

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/333667205>

Optimizing reproductive performance and embryonic development of red swamp crayfish *Procambarus clarkii* by manipulating water temperature

Preprint · June 2019

CITATIONS

0

READS

252

9 authors, including:



Jin Shiyu

Chinese Academy of Sciences

13 PUBLICATIONS 145 CITATIONS

[SEE PROFILE](#)



Lisa Jacquin

Paul Sabatier University - Toulouse III

57 PUBLICATIONS 1,189 CITATIONS

[SEE PROFILE](#)



Mantang Xiong

Chinese Academy of Sciences

12 PUBLICATIONS 116 CITATIONS

[SEE PROFILE](#)



Ruojing Li

The University of Sydney

7 PUBLICATIONS 71 CITATIONS

[SEE PROFILE](#)



Optimizing reproductive performance and embryonic development of red swamp crayfish *Procambarus clarkii* by manipulating water temperature

Shiyu Jin^{a,b,c,d}, Lisa Jacquin^c, Feng Huang^{a,b,d}, Mantang Xiong^{a,b,d}, Ruojing Li^{a,b,d}, Sovan Lek^c, Wei Li^{a,b,d}, Jiashou Liu^{a,b,d}, Tanglin Zhang^{a,b,d,*}

^a State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

^b University of Chinese Academy of Sciences, Beijing 100049, China

^c Laboratoire Evolution et Diversité Biologique (EDB), UMR 5174, Université de Toulouse, CNRS, IRD, UPS, Toulouse 31062, France

^d Hubei Provincial Research Center for Integrated Rice Field Aquaculture Engineering, Wuhan 430072, China

ARTICLE INFO

Keywords:

Optimal water temperatures
Artificial reproduction
Broodstock and embryos management
Embryos hatching
Temperature-dependent developmental model

ABSTRACT

Aquaculture of red swamp crayfish, *Procambarus clarkii* (Girard, 1852), has developed rapidly worldwide in recent years with promising prospects. However, limited knowledge about temperature effects on reproductive performance and embryonic development has hindered the development of crayfish aquaculture. The two present studies were conducted to identify optimal water temperatures (17 °C, 21 °C, 25 °C, 29 °C and 33 °C) for reproductive performance (experiment 1) and embryonic development (experiment 2) of *P. clarkii*. Totally, there were 12 replicates, with 480 adults and embryos from 60 ovigerous crayfish selected for experiment 1 and 2, respectively. In the first experiment, the survival of adult crayfish was not significantly affected by the temperatures tested. However, significantly higher feeding rates, spawning rates, and fecundity were obtained at 21 °C and 25 °C when compared to those at 29 °C and 33 °C. Polynomial models and loess regression fitted to the experimental data showed that highest spawning rates and fecundity occurred at 21 °C while shortest duration from mating to spawning was found at 33 °C. In the second experiment, we found that optimal embryonic development was at 25 °C with shorter hatching time and no abnormalities observed. However, while embryos showed abnormalities and subsequently died at 29 °C and 33 °C. We further built a temperature-dependent developmental model for *P. clarkii* embryos: D (developmental time, days) = 3,140,837(T-2.03)^{-3.76}. Based on these results, the temperature range 21 °C – 25 °C was recommended for adult crayfish reproduction and 25 °C was recommended for embryonic development. This study indicates that manipulating water temperature is an effective alternative to current artificial reproduction techniques (e.g. eyestalk ablation and injection hormones) to induce spawning and embryonic development and thus provides mass production of juvenile *P. clarkii* for aquaculture.

1. Introduction

Crustacean aquaculture has developed rapidly and global production has reached 7.9 million tons in 2016 (FAO, 2018). Among commercially farmed species, red swamp crayfish, *Procambarus clarkii* (Girard, 1852), is the second most produced species and accounts for 12% of total crustacean aquaculture production (FAO, 2018). As the top-ranking aquaculture country, China has witnessed the rapid development of *P. clarkii* culture industry, with the production increasing from 0.26 million tons in 2007 to 0.85 million tons in 2016 (USD 8.14 billion, Fisheries Department of Ministry of Agriculture, 2017). This encourages the development of optimal artificial reproduction

techniques, which are the key steps for improving reproductive outputs and juvenile crayfish production in aquaculture (Rakaj et al., 2019). However, we still lack basic knowledge on how crayfish reproductive performance and embryonic development respond to different culture conditions (especially water temperature). Such knowledge will be helpful to facilitate the management of crayfish broodstock and embryos in aquaculture. In addition, this species is one of most invasive species in the world and has been listed as “100 of the worst” invasive alien species in Europe (DAISIE, 2010; Nentwig, 2009). More information on the reproduction and embryonic development will help to understand populations status and predict juveniles recruitment time. Thus population control methods (e.g. fishing) with emphasis on young

* Corresponding author at: State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China.

E-mail address: tlzhang@ihb.ac.cn (T. Zhang).

crayfish and exact time (e.g. reproductive seasons) will be therefore of the high priority and more effective to control population sizes (Rogowski et al., 2013). Furthermore, the related information is also helpful to predict the potential distribution areas and thus management efforts can be made to prevent their further introduction, establishment, and spread (Egly et al., 2019).

Currently, the biggest challenge in *P. clarkii* aquaculture is the limited supplies of juveniles (Song et al., 2015). Up to now, most juvenile *P. clarkii* in aquaculture are obtained from spontaneous reproduction which is limited by seasonal availability (Xu et al., 2011). This hinders the development of the crayfish industry (Smith et al., 2002). It is, thus, of great importance to develop artificial reproduction techniques to trigger a mass production of juveniles. This would be important to meet the demands of commercial production and improve crayfish culture sustainability (Liu et al., 2013a). The crayfish gonad maturation is controlled by two antagonistic neuropeptides: gonad inhibiting hormone (GIH) and gonad stimulating factor (GSF) (Eastman-Reks and Fingerman, 1984; Chaves, 2000). GIH is secreted from the X-organ sinus gland complex, located in the eyestalk of crustaceans. GSF is produced by brains and thoracic ganglion, which has significant effects on stimulating gonads development. Based on this reproductive rationale, there are currently two techniques used to induce the reproduction of *P. clarkii*: eyestalk ablation and hormones injection. The eyestalk ablation, by elimination of GIH to accelerate gonad development, is widely used to induce crayfish reproduction (Chaves, 2000). Besides *P. clarkii*, it has been also extensively used on various crustacean species such as *Cherax quadricarinatus*, *Penaeus monodon*, and *Penaeus semisulcatus* (Aktaş and Kumlu, 1999; Browdy, 1992; Browdy and Samocha, 1985; Liu et al., 2014; Lumare, 1979; Muthu and Laxminarayana, 1977; Sagi et al., 1997; Wen et al., 2015). Hormones injection is through injecting hormones involved in the control of crayfish reproduction to stimulate gonad maturation and spawning. Various hormones such as serotonin (also called 5-hydroxytryptamine), progesterone, 17 α-hydroxyprogesterone, human chorionic gonadotropin (HCG), and domperidone have been proved to significantly induce gonad development and spawning of crayfish (Yano, 1985; Wongprasert et al., 2006; Zhang, 2011; Liu et al., 2014; Liu et al., 2013b). However, eyestalk ablation and hormones injection the two techniques led to death and permanent damage of adult females and also had negative effects on offspring quality (Makinouchi and Honculada-Primavera, 1987; Liu et al., 2013b; Liu et al., 2014; Zhang, 2011). Furthermore, they might cause endocrine and potentially ethical problems. There is thus now an urgent need to find new techniques to produce a mass of high quality juveniles while ensuring animal welfare.

One potential means would be to optimize culture conditions especially water temperature to induce reproduction and ensure optimal embryonic development. It was proved that reproductive processes such as ovarian development, mating and spawning activities of *P. clarkii* were highly related to temperature, with variability in spawning events in different locations. For instance, *P. clarkii* had only one spawning event yearly in Germany (Chucholl, 2011), Italy (Dörr et al., 2006), and UK (Richter, 2000), while two or more spawning events occurred in USA (Huner, 2002; Penn, 1943), Portugal (Anastácio and Marques, 1995; Sousa et al., 2013), Kenya and Spain (Cano and Ocete, 1997; Gutierrez-Yurrita and Montes, 1999; Gutierrez-Yurrita et al., 1999; Lowery and Mendes, 1977; Oluoch, 1990). Furthermore, embryogenesis and hatching also highly depended on temperature, which could be accelerated or delayed under different water temperature conditions (Planas et al., 2012; Tong et al., 2000). Typically, increasing temperature in a certain range shortened embryos hatching time while temperature below or above a specific threshold delayed hatching and even caused abnormalities and/or mortality (Das et al., 2006; Folkvord et al., 2015; Lin et al., 2006; Pandian and Katre, 1972; Seuffert et al., 2012; Sfakianakis et al., 2004). This was particularly true in China. For instance, it took three months for *P. clarkii* embryos hatching in Poyang lake (annual min-max and mean water temperature:

3.52 °C—31.18 °C, 18.37 °C, Hu, 2009; Li et al., 2012; Xiao et al., 2011), while it took four months in Huangjin Lake (annual min-max and mean water temperature 7.0–34.1 °C, 17.4 °C, unpublished data provided by Qidong Wang and Kai Feng, Gong et al., 2008; Lv, 2006). These studies suggest the potential for improving *P. clarkii* reproductive performance and embryonic development by manipulating water temperature in controlled conditions. However, only few studies have attempted to determine temperature effects on hatching time of *P. clarkii* embryos (Lv et al., 2004, 2006; Suko, 1956; Wang, 2012). More detailed information would be an important prerequisite for the development of artificial reproduction techniques. We thus hypothesized that the manipulation of water temperature would be an effective alternative to improve reproductive performance and embryonic development of *P. clarkii*.

The objectives of the present study were to: (1) evaluate the effects of water temperature on the reproductive performance of adult *P. clarkii* (survival, feeding rates, spawning rates, duration from mating to spawning and fecundity); (2) determine the effects of water temperature on embryonic development (morphological abnormalities, relationship between embryonic development and temperature); (3) build a temperature-dependent developmental model for *P. clarkii* embryos to better predict their hatching time.

To tackle these questions, we reared *P. clarkii* under five different temperatures (17 °C, 21 °C, 25 °C, 29 °C, and 33 °C), which were the typical temperature range during reproductive seasons in the wild (Qianjiang, China, see supplementary material 1). The present study will hopefully provide theoretical basic knowledge for optimizing crayfish reproductive performance and embryos culture conditions in crayfish aquaculture.

2. Material and methods

2.1. Broodstock and embryos collection and holding

Adult crayfish (weight: 31.03 ± 1.95 g, total length: 105.41 ± 1.20 mm, mean \pm SE) used in experiment 1 and experiment 2 were collected during the peak of ovarian maturation from the Selection and Reproduction Center of Crayfish (30.41°N, 112.75°E), Qianjiang, China. After transportation to the laboratory, crayfish were randomly paired and each paired crayfish (one male crayfish and one female crayfish) was kept separately in small tanks ($35 \times 30 \times 25$ cm). They were then acclimated to the experimental conditions for two weeks in five recirculation systems with constant aeration, during which they were fed a 30% protein commercial crayfish diet twice daily. In the beginning, all crayfish were reared under the same temperature conditions (23 °C) in the five recirculation systems, and then water temperatures were adjusted gradually at a rate of 1 °C per day until the experimental temperatures were reached and then maintained thereafter. All paired crayfish were checked every hour so that the accurate dates for mating and spawning could be determined. Embryos used in experiment 2 were obtained from 60 ovigerous females. They were incubated attached to the pleopods of females (thereby under the same temperature conditions as females). Eggs from each female were used as an independent replicated experimental unit. At the beginning of the experiment, we randomly dissected 20 ovaries from female crayfish to determine ovarian developmental stages through histological analyses. They were first weighed to calculate the gonadosomatic index (GSI, 3.18 ± 0.15 , mean \pm SE) and then fixed in Bouin's solution (Wuhan Servicebio Technology Company, China). The samples were dehydrated in 50%, 70%, 85%, 90%, 95%, and 100% ethanol and embedded in paraffin blocks. Finally, the slides were stained with hematoxylin and eosin (Kiernan, 1999; Suvarna et al., 2012). The histological analyses were conducted on micrographs under an Olympus BX53 microscope. The ovarian development of *P. clarkii* was divided into seven stages (Kulkarni et al., 1991): stage I, stage II, stage III, stage IV, stage V, stage VI, and stage VII. The results are shown in

supplementary material 2, with 3 crayfish ovaries developing to stage IV and 17 crayfish ovaries developing to stage V or VI (considered as mature ovaries).

2.2. Culture conditions

In the laboratory, adult crayfish were reared in five independent closed recirculation systems, operating at a fixed temperature of 17 °C, 21 °C, 25 °C, 29 °C, and 33 °C. This temperature range was chosen to represent the average water temperature during the reproductive seasons of *P. clarkii* in Qianjiang, China (mean temperature of 31.25 °C in August, 26.56 °C in September, and 19.94 °C in October, see supplementary material 1), which was recorded every two hours by data HOBO loggers (UA-002-64, HOBO Pendant temperature/light 64 K data logger Onset, Bourne, MA, USA).

Each system consisted of 16 large tanks (35 × 120 × 25 cm, experiment 1) and 64 small tanks (35 × 30 × 25 cm, experiment 2). Each tank served as an independent replicated experimental unit. In each tank, PVC pipes were provided for shelters of crayfish (four pipes in each large tanks and one pipe in each small tank). Tap water with ultraviolet sterilization and aeration for chlorine elimination was delivered to each tank at a constant rate of 1 L/min during the study. Tanks were cleaned every day. Photoperiod was maintained at a 12:12 (light: dark) cycle. Water temperatures during the whole experimental period were controlled with high precision, which were recorded every two hours with data loggers and shown in supplementary material 3. The pH, dissolved oxygen, and hardness were measured daily by a YSI probe (Yellow Springs Instruments, Yellow Springs, OH, USA). The concentration of ammonia nitrogen was determined using the standard method (APHA et al., 1989). Water quality variables during the whole experiment were within the suitable ranges: dissolved oxygen 5.60 ± 0.9 mg/L, pH 7.12 ± 0.21, hardness 125 ± 7 mg/L, and ammonia nitrogen 0.54 ± 0.13 mg/L.

2.3. Experiment 1

2.3.1. Experimental design

Experiment 1 was designed to evaluate the effects of water temperature on the reproductive performance of *P. clarkii*. It was conducted from September to October 2017 for 50 days under five constant temperatures (17 °C, 21 °C, 25 °C, 29 °C, and 33 °C), with 12 replicates of each treatment (total $N = 480$, 240 females and 240 males). Each replicate consisted of four paired female and male crayfish. The crayfish were fed twice daily with an artificial diet purchased from Charoen Pokphand Group (WHS001–2016, 30.23% protein, 10.74% lipid, 10.18% moisture, and 8.70% ash). All crayfish were checked every day so that their mortality, accurate dates for mating and spawning could be determined. Tanks were cleaned every day.

2.3.2. Data collection and measurement

At the beginning and the end of the experiment, crayfish weight was determined by a 0.01 g precision scale. Feeding rates were measured following the methods described in a previous study (Van Ham et al., 2003). Specifically, crayfish were fed with an excess quantity of weighted artificial diet until feeding activities stopped within one hour. Then, the remaining artificial diet was removed, dried and reweighted. Finally, we determined the given amount of artificial diet to calculate feeding rates. The duration from mating to spawning was calculated as the number of days from mating to spawning. After spawning, all eggs were counted to determine the fecundity of female *P. clarkii*. Other parameters were calculated as follows:

$$\text{Survival (\%)} = 100 \times (\text{final crayfish number} / \text{initial crayfish number})$$

$$\begin{aligned} \text{Feeding rate (\%body weight/day)} &= 100 \times \frac{\text{total feed intake (dry matter, g}}{\text{days}} \\ &\quad / [(\text{initial body weight (wet weight, g)}} \\ &\quad + \text{final body weight (wet weight, g)}) / 2] \end{aligned}$$

$$\begin{aligned} \text{Spawning rate (\%)} &= 100 \times \frac{(\text{final spawning crayfish number}}{\text{initial female crayfish number}) \end{aligned}$$

2.4. Experiment 2

2.4.1. Experimental design

Experiment 2 was designed to determine the optimal temperature for embryonic development. It was conducted from September to December 2017 (90 days) at 17 °C, 21 °C, 25 °C, 29 °C, and 33 °C. There were 12 replicates for each temperature treatment, and each replicate included one ovigerous crayfish (a total of 60 females for experiment 2). Eggs from the same ovigerous female crayfish served as an independent replicate. Once females spawning, the eggs were sampled for monitoring embryonic development. Ovigerous crayfish rearing methods were identical to those for experiment 1.

2.4.2. Data collection and measurement

For the 21 °C and 25 °C treatments, 30 eggs were collected for each sampling to determine developmental stages under the dissecting microscope LEICA MVX10 (M205FA). Because embryos at 17 °C developed slowly with insufficient embryos to be sampled later, sometimes only 10 eggs were sampled. Photographs of eggs were taken to determine their developmental stages. During the 36 h of spawning, eggs were examined every two hours and thereafter, daily until hatching.

In order to provide accurate time for each stage of embryos development, we first classified embryonic development into 9 stages according to previous studies (Dai et al., 2009; Feng et al., 2007; Harper and Reiber, 2006; Lei et al., 2009): I, zygote; II, cleavage; III, blastula; IV, semicircular furrow; V, circular furrow; VI, gastrula; VII, nauplius; VIII, zoea; and IX, hatching. Characteristics of each developmental stage are shown in Fig. 1. Then we recorded the duration of development for each stage. The end of each stage was defined as the time at which 50% of the embryos sampled had passed into the next stage. This index is often chosen to compare embryonic development when different numbers of eggs are sampled in different studies (Geffen et al., 2006; Webb et al., 2007; Yang and Chen, 2005).

Based on our data, the predictive exponential model (Bělehrádek's equation) of the developmental time was established as follows: $D = a(T - \alpha)^b$, where a , b , and α were constants, D was the development time (days) and T was the temperature (°C) (Belehradek, 1957). It was commonly used to describe the relationship between temperature (°C) and embryonic development time (Yamakawa and Matsuda, 1997). Based on the relationship of embryonic development and temperature, we estimated the Bělehrádek equation parameters following the methods described by previous studies (Corkett and McLaren, 1970; Ozaki and Ikeda, 1997; Yamakawa and Matsuda, 1997). Specifically, a represented for the differences in mean slope (shifts on the development scale) and b depicted the degree of curvilinearity over the vital temperature range. The α was "theoretical biological zero temperature" (theoretical temperature below which eggs stop their development). The equation was first converted to logarithm: $D = \log_{10}a + b\log_{10}(T-\alpha)$. Then, it was fitted to get constants by successive approximation to that value of α having the smallest sums of squares of deviations of observed hatching times.

2.5. Statistical analysis

We used non-parametric Kruskal-Wallis tests followed by pairwise Wilcoxon Rank Sum tests (post hoc test) to detect the differences in survival, feeding rates, spawning rates, duration from mating to the

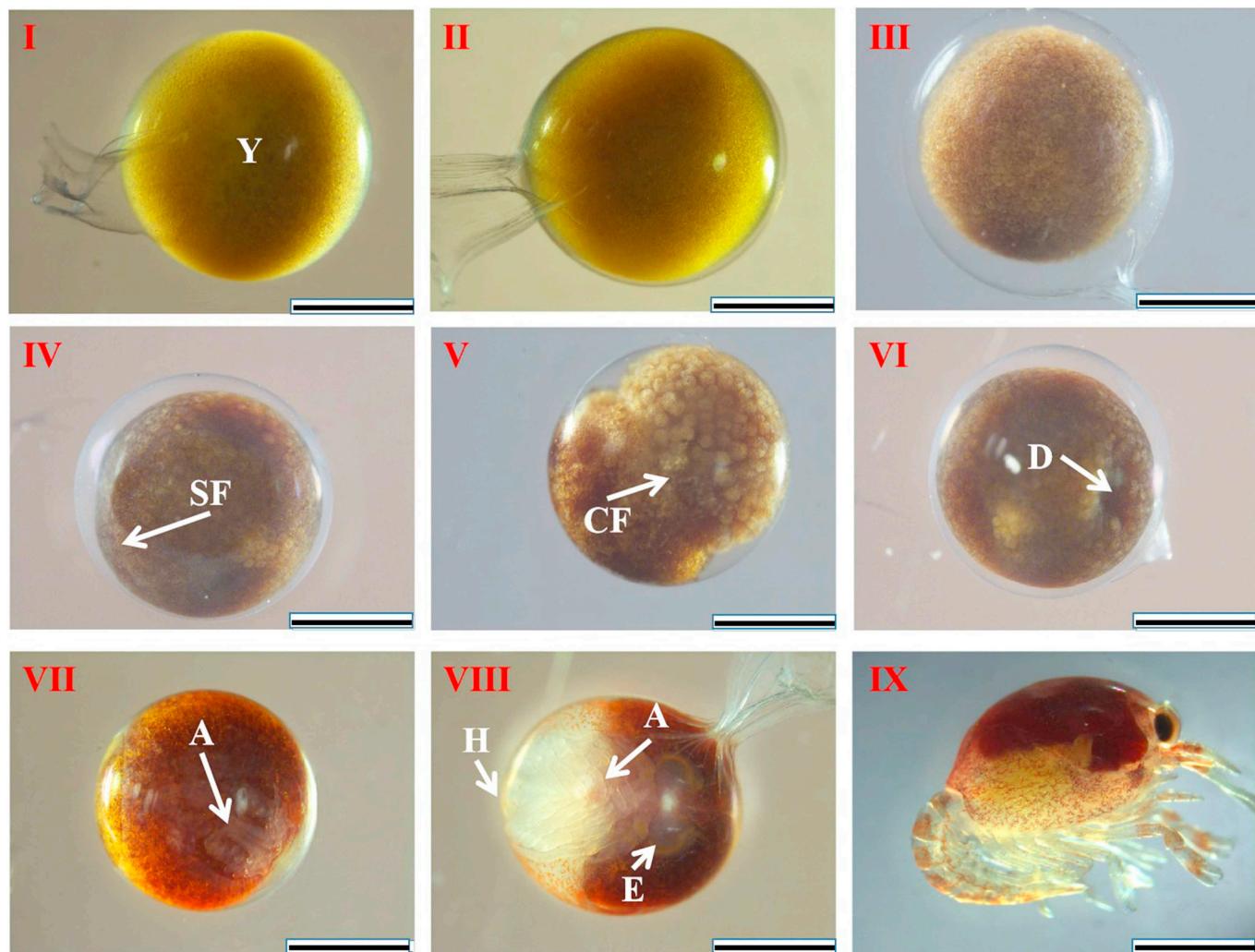


Fig. 1. Morphological characteristics of *Procambarus clarkii* embryos in nine different developmental stages. I, zygote, opaque and full of yolk (Y); II, cleavage; III, blastula; IV, semicircular furrow (SF, due to blastula invagination); V, circular furrow (CF); VI, gastrula with dent (D) visible (the sign of gastrula); VII, nauplius with appearance of appendages (A); VII, zoea showing the heart (H) region, a pair of round eyes (E), appendages (A) and enlarged transparent area; IX, hatching. Scale bars are 1 mm.

spawning, fecundity, and embryos hatching time among different temperature treatments. Independent samples *t*-tests were used to analyze the differences in survival between sexes. In order to estimate optimal temperature for *P. clarkii* reproductive performance, polynomial models were fitted to the data of spawning rates and fecundity, and loess regression was fitted to the data of duration from mating to spawning. We used non-metric multidimensional scaling analysis (NMDS) to ordinate samples of embryos developmental stages under different temperatures. Results were presented according to five levels of experimental temperatures. Stress (mismatch in the relationship between the distance in the original space and the reduced ordination space) is normally a factor indicating the quality of NMDS analysis, and lower values (< 0.2) generally result in good interpretations (McCune et al., 2002; Wittig and Becker, 2010). Statistical differences were set to 0.05 and all statistical analyses were performed in the software R version 3.3.2 (R Core Team, 2017).

3. Results

3.1. Experiment 1

3.1.1. Survival

Adult crayfish survival was not significantly affected by temperature

for both females and males (Kruskal-wallis test, females: $\chi^2 = 4.27$, $P = 0.37$; males: $\chi^2 = 3.01$, $P = 0.56$). Furthermore, no significant differences between sexes were observed (Independent samples *t*-tests, 17 °C: $t = 1.68$, $P = 0.11$; 21 °C: $t = 1.26$, $P = 0.22$; 25 °C: $t = 1.15$, $P = 0.26$; 29 °C: $t = 1.70$, $P = 0.11$; 33 °C: $t = 1.17$, $P = 0.25$. Original data see supplementary material 4).

3.1.2. Feeding rates

The feeding rates of adult crayfish were significantly affected by temperature (Kruskal-wallis test, $\chi^2 = 43.51$, $P < 0.001$). Specifically, at 21 °C and 25 °C, feeding rates of adults were significantly higher than those at other temperatures (pairwise Wilcoxon test, all $P < 0.001$) (Supplementary material 5).

3.1.3. Spawning rates

Spawning events occurred from 17 °C to 33 °C, but spawning rates were significantly affected by temperature (Kruskal-wallis test, $\chi^2 = 31.04$, $P < 0.001$). More specifically, the spawning rates of *P. clarkii* at 29 °C and 33 °C were significantly lower than those at 17 °C, 21 °C, and 25 °C (pairwise Wilcoxon test, 17–29 °C: $P = 0.002$; 17–33 °C: $P < 0.001$; 21–29 °C: $P < 0.001$; 21–33 °C: $P < 0.001$; 25–29 °C: $P = 0.001$; 25–33 °C: $P < 0.001$). The spawning rates were also fitted by a polynomial model. Based on the model, the optimal

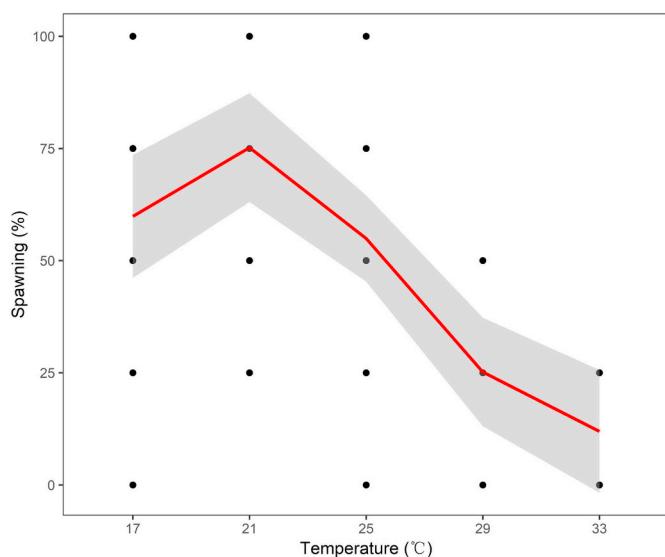


Fig. 2. Scatterplot of spawning rates of female *Procambarus clarkii* exposed to five different temperatures. Total sample sizes were 109, with 29 samples for 17 °C (2, 3, 3, and 3 samples overlapped in the spawning rates values of 25%, 50%, 75%, and 100%, respectively), 35 for 21 °C (3, 4, and 4 samples overlapped in 50%, 75%, and 100%, respectively), 28 for 25 °C (4 and 5 samples overlapped in 50% and 75%, respectively), 11 for 29 °C (3, 7, and 2 samples overlapped in 0%, 25%, and 50% respectively), and 6 for 33 °C (6 samples overlapped in 0% and 25%, respectively). Red line denotes the fitted values from the polynomial model and the grey area denotes 95% confidence interval. The relationship between spawning rates and temperature is shown as: $Y = 45.42 - 159.75X - 61.72X^2 + 57.05X^3$ ($F = 19.14$, $P < 0.001$, $r^2 = 0.48$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

spawning rate occurred at 21 °C. The relationship between spawning rates and temperature is shown as: $Y = 45.42 - 159.75X - 61.72X^2 + 57.05X^3$ ($F = 19.14$, $P < 0.001$, $r^2 = 0.48$, Fig. 2).

3.1.4. Duration from mating to spawning

The duration from mating to spawning of crayfish was significantly affected by temperature (Kruskal-Wallis test, $\chi^2 = 27.77$, $P < 0.001$). At 29 °C, it was significantly shorter than other treatments (pairwise Wilcoxon test, 17 °C: $P < 0.001$; 21 °C: $P < 0.001$; 25 °C: $P < 0.001$; 33 °C: $P = 0.003$) while at 33 °C, it was significantly shorter than those at 17 °C (pairwise Wilcoxon test, $P = 0.006$). We used loess regression to fit the observed data, which showed that crayfish at 17 °C had the longest duration while crayfish at 33 °C had the shortest duration ($span = 0.75$, Fig. 3).

3.1.5. Fecundity

Fecundity of female *P. clarkii* ranged from 163 to 624 in the present study. They were significantly higher at 21 °C and 25 °C when compared to other treatments, and *P. clarkii* at 17 °C also had significantly higher fecundity compared to 29 °C and 33 °C (Kruskal-Wallis test and pairwise Wilcoxon test, $\chi^2 = 60.64$, 29 °C — 33 °C: $P = 0.01$, others: $P < 0.001$). The polynomial model showed that the optimal temperature for improving fecundity was 21 °C. The relationship between fecundity and temperature is shown as: $Y = 442.38 - 536.62X - 745.43X^2 + 197.35X^3$ ($F = 75.48$, $P < 0.001$, $r^2 = 0.67$, Fig. 4).

3.2. Experiment 2

3.2.1. Morphological abnormalities

During the early stages of embryo development (< 72 h), we observed abnormalities and death of all eggs at 29 °C and 33 °C. These abnormalities included abnormal cleavage (Fig. 5A), blastula lesions

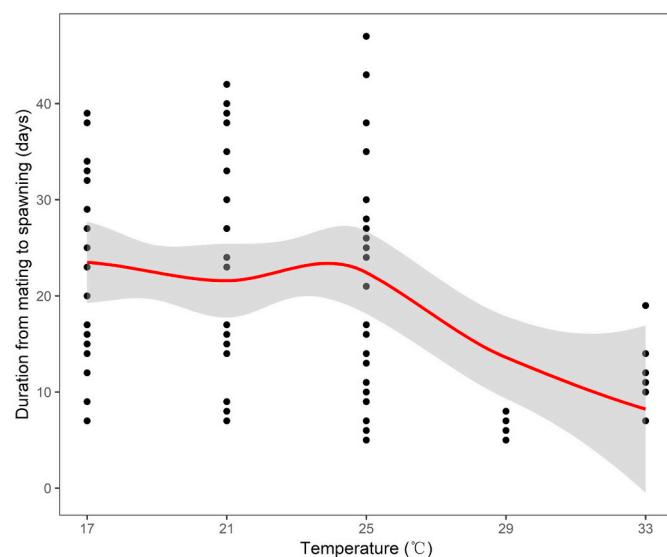


Fig. 3. Scatterplot of duration from mating to spawning of female *Procambarus clarkii* at five different temperatures. Total sample sizes were 109, with 29, 35, 28, 11, and 6 samples for 17 °C, 21 °C, 25 °C, 29 °C, 33 °C, respectively. Red line denotes the fitted values from the loess regression and the grey area denotes 95% confidence interval ($span = 0.75$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

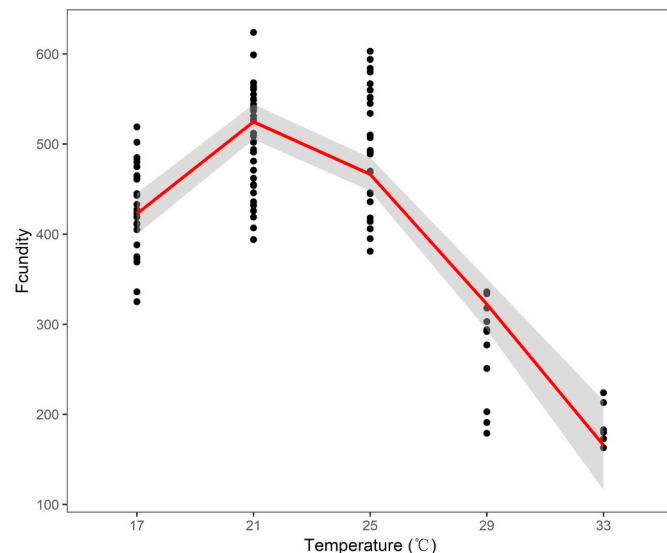


Fig. 4. Scatterplot of the fecundity of female *Procambarus clarkii* exposed to five different temperatures. Total sample sizes were 109, with 29 for 17 °C, 35 for 21 °C, 28 for 25 °C, 11 for 29 °C, and 6 for 33 °C, respectively. Red line denotes the fitted values from the polynomial model and the grey area denotes 95% confidence interval. The relationship between fecundity and temperature is shown as: $Y = 442.38 - 536.62X - 745.43X^2 + 197.35X^3$ ($F = 75.48$, $P < 0.001$, $r^2 = 0.67$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 5B), punctured membranes (Fig. 5C), abnormal invagination of blastula (Fig. 5D), and gastrulation lesions (Fig. 5E). However, no abnormalities were observed in embryos at 17 °C, 21 °C, and 25 °C.

3.2.2. Relationship between embryonic development and temperature

The NMDS analysis on embryos developmental stages at five different temperatures revealed that successful hatching of *P. clarkii* only

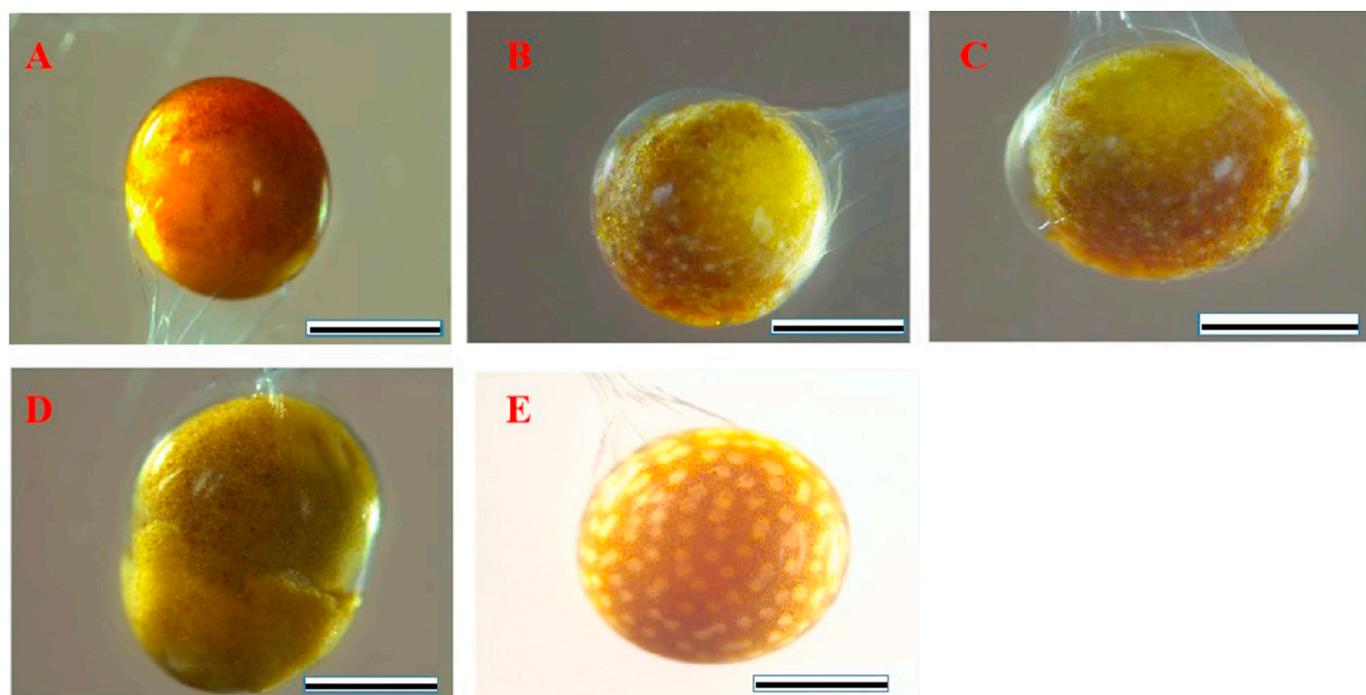


Fig. 5. Morphological abnormalities of *Procambarus clarkii* embryos exposed to 29 °C and 33 °C. (A) abnormal cleavage, (B) blastula lesions, (C) punctured membranes, (D) abnormal invagination of blastula, (E) gastrulation lesions. Scale bars are 1 mm.

occurred when they were exposed to 17 °C, 21 °C, and 25 °C (stress = 0.04, Fig. 6). The development of embryos at 29 °C and 33 °C was aborted and they were dead before hatching. Embryos hatching time was significantly shortened when *P. clarkii* exposed to 25 °C (Kruskal-Wallis and pairwise Wilcoxon Rank Sum tests, $\chi^2 = 31.07$, 17 °C — 25 °C: $P < 0.001$; 21 °C — 25 °C: $P < 0.001$).

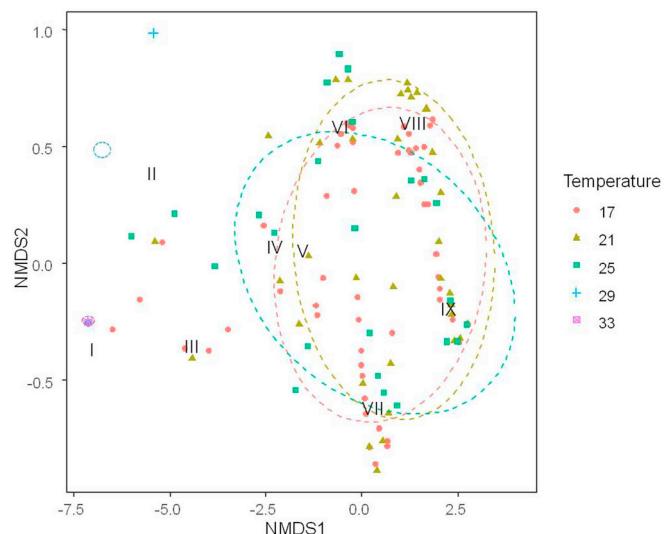


Fig. 6. Non-metric multidimensional scaling (NMDS) plot based on embryos developmental stages for female *Procambarus clarkii* exposed to five different temperatures (17 °C, 21 °C, 25 °C, 29 °C, and 33 °C). Each point (different shapes and colors representing that they were exposed to different water temperatures) in the two-dimensional space represents an individual embryo developmental stage. Ellipses indicate 68% confidence intervals of embryos developmental stages exposed to different water temperature. I ~ IX represents *P. clarkii* embryos developmental stages. Specifically, I, zygote; II, cleavage; III, blastula; IV, semicircular furrow; V, circular furrow; VI, gastrula; VII, nauplius; VIII, zoea; and IX, hatching. Stress is 0.04 for NMDS analysis, indicating good interpretations of the results.

3.2.3. Temperature-dependent developmental model

The 50% developmental time of the sampled eggs is an important index to compare embryonic development. When exposed to 17 °C, the embryonic development took significantly more time compared to 21 °C and 25 °C. The average time taken for 50% of embryos hatching at 17 °C was 85 days, while they were 29 days for 21 °C and 21 days for 25 °C (Fig. 7).

Based on the relationship of embryos developmental time and temperature, we built a predictive exponential model as follows: $D = 3,140,837(T-2.03)^{-3.76}$ ($r^2 = 0.96$, $F_{1, 34} = 765.8$, $P < 0.001$, Fig. 7), where D was the embryonic development duration from spawning to hatching in days and T was the hatching temperature in °C. The model described the curvilinear relationship between the duration of embryonic development and temperature, and it fitted the experimental data very well, with a very high value of $r^2 = 0.96$. In addition, it indicated that the theoretical biological zero temperature of 2.03 °C for embryonic development of *P. clarkii*. This meant that under this temperature, embryonic development would be aborted.

4. Discussion

4.1. Optimal temperature for female reproductive performance

The results of experiment 1 showed that female *P. clarkii* at 21 °C and 25 °C had significantly higher reproductive outputs than other treatments. According to the polynomial models and loess regression, crayfish at 17 °C had a long duration from mating to spawning while they had significantly lower spawning rates and fecundity at 29 °C and 33 °C. Taken together, we thus suggest the optimal temperature range of 21 °C – 25 °C for improving reproductive performance of female *P. clarkii*.

Temperature is generally a crucial factor influencing the spawning activities of crayfish (Carmona-Osalde et al., 2004; Liu et al., 2013a; Tropea et al., 2010). In the current study, the spawning rates of *P. clarkii* exposed to 21 °C and 25 °C were significantly higher than those at other temperatures. This was different from a previous study reporting that 16–18 °C could significantly induce spawning of *P. clarkii* (Liu

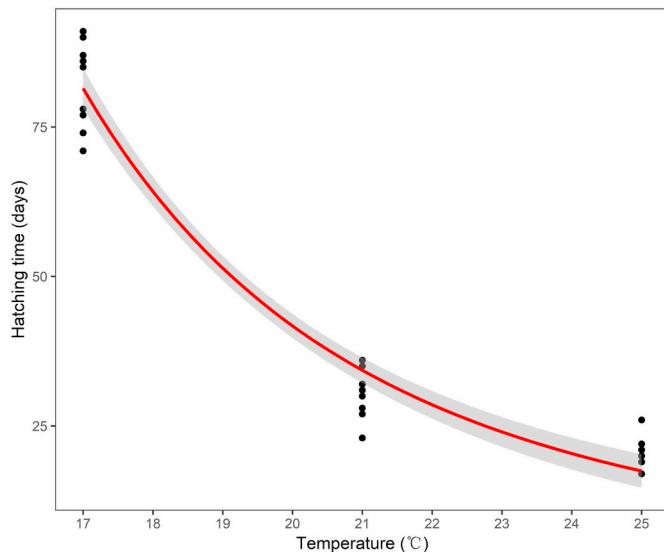


Fig. 7. Scatterplot of hatching time of *Procambarus clarkii* embryos across temperatures fitted by the predictive exponential model ($r^2 = 0.96$). Each black point represents 50% sampled eggs hatching time from each replicate in different temperatures of the current study ($N = 36$). The solid red curve represents the estimated results from the model and the grey areas represent the 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2013a). Similar results could also be found on other species such as crayfish *Cherax quadricarinatus* (Tropea et al., 2010), *Procambarus llamasii* (Carmona-Osalde et al., 2004), crabs *Callinectes sapidus* (Bembe et al., 2017), *Genus menippe* (Bert et al., 2016), shrimps *Penaeus semisulcatus* (Aktaş et al., 2003), *Exopalaemon carinicauda* (Liang et al., 2017), and lobster *Panulirus japonicus* (Matsuda et al., 2002). We inferred that the discrepancy among studies might be due to the fact that spawning activities were not only dependent on temperature, but that other environmental factors (e.g. photoperiod, foods, and salinity) not tested in this study could also interact with temperature and then influence spawning activities (Gutierrez-Yurrita and Montes, 1999; Harlioğlu and Duran, 2010; Liu et al., 2013a; Meineri et al., 2014). Furthermore, differences between populations in different studies could also be responsible for the discrepancy as each population might be adapted to different environmental conditions, which thus might result in variability in life history traits such as spawning activities (Alcorlo et al., 2008; Chucholl, 2011; Peruzza et al., 2015). In this case, it appears that different *P. clarkii* populations may have different optimal temperatures for spawning, thus resulting in the discrepancy between our study and previous ones.

Our study also showed that the duration from mating to spawning were significantly shortened at 29 °C and 33 °C (mean duration were 6 and 12 days, respectively). However, in the wild, the mean duration from mating to spawning for *P. clarkii* in China was much longer (approximately two months in Xuyu and one month in Wuhan, Gong et al., 2008; Xu et al., 2014). This could be due to the fact that temperature was continuously decreasing in the wild while it was kept constant all the time in our study. Furthermore, protein and lipid-rich artificial diet used in our study may shorten the duration (30.23% and 10.74% for crude protein and lipid contents). However, in the wild, *P. clarkii* fed on natural foods such as macrophytes, which contained lower protein and lipid contents (Carreira et al., 2014; Carvalho et al., 2016). For instance, a previous study demonstrated that protein and lipid contents were 2.57% and 0.44% for *Hydrilla verticillata*, 2.40% and 0.54% for *Ceratophyllum demersum*, 3.77% and 0.79% for *Elodea Canadensis*, 1.39% and 0.45% for *Vallisneria spiralis* (Zhang et al., 2016). For experiment 1, we also found an interesting phenomenon regarding no significant differences observed in survival among treatments. These results were

different from what were reported by several previous studies (Gherardi and Paglianti, 2004; Han et al., 2011; Mazlum and Eversole, 2005; Zhang et al., 2015). We inferred that it may be due to the different experimental designs and culture conditions (e.g. constant or ambient temperature variations, different temperature ranges tested, experimental *P. clarkii* sizes, and even whether other environmental factors synchronically action with temperature). For instance, some authors set the experimental minimum temperature (10 °C) lower than ours (17 °C), which thus might more or less relate to different survival results (Han et al., 2011; Mazlum and Eversole, 2005). Furthermore, in our study, the temperature tested (17 °C, 21 °C, 25 °C, 29 °C, and 33 °C) were within the temperature range that the experimental *P. clarkii* experienced during their reproductive seasons in the wild. In this case, the *P. clarkii* in the current study might have tolerance and resistance to these temperatures, which in turn resulted in the no differences in survival results.

The ability to induce spawning spontaneously is a key step for large-scale production of juvenile crayfish in aquaculture. Currently, eyestalk ablation and hormones injection are widely used to induce spawning of crustaceans including *P. clarkii*. The current study demonstrated that manipulating water temperature could achieve similar effects on inducing spawning of *P. clarkii* (mean spawning rates: 72% and 58.33% for 21 °C and 25 °C) when compared with eyestalk ablation and hormones injection (mean spawning rates with eyestalk ablation: 63.33%, HCG injection: 77.5%, LD injection: 55%, domperidone injection: 66.67%, domperidone and serotonin injection: 59.26% and 17 α-hydroxyprogesterone injection: 20%) (Liu et al., 2014; Liu et al., 2013b; Zhang, 2011). In addition, hormones injection and eyestalk ablation compromised with lower adults survival (mean survival range from 15.56% to 51.11% in previous studies while 83.9% in our study) and even decreased fertilization rates and offspring sizes (especially for nauplii) (Fornies et al., 2001; Magana-Gallegos et al., 2018; Mylonas et al., 1992). Such cases could also be found in other crustacean species (Pillai et al., 2011; Weng et al., 2012; Vaca and Alfaro, 2000; Wen et al., 2009). All these results show that temperature manipulation could be a more efficient and ethical alternative technique for *P. clarkii* reproduction. Although the present study convinced that 21 °C – 25 °C was optimal for improving female *P. clarkii* reproductive performance, we could not exclude the point that different developmental stages of female crayfish ovaries (3 crayfish ovaries developing to stage IV and 17 crayfish ovaries developing to stage IV or stage V) at the beginning of the experiment might influence the results of spawning rates and duration from mating to spawning to a certain degree during a 50-day experimental period. More studies are encouraged to address this question and confirm whether asynchronous ovaries development has potential effects on crayfish spawning activities and the duration from mating to spawning. Anyway, these results support our hypothesis that water manipulation is an efficient alternative technique of reproduction, and 21 °C–25 °C is suggested for improving the the reproductive performance of female *P. clarkii*.

4.2. Optimal temperature on embryonic development

Results from experiment 2 and temperature-dependent developmental model showed that the optimal temperature for embryonic development was 25 °C. The model was described as $D = 3,140,837(T - 2.03)^{-3.76}$.

In the present study, embryos hatching time was shortened as temperature increased within the defined temperature range (17–25 °C). Optimal embryonic development was observed at 25 °C (mean duration of 21 days) while it was delayed (85 days) at 17 °C. This suggests that the embryonic development of *P. clarkii* could be accelerated by manipulating water temperature. The results were consistent with previous studies reporting faster development with increasing temperatures within a suitable range: 23–30 days at 21 °C and 15–20 days at 25.8 °C for *P. clarkii* (Lv et al., 2006; Suko, 1956; Wang,

2012). Hatching temperature was previously shown to have similar effects on embryonic development of other crustacean species (Branford, 1978; Brillon et al., 2005; Perkins, 1972; Sachlikidis et al., 2010; Stevens et al., 2008; Tong et al., 2000; Webb et al., 2007) and fish (Brown et al., 2011; Morehead and Hart, 2003; Peña et al., 2014; Wen et al., 2013; Yang and Chen, 2005). All these findings further indicate that manipulating water temperature to induce spawning and embryos hatching is a potentially effective way to provide mass production of juveniles in a limited time.

4.3. Temperature-induced abnormality and death of embryos

Abnormality of embryos is one of the most serious problems in aquaculture, which is mainly due to suboptimal culture conditions (Cobcroft et al., 2001; Fraser and De Nys, 2005). For instance, high temperature could induce abnormalities of embryos especially during cleavage, blastomere and gastrulation stages of many hatchery-reared species (Aritaki and Seikai, 2004; Huang et al., 2010; Sfakianakis et al., 2004; Wang and Tsai, 2000). In the current study, *P. clarkii* exposed to the high temperatures (29 °C and 33 °C) during embryonic development also showed abnormalities and ceased to develop while no abnormalities were detected at lower temperatures (17 °C, 21 °C, and 25 °C). Similar phenomena have also been reported in many fish species such as *Solea senegalensis* (Dionisio et al., 2012), *Danio rerio* (Casper et al., 2015), *Vimba vimba* (Lugowska and Kondera, 2018), *Sparus aurata* (Georgakopoulou et al., 2010), and *Dicentrarchus labrax* (Georgakopoulou et al., 2007).

High mortalities of embryos also occurred when hatching temperatures were out of the suitable ranges (Lahnsteiner et al., 2012; Lugowska and Witeska, 2018). In our study, all the embryos failed to hatch above 29 °C while a previous study showed that 40% of the embryos of *P. clarkii* died at 30 °C, and 100% died at 41 °C (Lv et al., 2004). This discrepancy and reduced thermal tolerance in our study might be attributed to different maternal thermal history, which has been considered as the most important factor influencing thermal tolerance, thus resulting in the different results of embryos thermal tolerance between studies (Lutterschmidt and Hutchison, 1997; Soundarapandian et al., 2014). Previous studies also found that animals exposed to dynamic temperature changes would have faster acclimation rates and thus increase their thermal tolerance (Beitinger et al., 2000; Heath, 1963; Hutchison and Ferrance, 1970; Mora and Maya, 2006). The different duration that crayfish embryos exposed to suboptimal temperature conditions could also affect their survival and abnormalities. In the present study, we did not observe abnormalities when embryos were exposed to 17 °C, 21 °C, and 25 °C, which suggested that embryos at these temperatures displayed better ontogeny. Based on these results, we thus recommend performing embryos hatching at 25 °C and avoiding hatching temperatures higher than 29 °C to perform balanced embryonic development.

4.4. Embryo developmental model

The relationship between temperature and developmental time was best described by a nonlinear model that fitted the experimental data very well. This model is useful to predict embryos hatching time based on temperatures and would hopefully help farmers to predict juveniles recruitment time and optimize their culture conditions. According to the Match/Mismatch theory, a mismatch of hatching time and food availability would subsequently lead to low survival and poor growth (Cushing, 1990). In the wild, the diets of juvenile *P. clarkii* include a variety of zooplankton (e.g. *Daphnia magna*), and macrophytes (e.g. *Myriophyllum spicatum*) (Carreira et al., 2014; Carvalho et al., 2016; Dan et al., 2007). The abundance of these food sources has pronounced influences on survival of juveniles (Fiksen and Jørgensen, 2011; González-Ortegón et al., 2015). With this model, farmers and scientists will be able to predict the occurrence time of juveniles in farmed and

natural ponds. This could help match food resources and optimize feeding strategies in aquaculture to make multiple hatchery productions thus increasing potential production.

5. Conclusions

A sustainable and continuous supply of juvenile crayfish is now needed for the development of *P. clarkii* culture industry. Our study suggests that manipulating water temperature is an effective way to induce spawning and optimize embryonic development to improve juvenile crayfish production, which is of high interest for sustainable aquaculture. In the present study, the optimal temperatures for improving *P. clarkii* reproductive performance were 21 °C – 25 °C. Furthermore, the optimal temperature for embryonic development was 25 °C to shorten embryonic development time while avoiding embryos abnormalities and death. We also built a temperature-dependent developmental model, which could help farmers to predict juveniles recruitment time depending on their culture conditions. Other factors such as photoperiod, food quality, and salinity will also affect the reproductive performance and embryonic development of *P. clarkii*, and further experimental studies aiming at optimizing the culture conditions for *P. clarkii* aquaculture should be encouraged.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aquaculture.2019.04.066>.

Declarations of interest

None. The funding sponsors had no roles in the design of the study; in the collection, analysis, or interpretation of data; in the writing of the manuscript, nor in the decision to publish the results.

Declarations of submission

All authors approved the authorship and submission of the manuscript for peer review. The authors confirm that this manuscript has not been published and is not currently under consideration by any other journals.

Authorship

Shiyu Jin and Tanglin Zhang conceived and designed the investigation; Shiyu Jin, Feng Huang, Mantang Xiong, and Ruojing Li conducted the test; Shiyu Jin and Lisa Jacquin drafted the initial manuscript; Sovan Lek contributed to the data analysis; Wei Li, Sovan Lek, Jiashou Liu, and Tanglin Zhang provided guidance for data analysis, provided critical feedback on the manuscript and approved the final manuscript.

Acknowledgements

This work was financially supported by the Technical Innovation Project of Science and Technology Department of Hubei Province (Grant numbers. 2018ABA102; 2016ABA123), and STS Project (Grant number KFJ-STS-ZDTP-049) of Chinese Academy of Sciences. The authors would like to acknowledge the great help of Xianghong Dong, Ting Yuan, Tao Xiang, Jing Qian and China Scholarship Council for their great assistance in the study. Finally, we also would like to acknowledge Qidong Wang and Kai Feng for providing the temperature data of Huangjin Lake.

References

- Aktaş, M., Kumlu, M., 1999. Gonadal maturation and spawning of *Penaeus semisulcatus* (Penaeidae: Decapoda). Turkish J. Zool. 23, 61–66.
- Aktaş, M., Kumlu, M., Eroldogan, O., 2003. Off-season maturation and spawning of *Penaeus semisulcatus* by eyestalk ablation and/or temperature–photoperiod regimes.

- Aquaculture 228, 361–370. [https://doi.org/10.1016/S0044-8486\(03\)00314-4](https://doi.org/10.1016/S0044-8486(03)00314-4).
- Alcorlo, P., Geiger, W., Otero, M., 2008. Reproductive biology and life cycle of the invasive crayfish *Procambarus clarkii* (Crustacea: Decapoda) in diverse aquatic habitats of South-Western Spain: implications for population control. Fundam. Appl. Limnol. (3), 197–212. <https://doi.org/10.1127/1863-9135/2008/0173-0197>.
- Anastácio, P.M., Marques, J.C., 1995. Population biology and production of the red swamp crayfish *Procambarus clarkii* (girard) in the lower mondego river valley, Portugal. J. Crustac. Biol. 15, 156–168. <https://doi.org/10.2307/1549018>.
- APHA, et al., 1989. Standard Methods for the Examination of Water and Wastewater, 17th ed. American Public Health Association, American Water Works Association, Water Pollution Control Federation, Washington, D.C.
- Aritaki, M., Seikai, T., 2004. Temperature effects on early development and occurrence of metamorphosis-related morphological abnormalities in hatchery-reared brown sole *Pseudopleuronectes herzensteini*. Aquaculture 240, 517–530. <https://doi.org/10.1016/j.aquaculture.2004.06.033>.
- Beitingier, T.L., Bennett, W.A., McCauley, R.W., 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environ. Biol. Fish. 58, 237–275. <https://doi.org/10.1023/A:100767632585>.
- Belehradek, J., 1957. Physiological aspects of heat and cold. Annu. Rev. Physiol. 19, 59–82. <https://doi.org/10.1146/annurev.ph.19.030157.000423>.
- Bembe, S., Liang, D., Chung, J.S., 2017. Optimal temperature and photoperiod for the spawning of blue crab, *Callinectes sapidus*, in captivity. Aquac. Res. 48, 5498–5505. <https://doi.org/10.1111/are.13366>.
- Bert, T.M., Gerhart, S.D., Crawford, C., 2016. Reproduction in female stone crabs (Genus *Menippe*) from Tampa bay, Florida: interannual, seasonal, and temperature-related variation. J. Shellfish Res. 35, 519–537. <https://doi.org/10.2983/035.035.0225>.
- Branford, J., 1978. Incubation period for the lobster *Homarus gammarus* at various temperatures. Mar. Biol. 47, 363–368. <https://doi.org/10.1007/BF00388928>.
- Brillon, S., Lambert, Y., Dodson, J., 2005. Egg survival, embryonic development, and larval characteristics of northern shrimp (*Pandalus borealis*) females subject to different temperature and feeding conditions. Mar. Biol. 147, 895–911. <https://doi.org/10.1007/s00227-005-1633-6>.
- Browdy, C., 1992. A review of the reproductive biology of *Penaeus* species: perspectives on controlled shrimp maturation system for high quality nauplii production. Proc. Special Session Shrimp Farm. 1992, 22–51.
- Browdy, C., Samocha, T., 1985. The effect of eyestalk ablation on spawning, molting and mating of *Penaeus semisulcatus* de Haan. Aquaculture 49, 19–29. [https://doi.org/10.1016/0044-8486\(85\)90187-5](https://doi.org/10.1016/0044-8486(85)90187-5).
- Brown, C.A., Gothreaux, C.T., Green, C.C., 2011. Effects of temperature and salinity during incubation on hatching and yolk utilization of Gulf killifish *Fundulus grandis* embryos. Aquaculture 315, 335–339. <https://doi.org/10.1016/j.aquaculture.2011.02.041>.
- Cano, E., Ocete, M.E., 1997. Population biology of red swamp crayfish, *Procambarus clarkii* (girard, 1852) in the guadalquivir river marshes, Spain. Crustaceana 70, 553–561. <https://doi.org/10.1163/156854097x00672>.
- Carmona-Osalde, C., Rodriguez-Serna, M., Olvera-Novoa, M.A., Gutierrez-Yurrita, P.J., 2004. Gonadal development, spawning, growth and survival of the crayfish *Procambarus llanasi* at three different water temperatures. Aquaculture 232, 305–316. [https://doi.org/10.1016/S0044-8486\(03\)00527-1](https://doi.org/10.1016/S0044-8486(03)00527-1).
- Carreira, B.M., Dias, M.P., Rebelo, R., 2014. How consumption and fragmentation of macrophytes by the invasive crayfish *Procambarus clarkii* shape the macrophyte communities of temporary ponds. Hydrobiologia 721, 89–98. <https://doi.org/10.1007/s10750-013-1651-1>.
- Carvalho, F., Cláudia, P., Cássio, F., Sousa, R., 2016. Direct and indirect effects of an invasive omnivore crayfish on leaf litter decomposition. Sci. Total Environ. 541, 714–720. <https://doi.org/10.1016/j.scitotenv.2015.09.125>.
- Casper, P., Verbueken, E., Saada, M.A., Casteleyn, C.R., Ginneken, C.J.V., Knapen, D., Cruchtena, S.J.V., 2015. Incubation at 32.5°C and above causes malformations in the zebrafish embryo. Reprod. Toxicol. 56, 56–63. <https://doi.org/10.1016/j.reprotox.2015.05.006>.
- Chaves, A.R., 2000. Effect of x-organ sinus gland extract on S-35 methionine incorporation to the ovary of the red swamp crawfish *Procambarus clarkii*. Comp. Biochem. Physiol. 3, 407–413.
- Chucholl, C., 2011. Population ecology of an alien "warm water" crayfish (*Procambarus clarkii*) in a new cold habitat. Knowl. Manag. Aquat. Ecosyst. 401, 29. (P1-P21). <https://doi.org/10.1051/kmae/2011053>.
- Cobcroft, J., Pankhurst, P., Sadler, J., Hart, P., 2001. Jaw development and malformation in cultured striped trumpetfish *Lutjanus lineatus*. Aquaculture 199, 267–282. [https://doi.org/10.1016/S0044-8486\(01\)00592-0](https://doi.org/10.1016/S0044-8486(01)00592-0).
- Corkett, C., McLaren, I., 1970. Relationships between development rate of eggs and older stages of copepods. J. Mar. Biol. Assoc. U. K. 50, 161–168. <https://doi.org/10.1017/S0025315400000680>.
- Cushing, D., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26, 249–293. [https://doi.org/10.1016/S0065-2881\(08\)60202-3](https://doi.org/10.1016/S0065-2881(08)60202-3).
- Dai, Y., Wang, T.T., Wang, Y.F., Gong, X.J., Yue, C.F., 2009. Activities of digestive enzymes during embryonic development in the crayfish *Procambarus clarkii* (Decapoda). Aquac. Res. 40, 1394–1399. <https://doi.org/10.1111/j.1365-2109.2009.02237.x>.
- DAISIE Delivering Alien Invasive Species in Europe, 2010. Available from: <http://www.europe-alien.org/speciesTheWorst.do>, Accessed date: 1 August 2010.
- Dan, L., Zhang, S.P., Yang, Q., Zhu, Y.F., 2007. Feeding habit and behavior of *Procambarus clarkii*. Hubei Agric. Sci. 46, 436–438.
- Das, T., Pal, A., Chakraborty, S., Manush, S., Dalvi, R., Sarma, K., Mukherjee, S., 2006. Thermal dependence of embryonic development and hatching rate in *Labeo rohita* (Hamilton, 1822). Aquaculture 255, 536–541. <https://doi.org/10.1016/j.aquaculture.2006.01.013>.
- Dionísio, G., Campos, C., Valente, L., Conceição, L., Cancela, M., Gavaia, P.J., 2012. Effect of egg incubation temperature on the occurrence of skeletal deformities in *Solea selegalensis*. J. Appl. Ichthyol. 28, 471–476. <https://doi.org/10.1111/j.1439-0426.2012.01996.x>.
- Dörr, A.J.M., La Porta, G., Pedicillo, G., Lorenzoni, M., 2006. Biology of *Procambarus clarkii* (Girard, 1852) in Lake Trasimeno. Bull. Fr. Peche Piscic. 380–381, 1155–1167. <https://doi.org/10.1051/kmae:2006018>.
- Eastman-Reks, S., Fingerman, M., 1984. Effects of neuroendocrine tissue and cyclic AMP on ovarian growth in vivo and in vitro in the fiddler crab, *Uca pugilator*. Comp. Biochem. Physiol. A Physiol. 4, 679–684. [https://doi.org/10.1016/0300-9629\(84\)90468-7](https://doi.org/10.1016/0300-9629(84)90468-7).
- Egly, R.M., Annis, G.M., Chadderton, W.L., Peters, J.A., Larson, E.R., 2019. Predicting the potential distribution of the non-native red swamp crayfish *Procambarus clarkii* in the Laurentian Great Lakes. J. Great Lakes Res. 45, 150–159. <https://doi.org/10.1016/j.jglr.2018.11.007>.
- FAO, 2018. The State of World Fisheries and Aquaculture 2018 - Meeting the Sustainable Development Goals., Rome. (Licence: CC BY-NC-SA 3.0 IGO).
- Feng, M., Xugan, W., Yongxu, C., Jianfeng, L., 2007. External morphological character during the embryonic development of *Procambarus clarkii*. J. Fish. China 31, 6–11 (in Chinese).
- Fiksen, Ø., Jørgensen, C., 2011. Model of optimal behaviour in fish larvae predicts that food availability determines survival, but not growth. Mar. Ecol. Prog. 43, 207–219. <https://doi.org/10.3354/meps09148>.
- Fisheries Department of Ministry of Agriculture, 2017. China Fishery Statistical Yearbook: 2017. China Agriculture Press, Beijing.
- Folkvord, A., Gundersen, G., Albretsen, J., Asplin, L., Kaartvedt, S., Giske, J., 2015. Impact of hatch date on early life growth and survival of Mueller's pearlside (*Maurolicus muelleri*) larvae and life-history consequences. Can. J. Fish. Aquat. Sci. 73, 163–176. <https://doi.org/10.1139/cjfas-2015-0040>.
- Fornies, M.A., Mananos, E., Carrillo, M., Rocha, A., Laureau, S., Mylonas, C.C., Zohar, Y., Zanuy, S., 2001. Spawning induction of individual european sea bass females (*Dicentrarchus labrax*) using different gnrha-delivery systems. Aquaculture 202, 221–234. [https://doi.org/10.1016/S0044-8486\(01\)00773-6](https://doi.org/10.1016/S0044-8486(01)00773-6).
- Fraser, M., De Nys, R., 2005. The morphology and occurrence of jaw and operculum deformities in cultured barramundi (*Lates calcarifer*) larvae. Aquaculture 250, 496–503. <https://doi.org/10.1016/j.aquaculture.2005.04.067>.
- Geffen, A., Fox, C., Nash, R., 2006. Temperature-dependent development rates of cod *Gadus morhua* eggs. J. Fish Biol. 69, 1060–1080. <https://doi.org/10.1111/j.1095-8649.2006.01181.x>.
- Georgakopoulou, E., Angelopoulou, A., Kaspiris, P., Divanach, P., Koumoundouros, G., 2007. Temperature effects on cranial deformities in European sea bass, *Dicentrarchus labrax* (L.). J. Appl. Ichthyol. 23, 99–103. <https://doi.org/10.1111/j.1439-0426.2006.00810.x>.
- Georgakopoulou, E., Katharios, P., Divanach, P., Koumoundouros, G., 2010. Effect of temperature on the development of skeletal deformities in Gilthead seabream (*Sparus aurata* Linnaeus, 1758). Aquaculture 308, 13–19. <https://doi.org/10.1016/j.aquaculture.2010.08.006>.
- Gherardi, F., Paglianti, A., 2004. Combined effects of temperature and diet on growth and survival of young-of-year crayfish: a comparison between indigenous and invasive species. J. Crustac. Biol. 24, 140–148. <https://doi.org/10.1651/c-2374>.
- Gong, S., Lv, J., Sun, R., Li, L., Xugang, H., 2008. The study on reproductive biology of *Procambarus clarkii*. Freshwater Fish. 6, 23–25 (in Chinese).
- González-Ortegón, E., Giménez, L., Blasco, J., Le Vay, L., 2015. Effects of food limitation and pharmaceutical compounds on the larval development and morphology of *Palaeomon serratus*. Sci. Total Environ. 503, 171–178. <https://doi.org/10.1016/j.scitotenv.2014.08.118>.
- Gutierrez-Yurrita, P.J., Montes, C., 1999. Bioenergetics and phenology of reproduction of the introduced red swamp crayfish, *Procambarus clarkii*, in Donana National Park, Spain, and implications for species management. Freshw. Biol. 42, 561–574. <https://doi.org/10.1046/j.1365-2427.1999.00484.x>.
- Gutierrez-Yurrita, P.J., Martínez, J.M., Bravo-Utrera, M.A., Montes, C., Ilheu, M., Bernardo, J.M., 1999. The status of crayfish populations in Spain and Portugal. In: Gherardi, F., Holdich, D.M. (Eds.), Crayfish in Europe as Alien Species: How to Make the Best of a Bad Situation. A. A. Balkema, Rotterdam, Netherlands, pp. 161–192.
- Han, X.L., Li, X.R., Cheng, D.C., Li, B., Xu, J.R., 2011. Effect of temperature on mating, oogenesis, hatching and larvae development of red swamp crayfish (*Procambarus clarkii*). Hubei Agric. Sci. 10, 2078–2080.
- Harlioğlu, M.M., Duran, T.C., 2010. The effect of darkness on mating and pleopodal egg production time in a freshwater crayfish, *Astacus leptodactylus* Eschscholtz. Aquac. Int. 18, 843–849. <https://doi.org/10.1007/s10499-009-9305-z>.
- Harper, S., Reiber, C., 2006. Cardiac development in crayfish: ontogeny of cardiac physiology and aerobic metabolism in the red swamp crayfish *Procambarus Clarkii*. J. Comp. Physiol. B. 176, 405–414. <https://doi.org/10.1007/s00360-005-0062-7>.
- Heath, W.G., 1963. Thermoperiodism in sea-run cutthroat trout (*Salmo clarki clarki*). Science 142, 486–488. <https://doi.org/10.1126/science.142.3591.486>.
- Hu, M.L., 2009. Characteristics of Water Level, Water Environment and Effects on Fish Communication and Migration in the Hukou Area of Poyang Lake. Nanchang University.
- Huang, H.G., Hu, Z.X., Huang, Z.C., Wu, M.Y., Huang, L.T., 2010. Effects of temperature on embryonic and larvae development of *Polyodon spathula*. J. Guangdong Ocean Univ. 1 (010).
- Huner, J.V., 2002. *Procambarus*. In: Holdich, D. (Ed.), Biology of Freshwater Crayfish. Blackwell Sciene Ltd., Oxford, pp. 541–584.
- Hutchison, V.H., Ferrance, M.R., 1970. Thermal tolerances of *Rana pipiens* acclimated to daily temperature cycles. Herpetologica 1, 1–8.
- Kiernan, J.A., 1999. Histological and Histochemical Methods: Theory and Practice. Scion

- Publishing, Banbury.**
- Kulkarni, G.K., Glade, L., Fingerman, M., 1991. Oogenesis and effects of neuroendocrine tissues on invitro synthesis of protein by the ovary of the red swamp crayfish (GIRARD). *J. Crustac. Biol.* 11, 513–522. <https://doi.org/10.2307/1548520>.
- Lahnsteiner, F., Kletzl, M., Weismann, T., 2012. The effect of temperature on embryonic and yolk-sac larval development in the burbot *Lota lota*. *J. Fish Biol.* 81, 977–986. <https://doi.org/10.1111/j.1095-8649.2012.03344.x>.
- Lei, X., Xiao, M., Hu, H., Lan, L., 2009. The study of embryonic development of red swamp crayfish *Procambarus clarkii* and impact factors. *Jiangxi Fishery Sci. Technol.* 25–29 (in Chinese).
- Li, X.H., Zhang, Q., Xu, C.Y., 2012. Suitability of the TRMM satellite rainfalls in driving a distributed hydrological model for water balance computations in Xinjiang catchment, Poyang lake basin. *J. Hydrol.* 426, 28–38. <https://doi.org/10.1016/j.jhydrol.2012.01.013>.
- Liang, J.P., Li, J., Li, J.T., Liu, P., Liu, D.Y., Dai, F.Y., 2017. Controlled propagation of ridgetail white prawn *Exopalaemon carinicauda*. *Fish. Sci.* 3, 209–295.
- Lin, Q., Lu, J., Gao, Y., Shen, L., Cai, J., Luo, J., 2006. The effect of temperature on gonad, embryonic development and survival rate of juvenile seahorses, *Hippocampus kuda* Bleeker. *Aquaculture* 254, 701–713. <https://doi.org/10.1016/j.aquaculture.2005.11.005>.
- Liu, S.L., Gong, S.Y., Li, J.M., Huang, W.H., 2013a. Effects of water temperature, photoperiod, eyestalk ablation, and non-hormonal treatments on spawning of ovary-matured red swamp crayfish. *N. Am. J. Aquac.* 75, 228–234. <https://doi.org/10.1080/1522055.2012.746247>.
- Liu, W., Chen, S., Mao, J., Zhang, D., Zhou, G., 2013b. Effects of 17 α-hydroxyprogesterone on the synchronous spawning of red swamp crayfish *Procambarus clarkii*. *J. Jiangsu Agric. Sci.* 41, 241–243 (in Chinese).
- Liu, S., Gong, S., Li, J., Huang, W., 2014. Inducing synchronous ovarian maturation in the crayfish, *Procambarus clarkii*, via eyestalk interventional injection as compared with eyestalk ablation and combined injection of serotonin and domperidone. *Aquac. Res.* 45, 1402–1414. <https://doi.org/10.1111/are.12086>.
- Lowery, R.S., Mendes, A.J., 1977. *Procambarus clarkii* in Lake Naivasha, Kenya, and its effects on established and potential fisheries. *Aquaculture* 11, 111–121. [https://doi.org/10.1016/0044-8486\(77\)90069-2](https://doi.org/10.1016/0044-8486(77)90069-2).
- Lugowska, K., Kondera, E., 2018. Early development of vimba (*Vimba vimba*) at different temperatures and temperature-related anomalies. *Aquac. Res.* 49, 2336–2344. <https://doi.org/10.1111/are.13670>.
- Lugowska, K., Witeska, M., 2018. The effect of temperature on early development of barbel *Barbus barbus* (L.). *Aquac. Res.* 49, 2495–2502. <https://doi.org/10.1111/are.13709>.
- Lumare, F., 1979. Reproduction of *Penaeus kerathurus* using eyestalk ablation. *Aquaculture* 18, 203–214. [https://doi.org/10.1016/0044-8486\(79\)90012-7](https://doi.org/10.1016/0044-8486(79)90012-7).
- Lutterschmidt, W.I., Hutchison, V.H., 1997. The critical thermal maximum: history and critique. *Can. J. Zool.* 75, 1561–1574. <https://doi.org/10.1139/z97-783>.
- Lv, J., 2006. *Reproduction Biology, Embryo and Larval Development of Procambarus clarkii*. Huazhong Agricultural University.
- Lv, J., Song, S., Tang, J., Ge, J., Pan, J., 2004. Analysis on temperature factor in hatching of *Procambarus clarkii*. *J. Nanjing Agric. Univ.* 40, 226–231 (in Chinese).
- Lv, J., Gong, S., Li, L., 2006. Study on the embryonic development of red swamp crayfish *Procambarus clarkii*. *J. Yangtze Univ.* 3, 179–182 (in Chinese).
- Magana-Gallegos, E., Bautista-Bautista, M., Gonzalez-Zuniga, L.M., Arevalo, M., Cuzon, G., Gaxiola, G., 2018. Does unilateral eyestalk ablation affect the quality of the larvae of the pink shrimp *Farfantepenaeus brasiliensis* (Lettreille, 1817) (Decapoda: Dendrobranchiata: Penaeidae)? *J. Crustac. Biol.* (4), 401–406. <https://doi.org/10.1093/jcbiol/ruy043>.
- Makinouchi, S., Honculada-Primavera, J., 1987. Maturation and spawning of *Penaeus indicus* using different ablation methods. *Aquaculture* 62, 73–81. [https://doi.org/10.1016/0044-8486\(87\)90186-4](https://doi.org/10.1016/0044-8486(87)90186-4).
- Matsuda, H., Takenouchi, T., Yamakawa, T., 2002. Effects of photoperiod and temperature on ovarian development and spawning of the Japanese spiny lobster *Panulirus japonicus*. *Aquaculture* 205, 385–398. [https://doi.org/10.1016/S0044-8486\(01\)00687-1](https://doi.org/10.1016/S0044-8486(01)00687-1).
- Mazlum, Y., Eversole, A.G., 2005. Growth and survival of *Procambarus acutus acutus* (girard, 1852) and *P. clarkii* (girard, 1852) in competitive settings. *Aquac. Res.* 36, 537–545. <https://doi.org/10.1111/j.1365-2109.2005.01250.x>.
- McCune, B., Grace, J.B., Urban, D.L., 2002. *Analysis of Ecological Communities*. MJM Software Design, Oregon, USA.
- Meineri, E., Rodriguez-Perez, H., Hilaire, S., Mesleard, F., 2014. Distribution and reproduction of *Procambarus clarkii* in relation to water management, salinity and habitat type in the Camargue. *Aquat. Conserv. Marine Freshwater Ecosyst.* 24, 312–323. <https://doi.org/10.1002/aqc.2410>.
- Mora, C., Maya, M.F., 2006. Effect of the rate of temperature increase of the dynamic method on the heat tolerance of fishes. *J. Therm. Biol.* 31, 337–341. <https://doi.org/10.1016/j.jtherbio.2006.01.005>.
- Morehead, D., Hart, P., 2003. Effect of temperature on hatching success and size of striped trumpetfish (*Latris lineata*) larvae. *Aquaculture* 220, 595–606. [https://doi.org/10.1016/S0044-8486\(02\)00636-1](https://doi.org/10.1016/S0044-8486(02)00636-1).
- Muthu, M., Laxminarayana, A., 1977. Induced maturation and spawning of Indian penaeid prawns. *Indian J. Fish.* 24, 172–180.
- Mylonas, C.C., Hinshaw, J.M., Sullivan, C.V., 1992. GnRH-induced ovulation of brown trout (*Salmo trutta*) and its effects on egg quality. *Aquaculture* (3–4), 379–392. [https://doi.org/10.1016/0044-8486\(92\)90268-P](https://doi.org/10.1016/0044-8486(92)90268-P).
- Nentwig, W., 2009. *Handbook of Alien Species in Europe*. Springer Verlag, Berlin.
- Oluoch, A.O., 1990. Breeding biology of the Louisiana red swamp crayfish *Procambarus clarkii* Girard in Lake Naivasha, Kenya. *Hydrobiologia* 208, 85–92. <https://doi.org/10.1007/BF00008447>.
- Okazi, K., Ikeda, T., 1997. The effect of temperature on the development of eggs and nauplii of the mesopelagic copepod *Paraeuchaeta elongata*. *Plankton Biol. Ecol.* 44, 91–95.
- Pandian, T., Katre, S., 1972. Effect of hatching time on larval mortality and survival of the prawn *Macrobrachium idae*. *Mar. Biol.* 13, 330–337. <https://doi.org/10.1007/BF00348081>.
- Peña, R., Dumas, S., Zavala-Leal, I., Contreras-Olguín, M., 2014. Effect of incubation temperature on the embryonic development and yolk-sac larvae of the Pacific red snapper *Lutjanus peru* (Nichols & Murphy, 1922). *Aquac. Res.* 45, 519–527. <https://doi.org/10.1111/j.1365-2109.2012.03255.x>.
- Penn, G.H., 1943. A study of the life history of the Louisiana red-crawfish, *Cambarus clarkii* Girard. *Ecology* 24, 1–18. <https://doi.org/10.2307/1929856>.
- Perkins, H.C., 1972. Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne Edwards). *Fish. Bull.* 70, 95–99.
- Peruzzo, L., Piazza, F., Manfrin, C., Bonzi, L.C., Battistella, S., Giulianini, P.G., 2015. Reproductive plasticity of a *Procambarus clarkii* population living 10 °C below its thermal optimum. *Aquat. Invasions* (2), 199–208. <https://doi.org/10.3391/ai.2015.10.2.08>.
- Pillai, B.R., Sahoo, L., Sahu, S., Mohanty, S., Vijaykumar, D., Sahu, S., 2011. Effect of unilateral eyestalk ablation on ovarian maturation and occurrence of berried females in *Macrobrachium rosenbergii* (de man). *Indian J. Fisheries* 57, 77–80. <https://doi.org/10.1016/j.aquaculture.2010.08.012>.
- Planas, M., Blanco, A., Chamorro, A., Valladares, S., Pintado, J., 2012. Temperature-induced changes of growth and survival in the early development of the seahorse *Hippocampus guttulatus*. *J. Exp. Mar. Biol. Ecol.* 438, 154–162. <https://doi.org/10.1016/j.jembe.2012.10.003>.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. <https://www.r-project.org/>.
- Rakaj, A., Fianchini, A., Boncagni, P., Scardi, M., Cataudella, S., 2019. Artificial reproduction of *Holothuria polita*: a new candidate for aquaculture. *Aquaculture* 498, 444–453. <https://doi.org/10.1016/j.aquaculture.2018.08.060>.
- Richter, K., 2000. *Ecological and Behavioural Studies on the Red Swamp Crayfish, Procambarus clarkii (Girard) as Introduced Species in Britain*. University of North London.
- Rogowski, D.L., Sitko, S., Bonar, S.A., 2013. Optimising control of invasive crayfish using life-history information. *Freshw. Biol.* 58, 1279–1291. <https://doi.org/10.1111/fwb.12126>.
- Sachlikidis, N., Jones, C., Seymour, J., 2010. The effect of temperature on the incubation of eggs of the tropical rock lobster *Panulirus ornatus*. *Aquaculture* 305, 79–83. <https://doi.org/10.1016/j.aquaculture.2010.04.015>.
- Sagi, A., Shoukrun, R., Levy, T., Barki, A., Hulata, G., Karplus, I., 1997. Reproduction and molt in previously spawned and first-time spawning red-claw crayfish *Cherax quadricarinatus* females following eyestalk ablation during the winter reproductive-arrest period. *Aquaculture* 156, 101–111. [https://doi.org/10.1016/S0044-8486\(97\)00065-3](https://doi.org/10.1016/S0044-8486(97)00065-3).
- Seuffert, M.E., Saveanu, L., Martín, P.R., 2012. Threshold temperatures and degree-day estimates for embryonic development of the invasive apple snail *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). *Malacologia* 55, 209–217. <https://doi.org/10.4002/040.05.0203>.
- Sfakianakis, D., Koumoundouros, G., Divanach, P., Kentouri, M., 2004. Osteological development of the vertebral column and of the fins in *Pagellus erythrinus* (L. 1758). Temperature effect on the developmental plasticity and morpho-anatomical abnormalities. *Aquaculture* 232, 407–424. <https://doi.org/10.1016/j.aquaculture.2003.08.014>.
- Smith, G.H., Ritar, A.J., Thompson, P.A., Dunstan, G.A., Brown, M.R., 2002. The effect of embryo incubation temperature on indicators of larval viability in Stage I phyllosoma of the spiny lobster, *Jasus edwardsii*. *Aquaculture* 209, 157–167. [https://doi.org/10.1016/S0044-8486\(01\)00758-X](https://doi.org/10.1016/S0044-8486(01)00758-X).
- Song, G.T., Ding, F.Q., Wu, S., Chen, J., Wang, X., Hou, G.J., 2015. Studies of crucial artificial techniques of red swamp crayfish *Procambarus clarkii*. In: *Fisheries Science and Technology Information*. vol. 42, pp. 108–112. <https://doi.org/10.16446/j.cnki.1001-1994.2015.02.012>.
- Soundarapandian, P., Dinakaran, G., Varadharajan, D., 2014. Effect of temperatures on the embryonic development, morphometrics and survival of *Macrobrachium idella* idella (Hilgendorf, 1898). *J. Aquac. Res. Dev.* 5, 1.
- Sousa, R., Freitas, F.E.P., Mota, M., Nogueira, A.J.A., Antunes, C., 2013. Invasive dynamics of the crayfish *Procambarus clarkii* (Girard, 1852) in the international section of the River Minho (NW of the Iberian Peninsula). *Aquat. Conserv. Marine Freshwater Ecosyst.* 23, 656–666.
- Stevens, B.G., Swiney, K.M., Buck, L., 2008. Thermal effects on embryonic development and hatching for blue king crab *Paralithodes platypus* (Brandt, 1850) held in the laboratory, and a method for predicting dates of hatching. *J. Shellfish Res.* 27, 1255–1263. <https://doi.org/10.2983/0730-8000-27.5.1255>.
- Suko, T., 1956. Studies on the development of the crayfish. IV. The development of winter eggs. *Sci. Rep. Saitama Univ.* 2, 213–219.
- Suvarna, K.S., Layton, C., Bancroft, J.D., 2012. *Bancroft's Theory and Practice of Histological Techniques*. Elsevier Health Sciences, England.
- Tong, L.J., Moss, G.A., Pickering, T.D., Paewai, M.P., 2000. Temperature effects on embryo and early larval development of the spiny lobster *Jasus edwardsii*, and description of a method to predict larval hatch times. *Mar. Freshw. Res.* 51, 243–248. <https://doi.org/10.1071/MF99049>.
- Tropea, C., Piazza, Y., Greco, L.S.L., 2010. Effect of long-term exposure to high temperature on survival, growth and reproductive parameters of the “redclaw” crayfish *Cherax quadricarinatus*. *Aquaculture* 302, 49–56. <https://doi.org/10.1016/j.aquaculture.2010.01.027>.
- Vaca, A.A., Alfaro, J., 2000. Ovarian maturation and spawning in the white shrimp,

- Penaeus vannamei*, by serotonin injection. Aquaculture 182, 373–385. [https://doi.org/10.1016/S0044-8486\(99\)00267-7](https://doi.org/10.1016/S0044-8486(99)00267-7).
- Van Ham, E.H., Berntssen, M.H., Imsland, A.K., Parpoura, A.C., Bonga, S.E.W., Stefansson, S.O., 2003. The influence of temperature and ration on growth, feed conversion, body composition and nutrient retention of juvenile turbot (*Scophthalmus maximus*). Aquaculture 217, 547–558. [https://doi.org/10.1016/S0044-8486\(02\)00411-8](https://doi.org/10.1016/S0044-8486(02)00411-8).
- Wang, Q., 2012. Studies on Reproductive Mechanism and Culture Ecology of Red Swamp Crayfish *Procambarus clarkii*. School of Life Science. Nanjing Normal University, Nanjing.
- Wang, L.H., Tsai, C.L., 2000. Effects of temperature on the deformity and sex differentiation of tilapia, *Oreochromis mossambicus*. J. Exp. Zool. 286, 534–537. [https://doi.org/10.1002/\(SICI\)1097-010X\(20000401\)286:5<534::AID-JEZ11>3.0.CO;2-2](https://doi.org/10.1002/(SICI)1097-010X(20000401)286:5<534::AID-JEZ11>3.0.CO;2-2).
- Webb, J.B., Eckert, G.L., Shirley, T.C., Tamone, S.L., 2007. Changes in embryonic development and hatching in *Chionoecetes opilio* (snow crab) with variation in incubation temperature. Biol. Bull. 213, 67–75. <https://doi.org/10.2307/25066619>.
- Wen, W., Huang, J., Yang, Q., Zhou, F., Chen, X., 2009. Effect of serotonin on ovarian maturation in *Penaeus monodon*. South China Fisheries Sci. 5, 59–63 (in Chinese).
- Wen, W., Huang, X., Chen, Q., Feng, L., Wei, L., 2013. Temperature effects on early development and biochemical dynamics of a marine fish, *Inimicus japonicus*. J. Exp. Mar. Biol. Ecol. 442, 22–29. <https://doi.org/10.1016/j.jembe.2013.01.025>.
- Wen, W.G., Qiu, L.H., Yang, Q.B., Huang, J.H., Zhou, F.L., 2015. Effect of eyestalk ablation on ovarian maturation and spawning in green tiger shrimp *Penaeus semisulcatus* (De Haan 1844). Indian J. Fish. 62, 141–145.
- Weng, X., Li, C.X., Zhou, W.J., Li, Z.J., Li, Y.N., Yang, J., 2012. Effects of different methods in penaeid shrimp broodstock eyestalk ablation on survival rates. Guangdong Agri. Sci. 39, 132–133.
- Wittig, R., Becker, U., 2010. The spontaneous flora around street trees in cities - a striking example for the worldwide homogenization of the flora of urban habitats. Flora Morphol. Distrib. Funct. Ecol. Plants 205, 704–709. <https://doi.org/10.1016/j.flora.2010.07.002>.
- 2009.09.001.
- Wongprasert, K., Asuvapongpatana, S., Poltana, P., Tiensuwan, M., Withyachumnarnkul, B., 2006. Serotonin stimulates ovarian maturation and spawning in the black tiger shrimp *Penaeus monodon*. Aquaculture 261, 1447–1454. <https://doi.org/10.1016/j.aquaculture.2006.08.044>.
- Xiao, M., Lei, X., Rao, Y., Jiang, Q., 2011. Study on the reproductive traits of *Procambarus clarkii* in Poyang lake. China Fisheries 59–60 (in Chinese).
- Xu, J.T., Yan, B.L., Xu, G.C., 2011. The situation and prospects of aquaculture industry for red swamp crayfish *Procambarus clarkii*. Fisheries Sci. Technol. Inform. 38, 172–180 (in Chinese).
- Xu, Z.H., Zhou, X., Shui, Y., Zhao, C.Y., 2014. The study on reproductive behaviour ecology of red swamp crayfish *Procambarus clarkii*. J. Fishery Sci. China 02, 382–389 (in Chinese).
- Yamakawa, T., Matsuda, H., 1997. Improved Bélehrádek Equation for a comprehensive description of the relationship between environmental factors and metabolic rates. Fish. Sci. 63, 725–730. <https://doi.org/10.2331/fishsci.63.725>.
- Yang, Z., Chen, Y., 2005. Effect of temperature on incubation period and hatching success of obscure puffer *Takifugu obscurus* (Abe) eggs. Aquaculture 246, 173–179. <https://doi.org/10.1016/j.aquaculture.2004.12.030>.
- Yano, I., 1985. Induced ovarian maturation and spawning in greasyback shrimp, *Metapenaeus ensis*, by progesterone. Aquaculture 47, 223–229. [https://doi.org/10.1016/0044-8486\(85\)90068-7](https://doi.org/10.1016/0044-8486(85)90068-7).
- Zhang, J., 2011. Study on the Key Techniques of the Industrialized Reproduction and its Culture for *Procambarus clarkii*. Yangzhou University.
- Zhang, L.G., Zhong, J.W., Zhu, Y.A., 2015. Effects of temperature on survival and growth of juvenile red swamp crayfish *Procambarus clarkii*. Hebei Fisheries 1, 4–5.
- Zhang, L., Zhang, W.Q., Wu, F.R., Wang, R., Hou, W.Q., Zhang, J.B., Cheng, Y.X., Wu, X.G., 2016. The Comparaison of nutritional composition of commonly used aquatic plants in aquaculture ponds of adult Chinese Mitten Crab *Eriocheir sinensis*. J. Zhejiang Ocean Univ. 35, 113–121.