Effects of salinity and temperature on the recruitment of *Aurelia coerulea* planulae

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**ABSTRACT**

The recruitment of scyphomedusae planulae to the benthic polyp stage is important for population size and may be affected under projected climate change scenarios. In a laboratory study, we determined the combined effects of elevated temperature and reduced salinity on the behaviour, survival and settlement of *Aurelia coerulea* planulae. Three temperature levels (21, 24 and 27°C) and two salinity levels (31 and 22) were used. Reduced salinity had a significant negative effect on the swimming behaviour and settlement of *A. coerulea* planulae. The planulae moved quickly and preferred to settle under ambient salinity conditions. The settlement rate of *A. coerulea* planulae was high during the current ambient summer temperature (24°C), and elevated temperature increased the mortality rate and reduced their settlement rate. *A. coerulea* planulae were significantly smaller under the combined conditions of elevated temperature and reduced salinity. Our study provides information on the response of *A. coerulea* planulae to temperature and salinity, which is helpful for understanding how environmental factors will influence the recruitment dynamics of *A. coerulea*.

**Introduction**

The moon jellyfish *Aurelia* spp. belongs to the phylum Cnidaria (Class: Scyphozoa) and is the most common scyphozoan jellyfish in global coastal waters (Lucas 2001). Based on phylogenetic analysis, there are at least 13 cryptic species in the genus *Aurelia*; among these species, *A. coerulea* occurs in the major warm temperate regions, which includes China, Japan, Korea, Australia and California (Dawson et al. 2005; Ki et al. 2008; Dong et al. 2015; Scorrano et al. 2016). Recently, blooms of *A. coerulea* medusae have been reported in the East Asian margin seas, including the coastal waters of China, Japan and Korea, and these blooms can negatively impact coastal power plant operations, local fisheries and aquaculture (Uye and Ueta 2004; Dong et al. 2010; Uye 2011; Purcell et al. 2013). Multiple factors have been suggested to be possible causes of the *A. coerulea* blooms in these regions, including overfishing, eutrophication, global warming, habitat modification and the invasion of alien species (Lo et al. 2008; Dong et al. 2010; Uye 2011).

Most scyphomedusae have a complex life cycle that alternates between a sexual reproduction stage and an asexual reproduction stage. The recruitment success during the early life stages (i.e. planula, polyp and ephyra) of scyphomedusae can have a major effect on the abundance of the adult medusa population and can contribute to jellyfish blooms (Lucas et al. 2012). It is well documented that seawater temperature can affect the survival, growth and asexual reproduction of *Aurelia* spp. polyps (e.g. Liu et al. 2009; Han and Uye 2010; Schiariti et al. 2014; Hubot et al. 2017). Seawater temperature can also affect the growth of *Aurelia* spp. ephyrae (Widmer 2005; Fu et al. 2011; Algueró-Muñiz et al. 2016).

*Aurelia* spp. planulae, released by mature female medusae, usually settle on suitable substrate within one week (Brewer 1978; Conley and Uye 2015). During this stage, environmental factors (temperature, salinity, light and DO), substrate properties (physical properties and bacterial biofilms) and biological factors (conspecifics, competitors and predators) may affect the survival, settlement and metamorphosis of *Aurelia* spp. planulae (Lucas et al. 2012). Previous studies have investigated the settlement substrate preferences (Holst and Jarms 2007; Hoover and Purcell 2009) and the effects of bacteria on the induction of settlement of *Aurelia aurita* (Kroiker and Berking 1999). Only a few recent studies...
have reported how seawater temperature or salinity influences the survival and settlement of Aurelia spp. planulae (Webster and Lucas 2012; Conley and Uye 2015). In Aurelia aurita collected from southern England, significantly fewer numbers of planulae settled under the highest temperature conditions (Webster and Lucas 2012). Conley and Uye reported that salinity was a principle factor that affected planulae dispersion and distribution of A. coerulea in temperate monsoon regions (Conley and Uye 2015).

Sexual recruitment of A. coerulea in Chinese coastal waters mainly occurs during the warmest time in the summer. Heavy rainfall and storms frequently occur during the summer, which could cause extremely low sea-surface salinity in the coastal waters. For example, the seawater salinity can be reduced to 22 or below during the summer in coastal sea cucumber culture ponds, where high densities of A. coerulea medusae have been reported (Yuan et al. 2010; Dong et al. 2014; Peng 2015). Furthermore, relatively more severe precipitation is expected to accompany a warming climate (Donat et al. 2016). Therefore, it is necessary to understand the combined effects of elevated temperature and reduced salinity on the recruitment dynamics of A. coerulea planulae.

In this study, we investigated the combined effects of temperature and salinity on the swimming behaviour, settlement and survival of A. coerulea planulae. We addressed the following two questions. (1) Do the behaviour, settlement and survival of A. coerulea planulae change in response to temperature and salinity stress? (2) Do future increases in temperature contribute to the increase of the A. coerulea population? The null hypotheses tested were that temperature and salinity did not affect the swimming behaviour, settlement or survival of A. coerulea planulae.

Materials and methods

A. coerulea collection and planulae cultivation

Five mature A. coerulea medusae with visible planulae were collected by a hand net at Sishili Bay, northern Yellow Sea, China (37°29.40′ N; 121°2.89′ E) in August 2016. Medusae were maintained in a 30 I plastic container filled with 160 μm filtered seawater (salinity 31) and transported to a controlled temperature laboratory (24°C) in the Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences. The planulae of A. coerulea were obtained following the methods of Conley and Uye (2015). On the second day, medusa incubation seawater was filtered through a 500 μm mesh to remove mucus and gelatinous tissue, and the planulae were concentrated with the use of a 38 μm mesh. Thereafter, the concentrated planulae were rapidly washed with 0.45 μm filtered natural seawater and transferred to a graduated cylinder (1000 ml volume). The planulae were pipetted into a beaker with 0.45 μm filtered natural seawater (salinity 31) and used in the following experiments.

Experimental design and procedures

A factorial experimental design was conducted with two main effects: temperature (21, 24 and 27°C) and salinity (31 and 22). The average seawater temperature at Sishili Bay during the summer spawning time (July–September) was approximately 24°C. The reduced temperature (21°C) represents the average minimum temperature in July. The elevated temperature (27°C) is approximately 3°C higher than the recorded average highest temperature at the study site. The salinity of 31 represents the ambient salinity level at Sishili Bay, while the reduced salinity of 22 represents the lowest salinity due to high precipitation during the summer (Yuan et al. 2010; Peng 2015). Seawater with low salinity was prepared by diluting 0.45 μm filtered natural seawater with a volume of Milli-Q water. The salinity was measured with a YSI-600 multiparameter water quality probe (YSI, Yellow Springs, OH).

To determine the effects of different treatments on the swimming behaviour of A. coerulea planulae, video motion analysis was performed following the protocol of Lönnstedt and Eklöv (2016) with minor revisions. Briefly, five planulae were randomly selected and kept in a 10 ml plastic tube containing 0.45 μm filtered seawater equilibrated to the respective salinity levels. Three replicate tubes were used in each of the six treatments. Then, the tubes with planulae were maintained overnight in three different incubators (BSG-800, Boxun, Shanghai) that were set to 21, 24 and 27°C, respectively. After 24 h, the swimming activity of the planulae was analysed in one temperature-controlled room that was set to 21, 24 and 27°C. Five planulae from each replicate of each treatment were selected for recording. For each recording session, a single planula was randomly selected and placed in a glass aquarium (20 × 20 cm; 5 mm × 5 mm grid drawn on the bottom), which was at the same salinity of 0.45 μm filtered seawater. The videos were recorded using an Olympus SZX10 stereo microscope fitted with an Optec TP510 digital camera. The total number of lines crossed on a grid present at the bottom of the aquarium (5 × 5 mm) was recorded for each three-minute sampling period and served as an indicator of larval swimming behaviour. The entire test was conducted on the same day.
The settlement assays were conducted using 24 culture plates (24-well plates; Canvic, Shanghai). Each of the wells was filled with 10 ml of 0.45 μm filtered seawater equilibrated to the respective salinity levels. *A. coerulea* planulae were individually transferred into each well. A 3 cm diameter polyethylene terephthalate (PET) plate was added on the water surface as a settlement substrate. Before beginning the experiments, the PET plates were conditioned in natural seawater to allow a bacterial film to form. Four replicates, each containing one tray of 24 planulae, were used for each temperature and salinity combination. The culture plates with planulae were then maintained in three different incubators which were set to 21, 24 and 27°C with a light regime of 12 h light/12 h dark. Examinations of the number of dead and settled planulae were conducted every 24 h for a period of seven days. Mortality was defined as the percentage of planulae missing after 24 h (Edmunds et al. 2001). This definition assumes that missing planulae degraded and disintegrated, and were lost to the water. The seawater was changed every two days by gently pipetting old seawater out of the rearing containers and pipetting 0.45 μm filtered seawater in under the microscope. The seawater temperature, salinity and pH were measured in the filtered seawater samples at the beginning of the experiment and at each subsequent water exchange.

To determine the effects of different treatments on the morphology of *A. coerulea* planulae, two planulae were sampled randomly from each replicate and measured at both the beginning and end of the experiment. The length and width of the sampled planulae were measured using an Olympus SZX10 stereo microscope fitted with an Optec TP510 digital camera. The planulae larval sizes were estimated using the formula for an ellipsoid \[ \frac{4}{3} \times \pi \times \frac{\text{length}}{2} \times \left(\frac{\text{width}}{2}\right)^2 \]. The change in the larval size of *A. coerulea* planulae was examined using larval size data on day 0 and day 7.

### Data analysis

The effects of two factors (temperature and salinity) and their interactions on the swimming speed, settlement, mortality and size of *A. coerulea* planulae were examined using two-way analysis of variance (ANOVA). Post-hoc analyses for significant factors in the ANOVAs were completed using Fisher’s least significant difference test. For all analyses, the homogeneity of variances and normality of residuals were assessed with Levene’s and Shapiro–Wilk tests, respectively. When necessary, variances were homogenized using a square-root transformation. All statistical analyses were performed using SPSS statistics software, version 19 (IBM, Armonk, NY, USA).

### Results

#### Behaviour

The effect of the temperature-salinity interaction on the swimming speed of *A. coerulea* planulae was

### Table 1

Results from a two-way ANOVA on differences in the mean number of lines crossed, settlement rates (%), mortality rates (%) and size of *Aurelia coerulea* planulae under different temperature (21, 24, and 27°C) and salinity (22 and 31) treatments. df, degree of freedom; MS, mean square; F, F-value; P, P-value.

| Source               | df  | MS    | F     | P     |
|----------------------|-----|-------|-------|-------|
| Number of lines crossed |     |       |       |       |
| Temperature          | 2   | 4.389 | 0.277 | 0.763 |
| Salinity             | 1   | 133.389 | 8.425 | 0.013*|
| Temperature × salinity | 2   | 5.056 | 0.319 | 0.733 |
| Error                | 12  | 15.833 |       |       |
| Settlement (%)       |     |       |       |       |
| Temperature          | 2   | 0.148 | 7.203 | 0.001*|
| Salinity             | 1   | 0.563 | 27.349| 0.000*|
| Temperature × salinity | 2   | 0.008 | 0.380 | 0.684 |
| Error                | 162 | 0.021 | –     | –     |
| Mortality (%)        |     |       |       |       |
| Temperature          | 2   | 0.204 | 7.469 | 0.001*|
| Salinity             | 1   | 0.003 | 0.098 | 0.754 |
| Temperature × salinity | 2   | 0.033 | 1.191 | 0.306 |
| Error                | 162 | 0.027 | –     | –     |
| Larval size          |     |       |       |       |
| Temperature          | 2   | 0.000 | 6.995 | 0.002*|
| Salinity             | 1   | 0.000 | 0.628 | 0.432 |
| Temperature × salinity | 2   | 0.000 | 8.486 | 0.001*|
| Error                | 42  | 0.000 | –     | –     |

Asterisks denote significant differences (P < 0.05).
not significant (\(P > 0.05;\) Table I). The results from the two-way ANOVA analysis indicate that salinity had a significant effect on the swimming speed of the A. coerulea planulae (\(P < 0.05;\) Table I; Figure 1). A. coerulea planulae moved more rapidly at high salinity (32) than at low salinity (22) at all three temperatures (Figure 2). A statistically significant difference in the swimming speed of A. coerulea planulae was detected at a temperature of 21°C (\(P < 0.05;\) Figure 1).

**Settlement**

The day-to-day settlement from planulae to polyps at different temperature–salinity combinations is shown in Figure 2. The settlement of A. coerulea planulae was influenced by salinity (\(P < 0.001;\) Table I) and temperature (\(P = 0.001;\) Table I), but there were no statistically significant interactive effects (\(P > 0.05;\) Table I). The settlement rate of A. coerulea planulae was higher at the salinity of 31 than at the salinity of 22 at all three temperatures (Figure 2). At 21°C, significant differences in settlement rate between the two levels of salinity were detected from day 2 to day 7 (Figure 2). The settlement of A. coerulea planulae was highest at ambient temperature (24°C) and lowest at the elevated temperature of 27°C (Figure 2). This pattern was especially significant on days 1, 2 and 3 at the salinity of 22 (Figure 2).

**Mortality**

The results from the two-way ANOVA showed that the mortality rate of A. coerulea planulae (\(P = 0.001;\) Table I), while salinity had no significant effect on the mortality rate of A. coerulea planulae (\(P > 0.05;\) Table I). The mortality rate of A. coerulea planulae was higher at the elevated temperature of 27°C than at other temperatures, and this effect was statistically significant on day 7 at the salinity of 22 (\(P < 0.05;\) Figure 3). There were no significant interactions between the effects of temperature and salinity on the mortality of A. coerulea planulae (\(P > 0.05;\) Table I).

**Larval size**

Results from the two-way ANOVA revealed that temperature was the main factor affecting the larval size of A. coerulea over the duration of 7 days (\(P < 0.05;\) Table I). Larval sizes were significantly smaller at 27°C and salinity of 22 (\(P < 0.001;\) Figure 4).

**Discussion**

A. coerulea is a common scyphozoan jellyfish that is typically found in the coastal bays, marine lakes and aquaculture ponds of the Bohai and Yellow Seas (Dong et al. 2014). The early life stages (i.e. planulae, polyps and ephyrae) are more sensitive to stress compared to the adult medusa, and therefore are suggested to be key stages that affect the population size of A. coerulea medusae (Lucas, 2012). A. coerulea can produce planulae larvae sexually, which are released into the seawater during the summer time (Lucas 2001), when heavy rainfall, river run-off and storms may significantly decrease the seawater salinity. Therefore, A. coerulea planulae are likely to encounter low-salinity conditions and elevated temperatures during the planktonic and settling time. The results presented here suggest that the swimming behaviour and settlement of A. coerulea planulae were negatively affected by reduced salinity and that the survival and settlement of A. coerulea planulae were negatively affected by elevated temperatures.

**Effects of salinity on A. coerulea planulae**

Salinity is one key abiotic factor affecting the survival, development and settlement of many marine invertebrate larvae, particularly in bays and estuaries which undergo considerable salinity variations (Vazquez and Young 2000; Holst and Jarms 2010; Conley and Uye 2015). Our results showed that the survival of A. coerulea planulae was not influenced by the reduced salinity of 22. The result was in accordance with results from Colney and Uye (2015), which indicated that A. coerulea planulae in Japanese waters could survive at salinities above 15 (Conley and Uye 2015). A. coerulea planulae were less active under reduced salinity conditions. Similarly, Conley and Uye (2015) revealed that hyposalinity significantly reduced the swimming speed of A. coerulea planulae in Japanese coastal waters. The results from Holst and Jarms (2010) showed Aurelia aurita planulae in the Baltic Sea have reduced swimming after a salinity reduction from 32 to 10. This pattern was also detected in the planulae of two other scyphozoan jellyfish species: Cyanea capillata and C. lamarckii in the Baltic Sea (Holst and Jarms 2010).

Meanwhile, reduced salinity decreased the settlement rate of A. coerulea planulae in our experiments. Conley and Uye (2015) showed that A. coerulea planulae in Japanese waters had a lower settlement rate at a salinity of 15 than at a salinity of 32. Percentages of
Cyanea lamarckii, C. capillata and Chrysaora hysoscella planulae settlement were higher at high salinity (32) than at low salinity (20, 15 and 10) (Holst and Jarms 2010).

The mechanism that underlies the physiological response of A. coerulea planulae to low salinity is not known. Randall and Szmant (2009) suggest that the reduction in coral larvae movement may reduce the opportunity of planulae to settle on suitable substrate. Furthermore, a previous study on additional invertebrate larvae suggested that reduced salinity might cause osmotic shock and induce locomotor activity of larvae (Kashenko 1997). Therefore, low salinity may cause physiological stress in A. coerulea planulae and influence the settlement of A. coerulea planulae. Our results suggest that A. coerulea polyps probably occur under seawater conditions of relatively high salinities.

Effects of temperature on A. coerulea planulae
A number of studies have been conducted to investigate the effect of seawater temperature on the asexual reproduction of Aurelia spp. polyps in different regions (Liu et al. 2009; Purcell et al. 2012; Schiariiti et al. 2014) and on the growth of ephyrae (Widmer 2005; Fu et al. 2011; Algueró-Muñiz et al. 2016). However, relatively few studies have been conducted on the effect of temperature on jellyfish planulae despite their necessity for the establishment of new polyp populations (Webster and Lucas 2012; Gambill et al. 2018). Our results demonstrated that elevated temperature could negatively affect the development, survival and settlement of planulae. A. coerulea planulae shrunk in size and became significantly smaller over seven days.
under the combination of elevated temperature (27°C) and reduced salinity (22). This morphological change suggests that elevated temperature and reduced salinity may affect larval physiology and the development of *A. coerulea* planulae. Furthermore, elevated seawater temperature reduced the survival rate of *A. coerulea* planulae, especially in combination with reduced salinity (22).

The settlement rate of *A. coerulea* planulae decreased under elevated seawater temperature and was highest at ambient seawater temperature (24°C) in summer. These results are in accordance with those of Webster and Lucas (2012), who reported significantly fewer *Aurelia aurita* planulae in southern England settled under the highest temperature, which was similar to the current seawater temperature.
range. High temperatures may also impair functional enzymes and proteins during coral larvae development, which are important for the initial stage of settlement (Negri et al. 2007).

Our results showed that a high settlement rate and relatively low mortality rate occurred at 24°C, which suggested that the current ambient seawater temperature in the summer was appropriate for the population recruitment of *A. coerulea* planulae. However, *A. coerulea* planulae were sensitive to additional, projected elevation in temperature, especially under reduced salinity conditions. Therefore, with global ocean warming and related phenomena such as more frequent extreme precipitation events, elevated seawater temperatures will not contribute to the population increase of *A. coerulea*.

Some studies have also been conducted to investigate the effects of temperature and/or salinity on different life history stages of *A. coerulea*, often with inconsistent results (Liu et al. 2009; Han and Uye 2010; Fu et al. 2011; Schiariti et al. 2014; Wang et al. 2015; Wang and Li 2015; Hubot et al. 2017). For example, several studies showed warm temperature increased the asexual reproduction in *A. coerulea* polyps of Japanese, French and Chinese strains (Han and Uye 2010; Schiariti et al. 2014; Wang and Li 2015). However, in other studies, *A. coerulea* polyps of Chinese and Italian strains showed no significant effect of temperature on the asexual reproduction (Wang et al. 2015; Hubot et al. 2017). Additionally, the production of new buds of *A. coerulea* polyps in Taiwan decreased under unusually high temperatures (Liu et al. 2009). Results from Holst (2012) showed that the elevated winter temperature of 5°C increased the ephyra production per polyp and produced higher numbers of strobilating polyps in *Aurelia aurita*. The different experimental conditions and strains used in these studies restrict the comprehensive analysis of future temperature scenarios on the population dynamics of *A. coerulea*. Therefore, it is still difficult to predict population size changes of *A. coerulea* under changing climate conditions in the future. Additional research on how different stages of the life cycle will be affected under the same projected temperature scenarios is needed to address the question of whether elevated temperature contributes to the blooms of *A. coerulea*.

**Acknowledgements**

Z.J.D. gratefully acknowledges the visiting scholarship program from China Scholarship Council and Dr. Kylie Pitt at Griffith University as host for the visit.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

**Funding**

This work was supported by grants from the National Natural Science Foundation of China (No. 41576152) and Science and Technology Service Network Initiative (STS) Project (No. KFJ-STS-ZDTP-023).

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