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Effect of temperature and food type on asexual reproduction in *Aurelia* sp.1 polyps

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Abstract Environmental factors such as temperature and food type affect the rate of asexual reproduction of jellyfish at the polyp stage. Combinations of three temperatures (10, 15, and 20°C) and four food treatments (*Prorocentrum donghaiense*, *Skeletonema costatum*, *Artemia* sp. nauplii, and no food) were established to examine the asexual reproduction strategy of *Aurelia* sp.1. The results allowed us to reject two null hypotheses: no effect of temperature and no effect of food. A change from 20 to 15 or 10°C induced polyps to release ephyrae when food was present, while polyps without food did not strobilate. Polyps with *Artemia* sp. nauplii as prey produced more polyps through buds and podocysts, as well as more ephyrae through strobilation. At 20°C, the mortality rates of polyps exceeded 50%, except for those served by *Artemia* sp. nauplii. The number of polyps increased rapidly with *Artemia* sp. nauplii as prey. We conclude that when animal prey is limited, plants can serve as a nutrient source and satisfy the energy requirements for polyps at lower temperatures (10 or 15°C). Phytoplankton cannot provide adequate nutrition to polyps at higher temperature (20°). Abundant animal prey and suitable temperatures are essential conditions for polyps to strobilate and release ephyrae, leading to jellyfish blooms.

Keywords *Aurelia* sp.1 · Temperature · Food type · Asexual reproduction · Bloom

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Introduction

In the past 20 years, published studies on gelatinous zooplankton (jellyfish and Ctenophores) have increased in number (Condon et al., 2012). In particular, in recent decades, an abundance of jellyfish has been noted in marine ecosystems worldwide (Uye & Shimauchi, 2005). Blooms of jellyfish cause damage to marine ecosystems and have economic impact. For example, their gelatinous bodies clog cooling systems in coastal industrial facilities (Dong et al., 2012). Jellyfish have negative effects on the tourism industry

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because they sting swimmers (Purcell et al., 2007). Jellyfish blooms negatively affect the health of marine ecosystems because they compete with fish for food and they feed on fish larvae and small fish (Sabates et al., 2010). Many ecologists consider that increasing numbers of jellyfish could even result in an ecological problem, by replacing fish and coming to dominate marine ecosystems (Michael et al., 2013).

The common moon jellyfish, *Aurelia aurita* (Linnaeus) s. l., is a cosmopolitan species-complex with a worldwide distribution in neritic waters between 70°N and 40°S (Kramp, 1961; Lucas, 2001). Mitochondrial and nuclear DNA sequence data indicate that there are many sibling species of *A. aurita* s. l. worldwide, and the species found in the seas of Japan, Korea, and China is *Aurelia* sp.1 (Dawson & Martin, 2001; Dawson et al., 2005; Ki et al., 2008). As it is common in coastal waters, its damaging effects are particularly apparent (Sun et al., 2011). The life cycle of *A. aurita* consists of an alternation between an attached asexual polyp phase and a planktonic sexual medusa phase. The population size, survival rate, and the habitat of the polyps all influence the size of the adult medusa population (Kawahara et al., 2006). At the stage of asexual reproduction, parent polyps form new polyps through buds and stolons, and also release ephyrae, which develop into medusae (Malej et al., 2012). Thus, the existence of a large number of polyps underlies the production of large quantities of jellyfish. Reproductive and survival rates affect the population size of medusae (Lucas, 2001). Environmental factors are critical for strobilation, and polyps may be adapted to the specific conditions in the areas they inhabit. When the temperature is suitable for strobilation, ephyrae are released (Willcox et al. 2007a, b, Purcell et al., 2012). It was noted that the temperature played a decisive role in determining the size of a temperate population of *A. aurita* s.l. medusae, strobilation occurring when the temperature increased (Miyake et al., 2002).

Several studies have suggested that medusae of *A. aurita* regulate the quantity of phytoplankton indirectly by grazing on the zooplankton. Phytoplankton plays a critical role in the circulation of materials and energy flow in marine ecosystems (Jassby et al., 2002). Many species such as *Prorocentrum donghaiense*, *Skeletonema costatum* sensu lato, *Karenia mikimotoi, Alexandrium catenella, Noctiluca scintillans*, and *Scrippsiella trochoidea* can form red tides, reaching high concentrations at different times and locations (Zhou et al., 2008). Although these organisms are the primary producers in marine ecosystems at the base of the food web, few studies have examined the direct effects of jellyfish feeding on phytoplankton, particularly by ephyrae or polyp stages (Båmstedt et al., 2001). Båmstedt et al. (2001) reported that ephyrae are able to feed on phytoplankton, but no quantitative data were provided. In contrast, Zheng et al. (2012) found that polyps of *Aurelia* sp.1 were able to feed on *P. donghaiense* and *S. costatum* sensu lato. As reproduction of polyps plays a key role in jellyfish blooms, further research into the relationships among polyps, ephyrae, and phytoplankton is necessary (Wang et al., 2012). Polyps are observed on the undersides of docks in harbors (Miyake et al., 2002), but we know little about the responses of the polyp stage to different environmental factors in natural waters. Laboratory investigations have shown that environmental factors and stressors, such as temperature, pH, salinity, and light intensity, affect the induction, magnitude, and timing of the strobilation process (Liu et al., 2009; Holst, 2012).

No previous studies had been conducted on the long-term cultivation of *Aurelia* sp.1 polyps with phytoplankton as a food source. The aim of this study was to explore the relationship between jellyfish and red tides through laboratory simulation. To test the relationships, we hypothesized that the food and temperature had no effect on growth. We cultured *Aurelia* sp.1 polyps at three temperatures and with four food treatments, *P. donghaiense*, *S. costatum* sensu lato, *Artemia* sp. nauplii, and no food. We examined the effect of temperature and food type on asexual reproduction, whether phytoplankton can serve as food for polyps, and the relationship between phytoplankton and the release of ephyrae.

Materials and methods

Aurelia sp.1 polyps were obtained from Institute of Oceanology, Chinese Academy of Sciences, Qingdao. The polyps were produced from medusae collected from nearby Jiaozhou Bay and were attached to the plates cultivated in the laboratory for more than 1 year. Prior to the experiment, we cut out sections of the plates (2 × 3 cm) with healthy polyps, retaining 18 polyps of similar size, and eliminating the remaining polyps,

buds, and podocysts. To prevent the prior conditions from stimulating strobilation, polyps were kept for more than 1 month in a darkened incubator at 20°C without food before starting the experiment.

Two orthogonal treatment sets were established. The first was temperature with three levels (10, 15, and 20°C) spanning the temperature range in late spring and early summer in northern Chinese waters. The second treatment set consisted of four food conditions (*P. donghaiense*, *S. costatum* sensu lato, *Artemia* sp. nauplii, and unfed) (Sarno et al., 2007). Eighteen polyps with 16 tentacles were arbitrarily allocated to each of the twelve combinations of temperature and food supply, with three replicates of each combination. Polyps were placed in 1-l *Nalgene* wide-mouth bottles and cultured with 0.45 μm filtered seawater from Jiaozhou Bay. The salinity of water used in this experiment was about 31. The experiment began on 4th October 2011.

Incubators were used to maintain the three temperatures. Photoperiod was maintained at 12 h light:12 h dark, simulating the light conditions in late spring and early summer. Initially, the polyps were moved into their treatment temperatures but kept in the dark and unfed for 1 week. Thereafter, polyps were fed daily with the appropriate food at high density (*P. donghaiense* 1×10^4 cells/ml, *S. costatum* 6×10^4 cells/ml, *Artemia* sp. nauplii (10 ind./ml). Each day, the polyps were transferred to a new bottle of fresh filtered seawater (pore size 0.45 μm) of the same temperature and salinity 1 h after feeding. During data collection, they were exposed to indirect room light and microscope illumination for about 5 min, once per week. The numbers of new buds, polyps with buds, and podocysts were counted once per week; ephyrae were counted in each bottle at each water change. After counting, ephyrae were removed but new buds and podocysts were not removed and were retained as natural growth. The experiment lasted 77 days.

Several characteristics were defined for analysis: The time from the beginning of the experiment to the death of half of the polyps was the "survival period" (SP); the time from the beginning of the experiment to the beginning of strobilation was the "pre-strobilation period" (Pre-str); the time from the beginning of strobilation to the release of the first ephyrae was the "bet-strobilation period"; and the time from the first release of ephyrae to the release of the last ephyrae was the "strobilation period"(Str). Microsoft Excel was used for descriptive statistics and the data were analyzed by two-way analysis of variance (ANOVA) using SPSS. A post hoc test (Tukey's HSD test) was used to identify which treatments (temperature and food type) were causing the overall effect of group differences in the ANOVA test.

Results

The effects of combinations of temperature (10, 15, and 20°C) and food treatments (*P. donghaiense*, *S. costatum*, *Artemia* sp. nauplii, and unfed) on polyps were examined (Table 1). Effects of temperature, food, and temperature × food were significant for the pre-strobilation period, the strobilation period, the survival period, and the number of ephyrae ($P < 0.01$); there were no significant effects of temperature on Polyps ($P > 0.05$).

SP (survival period) is the time from the beginning of the experiment to the death of half of the polyps. Pre-str is the time from the beginning of the experiment to the beginning of strobilation. And Str is the time from the first release of ephyrae to the release of the last ephyrae.

A post hoc test (Tukey's HSD test) showed that the average number of polyps diverged significantly for *Artemia* sp. nauplii compared to other food types. In addition, there were no significant differences among the average number of polyps for *S. costatum*, *P. donghaiense*, and unfed, while no significant variation was found in average number of polyps for three temperature treatments (Table 2).

A post hoc test (Tukey's HSD test) showed that Pre-str diverged significantly for *Artemia* sp. nauplii compared to other food types. In addition, there were no significant differences among pre-str for *S. costatum*, *P. donghaiense*, and unfed, while Pre-str diverged significantly for three temperature treatments (Table 3).

A post hoc test (Tukey's HSD test) showed that Str diverged significantly for *Artemia* sp. nauplii compared to *P. donghaiense* and unfed food types. In addition, there were no significant differences among Str for *S. costatum*, *P. donghaiense*, and unfed, while no significant variation was found in Str for *Artemia* sp. nauplii and *P. donghaiense*. Str diverged significantly for 15°C compared to 10 and 20°C treatment, while no significant variation was found in Str for temperatures 10 and 20°C(Table 4).

Table 1 Results of two-way ANOVA on the effects of temperature and food type on polyp

Variable tested					
	Polyps	Pre-str	Str	SP	Ephyrae
Temperature	$F(2,11) = 7.1$ $P = 0.277$	$F(2,11) = 120.7$ $P < 0.001$	$F(2,11) = 79.9$ $P < 0.001$	$F(2,11) = 4.6$ $P = 0.002$	$F(2,11) = 12.2$ $P = 0.045$
Food	$F(3,11) = 454.9$ $P < 0.001$	$F(2,11) = 79.5$ $P < 0.001$	$F(2,11) = 67.9$ $P < 0.001$	$F(2,11) = 1.0$ $P = 0.005$	$F(2,11) = 22.4$ $P < 0.001$
Temperature × food	$F(6,11) = 14.7$ $P < 0.001$	$F(6,11) = 17.3$ $P < 0.001$	$F(6,11) = 14.5$ $P < 0.001$	$F(6,11) = 0.8$ $P < 0.001$	$F(6,11) = 10.7$ $P < 0.001$

Polyps is the number of polyps observed in the experiment. SP is the time from the beginning of the experiment to the death of half of the polyps. Pre-str is the time from the beginning of the experiment to the beginning of strobilation. Str is the time from the first release of ephyrae to the release of the last ephyrae. Ephyrae is the number of ephyrae produced in the experiment

Table 2 Results of post hoc tests (Tukey's HSD test) on the on average number of polyps in all treatments

Food type	Average	Food type		
		P. donghaiense	*S. costatum*	Unfed
Artemia sp. nauplii	164.85	0.000	0.000	0.000
P. donghaiense	19.74		0.931	0.837
S. costatum	14.07			0.995
unfed	11.847			

Temperature (°C)	Average	Temperature	
		15°C	20°C
10	49.50	0.42	0.99
15	63.67		0.52
20	52.33		

Table 3 Results of post hoc tests (Tukey's HSD test) on the on Pre-str in all treatments

Food type	Average	Food type		
		P. donghaiense	*S. costatum*	Unfed
Artemia sp. nauplii	44.51	0.213	0.156	0.000
P. donghaiense	52.29		0.857	0.000
S. costatum	53.40			0.001
unfed	77.00			

Temperature (°C)	Average	Temperature	
		15°C	20°C
10	56.00	0.009	0.001
15	39.33		0.000
20	77		

A post hoc test (Tukey's HSD test) showed that SP diverged significantly for *S. costatum* compared to *Artemia* sp. nauplii, *P. donghaiense*, and unfed food classes. In addition, there were no significant differences among SP for *Artemia* sp. nauplii, *P. donghaiense*, and unfed. SP diverged significantly for 20°C compared to 10 and 15°C treatments, while no significant variation was found in SP for temperatures 10 and 15°C (Table 5).

Table 4 Results of post hoc tests (Tukey's HSD test) on the on Str in all treatments

Food type	Average	Food type		
		P. donghaiense	*S. costatum*	Unfed
Artemia sp. nauplii	20.45	0.007	0.159	0.000
P. donghaiense	5.12		0.517	0.564
S. costatum	11.12			0.053
Unfed	0			
Temperature (°C)	Average	Temperature		
		15°C		20°C
10	8.13	0.022		0.234
15	21			0.000
20	0			

Table 5 Results of post hoc tests (Tukey's HSD test) on the on SP in all treatments

Food type	Average	Food type		
		P. donghaiense	*S. costatum*	Unfed
Artemia sp. nauplii	77.00	0.253	0.001	0.564
P. donghaiense	73.40		0.017	0.564
S. costatum	63.29			0.004
unfed	75.74			
Temperature (°C)	Average	Temperature		
		15°C		20°C
10	77.00	0.374		0.011
15	77.00			0.000
20	63.00			

A post hoc test (Tukey's HSD test) showed that the average number of ephyrae diverged significantly for unfed compared to other food types. In addition, there were no significant differences among the average number of ephyrae for *Artemia* sp. nauplii, *S. costatum,* and *P. donghaiense*. Average number of ephyrae diverged significantly for 15°C compared to 20°C treatment, while no significant variation was found in the average number of ephyrae for temperatures 10 and 15°C, and 10 and 20°C (Table 6).

Survival period

Survival of polyps during the first few weeks was high. Among the twelve combinations, polyps died only in the 15°C-unfed, 20°C–*P. donghaiense*, 20°C–*S. costatum*, and 20°C-unfed treatments. The time from the beginning of the experiment to the death of half of the polyps was the "survival period" (SP). The shortest survival period was 42 days in the 20°C–*S. costatum* treatment. The survival period was 63 days in 20°C–*P. donghaiense* treatment and 70 days in the 20°C-unfed group (Fig. 1).

Number of polyps

During the 77 days of the experiment, the number of polyps increased in every group that was fed with *Artemia*, with higher rates of increase at higher temperatures (Fig. 2). Polyp number increased in the 10°C–*P. donghaiense* group and the 15°C–*P. donghaiense* group; in this case, the polyp number increased at the beginning of the experiment, but it decreased suddenly later in the experiment in the 20°C–*P. donghaiense* group. The number of polyps remained stable in the 10°C–*S. costatum* group and increased in the 15°C–*S.*

Table 6 Results of post hoc tests (Tukey's HSD test) on the on average number of ephyrae in all treatments

Food type	Average	Food type		
		P. donghaiense	*S. costatum*	Unfed
Artemia sp. nauplii	62.57	0.002	0.002	0.001
P. donghaiense	2.00		1.000	0.999
S. costatum	2.22			0.999
Unfed	0.00			

Temperature (°C)	Average	Temperature	
		15°C	20°C
10	12.75	0.304	0.830
15	39.42		0.031
20	0.00		

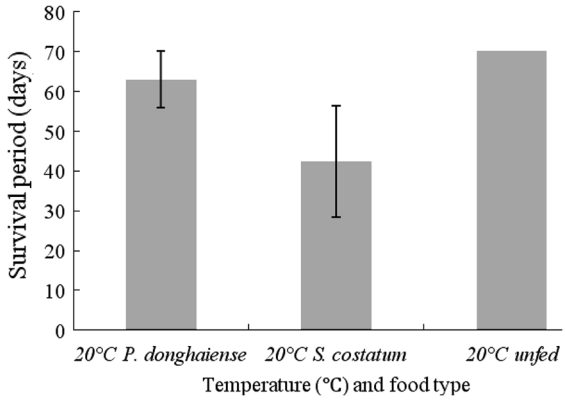

Fig. 1 Survival period of polyps in combinations of temperature and food. *Error bars* represent standard deviation

costatum group, but decreased in the 20°C–*S. costatum* treatment. Polyp number increased slowly in the 10°C-unfed group. In the 15°C-unfed treatment, the number increased slightly at the beginning of the experiment but decreased later (Fig. 2B). In the 20°C-unfed group, the number also increased initially but later decreased suddenly. The greatest increase in the number of polyps was observed in the *Artemia*-fed groups, at all three temperatures. At 10°C, the number of polyps increased in the group fed with *P. donghaiense*, and remained constant in the group fed with *S. costatum* and the unfed group. At 15°C, the number of polyps increased in groups fed with *P. donghaiense* and *S. costatum*, more greatly in the former group, and decreased in the unfed group. At 20°C, the polyp number decreased in the *P. donghaiense*, *S. costatum*, and unfed groups, but the change was not statistically significant. The number decreased by more than one half in the 20°C–*P. donghaiense*, 20°C–*S. costatum*, and 20°C-unfed combinations (Fig. 2C).

Occurrence rate of podocysts and ratio of existing numbers of podocysts and polyps

Podocysts occurred in each combination of the experiment (Fig. 3) and were observed in the unfed groups at each (weekly) observation time. The ratio of podocysts and polyps formation was highest in the unfed groups and lowest in the groups fed with *Artemia*. Polyps died and podocysts did not germinate in the 20°C–*P. donghaiense*, 20°C–*S. costatum*, and 20°C-unfed groups. The occurrence of podocysts and the ratio of existing numbers of podocysts and polyps were lower in the groups fed with *Artemia* than those fed with *P. donghaiense* and *S. costatum*.

Strobilation period

During the 77-day experiment, polyps strobilated in the 10 and 15°C groups supplied with food. Those in the 10°C-unfed, 15°C-unfed, and all of the 20°C groups did not strobilate. The period between the start of the experiment and the commencement of strobilation is referred to as the "pre-strobilation period" (Pre-str). Pre-strobilation periods were shorter in the 15°C groups than in the 10°C groups (Fig. 4). Relatively higher temperatures (15°C) favored

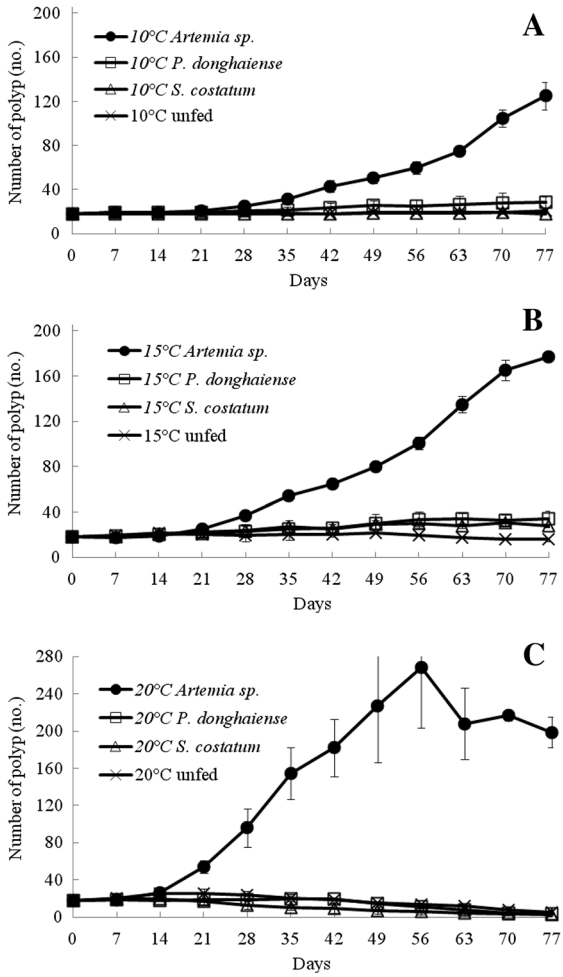

Fig. 2 **A**–**C** Changes in numbers of polyps under different conditions of temperature and food. *Error bars* represent standard deviation

strobilation, presumably because the time for the polyps to respond to environment factors was shorter. In the 10°C-*Prorocentrum donghaiense* group, strobilation occurred but some of the strobilae reverted to polyps before releasing ephyrae. Strobilation period was the longest in the 15°C-*Artemia* group.

Ephyra production

Polyps released ephyrae in the groups at 10 and 15°C supplied with food. No ephyrae were released in the 20°C groups, 10°C-unfed group, or 15°C-unfed group. Polyps produced more ephyrae at 15°C than at 10°C (Fig. 5). Polyps in groups fed with *Artemia* produced more ephyrae than in the other food groups. Polyps in the 15°C-*Artemia* group produced the largest number of ephyrae.

Discussion

In contrast to two earlier studies (Liu et al., 2009; Purcell et al., 2012), we did not remove new buds and podocysts, thus preserving the normal state of growth and reproduction. New polyps produced from buds and podocysts may undergo asexual reproduction, producing further buds, podocysts, and ephyrae. Thus, in the groups that provided favorable conditions for polyps, the cumulative numbers of polyps increased in the course of our experiment. This was similar to the growth and reproduction process in natural situations and provides new information relevant to the generation of jellyfish blooms.

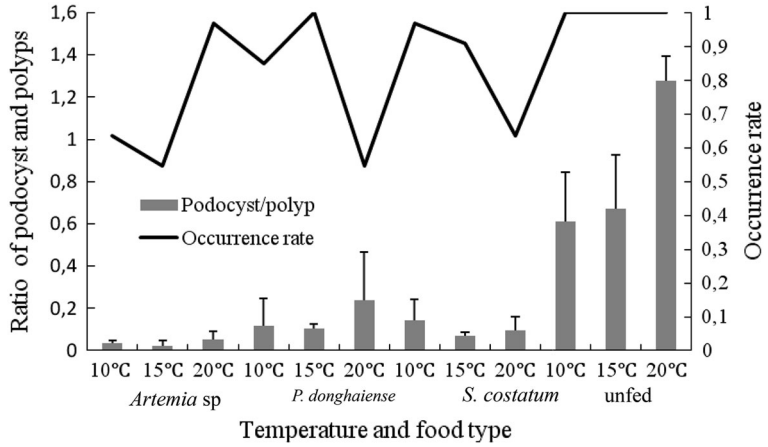

Fig. 3 Occurrence rate of podocyst and ratio of existing numbers of podocysts and polyps. *Error bars* represent standard deviation

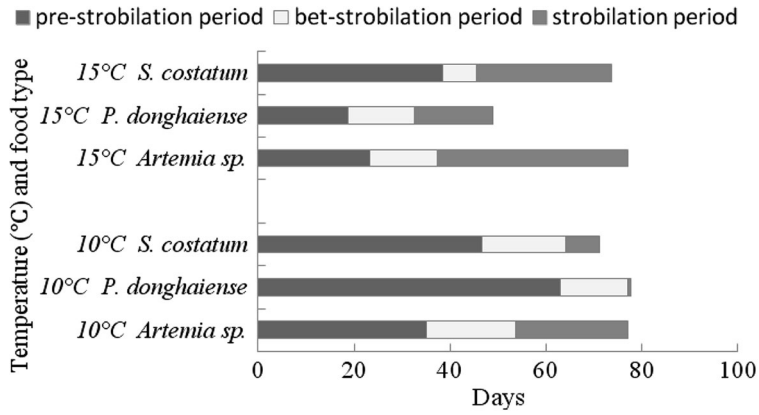

Fig. 4 Duration of pre-strobilation period (*black bars*), bet-strobilation (*white bars*), and strobilation period (*gray bars*) in a 77-day experiment with different combinations of temperature and food

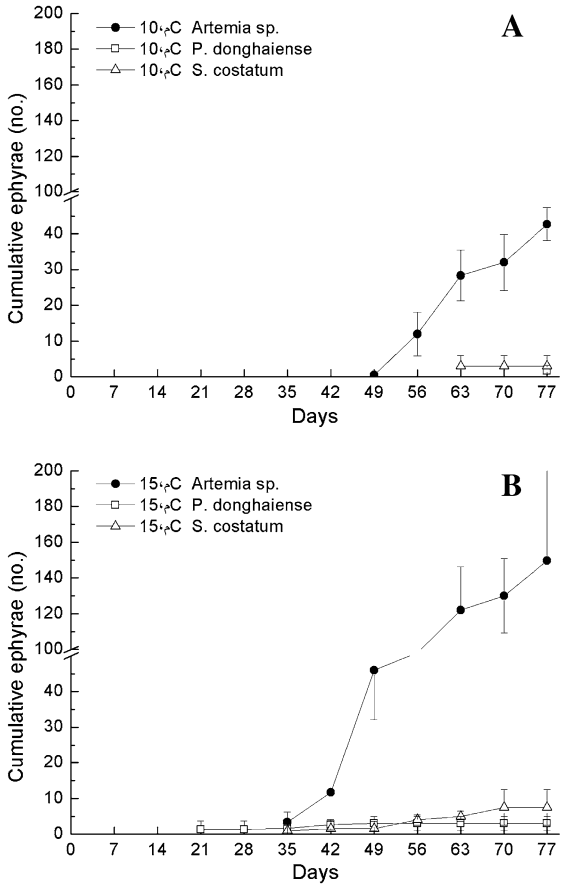

Fig. 5 **A**, **B** The cumulative numbers of ephyrae in treatments with different combinations of temperature and food. *Error bars* represent standard deviation

Effect of temperature

In this research, temperature was a key factor determining strobilation and release of ephyrae, i.e., the process that leads to the transformation of the attached asexual polyp phase into the planktonic sexual medusa phase. Polyps initially taken from water at 20°C were transferred to the experimental temperatures. Those in the groups at 20°C did not strobilate, but at 10 and 15°C, strobilation and release of ephyrae occurred, illustrating the crucial importance of temperature for strobilation. This observation is in accordance with previous reports (Liu et al., 2009; Willcox et al. 2007a, b).

The hypothesis that the temperature has no effect on the growth of polyps was rejected. Higher temperature (15°C) accelerated strobilation, with shorter induction time and release of greater numbers of ephyrae at 15°C than at 10°C. In our experiments, polyps changed their life cycle stage from the attached asexual polyp phase to the planktonic sexual medusa phase, when they were induced to strobilate and produce ephyrae at temperatures that declined to 15°C or below. We conclude that the temperature change is an indispensable condition for strobilation.

In summer, the high temperature of seawater and sufficient food are advantageous for polyps to expand the population. Large numbers of polyps are then ready to strobilate when the temperature rises in the following spring, providing the foundation for a jellyfish bloom. Polyps survived in all treatment groups at the lower temperatures of 10 and 15°C. However, mortality rates greater than 50% were observed for the polyps in the 20°C–*P. donghaiense*, 20°C–*S. costatum*, and 20°C-unfed groups. As there is little information on the death rate of polyps in natural waters, it is not easy to draw conclusions concerning the effect of phytoplankton on polyps at high temperatures. More research should be directed toward the

survival rates of polyps during red tide blooms in natural waters. The energy requirements of polyps are low at low temperatures, and a relatively low food supply is able maintain the survival of polyps. Energy requirements increase progressively with temperature increase (Liu et al., 2009).

Food type

Our study has investigated phytoplankton as a food source for culture of polyps. At low temperatures, *P. donghaiense* and *S. costatum* were able to maintain survival and asexual reproduction of polyps, and strobilation and release of ephyrae took place when temperature was suitable (10 or 15°C). At high temperature (20°C), the polyps in the *P. donghaiense* and *S. costatum* fed exhibited greater than 50% mortality, which was similar to the unfed groups. The hypothesis that food type has no effect on the growth of polyps was rejected and phytoplankton can serve as a nutrient source for polyps, but it represents a lower quality food than *Artemia* for the polyps.

There are reports that bottom-dwelling polyps capture food from the water column and also feed regularly on the substrate, polyps also consume algae (Hernroth & Grondahl, 1985). Polyps actively feed on micro-phytoplankton (*Gyrodinium instriatum* and *Cochlodinium convolutum*), but the feeding rate on these organisms (22–52 individual^{-1} h^{-1}) is significantly lower than that of ciliates with a similar equivalent spherical diameter (ESD) on the same type of organisms (Kamiyama, 2011). In the present study, polyps that were fed on *P. donghaiense* and *S. costatum* at 10 and 15°C were able to survive and reproduce through buds, podocysts, and strobilation. In the 10°C groups, the efficiency of predation might be reduced by weaker mobility of tentacles. The motility of *P. donghaiense* probably increased its chance of predation by polyps, but predation on *S. costatum*, which form assemblages on the bottom, might be limited.

Podocysts occurred in all treatments. Polyps in the groups without food produced the most podocysts. Larger numbers were produced in groups fed with *P. donghaiense* and *S. costatum*, compared with those fed on *Artemia*. Thein et al. (2012) noted that podocysts occurred under the conditions of poor food supply and suggested that starvation is the ultimate cause for podocyst formation (Thein et al., 2012). Therefore, it appeared that feeding on *Artemia* nauplii fulfilled the energy requirements of polyps, but *P. donghaiense* and *S. costatum* did not. Thus, phytoplankton appeared to be inadequate for polyp nutrition. Prey recognition, encounter rates, and transfer (handling) efficiency determine prey selection (Hansson, 2006; Regula et al., 2009). It is difficult to determine the minimum threshold prey size for *A. aurita* polyps. In our experiment, *P. donghaiense* (ESD 11.8 μm) and *S. costatum* (ESD 6.5 μm) maintained the survival of polyps at low temperature, and this was significantly different from unfed polyps. Zheng et al. (2012) found that the cell density could affect the feeding of polyps on *P. donghaiense* (ESD 11.8 μm) and *S. costatum* (ESD 6.5 μm). The species of phytoplankton and its cell density determine whether the polyp is able to use it. The species determines whether it triggers sufficient nematocyst discharges to capture the food and the cell density determines capture rate of the polyps.

Ecological effect

In this experiment, we selected two common red tide species of inshore China to study the effect of phytoplankton on the growth and asexual reproduction of *Aurelia* polyps. We conclude that when the biomass of zooplankton is limited, phytoplankton can serve as a nutrient source for polyps. However, phytoplankton represents a lower quality food for the polyps. Sufficient animal prey and suitable temperatures are essential conditions for polyp strobilation and the release of ephyrae leading to jellyfish blooms.

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References

Båmstedt, U., B. Wild & M. B. Martinussen, 2001. Significance of food type for growth of ephyrae *Aurelia aurita* (Scyphozoa). Mar Biol 139(4): 641–650.

Condon, R. H., W. M. Graham, C. M. Duarte, K. A. Pitt, C. H. Lucas, S. H. D. Haddock, K. R. Sutherland, K.

L. Robinson, M. N. Dawson, M. B. Decker, C. E. Mills, J. E. Purcell, A. Malej, H. Mianzan, S. I. Uye, S. Gelcich & L. P. Madin, 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. Bioscience 62(2): 160–169.

Dawson, M. N. & L. E. Martin, 2001. Geographic variation and ecological adaptation in *Aurelia* (Scyphozoa, Semaeostomeae): some implications from molecular phylogenetics. Hydrobiologia 451(1–3): 259–273.

Dawson, M. N., A. Sen Gupta & M. H. England, 2005. Coupled biophysical global ocean model and molecular genetic analyses identify multiple introductions of cryptogenic species. Proceedings of the National Academy of Sciences of the United States of America 102(34): 11968–11973.

Dong, Z. J., D. Y. Liu, Y. J. Wang, B. P. Di, X. K. Song & Y. J. Shi, 2012. A report on a Moon Jellyfish *Aurelia aurita* bloom in Sishili Bay, Northern Yellow Sea of China in 2009. Aquat Ecosyst Health 15(2): 161–167.

Hernroth, L. & F. Grondahl, 1985. On the biology of *Aurelia aurita* (L).3. Predation by Coryphella-Verrucosa (Gastropoda, Opisthobranchia), a major factor regulating the development of *Aurelia* populations in the Gullmar Fjord, Western Sweden. Ophelia 24(1): 37–45.

Hansson, L. J., 2006. A method for in situ estimation of prey selectivity and predation rate in large plankton, exemplified with the jellyfish *Aurelia aurita* (L.). Journal of Experimental Marine Biology and Ecology 328(1): 113–126.

Holst, S., 2012. Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. Hydrobiologia 690(1): 127–140.

Jassby, A. D., J. E. Cloern & B. E. Cole, 2002. Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem. Limnol Oceanogr 47(3): 698–712.

Kamiyama, T., 2011. Planktonic ciliates as a food source for the scyphozoan *Aurelia aurita* (s.l.): feeding activity and assimilation of the polyp stage. Journal of Experimental Marine Biology and Ecology 407(2): 207–215.

Kawahara, M., S. Uye, K. Ohtsu & H. Izumi, 2006. Unusual population explosion of the giant jellyfish *Nemopilemia nomurai* (Scyphozoa : Rhizostomeae) in East Asian waters. Marine Ecology Progress Series 307: 161–173.

Ki, J. S., D. S. Hwang, K. Shin, W. D. Yoon, D. Lim, Y. S. Kang, Y. Lee & J. S. Lee, 2008. Recent moon jelly (*Aurelia* sp.1) blooms in Korean coastal waters suggest global expansion: examples inferred from mitochondrial COI and nuclear ITS-5.8S rDNA sequences. ICES Journal of Marine Science 65(3): 443–452.

Kramp, P. L., 1961. Synopsis of Medusae of World. Journal of the Marine Biological Association of the United Kingdom 40(Nov):1–469.

Liu, W. C., W. T. Lo, J. E. Purcell & H. H. Chang, 2009. Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. Hydrobiologia 616: 247–258.

Lucas, C. H., 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. Hydrobiologia 451(1–3): 229–246.

Malej, A., T. Kogovsek, A. Ramsak & L. Catenacci, 2012. Blooms and population dynamics of moon jellyfish in the northern Adriatic. Cahiers de Biologie Marine 53(3): 337–342.

Michael, T., A. Villanueva, K. Joshi & S. Priya, 2013. Physical modeling of Mastigias papua feeding structures and simulation of their effect on bell stress and kinematics. Proc Spie 8686 doi:Unsp 868608 doi: 10.1117/12.2009933.

Miyake, H., M. Terazaki & Y. Kakinuma, 2002. On the polyps of the common jellyfish *Aurelia aurita* in Kagoshima Bay. J Oceanogr 58(3): 451–459.

Purcell, J. E., S. Uye & W. T. Lo, 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Marine Ecology Progress Series 350: 153–174.

Purcell, J. E., D. Atienza, V. Fuentes, A. Olariaga, U. Tilves, C. Colahan & J. M. Gili, 2012. Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. Hydrobiologia 690(1): 169–180.

Regula, C., S. P. Colin, J. H. Costello et al., 2009. Prey selection mechanism of ambush-foraging hydromedusae. Marine Ecology Progress Series 374: 135–144.

Sabates, A., F. Pages, D. Atienza, V. Fuentes, J. E. Purcell & J. M. Gili, 2010. Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. Hydrobiologia 645(1): 153–165.

Sarno, D., W. H. C. F. Kooistra, S. Balzano, P. E. Hargraves & A. Zingone, 2007. Diversity in the genus Skeletonema (Bacillariophyceae): III. Phylogenetic position and morphological variability of *Skeletonema costatum* and *Skeletonema grevillei*, with the description of Skeletonema ardens sp nov. J Phycol 43(1): 156–170.

Sun, X. X., S. W. Wang & S. Sun, 2011. Introduction to the China Jellyfish Project—the key processes, mechanism and ecological consequences of jellyfish bloom in China coastal waters. Chinese Journal of Oceanology and Limnology 29(2): 491–492.

Thein, H., H. Ikeda & S.-I. Uye, 2012. The potential role of podocysts in perpetuation of the common jellyfish *Aurelia aurita* s.l. (Cnidaria: Scyphozoa) in anthropogenically perturbed coastal waters. Hydrobiologia 690(1): 157–167.

Uye, S. & H. Shimauchi, 2005. Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the Inland Sea of Japan. J Plankton Res 27(3): 237–248.

Wang, Y. T., S. Sun & C. L. Li, 2012. Effects of temperature and food on asexual reproduction of the scyphozoan, *Aurelia* sp.1. Oceanologia et Limnologia Sinica 43: 900–904. (in Chinese with English abstract).

Willcox, S., N. A. Moltschamwskyj & C. Crawford, 2007a. Asexual reproduction in scyphistomae of *Aurelia* sp.: effects of temperature and salinity in an experimental study. Journal of Experimental Marine Biology and Ecology 353(1): 107–114.

Willcox, S., N. A. Moltschamwskyj & C. Crawford, 2007b. Asexual reproduction in scyphistomae of Aurelia sp.: effects of temperature and salinity in an experimental study. Journal of Experimental Marine Biology and Ecology 353(1): 107–114.

Zheng, S., X. X. Sun & S. Sun, 2012. The grazing of *Aurelia* sp.1 on *Skeletonema costatum* and *Prorocentrum donghaiense*. Oceanologia et Limnologia Sinica 43: 446–450. (in Chinese with English abstract).

Zhou, M. J., Z. L. Shen & R. C. Yu, 2008. Responses of a coastal phytoplankton community to increased nutrient input from the Changjiang (Yangtze) River. Continental Shelf Research 28(12): 1483–1489.