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Effects of temperature and salinity on the asexual reproduction of *Aurelia coerulea* polyps*

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Abstract *Aurelia coerulea* polyp is an important stage in the outbreaks of this species. To test the combined effects of salinity and temperature on the survival and asexual reproduction of polyps, we maintained 864 polyps at various salinities (15, 25, 33, and 40) and temperatures (9, 12, 15, 18, 21, and 24°C). Polyps could mostly survive in all treatment combinations except in salinity 15 treatments with low temperatures (9–15°C). Budding occurred at all temperatures (9–24°C), while strobilation only occurred at the low temperatures (9–15°C). The range of 12–15°C was suitable for strobilation and ephyrae release. The optimal range of salinity for asexual reproduction was 25–33. Low (15) or high (40) salinity could significantly reduce the numbers of new buds or ephyrae, and low salinity of 15 retarded and even prevented strobilation at low temperatures. The optimal treatment for budding and strobilation was 21°C-salinity 25 and 12°C-salinity 33, respectively. Salinity had less of an impact than temperature on asexual reproduction, except for the polyps in high or low osmotic pressure conditions.

Keyword: *Aurelia coerulea*; polyp; temperature; salinity; asexual reproduction

1 INTRODUCTION

Over the past two decades, blooms of jellyfish have increased in marine ecosystems worldwide (Purcell, 2005; Lo and Chen, 2008; Wang and Sun, 2015). Jellyfish outbreaks have been reported to damage marine ecosystems and the economy, especially in coastal waters (Dong et al., 2010; Bosch-Belmar et al., 2017). For example, high biomasses of several jellyfish species damage commercial fisheries by clogging nets or preying on fish eggs and larvae in many regions (Uye and Ueta, 2004; Dong et al., 2010), affect coastal tourism by closing beaches (Purcell et al., 2007), and interrupt power plant operations by clogging intake screens (Matsueda, 1969; Dong et al., 2012).

The scyphozoan genus *Aurelia* is one of the main contributors to such disasters and is a cosmopolitan species complex found in many coastal waters. Mitochondrial and nuclear DNA sequence data indicate that the *Aurelia* species that exhibits outbreaks in the coastal regions of East Asia is *A. coerulea* (Scorrano et al., 2016). The life cycle of *A. coerulea* is very complex and mainly consists of an alternation between planktonic medusa generation and benthic polyp generation. The population sizes,

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reproduction and survival, and spatial and temporal distributions of the polyps are very important to the biomass of adult medusa (Lucas, 2001; Ishii and Katsukoshi, 2010; Robinson and Graham, 2013; Wang and Sun, 2015).

Environmental factors (e.g., temperature, salinity, and food availability) affect *Aurelia* spp. polyps. Most previous studies have indicated that temperature plays a crucial role in the reproduction of polyps (e.g., Omori et al., 1995; Miyake et al., 2002; Willcox et al., 2007; Liu et al., 2009; Purcell et al., 2012; Wang and Sun, 2015). At warm temperatures, the polyps tend to reproduce daughter polyps by budding to enlarge the population, while the polyps trigger strobilation to reproduce planktonic ephyrae when the temperature decreases to below certain thresholds. The number of polyps is proportional to how many ephyrae will be generated in the future. Salinity is expected to be, in some cases, an important environmental factor determining the distribution of polyps in coastal waters (e.g., Watanabe and Ishii, 2001; Willcox et al., 2008; Sokołowski et al., 2016). Although field investigations on the relative influence of salinity on *Aurelia* polyps are lacking, salinity is proposed to be a principal factor that influences the mortality of polyps (Sokołowski et al., 2016) and the behavior, settlement of planulae and subsequent development of polyps (Conley and Uye, 2015; Dong et al., 2018a). In unsuitable salinity conditions, polyps may have to reduce their reproductive and growth rates so that they can allocate more energy to respond to physiological stress. In addition, Janas and Witek (1993) reported that lower salinity restricted the reproduction and distribution of *A. aurita* in the brackish waters of the Gulf of Gdańsk. The *Aurelia* medusae were also found to avoid water of extremely low salinity (Han and Uye, 2009; Albert, 2012). Food supply is also an important factor in the polyp population. Since Thiel (1962) first reported that the effects of food could impact the strobilation of *A. aurita*, many experiments have shown that the abundance of food is important to the number and ratio of budding and strobilation for *Aurelia* polyp reproduction (e.g., Purcell, 2007; Wang et al., 2015a, b), while temperature and salinity are the most important factors for the timing of strobilation and ephyrae release (Ma and Purcell, 2005; Willcox et al., 2007).

As a local *Aurelia* species, *A. coerulea* polyps are widely distributed in the coastal waters of East Asia, especially in harbors, estuaries and culture ponds with artificial reefs of the Bohai and Yellow Seas (Dong et al., 2012, 2018b). There are wide annual ranges of temperature and salinity (1–26°C, salinity 26–34 in Bohai Sea (Song, 2009; Yu et al., 2018); 7.5–25.5°C, salinity 24–32 in Yellow Sea (Xin, 2011)) in these coastal waters. The salinity can decrease to 13 (Sun et al., 2015) or even lower in estuaries, while it can reach 40 in the neighboring sea area of desalination plants (Wang et al., 2009). The aim of this study was to explore the combined effects of temperature and salinity conditions that are likely to occur in *A. coerulea* habitat on the polyps. We cultured the polyps at six temperatures (9, 12, 15, 18, 21, and 24°C) and four salinities (15, 25, 33, and 40) in laboratory conditions to examine eco-physiological responses, such as survival time, budding, strobilation, and ephyrae release. We also recorded the duration of different development phases, including strobilation prophase, strobilation interphase, and strobilation. We provided a complete picture of the reproductive strategy of *A. coerulea* polyps with different combinations of temperature and salinity to determine how those conditions would affect recruitment success to the polyp and medusae stages.

2 MATERIAL AND METHOD

2.1 Experimental set-up

Aurelia coerulea polyps were obtained from the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. The polyps developed from planulae collected from Jiaozhou Bay in August 2017 and adhered to the surface of corrugated plastic plates. The polyps were cultured at 20°C and a salinity of 30–33 in natural light for more than 1 year.

The seawater (salinity 33) used in the experiment was collected from Shilaoren Bay and was filtered through a 0.45-μm nitrocellulose filter before the experiment. Four salinities (15, 25, 33, and 40) were established during the experiment, which were adjusted by adding instant ocean sea salt or by mixing with deionized water to the setting salinity. The salinities were measured with a portable Multiparameter Water Quality Meter (YSI, USA).

Corrugated plastic plates were cut into several sections (approximately 2 cm×3 cm), and each small corrugated plate contained several polyps. All the polyps were cultured in a darkened incubator at 21°C and salinity of 33 without food for 3 days to ensure that the polyps maintained the same physiological state. The unhealthy polyps, new buds, podocysts, and impurities on the corrugated plates were removed

Table 1 Results of two-way ANOVA on the effects of salinity and high temperature on polyps

Variables tested	Temperature (°C)		Salinity		Temperature×salinity	
	Test statistic	*P* value	Test statistic	*P* value	Test statistic	*P* value
Survival time	F(2,11)=2.738	0.066	F(3,11)=0.915	0.434	F(6,11)=0.915	0.434
New buds	F(2,11)=40.918	<0.001	F(3,11)=48.140	<0.001	F(6,11)=18.326	<0.001

Survival time was from the beginning of the experiment to the death of a polyp. New buds were the number of buds observed in the experiment.

Table 2 Results of Tukey's HSD test on the effects of salinity and high temperature

Average value	Temperature (°C)			Salinity			
	18	21	24	15	25	33	40
Mean survival time (d)	30.00±0.00^{a}	30.00±0.00^{a}	28.50±5.33^{a}	29.04±5.00^{A}	28.96±3.77^{A}	30.00±0.00^{A}	30.00±0.00^{A}
Mean number of new buds (No.)	6.89±4.90^{a}	9.31±6.90^{b}	9.88±6.66^{b}	1.39±1.98^{A}	15.40±4.40^{B}	11.40±4.24^{C}	6.57±3.04^{D}

The lowercase letters indicate whether data are significantly different among temperatures (P<0.05). The capital letters indicate whether data are significantly different among salinities (P<0.05). The same letters indicate that the difference was not significant (P>0.05).

carefully using a dissecting needle before the experiment. Twelve of the healthiest polyps were left on each small corrugated plate.

2.2 Effects of temperature and salinity on polyps

Each small plate was directly placed in a 250-mL beaker containing 200-mL seawater at four salinities (15, 25, 33, and 40) at the beginning of experiments. Beakers were covered with plastic film with an air vent to maintain the stability of the culture system. Two separate experiments were conducted. Experiment 1 continued for 30 days and was designed to inspect the combined effects at high temperatures (18, 21, and 24°C). Experiment 2 continued for 52 days and was designed to examine the combined effects at low temperatures (9, 12, and 15°C). These beakers were placed at the six temperatures and were maintained in the incubators without light. Each combination contained three replicates. Polyps were fed with newly hatched *Artemia nauplii* in excess every 2 days to minimize the effects of food supply. After the polyps were fed for 1 h, the seawater and uneaten food in the beakers were discarded and replaced with seawater of the same temperature and salinity to maintain the water quality. All the polyps were observed every 2 days with a dissecting microscope to record the asexual reproduction process per polyp, such as the formation of new polyps, strobilation, and the number of ephyrae released. Any dead polyps, newly formed polyps or podocysts were excised with a dissecting needle and free ephyrae were removed with a pipette.

2.3 Statistical analysis

The effects of temperature and salinity on the survival time and asexual reproduction of polyps were analyzed by two-way analysis of variance (ANOVA). All data were square root transformed and tested for normality and homogeneity of variance. Tukey's honestly significant difference (HSD) test was used to identify the treatments (temperature and salinity) that caused the overall effect of the group differences in the ANOVA. All statistical tests were analyzed by using SPSS 17.0.

3 RESULT

3.1 High temperature with different salinity experiments

The combined effects of temperature (18, 21, and 24°C) and salinity (15, 25, 33, and 40) on polyps were tested. There were no significant effects of temperature, salinity, or temperature × salinity on the survival time of polyps; significant effects of temperature, salinity and temperature × salinity were found on the number of new buds (Table 1).

Polyps were able to mostly survive in all treatment combinations during the experiment. There were no significant differences among the survival times for the three temperature treatments or four salinity treatments (Table 2).

At the beginning of the experiment, the polyps needed a few days to adapt to the different combinations of temperature and salinity. The number of new buds in the treatments increased slowly in the first 10 days of the experiment, except for the buds in the 24°C-salinity 33 treatment, which increased slowly in the first 4 days and then increased rapidly (Fig.1). The cumulative number of new buds in the different treatments increased to different extents

Table 3 Results of two-way ANOVA on the effects of salinity and low temperature on polyps

Variables tested	Temperature (°C)		Salinity		Temperature×salinity	
	Test statistic	*P* value	Test statistic	*P* value	Test statistic	*P* value
Survival time	F(2,11)=0.294	0.746	F(3,11)=3.943	0.011	F(6,11)=0.587	0.740
New buds	F(2,11)=61.236	<0.001	F(3,11)=20.192	<0.001	F(6,11)=17.341	<0.001
Ephyrae	F(2,11)=35.759	<0.001	F(3,11)=11.345	<0.001	F(6,11)=3.946	<0.001
Pre-strobilation	F(2,11)=3.514	0.350	F(3,11)=21.412	<0.001	F(6,11)=6.237	<0.001
Bet-strobilation	F(2,11)=16.266	<0.001	F(3,11)=22.555	<0.001	F(6,11)=17.162	<0.001

Survival time was from the beginning of the experiment to the death of the polyp. New buds were the number of buds observed during the experiment. Ephyrae were the number of ephyrae produced in the experiment. Pre-strobilation was the time from the beginning of the experiment to the beginning of strobilation. Bet-strobilation was the time from the beginning of strobilation to the first release of ephyrae.

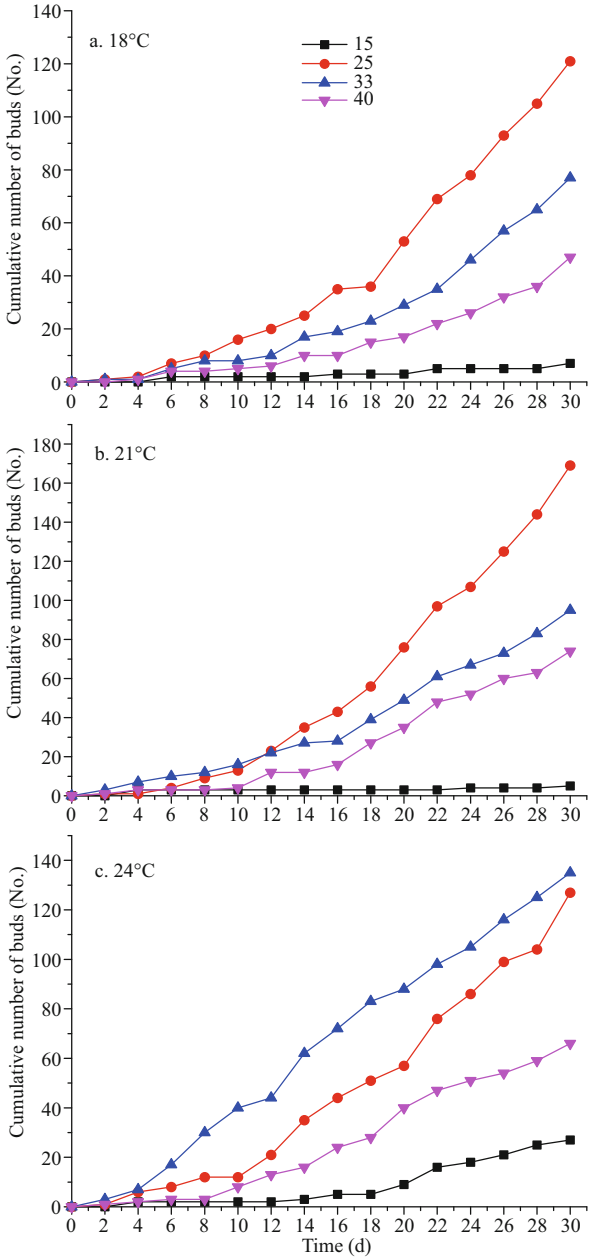

Fig.1 Cumulative number of buds in four salinity treatments (15, 25, 33, and 40) at 18°C (a), 21°C (b), and 24°C (c) during the 30-day experiment

during the 30 days of the experiment. At 18°C and 21°C, more buds were produced in salinity 25 than in the other salinity levels (Fig.1a, b); at 24°C, the number of new buds was higher in both salinity 33 and 25 treatments (Fig.1c). A very small number of buds was produced in salinity 15 in all three temperature treatments, and somewhat more buds were produced in the 24°C-salinity 15 treatment. Overall, the polyps produced more buds in warmer temperatures with suitable salinities (25, 33); low (15) or high (40) salinity reduced the number of buds (Table 2, Fig.1). The greatest number of buds was observed in the 21°C-salinity 25 treatment.

3.2 Low temperature with different salinity experiments

The effects of different combinations of low temperatures (9, 12, and 15°C) and salinities (15, 25, 33, and 40) on polyps were observed. The effects of temperature and temperature × salinity were not significant on survival time, while the effects of salinity on survival time were significant. The number of new buds and ephyrae differed significantly among the temperature, salinity, and temperature × salinity treatments. The effects of salinity and temperature × salinity were significant for the pre-strobilation period, while there were no significant effects of temperature on the pre-strobilation period. There were significant effects of temperature, salinity, and temperature × salinity on the bet-strobilation period (Table 3).

The effects of the three temperatures were not significant on the average survival time. The average survival time of polyps in salinity 15 was significantly shorter than the other salinity treatments. Significant variations were not found in the survival time for salinity 25, 33, and 40 treatments (Table 4).

The polyps in salinity 15 treatments did not produce new buds at the three temperatures. The polyps in

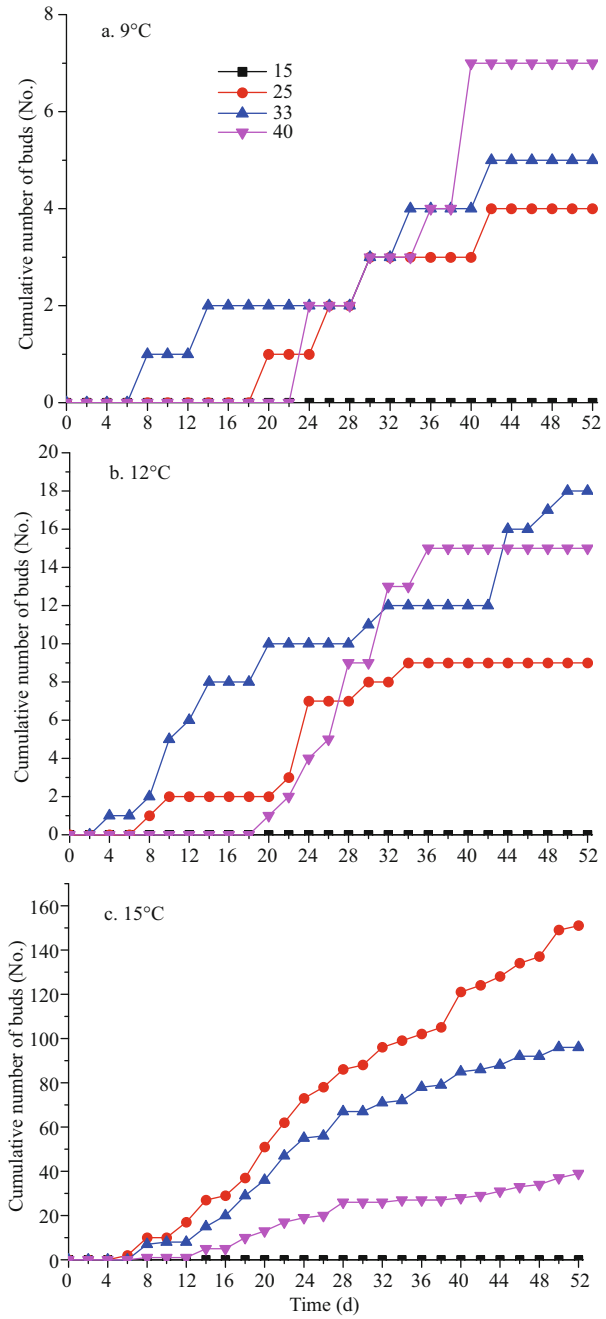

Fig.2 Cumulative number of buds in four salinity treatments (15, 25, 33, and 40) at 9°C (a), 12°C (b), and 15°C (c) during the 52-day experiment

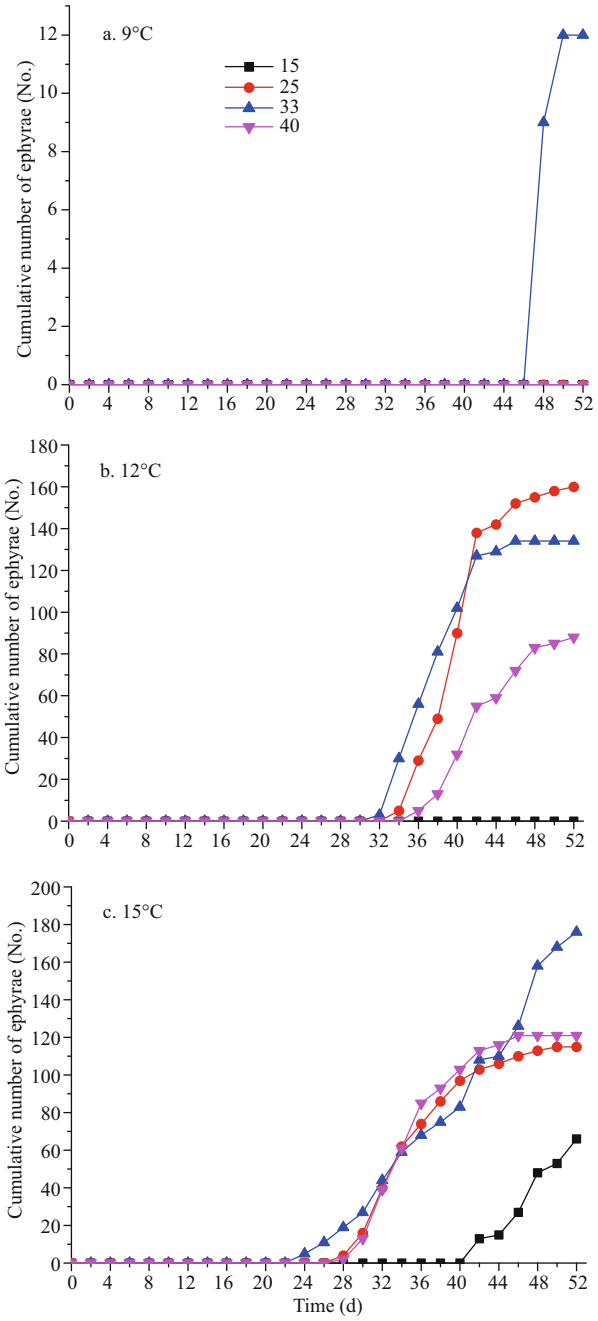

Fig.3 The cumulative number of ephyrae in the four salinity treatments (15, 25, 33, 40) at 9°C (a), 12°C (b), and 15°C (c) during a 52-day experiment

salinity 40 treatments needed more time (12–22 days) to adapt to the combinations than those in salinity 25 and 33 treatments, especially at 9°C and 12°C. With increasing temperature, the adaptation time of the polyps gradually shortened and the polyps produced more buds, particularly in salinity 25 treatments (Fig.2, Table 4). In the lower temperature (9°C and 12°C) treatments, polyps produced fewer buds (Fig.2a, b, Table 4), while the cumulative numbers of buds increased greatly in the warm temperature treatments (15°C) with salinities of 25–40, especially in the 15°C-salinity 25 treatment (Fig.2c).

At 9°C, ephyrae were not observed during the experiment, except a few ephyrae were released in the 9°C-salinity 33 treatment (Fig.3a). As the temperature increased, the cumulative numbers of ephyrae increased greatly, especially in salinity 25, 33, and 40 treatments. Although the average number of ephyrae was higher at 15°C, the variation was not significant between the 12°C and 15°C treatments

Table 4 Results of Tukey's HSD test on the effects of salinity and low temperature

Average value	Temperature (°C)			Salinity			
	9	12	15	15	25	33	40
Mean survival time (d)	46.06±14.47^{a}	46.47±13.68^{a}	48.67±11.33^{a}	39.93±18.11^{A}	49.11±10.59^{B}	50.30±8.85^{B}	49.90±9.39^{B}
Mean number of new buds (No.)	0.52±0.77^{a}	1.24±1.63^{a}	7.94±7.89^{b}	0.00±0.00^{A}	6.07±8.87^{B}	4.41±5.46^{B}	3.05±2.16^{C}
Mean number of ephyrae (No.)	0.39±1.05^{a}	11.24±8.40^{b}	13.28±10.12^{b}	2.44±4.95^{A}	10.19±10.68^{B}	11.93±10.23^{B}	10.45±8.19^{B}
Mean pre-strobilation period (d)	33.30±12.01^{a}	24.83±12.83^{b}	28.91±12.11^{ab}	42.82±12.89^{A}	25.08±12.21^{B}	24.33±8.66^{B}	25.05±8.04^{B}
Mean bet-strobilation period (d)	18.00±11.52^{a}	13.52±6.62^{b}	9.52±5.57^{c}	6.12±8.56^{A}	15.84±8.87^{B}	15.00±6.46^{B}	13.68±7.43^{B}

The lowercase letters indicate whether data are significantly different among temperatures (P<0.05). The capital letters indicate whether data are significantly different among salinities (P<0.05). The same letters indicate that the difference was not significant (P>0.05)

(Fig.3b, c, Table 4). At 12°C with salinities of 25, 33, and 40, 100% of polyps produced ephyrae, but at 9°C and 15°C with salinities of 25, 33, and 40, a few polyps were in the pre-strobilation period from the beginning to the end of the experiment. The largest number of ephyrae of all treatments was produced in the 15°C-salinity 33 treatment. The average number of new ephyrae in salinity 15 was significantly lower than those in other salinity treatments. In the 15°C-salinity 15 treatment, the polyps released a small number of ephyrae compared with the polyps in the 9°C-salinity 15 and 12°C-salinity 15 treatments, which did not produce ephyrae (Fig.3, Table 4).

Polyps could strobilate under different treatment combinations, except for polyps in the 9°C- salinity 15 and 12°C-salinity 15 treatments, which remained in pre-strobilation throughout the 52-day experiment. The polyps in the 9°C-salinity 25 and 9°C-salinity 40 treatments remained in bet-strobilation at the end of the experiment. The pre-strobilation period of polyps at 12°C with salinities of 25, 33, and 40 continued for 18–21 days, which was shorter than those observed in the other temperature-salinity combinations. The longest average pre-strobilation period and bet-strobilation were in the 9°C treatment. The bet-strobilation and strobilation periods were shorter at 15°C than those at 12°C, although polyps spent more time in the pre-strobilation period at 15°C. The average pre-strobilation period in salinity 15 treatment was the longest. Overall, warmer temperature and suitable salinity conditions shortened the total time of strobilation, while low temperature and stressful salinity combinations were not suitable for strobilation (Fig.4, Table 4).

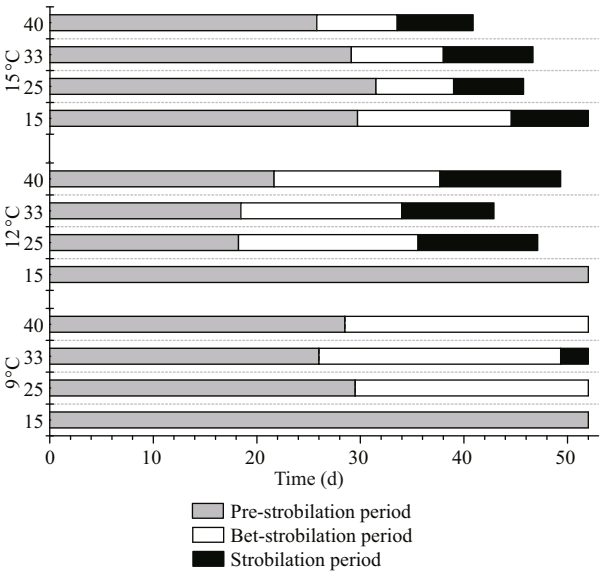

Fig.4 Pre-strobilation, bet-strobilation, and strobilation periods of polyps at three temperatures (9, 12, and 15°C) and four salinities (15, 25, 33, and 40) during a 52-day experiment

4 DISCUSSION

4.1 Effects of temperature

Polyps could mostly survive in all treatments (9–24°C) during the experiments (Tables 2 & 4), which indicated that the polyps could tolerate a wide range of temperatures. Pascual et al. (2015) found that the survival rates of three populations of *Aurelia aurita* polyps from the Mediterranean, Red and Baltic Seas were high and did not differ significantly across temperatures (14, 21, and 28°C) during a laboratory experiment.

Temperature is a primary factor in regulating, initiating, and controlling the shift between reproduction modes. At the temperatures greater than or equal to 18°C, the polyps in the treatments produced only buds, and at the temperatures less than or equal to 15°C, both strobilation and budding occurred. The results showed that asexual reproduction was strongly temperature dependent between budding and strobilation. A similar effect was noted in laboratory and in situ manipulative experiments in other studies (Watanabe and Ishii, 2001; Willcox et al., 2007; Han

and Uys, 2010; Wang et al., 2015a). In tropical waters, some results showed different temperature ranges of strobilation, in which the polyps could produce ephyrae at temperatures higher than 20°C (Liu et al., 2009; Pascual et al., 2015). In this study, the polyps of all treatments were fed in excess, and the average number of buds increased with increasing temperature. Although high temperatures (18, 21, 24°C) were sustained in the experiment for shorter (30 days) than low temperatures (52 days; 9, 12, 15°C), more buds were produced by polyps at high temperatures (Figs.1, 2). The peak cumulative number of buds appeared at 24°C, which was not significantly different from that at 21°C but was significantly higher than that at 18°C. The results indicate that polyps could rapidly expand the population by budding when food is abundant in summer.

During the experiment, the polyps produced a small number of ephyrae and buds at 9°C. The polyps at both 12°C and 15°C produced large numbers of ephyrae (P>0.05) (Fig.3, Table 4), while the cumulative number of buds at 12°C was far less than that at 15°C (P<0.05) (Fig.2, Table 4). Moreover, 100% of the polyps at 12°C with salinities of 25, 33, and 40 produced ephyrae by strobilation, while a small number of polyps at 15°C with salinities of 25, 33 and 40 were in the pre-strobilation period from the beginning to the end of the experiment. Therefore, 15°C might be a balance point between budding and strobilation for *A. coerulea* polyps. Polyps invested more energy in strobilation than budding as the temperature decreased, but at low temperatures, the strobilation period was prolonged and polyps produced fewer ephyrae (Wang et al., 2015a; Sokołowski et al., 2016). Hence, temperature played a vital role in not only when strobilation occurred but also the number of the ephyrae. In nature, strobilation takes place in winter or early spring after polyps are exposed to a prolonged period of cold-water temperatures. This internal biological rhythm of polyps may help the new ephyrae have a sufficient food supply during the following period; with the water temperature and biomass of zooplankton gradually rise. Funs et al. (2014) found that one protein (CL390) functioned as a temperature-sensitive ‘‘timer’’ and encoded the precursor of the strobilation hormone in *Aurelia aurita*. This protein gradually accumulates in polyps during the winter. Once CL390 transcription reaches a certain level, strobilation is nearly independent of seawater temperature (Brekhman et al., 2015), and higher temperatures promote the transcription of CL390 (Shi et al., 2017). This may partly explain why no strobilation was found in the coldest part of winter. These physiology and molecular biology results implied that higher seawater temperatures of the Bohai and Yellow Seas than usual in winter or early spring would be an important factor that would trigger *Aurelia* blooms in coastal waters.

4.2 Effects of salinity

Salinity stresses organisms when they are not at their optimal salinity levels (Purcell et al., 1999; Ma and Purcell, 2005; Devreker et al., 2009). As one type of coelenterate, the osmoregulation of *Aurelia* spp. is imperfect. The unfavorable osmotic pressure of seawater will interfere with the growth and reproduction of *Aurelia* spp. polyps. In the present study, the polyps could accommodate the salinity discontinuities, but the osmotic accommodation took more time when the polyps experienced suddenly high changes in salinity gradients (Figs.1, 2, 3). These findings were similar to those of a previous study by Mills (1984), who found the same phenomenon in medusae of *A. aurita*.

At high temperatures (18–24°C), although the survival time of polyps was not significant in all temperature-salinity combinations, the low salinity (15) significantly inhibited the numbers of buds produced by polyps. Interestingly, in the 24°C-salinity 15 treatment, the polyps were able to produce somewhat more buds. It was likely that the higher temperature stimulated the metabolism and activities of enzymes and proteins, which ensured that the polyps had the ability to combat unfavorable salinity conditions. At low temperatures (9–15°C), the cumulative numbers of buds significantly increased with increasing temperature but were not affected by salinities of 25–33. A similar result of was previously noted by Willcox et al. (2007). He also found that the proportion of polyps that were actively budding was dependent on salinity (25, 30, 35), with more active polyps at the highest salinity. In the present study, although we did not count the number of actively budding polyps, no significant difference was found in the number of new buds in salinity 25 and 33, while high salinity (40) significantly reduced the numbers of new buds. This may be due to the fact that the physiological plasticity and optimal salinity conditions were different among species of *Aurelia* spp. For example, *A. coerulea* showed a wider environmental adaptation than *A. relicta* (Hubot et al.,

2017). Even the same species living in a different climatic location may exhibit different responses to environmental changes (Pascual et al., 2015). The polyps did not produce new buds at a salinity of 15 at 9–15°C in our study. The survival time of polyps at a salinity of 15 was shorter than that in the other salinity treatments (25, 33, 40) (P<0.05), especially in the 12°C-salinity 15 treatment. These results implied that estuaries with a low-salinity environment are not conducive to survival and budding of polyps in the Bohai and Yellow Seas. Accordingly, Watanabe and Ishii (2001) observed high mortality of polyps and inhibition of budding at low salinity levels in an in situ experiment in Japan. Other previous studies on *Aurelia* spp. showed that medusae were almost completely absent from parts of the water column with salinities less than 20 (Lo and Chen, 2008; Han and Uye, 2009) due to their avoidance behavior when they encountered low salinity (Albert, 2012).

Polyps could strobilate in salinities of 25–40 at temperatures of 9–15°C. The polyps in the 15°C-salinity 15 treatment could produce ephyrae, while none of the polyps was able to strobilate in the 12°C-salinity 15 and 9°C-salinity 15 treatments (Fig.4). This result indicated that although temperature played a greater role than salinity in strobilation, salinity also affected polyp strobilation (Purcell, 2007). Previous results showed that low salinity (20) reduced and retarded the strobilation of *A. labiata* polyps in the laboratory (Purcell et al., 2007), and field data showed similar results (Purcell et al., 2009). It was likely that low temperature and stressful salinity conditions increased the energy demands of osmoregulation and decreased the energy allocated to reproduction. There were no significant effects of salinity on strobilation at 12–15°C in salinity 25–33 in our study, which implied that the suitable salinity range for strobilation of polyps was 25–33 and rapid changes in salinity due to events such as discharged brine from desalination plants or massive freshwater inflow may affect the strobilation of *A. coerulea* in the field. The physiological adaptability of polyps to the range of salinity change would regulate the distribution and dispersion of *A. coerulea* in the highly variable coastal waters of the Bohai and Yellow Seas. In addition, food is an important factor in the survival and asexual reproduction of *Aurelia* polyps. Previous studies showed that high efficiency of food utilization was important for the numbers of buds and ephyrae (e.g., Han and Uye, 2010; Wang et al., 2015a). During our study, we found that polyps in the low (15) or high (40) salinity treatments had shorter tentacles and poorer predation capacities than those in the other salinity treatments. Therefore, salinity probably affects growth and asexual reproduction by reducing predation efficiency. To facilitate a better understanding of these phenomena, further detailed studies on the effects of salinity and predation efficiency are needed.

5 CONCLUSION

Both temperature and salinity were important factors for the survival and asexual reproduction of *A. coerulea* polyps, whereas temperature played a key role in deciding the direction of reproduction and development. The number of new buds produced by polyps increased as the temperature increased. The polyps produced buds at only 18–24°C. The temperature range of 12–15°C is suitable for strobilation. The low (15) or high salinity (40) could reduce the numbers of new buds or ephyrae, and the low (15) salinity retarded and even prevented strobilation. The appropriate range of salinity for asexual reproduction was 25–33. The polyps produced the highest number of buds and ephyrae in the 21°C-salinity 25 and 12°C-salinity 33 treatments, respectively.

6 DATA AVAILABILITY STATEMENT

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

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References

Albert D J. 2012. Controlled activation of species typical behaviour to low salinity, seawater movement and seawater depth in *Aurelia labiata* (Scyphozoa) Jellyfish in Roscoe Bay, Canada. *Hydrobiologia*, **680**(1): 179-186.

Bosch-Belmar M, Azzurro E, Pulis K, Milisenda G, Fuentes V, Kéfi-Daly Yahia O, Micallef A, Deidun A, Piraino S. 2017. Jellyfish blooms perception in Mediterranean finfish aquaculture. *Marine Policy*, **76**: 1-7.

Brekhman V, Malik A, Haas B, Sher N, Lotan T. 2015. Transcriptome profiling of the dynamic life cycle of the scypohozoan jellyfish *Aurelia aurita*. *BMC Genomics*, **16**: 74.

Conley K, Uye S I. 2015. Effects of hyposalinity on survival

and settlement of moon jellyfish (*Aurelia aurita*) planulae. *Journal of Experimental Marine Biology and Ecology*, **462**: 14-19.

Devreker D, Souissi S, Winkler G, Forget-Leray J, Leboulenger F. 2009. Effects of salinity, temperature and individual variability on the reproduction of *Eurytemora affinis* (Copepoda; Calanoida) from the Seine estuary: a laboratory study. *Journal of Experimental Marine Biology and Ecology*, **368**(2): 113-123.

Dong Z J, Liu D Y, Keesing J K. 2010. Jellyfish blooms in China: dominant species, causes and consequences. *Marine Pollution Bulletin*, **60**(7): 954-963.

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

Dong Z J, Wang L, Liu Q Q, Sun T T. 2018a. Effects of salinity and temperature on the recruitment of *Aurelia coerulea* planulae. *Marine Biology Research*, **14**(5): 454-461.

Dong Z J, Wang L, Sun T T, Liu Q Q, Sun Y F. 2018b. Artificial reefs for sea cucumber aquaculture confirmed as settlement substrates of the moon jellyfish *Aurelia coerulea*. *Hydrobiologia*, **818**(1): 223-234.

Fuchs B, Wang W, Graspeuntner S, Li Y Z, Insua S, Herbst E M, Dirksen P, Böhm A M, Hemmrich G, Sommer F, Domazet-Lošo T, Klostermeier U C, Anton-Erxleben F, Rosenstiel P, Bosch T C G, Khalturin K. 2014. Regulation of polyp-to-jellyfish transition in *Aurelia aurita*. *Current Biology*, **24**(3): 263-273.

Han C H, Uye S I. 2009. Quantification of the abundance and distribution of the common jellyfish *Aurelia aurita* s.l. with a Dual-frequency IDentification SONar (DIDSON). *Journal of Plankton Research*, **31**(8): 805-814.

Han C H, Uye S I. 2010. Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* s.l. *Plankton & Benthos Research*, **5**(3): 98-105.

Hubot N, Lucas C H, Piraino S. 2017. Environmental control of asexual reproduction and somatic growth of *Aurelia* spp. (Cnidaria, Scyphozoa) polyps from the Adriatic Sea. *PLoS One*, **12**(6): e0178482.

Ishii H, Katsukoshi K. 2010. Seasonal and vertical distribution of *Aurelia aurita* polyps on a pylon in the innermost part of Tokyo Bay. *Journal of Oceanography*, **66**(3): 329-336.

Janas U, Witek Z. 1993. The occurrence of medusae in the southern Baltic and their importance in the ecosystem, with special emphasis on *Aurelia aurita*. *Oceanologia*, **34**: 69-84.

Liu W C, Lo W T, Purcell J E, Chang H H. 2009. Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. *Hydrobiologia*, **616**(1): 247-258.

Lo W T, Chen I L. 2008. Population succession and feeding of scyphomedusae, *Aurelia aurita*, in a eutrophic tropical lagoon in Taiwan. *Estuarine*, *Coastal and Shelf Science*, **76**(2): 227-238.

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.

Ma X P, Purcell J E. 2005. Temperature, salinity, and prey effects on polyp versus medusa bud production by the invasive hydrozoan *Moerisia lyonsi*. *Marine Biology*, **147**(1): 225-234.

Matsueda N. 1969. Presentation of *Aurelia aurita* at thermal power station. *Bulletin of the Marine Biological Station* of *Asamushi*, **13**: 187-191.

Mills C E. 1984. Density is altered in hydromedusae and ctenophores in response to changes in salinity. *The Biological Bulletin*, **166**(1): 206-215.

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

Omori M, Ishii H, Fujinaga A. 1995. Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES Journal of Marine Science*, **52**(3-4): 597-603.

Pascual M, Fuentes V, Canepa A, Atienza D, Gili J M, Purcell J E. 2015. Temperature effects on asexual reproduction of the scyphozoan *Aurelia aurita s.l.*: differences between exotic (Baltic and Red seas) and native (Mediterranean Sea) populations. *Marine Ecology*, **36**(4): 994-1 002.

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

Purcell J E, Hoover R A, Schwarck N T. 2009. Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions *in situ*. *Marine Ecology Progress Series*, **375**: 139-149.

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

Purcell J E, White J R, Nemazie D A, Wright D A. 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Marine Ecology Progress Series*, **180**: 187-196.

Purcell J E. 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association* of *the United Kingdom*, **85**(3): 461-476.

Purcell J E. 2007. Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata*. *Marine Ecology Progress Series*, **348**: 183-196.

Robinson K L, Graham W M. 2013. Long-term change in the abundances of northern Gulf of Mexico scyphomedusae *Chrysaora* sp. and *Aurelia* spp. with links to climate variability. *Limnology and Oceanography*, **58**(1): 235-253.

Scorrano S, Aglieri G, Boero F, Dawson M N, Piraino S. 2016. Unmasking *Aurelia* species in the Mediterranean Sea: an integrative morphometric and molecular approach.

Zoological Journal of the Linnean Society, **180**(2): 243-267.

Shi Y, Yu Z G, Zhen Y, Wang G S, Wang X G, Mi T Z. 2017. Effect of decreasing temperature on the strobilation of *Aurelia* sp.1. *Journal* of *Oceanology and Limnology*, **36**(2): 465-472.

Sokołowski A, Brulińska D, Olenycz M, Wołowicz M. 2016. Does temperature and salinity limit asexual reproduction of *Aurelia aurita* polyps (Cnidaria: Scyphozoa) in the Gulf of Gdańsk (southern Baltic Sea)? An experimental study. *Hydrobiologia*, **773**(1): 49-62.

Song W P. 2009. The Analysis of the Structure of T-S and the Current Characteristics in Baohai Sea during Winter and Summer. Ocean University of China, Qingdao. 70p. (in Chinese with English abstract)

Sun S, Zhang F, Li C L, Wang S W, Wang M X, Tao Z C, Wang Y T, Zhang G T, Sun X X. 2015. Breeding places, population dynamics, and distribution of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in the Yellow Sea and the East China Sea. *Hydrobiologia*, **754**(1): 59-74.

Thiel H. 1962. Untersuchungen über die Strobilisation von *Aurelia aurita* Lam. an einer Population der Kieler Förde. *Kieler Meeresforschungen*, **18**(2): 198-230.

Uye S I, Ueta U. 2004. Recent Increase of Jellyfish Populations and their Nuisance to Fisheries in the Inland Sea of Japan. *Bulletin of the Japanese Society of Fisheries Oceanography*, **68**: 9-19.

Wang N, Li C L, Liang Y, Shi Y Q, Lu J L. 2015a. Prey concentration and temperature effect on budding and strobilation of *Aurelia* sp.1 polyps. *Hydrobiologia*, **754**(1): 125-134.

Wang X M, Liu X H, Liang S K, Shi X Y. 2009. The effect of brine discharged from desalination plant on the distribution of the salinity in the Jiaozhou Bay. *Acta Oceanologica Sinica*, **31**(1): 44-51. (in Chinese with English abstract)

Wang Y T, Sun S. 2015. Population dynamics of *Aurelia* sp.1 ephyrae and medusae in Jiaozhou Bay, China. *Hydrobiologia*, **754**(1): 147-155.

Wang Y T, Zheng S, Sun S, Zhang F. 2015b. Effect of temperature and food type on asexual reproduction in *Aurelia* sp.1 polyps. *Hydrobiologia*, **754**(1): 169-178.

Watanabe T, Ishii H. 2001. *In situ* estimation of ephyrae liberated from polyps of *Aurelia aurita* using settling plates in Tokyo Bay, Japan. *Hydrobiologia*, **451**(1-3): 247-258.

Willcox S, Moltschaniwskyj N A, Crawford C M. 2008. Population dynamics of natural colonies of *Aurelia* sp. scyphistomae in Tasmania, Australia. *Marine Biology*, **154**(4): 661-670.

Willcox S, Moltschaniwskyj N A, Crawford C. 2007. 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.

Xin M. 2011. Distribution Characteristics of Biogenic Elements in the Yellow Sea and Comparison of Properties between the Southern and Northern Yellow Sea Cold Water Masses. The First Institute of Oceanography, SOA, Qingdao. 94p.

Yu Q, Lou A G, Zhang X Q, Li N. 2018. Numerical analysis on the impact of main river runoff on the plain distribution in the low-salinity area at north Liaodong Bay. *Transactions of Oceanology and Limnology*, (2): 88-96. (in Chinese with English abstract)