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Embryonic development of *Amphioctopus fangsiao* under elevated temperatures: Implications for resource management and conservation

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ABSTRACT

Amphioctopus fangsiao is an important fishery resource in northern coastal China, and this species has been developed for commercial fishing and aquacultural purposes. However, its embryos are vulnerable to ambient temperature, which leads to challenges in resource management and conservation. The present study investigated how high temperatures could affect the embryonic development (e.g., morphology, development time, and viability) of *A. fangsiao*. The results showed that the embryonic developmental rate was accelerated as the temperature increased. In addition, temperatures higher than the thermal threshold detrimentally affected the morphology and viability of eggs. Embryos maintained at 18, 21, and 24 °C successfully hatched at 40, 30, and 24 d after spawning, respectively. However, no embryos hatched at 27 °C. Elevated temperatures altered the trajectory of normal embryonic development and increased the percentage of eggs with abnormal morphology. Embryos maintained at 24 °C failed to undergo the second inversion during embryonic development and remained at the animal pole until stage XVII (15 d). Upon the completion of organogenesis at stage XIX, an elevated temperature, as the external stimulus, could promote the early hatching of embryos with poor physiological features (e.g., small size and large yolk sac). The results indicate that the thermal range for *A. fangsiao* embryonic development is 18–24 °C. Our findings on the relationship between embryonic stage and temperature might help fishery managers predict the emergence time of the hatchling population and promote the conservation of this species when establishing related fishery policies.

1. Introduction

Amphioctopus fangsiao is abundant from the southern coast of Hokkaido in Japan to Hainan Province in China (Segawa and Nomoto, 2002; Norman et al., 2014), and it is an important fishery resource in the coastal waters of northern China. Compared with other octopod species, *A. fangsiao* has advantageous fishery characteristics in that true larval stages are absent in hatchlings, which can quickly develop into adults after hatching. Furthermore, juveniles have fast growth rates (up to 8.3 % at 25 °C), and this contributes to steady yields in fishery resources (Segawa and Nomoto, 2002, as *Octopus ocellatus*; Wang et al., 2010; Dong et al., 2013). *A. fangsiao* also reproduces rapidly, with two reproduction peaks each year (April to May and September to October) (Segawa and Nomoto, 2002), which replenishes the fishery resources by natural breeding.

Ocean warming is a vital threat to marine biota, as it can gradually alter the marine ecosystems that these organisms have lived in for generations and drastically reshape their life processes (Rosa and Seibel, 2008). Compared with life stages that are influenced by temperature, the ontogenetic stages of marine biota have less adaptive capacity to fluctuations in oceanic temperature (Caverivière et al., 1999; Uriarte et al., 2012; Repolho et al., 2014). For cephalopods, the situation is even worse (Iglesias et al., 2007; Berger, 2010; Uriarte et al., 2011; Noyola et al., 2013; Villanueva et al., 2014). The embryonic metabolic costs of *Octopus vulgaris* increase significantly when the temperature increases from 18 to 21°C. An elevated temperature leads to cellular injuries that challenge the biochemical and physiological responses of this species (Repolho et al., 2014). Furthermore, temperatures higher than the thermal threshold can damage the physiological functions of eggs and consequently impede their normal development and the survival of hatchlings (Repolho et al., 2014).

Several studies have reported an inverse relationship between the

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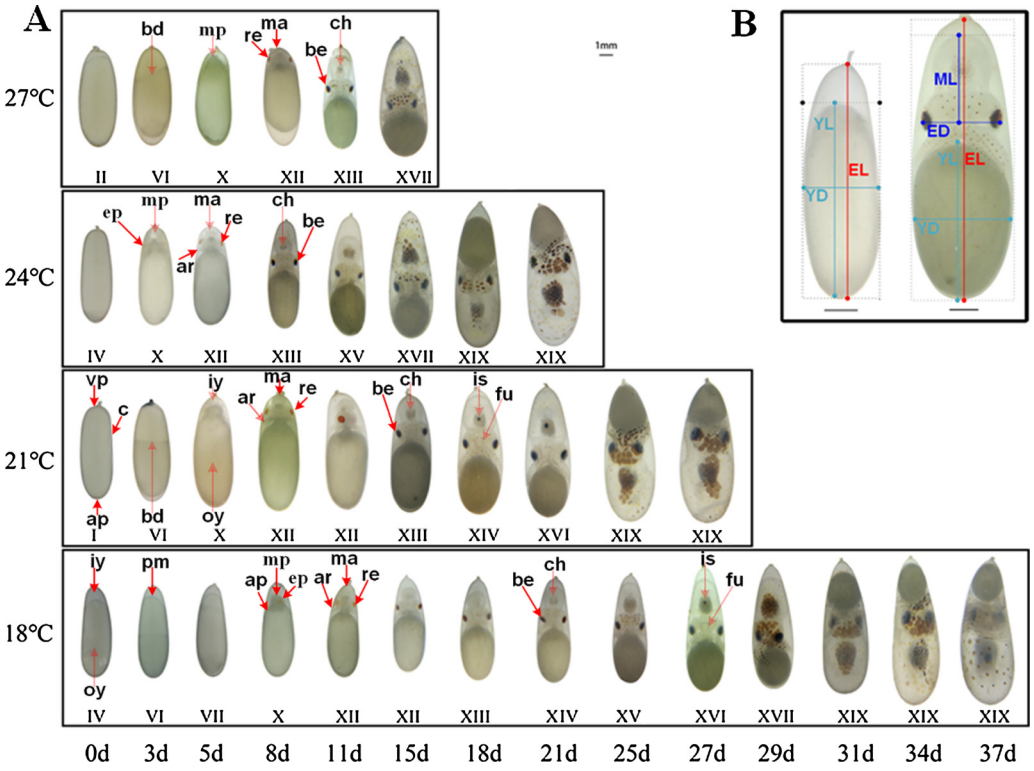

Fig. 1. A) Comparisons of embryonic development of *A. fangsiao* at 18, 21, 24 and 27°C. *ap*, animal pole; *apr*, arm primordia; *ar*, arm; *bd*, blastoderm cover egg surface in animal pole; *be*, blank eye; *c*, chorion; *ch*, chromatophores; *ep*, eye primoridia; *fu*, funnel; *is*, ink sac; *iy*, inner yolk; *ma*, mantle; *mp*, mantle primordium; *pm*, perivitelline membrane; *oy*, outer yolk; *re*, reddish eye; *vp*, vegetal pole. The embryonic illustrations represented the embryos accounting for more than 50 % of total observed eggs at each sampling point, the Roman numerals at the bottom of each picture was the embryo stage (as Naef) and the time of each sampling point was listed at the bottom of the picture. Scale bar = 1 mm. B) Morphometric analysis includes: egg length (EL), outer yolk sac length (YL), outer yolk sac width (YD), embryo mantle length (ML) and eye diameter (ED). Scale bar = 1 mm.

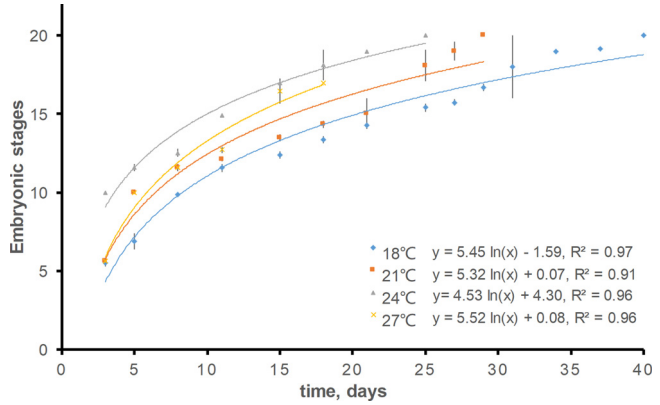

Fig. 2. Embryonic stages (Es) in relation to time (t), and t is the embryonic development time after spawning. R^2 is the coefficient of determination.

environmental temperature and the embryonic developmental time in octopod species (Boletzky, 1994; Wood and O'Dor, 2000). For example, the embryonic developmental time of *O. vulgaris* decreased by 13 d when the temperature increased from 18 to 21 °C (Repolho et al., 2014), whereas it was 75 % shorter at 21 °C than that at 12 °C for *Octopus mimus* (Uriarte et al., 2012). Thus, hatchlings might be born earlier when embryos are affected by increasing oceanic temperatures, and this information is critical for setting up fishery policies. The Fishing Closed Season (FCS), for example, is an effective way to restore marine fishery resources, especially for pregnant parents and hatchlings (Novak and Axelrod, 2017). Hence, fishery policymakers should consider the impact of temperature on the reproduction, specifically the embryonic development, of the main marine species. Moreover, the relationship between temperature and embryonic development can also guide the commercial culture of several species. For example, *Enteroctopus megalocyathus* is an important fishery resource on the coast of Northern Patagonia. However, its long embryonic developmental time impedes the successful culture of this species (Ortiz et al., 2006, 2011; Uriarte et al., 2014), suggesting that fisher managers can try to culture species, such as *Enteroctopus megalocyathus*, in warmer areas (i.e., within the optimal thermal range) to shorten their embryonic development.

In the present study, we investigated how high temperatures could affect the embryonic development (e.g., morphology, development time, and viability) of *A. fangsiao*. Our findings supply sufficient biological information for the conservation and commercial culture of this species in the future.

2. Materials and methods

2.1. Capturing and rearing of broodstock

In April 2018, subadult and adult individuals of *A. fangsiao* (male:female = 1:1, N = 50) were captured by local fishermen in artificial traps near the coastal waters of Lianyungang (N 34°, E 119°, Jiangsu Province, China), then transported to a private enterprise (Jiaxin Aquaculture Farm). The octopuses were maintained in 5 m^3 aerated cement pools (length × width × depth, 4 m × 1 m × 0.5 m). The individuals were fed clams (*Ruditapes philippinarum*) at a rate of 5 % body weight per day until they ceased to eat. Ceramic pots served as the refuge and the spawning place for the octopuses. The seawater was filtered and exchanged at a rate of 50 % per day, with water conditions as follows: a temperature of 1819 °C, a salinity of 32‰, a dissolved oxygen level > 5 mg L^{-1}, a pH of 7.8–8.1, and an ammonia nitrogen level < 0.2 mg L^{-1}.

2.2. Experimental incubation

Female octopuses weighed 93 ± 20.6 g (N = 12). Upon spawning, egg clutches (stages I–IV) were removed using sterilized forceps and suspended by a nylon rope in 25-L seawater tanks. Six hundred eggs were maintained at each trial level (200 eggs per tank). The selected eggs were similar in size (6 − 7 cm on average), development stage (stages I–II), and transparency without dirt on the surface. Because of the disparities in egg number and fertility among females, it was difficult to ensure uniformity across the different groups of eggs.

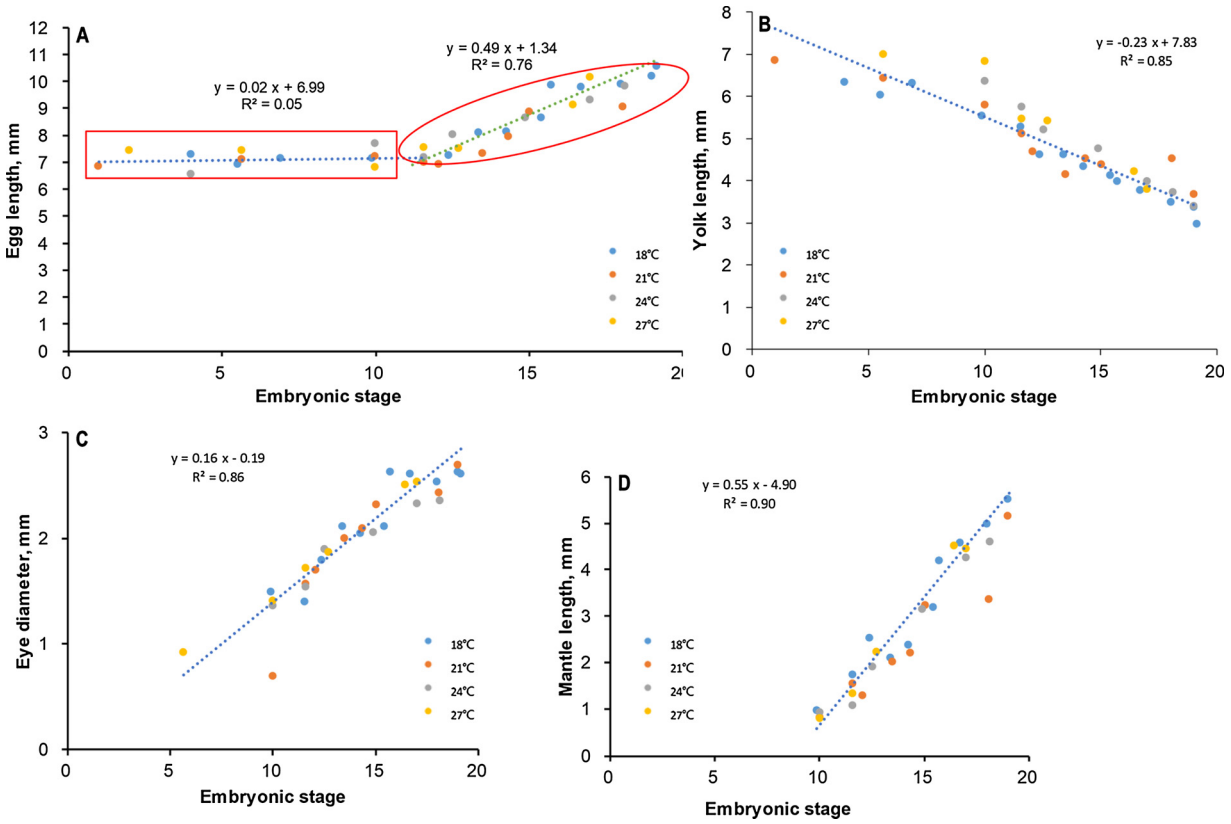

Fig. 3. Morphological characteristics in relation to embryo stages (as Naef). A) The egg length was 7.12 ± 0.30 mm at stage I–X, then has a linear relationship with embryo stage (stage XI-XX), with a maxim length of 10.53 mm at 18℃, stage XX. $P < 0.01$ (2-tailed). B) The yolk length was negative related to the embryo stages. $P < 0.05$ (2-tailed). C, D) The eye diameter and mantle length have a positive relationship with the embryo stages. $P < 0.01$ (2-tailed).

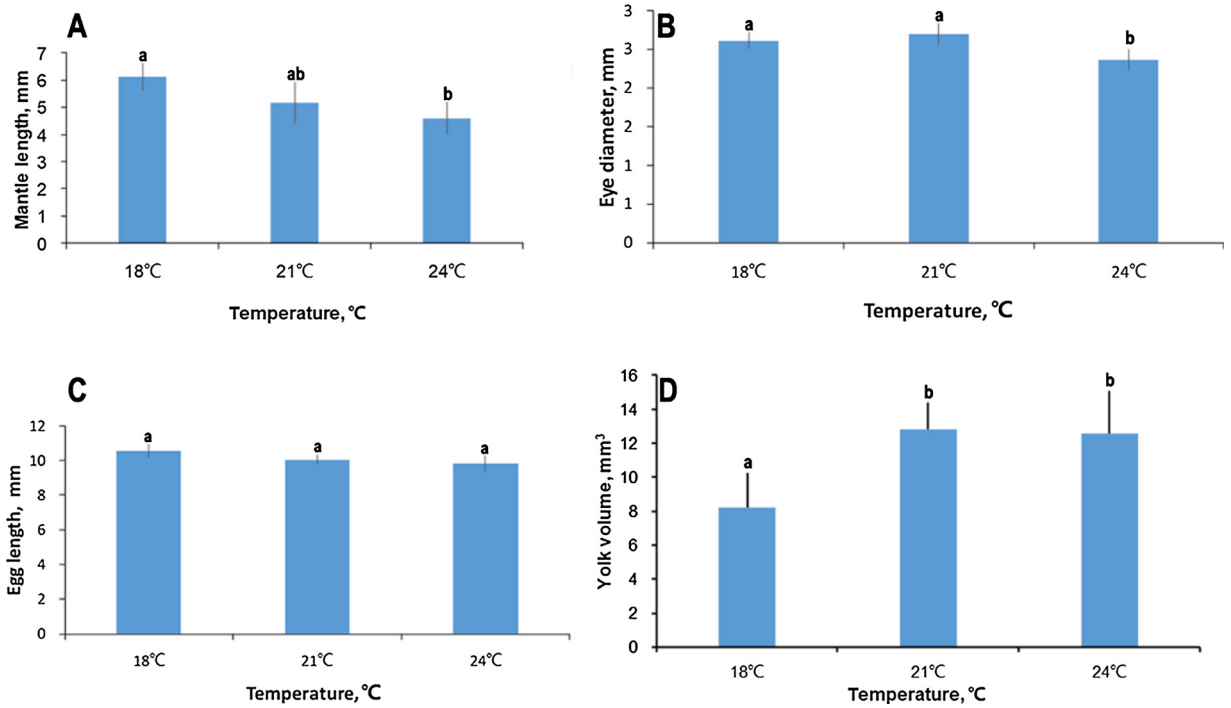

Fig. 4. Morphological characteristics at stage XIX in relation to temperature (18, 21 and 24 ℃). Different letters on average bars indicate significant differences ($P < 0.05$).

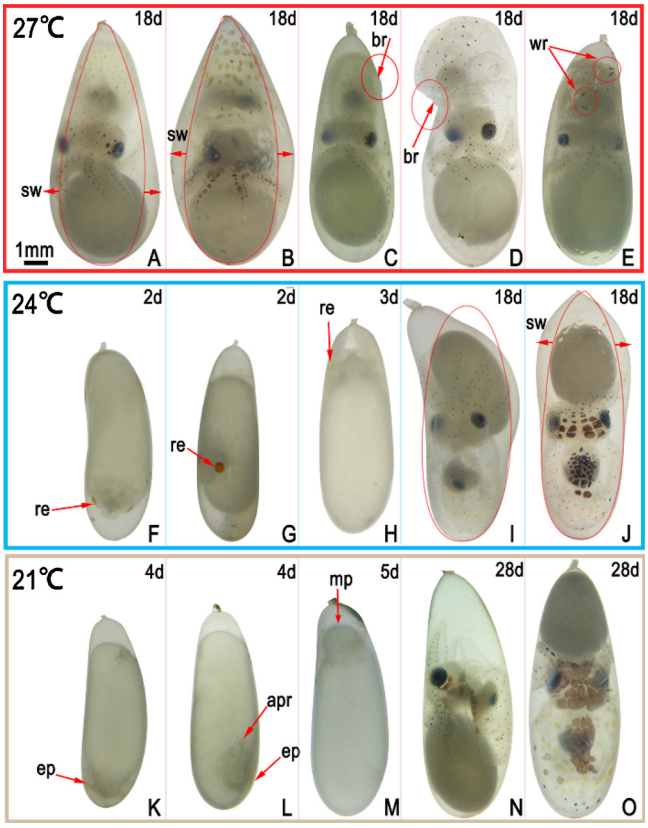

Fig. 5. Abnormal morphologies of embryos caused by temperature. A–E) Embryos at 27℃. *sw*, the eggs became swollen (*sw*); *br*, the chorion (18d, stage XVII as Naef) was abnormally broken (*br*); *wr*, worms (*wr*) on the surface of egg (18d, stage XVI-XVII as Naef). F–J) Embryos at 24℃. The eyes of embryo at stage VIII-IX (2d) became red, and the egg of 18d (stage XIX as Naef) became swollen (n = 12 of total observed N = 45). *re*, reddish eyes. K–O) Embryos at 21 ℃. *apr*, arm primordia of 4d (stage VIII as Naef); *ep*, eye primordia of 4d (stage VIII as Naef); *mp*, mantle primordium (5d, stage IX as Naef). Eggs (28d, stage XIII-XIX as Naef) were oval until hatching (n = 28 of total observed N = 30). The embryo age was listed at top right of each picture (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Therefore, the eggs for each incubation temperature were randomly selected from three individuals, and 12 females were used. This experiment was conducted in an aerated seawater flow-through system (Supplementary Data S1). The natural seawater was UV-sterilized after filtering and completely exchanged every two days. For the egg incubation system, the parameters of the chiller were as follows: an AC voltage of 110 − 240 V/50 − 60 Hz, a power of 72 W, and a temperature of 10 − 40 ˚C. The current velocity was 1 − 3 L/min, and the system was circularly refrigerated until the temperature was lower than the set temperature. The eggs swung freely by the bubble derived from the gas tube, which eliminated interactions between eggs and decreased the incidence of fungal and bacterial infections. Under natural conditions, the female octopuses spawned at 18 ˚C. Therefore, the experimental temperature was set between 18 and 27 ˚C. Initially, eggs were acclimated at 18 ˚C, with a temperature increase rate of 3 ˚C day^{-1} at each trial level. When the water reached the trial temperature (21, 24, and 27 ˚C), the heating stopped, and eggs were maintained at a constant temperature. During the acclimation period, the temperature in each system was controlled by an electronic chiller and submersible glass heater that was connected to a digital controller (± 0.1 ˚C) with thermocouple sensors. During the experiment, the eggs were maintained with a photoperiod of 12 h of light and 12 of dark.

2.3. Morphometric analyses and yolk quantification

To observe embryonic development, egg clutches were randomly collected from each tank with sterilized forceps every 2–4 days at 20:00 and placed into a dish with sterilized seawater maintained under low light conditions. The eggs for observation (N = 5–10) were photographed with a Nikon SMZ800 stereoscopic microscope, and the images were processed with ImageJ 1.52d (http://imagej.nih.gov/ij), Adobe Photoshop CC 2017, and Microsoft Visio 2016 software packages to determine the embryonic stages and morphometric characteristics, including the egg length (EL), mantle length (ML), eye diameter (ED), yolk length (YL), and yolk width (YD) throughout the experimental period until hatching (Fig. 1B). The embryonic stages were defined according to Naef (1928).

The relationship between the embryonic stage (Naef, 1928) and time (d) was described using an adjusted logarithmic model as follows:

embryonic stage (Es) = a + b·ln(t), where *a* and *b* are constants, and t is the embryonic development time (d).

The relationship between the morphological characteristic (e.g., EL, YL, ED, and ML) and embryonic stage (Es) was analyzed as follows:

morphological characteristic = a*Es + b, where a and b are constants.

The outer yolk sac volume (YV) was determined as follows:

yolk volume = $4/3 \cdot \pi \cdot l \cdot w^2$, where π is 3.1416, and *l* and *w* are half of the length and half of the width of the outer yolk sac, respectively (Uriarte et al., 2009).

2.4. Statistical analysis

The goodness–of–fit test was used to analyze the adjusted logarithmic model of the embryonic stage and time, and the relationships between morphological characteristics and embryonic stages. One–way analysis of variance (ANOVA) was performed on the morphometric characteristics (ML, ED, YV, and EL) of embryos at stage XIX.

3. Results

The embryos maintained at 18, 21, and 24 ℃ successfully hatched at 40, 30, and 24 d after spawning, and the hatching rates were 37 ± 8 %, 39 ± 6 %, and 13 ± 3 %, respectively. However, the embryos maintained at 27 ℃ failed to hatch.

3.1. Embryonic development

Eggs post–fecundation had active segmentation, and the eye primordia and mantle primordium of embryos at 24 ℃ differentiated from the yolk at 3 d (stage X) (Fig. 1). On the contrary, embryos maintained at 18, 21, and 27 ℃ were still at the gastrulation phase at 3 d, with blastodermic cells migrating over 60 % of the yolk surface (stage VI). The arms, mantle, and eyes of the embryos maintained at 24 ℃ could be recognized at 5 d (stage XII), whereas embryos maintained at 21 and 27 ℃ just completed the first inversion (stage X), without obvious organ primordia. Thereafter, embryos maintained at 24 ℃ reached stage XIII at 8 d, with visible black eyes and chromatophores on the dorsal and ventral areas of the head. However, these morphological characteristics were gained at 21, 15, and 11 d for embryos maintained at 18, 21, and 27 ℃, respectively. Embryos maintained at 24℃ started the second inversion at 17 d (stage XVIII) and completed the process at 18 d (stage XIX), whereas the second inversion ended at 31 and 25 d for embryos maintained at 18 and 21℃, respectively. Finally, embryos maintained at 24 ℃ hatched at 24 d (stage XX), which was 20 and 40 % shorter than those at 21 and 18 ℃, whereas embryos maintained at 27 ℃ failed to hatch.

The Es (stage I–XX) increased logarithmically in relation to the embryonic developmental time (Fig. 2), with a faster embryonic developmental rate at 24 ˚C (0.83 stages day^{-1} on average) than that at 18

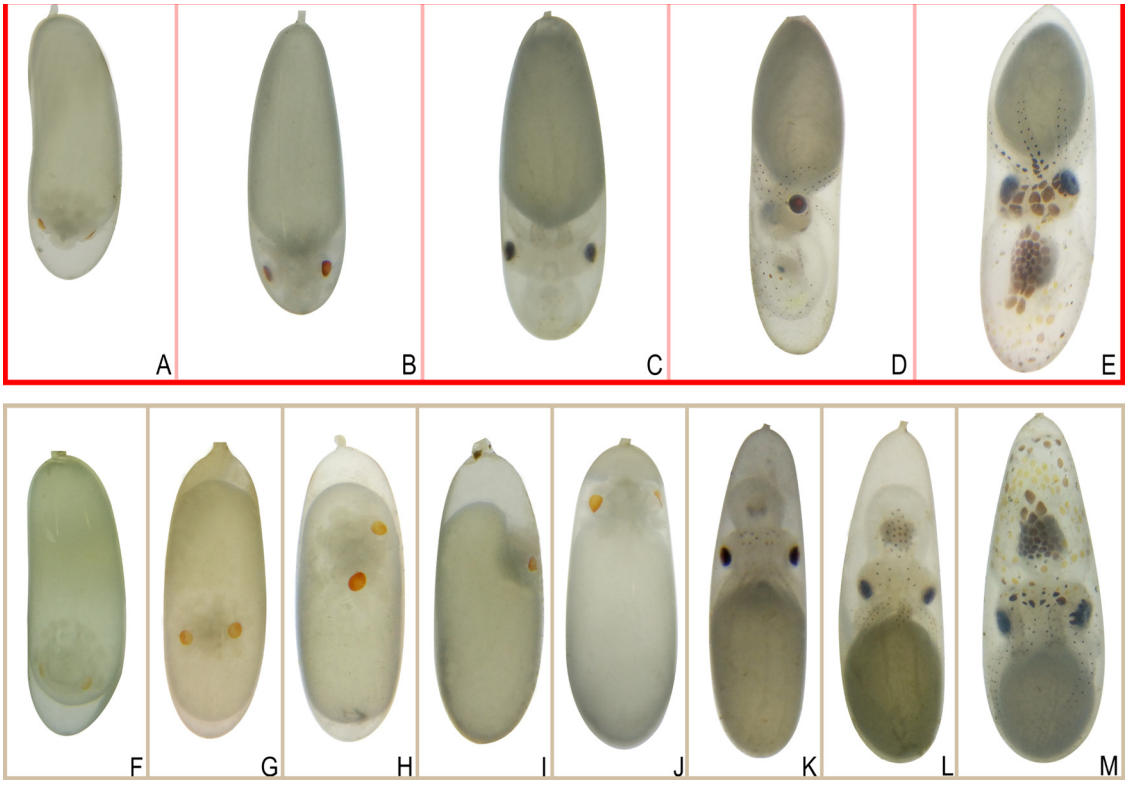

Fig. 6. Difference of embryo development at 24 °C. A–E) A–E represented embryos of 2, 5, 8, 11 and 15 days, respectively. Embryo of 2d (stage VIII) was observed to remain at the animal pole until 15d (stage XVII), without first inversion. F–M) F–I represented embryos within 2 days after hatching, and J–M showed embryos of 5, 8, 11, 15 days, respectively. Embryonic development initiated at the animal pole, then gradually turned to vegetal pole after first inversion.

(0.5 stages day^{-1} on average) and 21 °C (0.67 stages day^{-1} on average) ($P < 0.05$).

The EL measured 7.07 ± 0.38 mm at the beginning and reached 10.53 ± 0.39, 10.04 ± 0.27, and 9.81 ± 0.47 mm by stage XIX at 18, 21, and 24 °C, respectively (ANOVA, $P > 0.05$; Figs. 3A and 4). Initially, the EL grew slowly at stages I–X, with values approximately 7.12 ± 0.30 mm during this period. However, the EL increased linearly with the Es until stage XX ($EL = 0.49*Es$, $Es >$ stage X, $R^2 = 0.76$; Fig. 3A). The ML and ED increased linearly with the Es, with relationships of $ML = 0.16*Es–0.19$ ($R^2 = 0.90$) and $ED = 0.55*Es–4.90$ ($R^2 = 0.86$), respectively (Fig. 3C, D), while the YL showed a linear decrease with the Es, with a relationship of $YL = –0.23*Es+7.83$ ($R^2 = 0.85$) (Fig. 3B). For embryos at stage XIX, the ML and ED were affected by the temperature, with high values at 18°C and low values at 24°C ($P < 0.05$; Fig. 4A, B), whereas no difference was detected in the EL at different temperatures ($P > 0.05$; Fig. 4C). Moreover, embryos maintained at 21 and 24°C stored more yolk than those maintained at 18°C ($P < 0.05$; Fig. 4D).

3.2. Abnormal morphologies of embryos and eggs caused by temperature

At stages XVI–XVII (18 d), eggs at 27 °C became swollen and wider in diameter than normal eggs (Fig. 5A, B). In addition, the chorion was broken, causing the embryos to hatch earlier and to eventually die (Fig. 5C, D). Filaments and worms were observed on the surface of eggs maintained at 27 °C at stages XVI–XVII (18 d; Fig. 5E). Embryos maintained at 24 °C had reddish eyes at stages VIII–IX (2 d; Fig. 5F) and then the arms, eyes, and mantle started to differentiate from the yolk at stages IX–X (3 d; Fig. 5H). By contrast, organ primordia were observed at the animal pole in embryos maintained at 21 °C at stage VIII (4 d; Fig. 5K), which occurred later than that in same stage embryos maintained at 24 °C. No obvious differentiation of the mantle, arms, and eyes was detected at stage X (5 d; Fig. 5M). The shape of eggs maintained at 21°C was oval until stage XIX (28 d; Fig. 5N, O), whereas eggs maintained at 24°C appeared malformed at stage XIX (18 d; Fig. 5I, J). Under normal conditions, the embryo starts the first inversion from the animal pole around stages VIII, which settles on the base of the egg at stage IX, until the second inversion begins (Fig. 6F–M). Embryos maintained at 24°C were observed to remain at the animal pole until stage XVII (15 d; Fig. 6A–E), accounting for 25.9 % of all embryos (N = 7 of total observed N = 27).

4. Discussion

It has been reported that embryonic development is inversely related to the temperature (Boletzky, 1994; Caverivière et al., 1999; Uriarte et al., 2012 and 2014; Juárez et al., 2015), and linear and exponential relationships between the embryonic stage and time were established for *E. megalocyathus* (Uriarte et al., 2014) and *O. maya* (Juárez et al., 2015), respectively. In the present study, a logarithmic model was used to describe the relationship between the embryonic stage and time of *A. fangsiao*, which was also established for *O. mimus* (Uriarte et al., 2012). Based on the model shown in Fig. 2, fishery managers can estimate the emergence time of the hatchling population, which is important for the conservation of this species. Thus, policymakers can appropriately modify fishery policies (e.g., FCS) to maximally protect juveniles before they reach maturation.

The morphological characteristics (e.g., EL, YL, ML, and ED) of embryos were highly correlated with the embryonic stage throughout development. Organogenesis was completed at the end of stage XIX, and hatching occurred when triggered by an external stimulus, such as an elevated temperature. This can explain why smaller embryos with larger YVs hatched at 24°C than those at 18°C ($P < 0.05$, Fig. 4A, B). It should be noted that larger hatchlings can have an initial competitive advantage in terms of their prey–capture and predator–escape capacities. However, smaller hatchlings with shorter developmental times

can fulfill their energetic requirements from exogenous (i.e., prey) sources earlier than larger ones. They are also likely to survive longer, as juveniles are characterized by fast growth rates at the early stages of life. Further studies are needed to investigate the growth performance of hatchlings at different incubation temperatures to determine the best incubation protocol.

Elevated temperatures detrimentally affect egg morphology and viability. In general, octopod eggs are fusiform in shape (rounded at the animal pole and pointed at the vegetable pole). When the incubation temperature increased from 18℃ to 27℃, the proportion of eggs with abnormal morphology increased. At 27℃, the eggs swelled in width and eventually died before hatching. By contrast, eggs maintained at 18 and 21℃ retained their fusiform shape until hatching. In the incubation system, the sterilization measures failed to protect the eggs from microbial infection. At 27℃, filaments appeared on the surface of the eggs, which prohibited their exchange with the environment. This phenomenon might be related to the proliferation of microbes as the temperature increased, indicating that embryo viability was low under elevated temperatures (Uriarte et al., 2011 and 2014).

In the present study on *A. fangsiao*, the thermal threshold for embryo development was 24℃–27℃, and the hatching time, which was controlled by the incubation temperature, ranged from 24 to 40 d. Considering the limited yields in the parallel cultivation of feeds (e.g., mysids and crustacean zoeae), our findings advise fishery managers to regulate the hatching time of embryos by controlling the incubation temperature, thereby satisfying the feed needs of hatchlings. Other cost–effective feeds (e.g., clams) can be added into the diets of growing hatchlings, which can reduce the pressure on the feed supply and promote the regulation of production programs. Further studies are needed to improve incubation protocols (e.g., hatchery water supplies, incubation systems, and microbial management for pathogen control) in order to increase the hatching rate and to enhance the production of hatchlings.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2019.105479.

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