate from their ephyra to young medusa stages (ca. 0.1 d^{-1}, Ding & Chen 1981, Kawahara et al. 2006, Wang et al. 2015).

Ephyrae, metephyrae, and medusae of these scy-phozoans are primarily zooplanktivores (Uye & Shi-mauchi 2005, Uye 2008, Wang et al. 2010). However, recent studies have revealed that an *A. coerulea* medusa of 10 cm umbrella diameter can ingest as many as 57 *R. esculentum* ephyrae d^{-1} in the labora-tory (Li et al. 2012) and can ingest 1–2 d^{-1} of young *R. esculentum* medusae with umbrella diameters of 1–3 cm (Chi et al. 2013). Because of the later strobila-tion, *R. esculentum* ephyrae are subjected to inter-specific competition for food with and predation by post-ephyra stages of *A. coerulea* and *N. nomurai*. In the last 2 decades, both *A. coerulea* and *N. nomurai* have bloomed frequently, but *R. esculentum* blooms

have appreciably decreased (S. Wang et al. 2012, Dong et al. 2014), which might be attributed to increased impacts from the seasonally earlier *A. coerulea* and *N. nomurai* medusae.

CONCLUSIONS

An 8 mo monitoring of polyp populations of 3 bloom-forming scyphozoans (*Aurelia coerulea*, *Nemopilema nomurai*, and *Rhopilema esculentum*) established on settling plates and suspended in Jiaozhou Bay, China, revealed clear specificities in their population resiliency and the thermal thresholds triggering strobilation. The reproductive potential of *A. coerulea* was much higher, due to stolon extension and budding to generate new polyps, than those of *N. nomurai* and *R. esculentum.* The latter 2 could generate polyps asexually only by means of podocyst production. Thus, *A. coerulea* could survive biofouling and the impacts of predators coinciding especially with the late strobilation period, and its final polyp population increased to 1.5 times its initial density. The other 2 species were subjected to mortality great enough that they completely vanished. The thermal threshold triggering strobilation was lowest and widest in *A. coerulea*, as its strobilation started earliest and lasted longest, followed by *N. nomurai* and then *R. esculentum*. These physio-ecological characteristics of the polyp stage may be advantageous for more consistent formation of medusa blooms by *A. coerulea* than is observed for the other 2 species. For higher survival, polyps of *N. nomurai* and *R. esculentum* may need a better refuge from the settlement of biofouling animals. Perhaps when their polyps can survive abundantly is when they will give rise to medusa blooms.

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