

Combined Effects of Temperature and Salinity on the Growth and Pulsation of Moon Jellyfish (*Aurelia coerulea*) Ephyrae

Zhilu Fu^{1,2,*}, Jie Li^{3,4}, Jiale Wang^{3,4}, Junxiang Lai³, Yin Liu^{5,6}, Ming Sun^{5,7,8,*}

¹Key Laboratory of Protection and Utilization of Marine Resources, Guangxi University for Nationalities, Nanning, China

²Guangxi Key Laboratory of Utilization of Microbial and Botanical Resources, Guangxi University for Nationalities, Nanning, China

³Guangxi Key Laboratory of Marine Environmental Science, Guangxi Beibu Gulf Marine Research Center, Guangxi Academy of Sciences, Nanning, China

⁴School of Marine Science, Guangxi University, Nanning, China

⁵Liaoning Province Key Laboratory of Marine Biological Resources and Ecology, Liaoning Ocean and Fisheries Science Research Institute, Dalian, China

⁶College of Fisheries and Life Science, Dalian Ocean University, Dalian, China

⁷Key Laboratory of Experimental Marine Biology, Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China

⁸University of Chinese Academy of Sciences, Beijing, China

Email address:

fzl19@163.com (Zhilu Fu), sunming0408@163.com (Ming Sun)

*Corresponding author

To cite this article:

Zhilu Fu, Jie Li, Jiale Wang, Junxiang Lai, Yin Liu, Ming Sun. Combined Effects of Temperature and Salinity on the Growth and Pulsation of Moon Jellyfish (*Aurelia coerulea*) Ephyrae. *American Journal of Life Sciences*. Vol. 8, No. 5, 2020, pp. 144-151.

doi: 10.11648/j.ajls.20200805.19

Received: August 8, 2020; **Accepted:** August 20, 2020; **Published:** September 14, 2020

Abstract: Blooms of the scyphozoan jellyfish *Aurelia coerulea* have caused serious problems for the fishing industry and the power plants in the coastal waters of China. The population size of adult medusae is strongly influenced by their ability to survive the ephyra stage. In this study, the growth and pulsation of *A. coerulea* ephyrae from the northern Yellow Sea were analyzed under sixteen different temperature (10, 15, 20, and 25°C) and salinity (22, 25, 28 and 31 PSU) combinations over a 21-day experimental period. The temperature had a significant effect on the growth of ephyrae. The growth rate of ephyrae increased with increasing temperature. The effects of salinity and its interaction with temperature on the growth of ephyrae were not significant. The highest growth rate was recorded in the 25°C and 25 PSU group. The pulsation rate of ephyrae was also significantly influenced by temperature. The mean pulsation rates of newly released ephyrae were 24.2, 39.1, 52.5, and 73.15 beats min⁻¹ at 10, 15, 20, and 25°C, respectively. As ephyrae developed into medusae, the pulsation rates generally decreased. Salinity and its interaction with temperature did not have a significant effect on the pulsation of ephyrae. We conclude that a warm spring can cause an *A. coerulea* bloom in that year.

Keywords: *Aurelia coerulea*, Ephyrae, Growth, Pulsation, Temperature, Salinity

1. Introduction

Mass blooms of large jellyfish (Scyphozoa) have become increasingly common in oceans in many parts of the world, causing significant environmental and economic impacts. Jellyfish blooms can have considerable impacts on marine ecosystems since jellyfish compete for food with

zooplanktivorous fishes and predate directly on fish larvae and eggs [1, 2]. Hence, increases in jellyfish populations may lead to depletion of fish stocks and reductions in harvests [3-5]. In addition, dense aggregations of medusae can also cause serious problems for fisheries by clogging fishing gear and coastal power plants by blocking cooling water systems [6-8]. Therefore, it is important not only to clarify the mechanisms

of jellyfish population blooms but also to forecast future outbreaks and determine appropriate countermeasures.

The *Aurelia* spp. (class: Scyphozoa), commonly known as the moon jellyfish, is abundantly found in many temperate regions. It has been reported that genus *Aurelia* has at least 12 cryptic species, and the species found in China were previously recognized as *Aurelia* sp. 1 and recently changed to *Aurelia coerulea* [6]. In China, *A. coerulea* is one of the most common bloom-forming species. These species are mainly found across the shallow coastal waters of the Yellow Sea and the Bohai Sea, including Shandong, Liaoning, and Hebei provinces [7, 9]. In recent years, the local fishing industry and the coastal power plants have been negatively impacted by *A. coerulea* blooms, even causing power plant shutdown in severe cases [7, 9]. In 2007, a massive *A. coerulea* bloom was observed along the coastal waters of Shandong Province (Weihai city and Yantai city) between the months of June and September [10, 11]. In 2008, the intake screens of power plants in Qinhuangdao city and Weihai city were unclogged by removing more than 4000 tons wet weight and 20-50 tons of *A. coerulea* medusae, respectively [7]. Similarly, in 2009, more than 10 tons of medusae were removed from the intake screens of a power plant in Qingdao city, Shandong Province [7].

The recent increase in *A. coerulea* blooms in China may not be attributed to decadal climate change, which affects temporal variations in jellyfish biomass in the Bering Sea, but to environmental changes caused by human activities. Many previous studies have speculated the causes of jellyfish blooms include decreased fish stocks due to overfishing, increased zooplankton predation causing eutrophication, increased ocean water temperatures due to global warming, and increased numbers of polyp attachment sites due to marine construction. However, it is very difficult to specify which factors are primarily responsible since blooms may be caused by the interactions of multiple factors [4, 7, 12, 13].

The life cycle of *A. coerulea* alternates between a benthic polyp stage and a pelagic medusa stage. Their survival of the ephyra stage acts as a determining factor that impacts the population of adult medusae. Hence, it is necessary to investigate population dynamics during the ephyra stage to understand the causes of medusa blooms. Little information exists regarding the physio-ecology of the ephyrae of genus *Aurelia*. Previous studies have demonstrated that the growth of ephyrae of genus *Aurelia* can be affected by several environmental factors such as temperature, food and salinities [14-17]. Among these environmental factors, temperature had the greatest impact on growth ephyrae. Båmstedt et al. [14] studied the growth rate of *A. aurita* ephyrae at different temperatures and salinities and found a 5.4 times higher growth rate at 18°C than at 6°C. Another study analyzed the growth rate of *A. labiata* ephyrae between 8-28°C and found an initial increase till 21°C, followed by a gradual decrease [15]. For the pulsation rate of *A. aurita*, Dillon [18] found a significantly higher pulsation rate of *A. aurita* ephyrae at 20°C compared with 10°C; however, lower values were observed between 25 and 35°C. These results were consistent with a previous study where higher pulsation rates were observed for

A. aurita ephyrae between 11 and 25°C, but the values decreased at temperatures > 25°C [19]. The effect of salinity on the growth of *A. aurita* ephyrae did not show a clear trend [14]. Reduced salinity was associated with an acute effect of an increased pulsation rate, but this effect disappeared within 2 days [18]. Additionally, the impact of other parameters on the survival in the ephyra stage has not been evaluated. There are no published reports on the combined effects of temperature and salinity on growth and pulsation in this species.

In the coastal waters of northern China, *A. coerulea* ephyrae follow a season-specific appearance pattern, mainly in the middle or late spring [9, 16]. Large variations in recruitment are reflected in the population size of adult medusae. This variation is dependent upon the irregular mortality and growth rate in the ephyra stage. Since salinity and temperature might significantly impact the growth and locomotion of *A. coerulea* ephyrae in the northern Yellow Sea in China; thus, experimental investigations were performed to examine the combined effects of temperature and salinity on the growth and pulsation of *A. coerulea* ephyrae.

2. Materials and Methods

2.1. Ephyrae Preparation

Ephyrae of *A. coerulea* were obtained from stock cultures of polyps; they were originally derived from matured medusae obtained from the Heishijiao area, Dalian (northern Yellow Sea), China. Planulae of *A. coerulea* were placed in opaque plastic boxes containing approximately 20 L of filtered seawater with a salinity of 31 PSU. The planulae were incubated and allowed to settle on 0.5 mm thick opaque corrugated plates (40×35 cm in size) at 20-25°C. Post-transformation into the polyp stage, they ate *Artemia* spp. nauplii *ad libitum* once or twice weekly, and a seawater alternative. Finally, strobilation was induced at 15°C to release the ephyrae.

2.2. Experimental Design

A two-factor orthogonal design was used to determine the effect of temperature (10, 15, 20, and 25°C) and salinity (22, 25, 28, and 31 PSU) on the growth of *A. coerulea* ephyrae over a 21-day period. The four temperature levels span the temperature range from mid-spring to summer in the northern Yellow Sea, that is, the period from the release of ephyrae to development into adult medusae. The salinity levels represent the salinity range from the estuary to offshore waters in the northern Yellow Sea, where *A. coerulea* is naturally distributed. All further experiments were performed using ephyrae that released from their strobilae within 48 h. Ten ephyrae were arbitrarily placed in a 1 L glass beaker containing 0.45 µm of filtered seawater. In this study, 1-L glass beakers containing 10 ephyrae each were randomly allocated to 16 temperature and salinity groups, with one beaker assigned to each combination.

For the 10 and 15°C treatments, the beakers with ephyrae

were placed in incubators to maintain constant temperatures. For the 20°C treatment, the beakers were placed in a room that was kept at a constant 20°C. For the 25°C treatment, the beakers were submerged in water baths held at 25°C. Temperatures at each treatment were checked with thermometers twice per day to ensure a constant water temperature constant ($\pm 0.2^\circ\text{C}$). Additionally, experimental seawater samples with different salinities were prepared by adding purified water to filtered seawater.

Ephyrae were held at their treatment temperatures and transferred to their respective salinity conditions to acclimate to the experimental conditions for 24 h. After 24 h of acclimation, the ephyrae were fed adequate *Artemia* nauplii twice daily (approximately 300-1000 prey L^{-1}). The protocol was designed to maximize the growth rate that would generate a significant difference between the treatments. Post-feeding, the unfinished food was replaced with filtered seawater at identical salinity and temperature. The seawater used for replacement was placed in the corresponding incubator or room 1 day before use to reach the experimental temperature.

During the experiment, continuous observations of the survival, morphological changes, and food digestion of ephyrae were recorded in detail. At each 3-d interval, the bell diameter size of all ephyrae was measured. The bell diameter in this study was defined as the distance between two opposite lappet tips. A wide-mouthed pipette was used to place the ephyrae (< 10 mm) on a glass dish, allowed to relax, followed by measurement using a dissecting microscope and a grid with 0.01-mm gradations; ephyrae larger than 10 mm were individually placed on a small glass container, allowed to relax and then measured using a ruler with 1-mm gradations. Each measurement was completed within 1 min. After the measurement, beakers with ephyrae were quickly placed back under experimental conditions. The following equation was used to estimate the growth rate [15]:

$$\text{Growth rate (\% d}^{-1}\text{)} = \ln [(D_2/D_1)^3] / (t_2 - t_1) \times 100$$

where D_1 and D_2 represent the mean diameters from each treatment group in two subsequent analyses, and t_1 and t_2 (days) are the experimental days of two consecutive measurements, respectively.

2.3. Pulsation Rate

During the 21-d experiment, pulsation rates were also measured in 3-d intervals. Three ephyrae from each beaker were randomly selected for measurement, and each specimen was transferred into a beaker (1 L) containing seawater at a specific salinity and temperature, followed by counting pulsations using a manual tally counter in 1-min increments for 3 min. Each experiment was repeated thrice, and the mean pulsation rate was derived.

2.4. Statistics

Two-way ANOVA was performed after testing for data normality and variance equality (SPSS 26.0) to examine the combined effects of salinity and temperature on the growth

and pulsation of ephyrae. Tukey's pairwise comparisons were conducted to compare variables among experimental combinations if the overall results of ANOVA were significant ($p < 0.05$).

3. Results

3.1. Observations of Feeding and Digestion in Ephyrae Under Different Treatment Conditions

Feeding and digestion in *A. coerulea* ephyrae under different treatment conditions were observed with the naked eye. The feeding and digestion rates of ephyrae were significantly different under different temperature conditions. At 25°C, the highest food intake and the shortest digestion time were observed in ephyrae. Five minutes after feeding, *Artemia* nauplii were ingested in the stomach cavity of ephyrae; this ingestion determined when the color of the stomach cavity turned red. At 1 h after ingestion, the *Artemia* nauplii in the stomach cavity of ephyrae were completely digested. As the temperature decreased, the food intake of ephyrae decreased, and digestion slowed accordingly. For example, at 10°C, digestion in ephyrae was very slow. After 8 h of ingestion, undigested *Artemia* nauplii could still be seen in the stomach cavities of ephyrae.

3.2. Effects of Salinity and Temperature on the Growth of Ephyrae

At the beginning of the experiment, the mean diameter of *A. coerulea* ephyrae in all treatment groups was 2.52 ± 0.11 mm, and there was an insignificant difference between different treatment groups ($p > 0.05$). After 21 days, differences in ephyrae diameters were visible and significant among treatments (Figure 1). The diameter of the ephyrae was largest in the 25°C-25 PSU treatment group, reaching 27.2 ± 2.6 mm. Two-way ANOVA showed that temperature significantly influenced the growth of ephyrae ($p < 0.01$); however, salinity ($p > 0.05$) and its combined effect with temperature ($p > 0.05$) did not produce any significant differences.

Figure 2 shows the average growth rates, calculated based on the difference between the initial and final diameter of the ephyrae measured every three days. Warm temperature significantly increased the growth of ephyrae (two-way ANOVA, $p < 0.01$). The highest growth rate was observed at 25°C, which resulted in an increase in the diameter of ephyrae from 2.50 ± 0.16 mm to 21.8 ± 4.4 mm under all salinity conditions at the end of the 21-day experiment. A slower growth rate was observed for ephyrae grown at 10°C, with an overall growth rate of approximately 6.30-9.51%; they slightly increased from 2.55 ± 0.09 mm to 4.60 ± 0.52 mm by day 21. Ephyrae grown at 15 and 18°C in all salinities had rapid growth rates at the beginning of the experiment (days 1-6), ranging from 30.41-69.03%, and then the growth rates exhibited a decreasing trend. The overall growth rates ranged from 17.76-30.35%. In addition, some ephyrae in the 15, 20, and 25°C treatment groups deformed by everting their bells. The number of deformed ephyrae was lowest in the 15°C

treatment groups and similar among the 20 and 25°C treatment groups. The deformed ephyrae showed a reduction in the growth rate in subsequent experiments.

Salinity did not have a significant impact on the growth rate of ephyrae (two-way ANOVA, $p > 0.05$). At 15, 20, and 25°C, the average growth rates of ephyrae were highest in the 25 and 28 PSU treatments, ranging from 20.74-30.24%. Ephyrae grown in the 22 PSU groups had slightly lower growth rates at these three temperatures, ranging from 20.78-30.88%. Ephyrae in the 31 PSU grew the slowest, and the overall growth rates at these three temperatures ranged from 17.76-27.85%. However, at 10°C, the average growth rate of ephyrae was highest in the 31 PSU groups, followed by the 25 PSU groups, the 28 PSU groups, and lowest in the 22 PSU groups (Figure 2). The statistical analysis showed that the interaction of temperature and salinity did not have a significant effect on the growth of ephyrae (two-way ANOVA, $p > 0.05$).

3.3. Effect of Temperature and Salinity on the Rate of Pulsation in Ephyrae

The mean pulsation rates in newly released ephyrae were 24.2 ± 6.4 , 39.1 ± 3.8 , 52.5 ± 4.9 , and 73.15 ± 5.09 beats individual⁻¹ min⁻¹ at 10, 15, 20, and 25°C in all salinities, respectively (Figure 3), and there was a significant difference between the temperature groups (one-way ANOVA, $p < 0.01$). As the ephyrae grew, the mean pulsation rate gradually decreased. The trend was highly pronounced at higher water temperatures. Over the experimental period of 21 days, temperature showed a significant effect on the pulsation rates of ephyrae (two-way ANOVA, $p < 0.01$); however, no significant effects were observed for the impact of salinity and its combined effect with temperature (two-way ANOVA, $p > 0.05$).

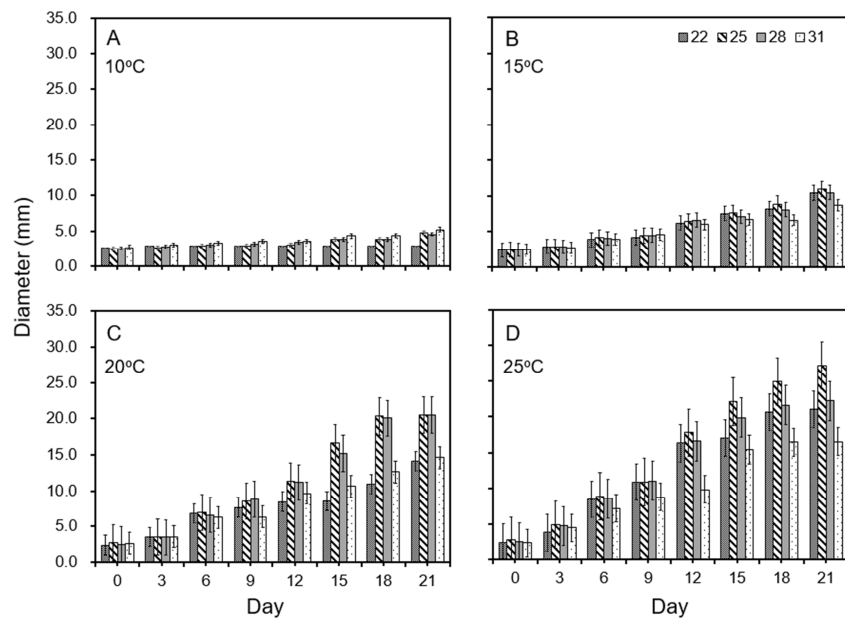


Figure 1. Means of body diameters increase of *Aurelia coerulea* ephyrae under 4 salinities at 10 (A), 15 (B), 20 (C) and 25°C (D) during a 21-d experiment.

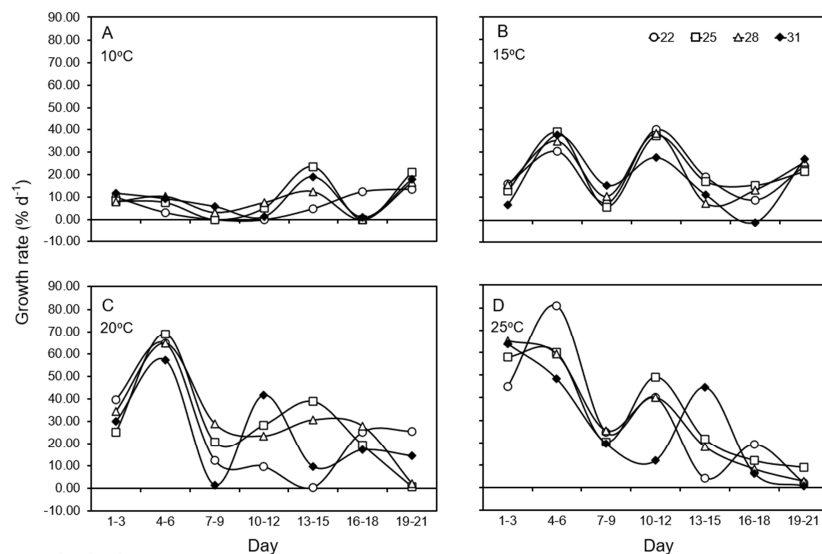


Figure 2. Change of growth rates of *Aurelia coerulea* ephyrae under 4 salinities at 10 (A), 15 (B), 20 (C) and 25°C (D) during a 21-d experiment.

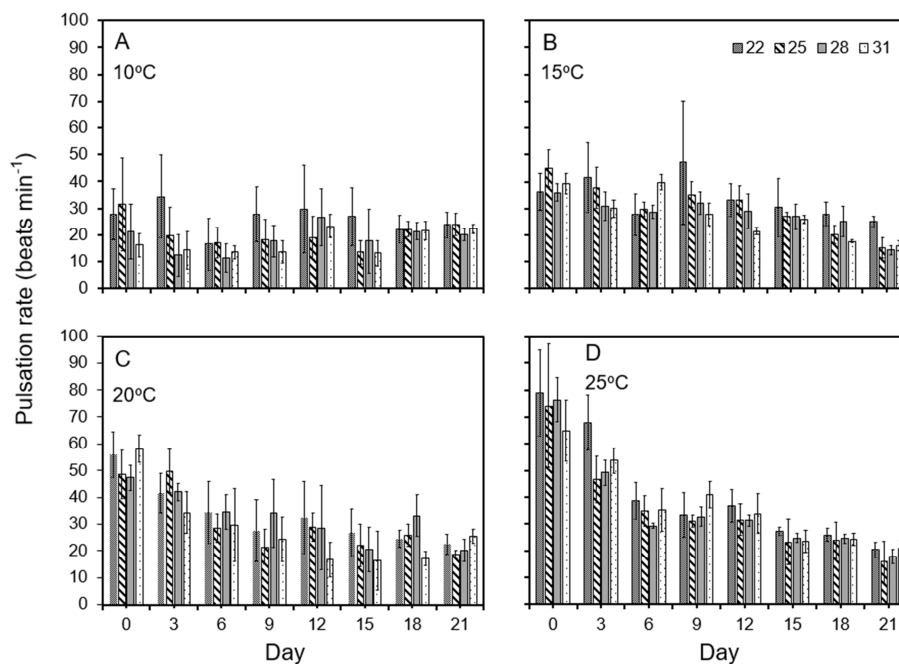


Figure 3. Change of pulsation rates of *Aurelia coerulea* ephyrae under 4 salinities at 10 (A), 15 (B), 20 (C) and 25°C (D) during a 21-d experiment.

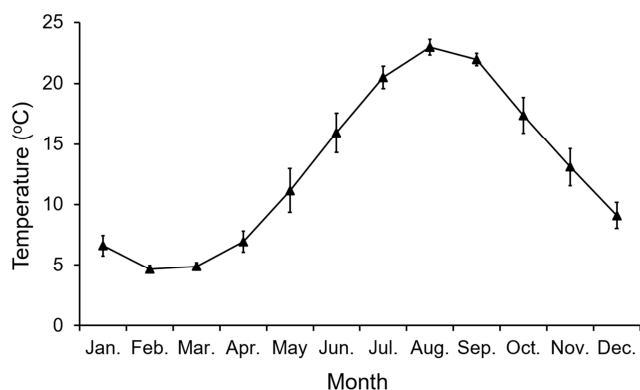


Figure 4. Annual sea surface water temperatures in Xinghai Bay, Dalian, northern Yellow Sea in 2017.

4. Discussion

4.1. Effect of Temperature and Salinity on the Growth Rate of Ephyrae

Unlike most previous studies on the growth of *A. aurita* ephyrae and medusae, which were restricted to several days [14, 15, 20–22], our study was a long-term experiment that was conducted for 21 days, covering the entire development period from 2.5-mm ephyrae to young medusae with a maximum diameter of approximately 3 cm. In our experiment, *A. coerulea* ephyrae were fed excess *Artemia* nauplii twice daily; this feeding strategy promoted the maximum growth rate in ephyrae, maximizing the differences between treatments. Most previous studies on the growth of ephyrae recorded the size of the ephyrae at the beginning and the end of the study. Our study measured the size of ephyrae and calculated the growth rate at 3-d intervals. Thus, our results have a significantly better statistical foundation than those of

previous studies.

Growth rates of ephyrae of the genus *Aurelia* have been recorded in only two studies [14, 15]. Båmstedt *et al.* [14] demonstrated that *A. aurita* ephyrae exhibited a rapid growth rate (up to 70% d⁻¹) initially, followed by reduction to 20 to 40% d⁻¹ consistent with the results for the ephyrae of *A. labiata* [15]. The growth rates were higher during the first 7 days of the experiment, reaching 41.35% d⁻¹, and then they decreased to ~17.82% d⁻¹ during days 7–14. In our study, the growth rate showed a similar trend. *A. coerulea* ephyrae had a rapid growth rate for the first 6 days; thereafter, the growth rate showed a general decreasing trend. This result is in accordance with previous studies. Moreover, the maximum growth rate recorded in our study was 81% d⁻¹, which is higher than those in previous studies. However, here, food was provided *ad libitum*, similar to previous studies. In the natural environment, this range of food concentration (> 300 prey L⁻¹) is not generally found, and thus, these results could be situations with a high abundance of food.

The differences in the growth of *A. coerulea* ephyrae at different temperatures were observable and noticeable in this study. Although the average size of ephyrae was the same in all groups at the beginning of the experiment, we observed that the average diameter of ephyrae was five times higher at 25°C than at 10°C at the end of the 21-day experiment. Ephyrae reared at different temperatures had different fates. For the first 12 days of the experiment, slow growth of ephyrae was observed at 10°C (Figure 2), followed by an increase between days 13–19, which may be attributed to the growth of larger guts and the subsequent ability to ingest an increased amount of food and energy to allocate to growth [15, 23]. It was observed that low temperatures led to a decrease in the feeding rates of *A. aurita* ephyrae. Ephyrae at 10°C did not appear to be active feeders, although *Artemia* nauplii were occasionally observed in their guts. Although the growth rate

of ephyrae at 10°C was slow, as they increased their diameter from 2.5 mm to only 4.60 mm, they grew well and did not exhibit any bell deformations or moribundity. Therefore, it appears that *A. coerulea* ephyrae in the field could survive at 10°C for a minimum of 21 days and then regrow if the temperature increased.

At 20 and 25°C, ephyrae showed a higher growth rate for the first 6 days; however, at 7-8 mm size, several ephyrae everted their bells and were unable to swim or feed effectively, leading to a reduced bell diameter. This phenomenon was also described by Widmer [15]. However, in the current study, the deformation caused by bell eversion in ephyrae occurred at 15°C, which was much lower than that reported by Widmer [15]. We attempted to mechanically restore their bells to a normal state, but some ephyrae could not recover. Widmer [15] concluded that the deformation was caused by heat stress. However, we do not fully agree with this conclusion since some of the ephyrae in the 15°C group also everted in their bells, although the number of deformed ephyrae was much lower than those in the 20 and 25°C groups. The mechanism of bell eversion in ephyrae remains unclear, and further studies are needed to clarify the cause of this phenomenon.

The optimum temperature for the growth of the genus *Aurelia* has been reported in many laboratory studies. For medusae, the optimum temperature for growth was reported to be 16.4°C (in *A. aurita* originally from Gullmarsfjorden, Sweden; [21]); for ephyrae, the optimum temperatures were reported to be 18°C (the *A. aurita* ephyrae origin is not recorded, but they are speculated to be from northern Europe; [14]) and 21°C (*A. labiata* ephyrae originally from Monterey Bay, US; [15]). In this study, the maximum growth rates of *A. coerulea* ephyrae (originally from the northern Yellow Sea, China) occurred at 25°C, which is in contrast with previous studies. We consider that the differences in optimal growth temperatures are caused by long-term adaptation of genus *Aurelia* to their respective environments.

Salinity within the tested range had no significant effect on the growth of *A. coerulea* ephyrae. Ephyrae grew well under all salinity conditions, indicating that the salinity range of 22-31 PSU is suitable for the growth of *A. aurita* ephyrae. The maximum growth rates were recorded in the 25 and 28 PSU groups, indicating that ephyrae may prefer to live in estuarine coastal areas. The salinity range tested in this study corresponded to salinity conditions likely to be encountered by naturally occurring colonies in the northern Yellow Sea. The tolerance of ephyrae to a range of salinity regimes allows them to survive and grow under different salinity conditions and thus maximize the population size of adult medusae in marine environments.

Interactions of temperature and salinity did not significantly affect the growth of *A. coerulea* ephyrae. However, the deformation of ephyrae caused by bell eversion tended to appear in the high salinity groups. The number of deformed ephyrae was highest in the 20°C-31 PSU and 25°C-31 PSU groups; no ephyrae showed deformations in the 22 PSU treatment groups. This result suggests that temperature and salinity might have additive effects on the deformation of

ephyrae.

4.2. Effects of Temperature and Salinity on the Pulsation of Ephyrae

A. coerulea detects their prey physically and do not possess the ability to detect their prey remotely. Thus, there is a strong correlation between swimming and feeding. Here, the maximum pulsation rate was found to be 78.9 beats min⁻¹. The maximum swimming speed of *A. coerulea* ephyrae was estimated to be 14.2 cm min⁻¹ based on 1.88 mm movement/pulsation [24]. This swimming speed was much slower than the escape speed of many zooplankton [24]. Studies have observed a continuous swimming pattern in *A. aurita* ephyrae since they are cruising predators [24]. Based on this pattern, *A. coerulea* ephyrae mainly capture slow-moving planktonic prey in the field, including immobile prey, such as fish eggs, and slow-moving prey, such as veliger larvae, barnacle nauplii, and hydromedusae. Copepod nauplii (escape speed: 120 cm min⁻¹) would not be expected to be major prey items, and copepodites and adult copepods that characteristically escape at >300 cm min⁻¹ are not generally consumed by *A. coerulea* ephyrae.

Temperature significantly influenced the pulsation rates of *A. coerulea* ephyrae. The pulsation rates increased with increasing temperatures from 10-25°C. This result is consistent with previous studies. However, as ephyrae developed into medusae, the pulsation rate decreased. This may be because as their body volume increases, their clearance rate, prey encounter rate, and prey capture success rate correspondingly increase. The effect of temperature on the pulsation rate of *A. coerulea* ephyrae also affected growth. The temperature-dependent growth observed in this study could be related to the irregular predation rate caused by temperature-dependent activity as *A. coerulea* are known to capture prey resulting from the swim propulsion activity-driven currents [21, 25].

Here, we observed that under all salinity conditions, ephyrae swam actively, and showed an insignificant difference in their rates of pulsation among the salinities tested. Dillion [18] showed that acute changes in salinity significantly increased pulsation rates. This difference could be attributed to the fact that the ephyrae in this study had a longer adaptation time compared with previous studies. At 22 to 31 PSU salinity, which is experienced by *A. aurita* ephyrae in the wild, ephyrae can swim actively to escape from predators and seek food.

4.3. *A. Coerulea* Ephyrae in the Wild

A. aurita is a eurythermal and euryhaline species that is distributed in water within a temperature range of 0-32°C and a salinity range of < 10 to 38 PSU [26]. The population dynamics of *A. coerulea* in Jiaozhou Bay, northern Yellow Sea has been reported by Wang and Sun [16]. They found that *A. coerulea* ephyrae occurred from May to June when the temperature ranged from 12 to 18°C. Moreover, Wang and Li [17] conducted a laboratory experiment and found that the

strobilation of *A. coerulea* occurred between 8-17°C. According to these results, the strobilation of *A. coerulea* in the Dalian area, northern Yellow sea, would be occurred between late April and late June when the *in situ* water temperature is between 8-17°C. Furthermore, previous studies in other regions have also reported that the beginning of the growth of *A. aurita* ephyrae in spring is determined by the water temperature [27]. The growth of *A. aurita* ephyrae in temperate areas remains stagnant in winter and early spring and rapidly increases in summer [26]. If we apply the results of this experiment to speculate the growth of *A. coerulea* ephyrae in the northern Yellow Sea, the rapid growth of *A. coerulea* is expected in mid-May when the temperature of the northern Yellow Sea is higher than 10°C (Figure 4). The results of this experiment also indicate that blooms of *A. coerulea* are more likely to occur in years when the water temperature is warm in spring.

5. Conclusions

The growth and pulsation of *Aurelia coerulea* ephyrae were examined at four temperatures and four salinities in laboratory experiments over the 21-d period. Temperature significantly affected the growth rates of ephyrae. Feeding of ephyrae was more active at higher temperatures, and digestion times decreased with an increase in temperature. The average diameters of ephyrae were the same at the beginning of the experiment. At the end of the 21-d experiment, the average diameters of ephyrae were 4.60, 10.18, 17.48, and 21.75 mm at 10, 15, 20, and 25°C, respectively. The growth rates showed a cyclical trend. Salinity and its interaction with temperature were not significantly affected the growth rates. The highest rate of pulsation for *A. coerulea* ephyrae was found to 78.9 beats min⁻¹, with a corresponding maximum swimming velocity of 14.2 cm min⁻¹. Since this swimming speed was much lower than the speed of common zooplanktons, such as copepods, it implied that ephyrae could only capture slow-moving prey. There was a significant impact of temperature on the pulsation rates, which generally decreased as ephyrae grown to medusae. Salinity and its interaction with temperature did not have a significant effect on the pulsation of ephyrae. We conclude that *A. coerulea* ephyrae in the northern Yellow Sea may occur between May and late June, and the warm spring can cause *A. coerulea* blooms in that year.

Acknowledgements

This research was funded by the Natural Science Foundation of Guangxi Province, China (2016GXNSFC A380015), Science and Technology Major Project of Guangxi (AA17202020), Xiangsihu Young Scholars Innovative Research Team of Guangxi University for Nationalities (2018RSCXSHQN02, 201706) and the Training Program for A Thousand Young and Middle-aged Backbone Teachers in Colleges and Universities in Guangxi.

References

- [1] Pereira, R., Teodósio, M. A. and Garrido, S. (2014) An Experimental Study of *Aurelia aurita* Feeding Behaviour: Inference of the Potential Predation Impact on a Temperate Estuarine Nursery Area. *Estuarine, Estuarine Coastal Shelf Science*, 146, 102-110.
- [2] Purcell, J. E. and Arai, M. N. (2001) Interactions of Pelagic Cnidarians and Ctenophores with Fish: A Review. *Hydrobiologia*, 451, 27-44.
- [3] Lynam, C. P., Gibbons, M. J., Axelsen, B. E., Sparks, C. A. J., Coetzee, J., Heywood, Benjamin G. and Brierley, A. S. (2006) Jellyfish Overtake Fish in a Heavily Fished Ecosystem. *Current Biology*, 16, 1976.
- [4] Richardson, A. J., Bakun, A., Hays, G. C. and Gibbons, M. J. (2009) The Jellyfish Joyride: Causes, Consequences and Management Responses to a More Gelatinous Future. *Trends in Ecology & Evolution*, 24, 312-322.
- [5] Uye, S.-i. (2011) Human Forcing of the Copepod-fish-jellyfish Triangular Trophic Relationship. *Hydrobiologia*, 666, 71-83.
- [6] Dong, Z. Blooms of the Moon Jellyfish *Aurelia*: Causes, Consequences and Controls. in Sheppard, C. (Eds), *World Seas: An Environmental Evaluation. Vol. III. Ecological Issues and Environmental Impacts*. Elsevier Ltd., London, 2019, pp. 163-171.
- [7] Dong, Z., Liu, D. and Keesing, J. K. (2010) Jellyfish Blooms in China: Dominant Species, Causes and Consequences. *Marine Pollution Bulletin*, 60, 954-963.
- [8] Purcell, J. E., Uye, S. I. and Lo, W. T. (2007) Anthropogenic Causes of Jellyfish Blooms and Their Direct Consequences for Humans: A Review. *Marine Ecology Progress Series*, 350, 153-174.
- [9] Dong, Z., Liu, D. and Keesing, J. K. Population Changes of *Rhopilema esculentum* with Special Reference to Its Fishery and Stock Enhancement, in: Pitt, K. A., Lucas, C. H. (Eds.), *Jellyfish blooms*. Springer Dordrecht, New York London, 2014, pp. 186-207.
- [10] Su, L. and Wang, Y. (2007) Exploring the Mystery of Moon Jellyfish Bloom at Yantai. *Beijing Sci-Tech-Report*, 37, 16-17.
- [11] Zheng, F. Y., Chen, S. Q. and Jia, N. I. (2010) Biological Characteristics of Moon Jellyfish (*Aurelia aurita* Linnaeus, 1758) and Its Bloom. *Advances in Marine Science*, 28, 126-132.
- [12] Purcell, J. (2012) Jellyfish and Ctenophore Blooms Coincide with Human Proliferations and Environmental Perturbations. *Annual review of marine science*, 4, 209-35.
- [13] Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S.-i., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R., Malej, A., Madin, L., Mianzan, H., Gili, J.-M., Fuentes, V., Atienza, D., Pagés, F., Breitburg, D., Malek, J., Graham, W. M. and Condon, R. H. (2013) Is Global Ocean Sprawl a Cause of Jellyfish Blooms? *Frontiers in Ecology and the Environment*, 11 (2), 91-97.
- [14] Båmstedt, U., Lane, J. and Martinussen, M. B. (1999) Bioenergetics of Ephyra Larvae of the Scyphozoan Jellyfish *Aurelia aurita* in Relation to Temperature and Salinity. *Marine Biology*, 135, 89-98.

- [15] Widmer, C. L. (2005) Effects of Temperature on Growth of North-East Pacific Moon Jellyfish Ephyrae, *Aurelia labiata* (Cnidaria: Scyphozoa). Journal of the Marine Biological Association of the United Kingdom, 85, 569-573.
- [16] Wang, Y.-T. and Sun, S. (2015) Population Dynamics of *Aurelia* sp. 1 Ephyrae and Medusae in Jiaozhou Bay, China. Hydrobiologia, 754, 147-155.
- [17] Wang, N. and Li, C. (2015) The Effect of Temperature and Food Supply on the Growth and Ontogeny of *Aurelia* sp. 1 Ephyrae. Hydrobiologia, 754, 157-167.
- [18] Dillon, T. (1977) Effects of Acute Changes in Temperature and Salinity on Pulsation Rates in Ephyrae of the Scyphozoan *Aurelia aurita*. Marine Biology, 42, 31-35.
- [19] Mangum, C., Oakes, M. and Shick, J. (1972) Rate-temperature Responses in Scyphozoan Medusae and Polyps. Marine Biology, 15, 298-303.
- [20] Hernroth, L. and Gröndahl, F. (1983) On the Biology of *Aurelia aurita* (L.) 1. Release and Growth of *Aurelia aurita* (L.) Ephyrae in the Gullmar Fjord, Western Sweden, 1982-83. Ophelia, 22, (2), 189-199.
- [21] Hansson, L. J. (1997) Effect of Temperature on Growth Rate of *Aurelia aurita* (Cnidaria, Scyphozoa) from Gullmarsfjorden, Sweden. Marine Ecology Progress Series, 161, 145-153.
- [22] Ishii, H. and Bamstedt, U. (1998) Food Regulation of Growth and Maturation in a Natural Population of *Aurelia aurita* (L.). Journal of Plankton Research, 20, 805-816.
- [23] Graham, W. M. and Kroutil, R. M. (2001) Size-based Prey Selectivity and Dietary Shifts in the Jellyfish, *Aurelia aurita*. Journal of Plankton Research, 23, 67-74.
- [24] Sullivan, B. K., Suchman, C. L. and Costello, J. H. (1997) Mechanics of Prey Selection by Ephyrae of the Scyphomedusa *Aurelia aurita*. Marine Biology, 130, 213-222.
- [25] Costello, J. H. and Colin, S. P. (1994) Morphology, Fluid Motion and Predation by the Scyphomedusa *Aurelia aurita*. Marine Biology, 121, 327-334.
- [26] Lucas, C. H. (2001) Reproduction and Life History Strategies of the Common Jellyfish, *Aurelia aurita*, in Relation to Its Ambient Environment. Hydrobiologia, 451, 229-246.
- [27] Möller, H. (1980) Population Dynamics of *Aurelia aurita* Medusae in Kiel Bight, Germany (FRG). Marine Biology, 60, 123-128.