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The influence of temperatures ranging from 25 to 36 °C on developmental rates, morphometrics and survival of freshwater prawn (*Macrobrachium rosenbergii*) embryos

S.M. Manush, A.K. Pal *, T. Das, S.C. Mukherjee

Fish Physiology, Pharmacology and Therapeutic Cell, Central Institute of Fisheries Education, Fisheries University Road, Versova, Mumbai-400 061, India

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Abstract

An in vivo study was conducted to assess effect of incubation temperature on embryonic development and hatching period of freshwater prawn (*Macrobrachium rosenbergii*). Brooders spawned on a single day were distributed among four temperature treatments, each with six replicates, and acclimated at a rate of 1 °C/day above and below ambient water temperature (30 °C) to reach test temperatures (25, 29, 33 and 36 °C) and maintained in separate rearing conditions until hatch. Sampling of developing embryos was done at 24-h intervals until mortality/hatching and observed under a light microscope. Major half axis, minor half axis, area and perimeter were measured at 48-h intervals. Embryonic development rates increased with increasing temperatures [y (time from early morula hatch; h) = 40.075x (temperature; °C) + 348.75; $R^2 = 0.993$). A rapid increase in major half axis, larval length, and faster hatching correlated with higher temperatures. Hence this study revealed that incubation temperature significantly influences the time to and duration of hatching and survival of *M. rosenbergii* eggs.

Keywords: Hatching duration; Embryonic development; Temperature; *M. rosenbergii*

1. Introduction

Freshwater prawn farming has become a significant and valuable sector of global aquaculture, contributing 0.3 million metric tons (MT) of all *Macrobrachium* species raised through aquaculture and is being increased with an annual expansion rate of 48% between 1999 and 2001 (New, 2003). The world production of *Macrobrachium rosenbergii* increased from 26, 588 MT in 1991 to 118, 501 MT in 2000 (FAO, 2002), which indicates the importance of this species in freshwater aquaculture. However, a reliable supply of healthy seed is one of the main limitations of *M. rosenbergii* culture.

Emission of greenhouse gases and carbon dioxide are expected to increase global mean temperature by 1.5–4.5 °C over the next half-century (Hounghton and Woodwell, 1989). The impact of such a large temperature shift on freshwater and marine fish and shellfish will affect their biological functions, as most of the species are poikilothermic in nature. Thermal tolerance of aquatic animals is also dependent on acclimation temperature and duration of acclimation (Manush et al., 2004; Das et al., 2004; Chatterjee et al., 2004). Over the years, attention has focused on the

* Corresponding author. Fax: +91 22 26361573.
E-mail address: akpal_53@rediffmail.com (A.K. Pal).

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thermal tolerance of embryos and larvae (Houde, 1989; Pepin, 1991), that are more sensitive to temperature changes than adult fishes (Brett, 1970). Our earlier investigation on *Labeo rohita* revealed similar results (Das et al., in press). Furthermore, it is evident that embryos of temperate species are more sensitive to extreme temperatures than embryos of tropical species (Hokanson and Kleiner, 1974; Irvin, 1974; Buddington et al., 1993). In general, thermal limits are narrower for early stages and reduced survival of embryos and juveniles can occur at temperatures that are within the tolerance range for adults (Elliott, 1981; Cossins and Bowler, 1987). It is reported that upper lethal temperatures of embryos, larvae (Subasinghe and Sommerville, 1992) and adults (Allanson and Noble, 1964) of the freshwater Mozambique tilapia (*Oreochromis mossambica*) varies in the range of 2 °C among different life stages.

When *M. rosenbergii* are reared in tanks, spawning occurs 4–7 times a year if the water temperature is maintained at 27–28 °C. At 25.9±2.1 °C, *M. rosenbergii* molt up to 8 times at intervals of 16.9±1.6 days prior to spawning (Ogasawara, 1984). All the members of *Macrobrachium* move towards freshwater during the juvenile stage. However, rearing brood mother prawns (i.e. bearing eggs on their pleopods) at salinity 2–5‰ increases the hatching rate of eggs. Fecundity of *M. rosenbergii* varies from 40,000 to 60,000 eggs (body weight 70–80 g) and 1,000,000 eggs (body weight 100 g). At the time of spawning, eggs of prawns are elliptical in shape and appear opaque and pale orange. At water temperature, 28 ±0.4 °C, the first polar body releases after 5–6 min and the fertilization membrane expands. The second polar body is then released. Eggs then undergo mitotic division and attain four cell stages, after which cleavage becomes visible under a light microscope. In *M. rosenbergii*, the cleavage is superficial (meroblastic, i.e., a large mass of centrally located yolk confines cleavage to the cytoplasmic rim of the egg) unlike in the case of *Penaeus japonicus.* At 27–28 °C, *M. rosenbergii* eggs attain the morula stage in about 20 h after fertilization (Ogasawara, 1984). Embryo development follows the normal blastula and gastrula stages, ending with the closing of the blastopore, which is visible at about 54 h after fertilization. The eggs then start cell differentiation. At 80 h, the embryo is visible. After 170 h, heartbeat is discernible and after 230 h, compound eyes appear (Ogasawara, 1984). From this stage onwards, different organs develop in the embryo. At 320 h, the embryo assumes the shape of a zoea (or early larval form). From this time, the primary half axis increases and after 430 h has attained maximum length and is ready to hatch (Ogasawara, 1984). The hatched embryo passes through 11 larval stages at salinity of 12±2‰ and attains post-larval stage to adapt again to freshwater. Currently, there are no comprehensive reports on the effect temperatures on embryonic development of *M. rosenbergii.* Hence, the present study was undertaken to assess the effect of incubation temperature on the embryonic development and hatching period of *M. rosenbergii.*

2. Materials and methods

2.1. Experimental animals

Gravid females of *M. rosenbergii* (mean size±S. E=35±2.9 g) having bright orange fertilized eggs in their brood pouch were used for the experiment.

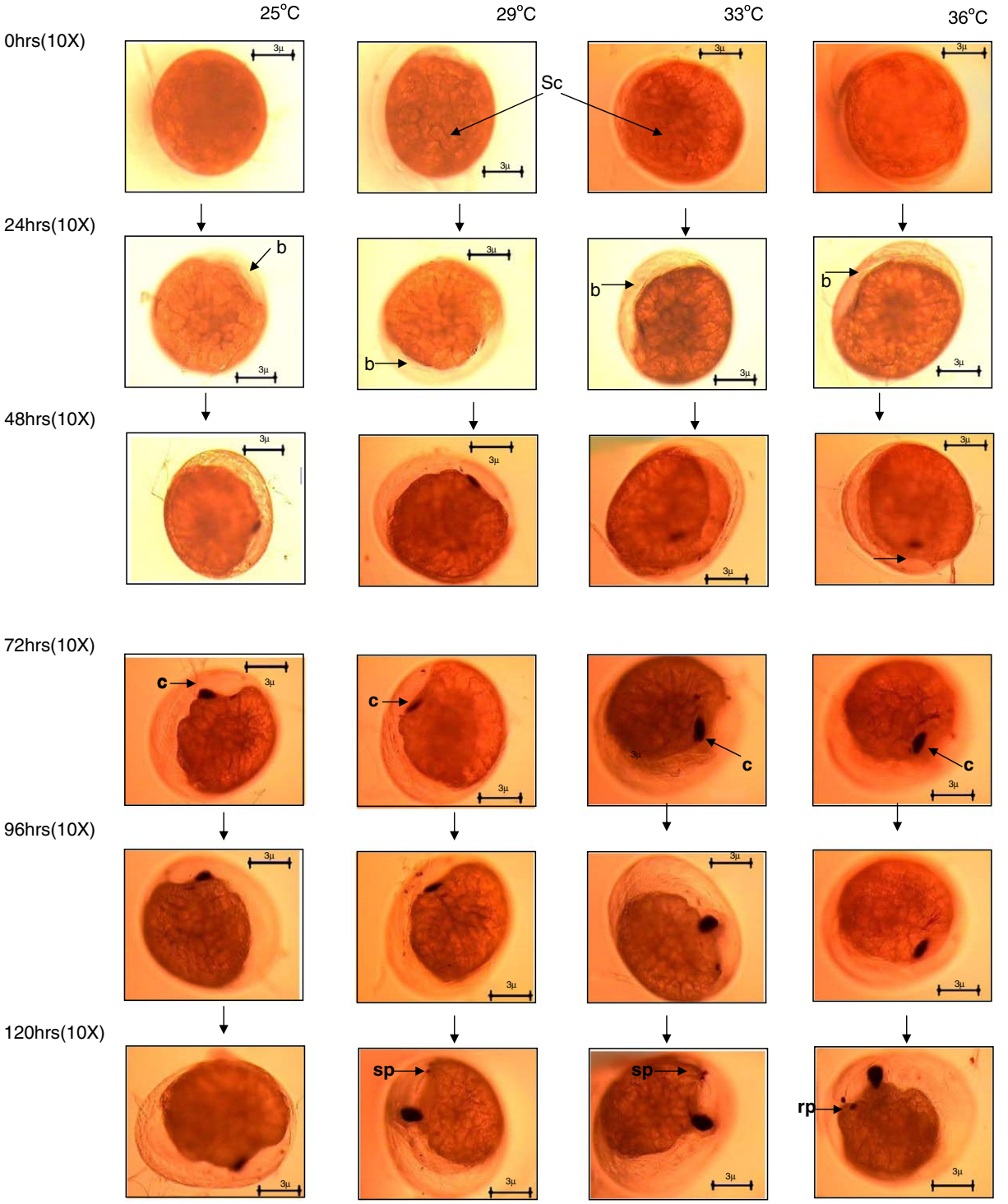
2.2. Experimental protocol

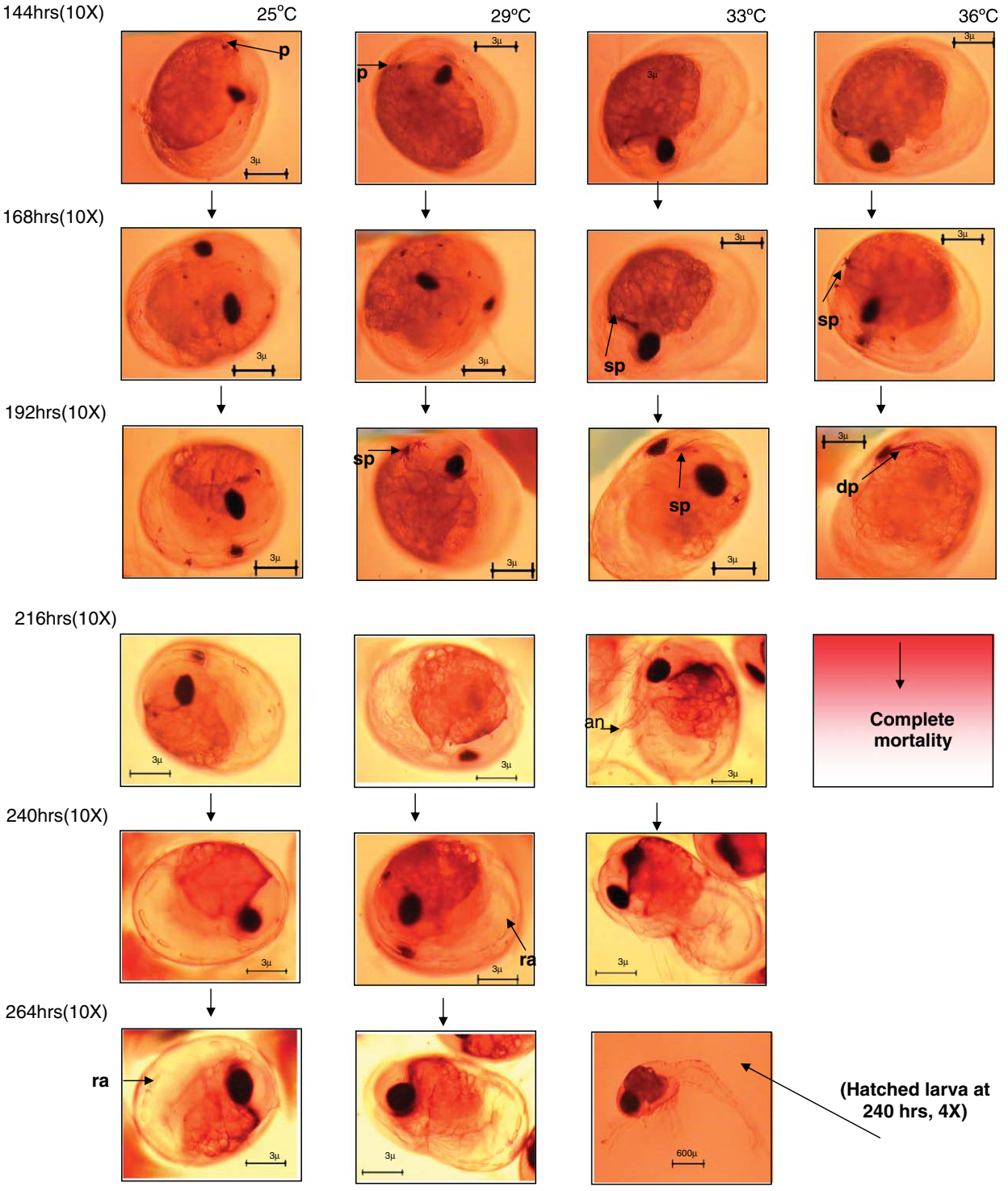
Twenty-four newly spawned brooders were distributed, one each into 175 L plastic pools to assess the effect of incubation temperature on embryonic stages of *M. rosenbergii*. Acclimation was carried out at one degree per day from ambient water temperature (30 °C) to reach test temperatures (25, 29, 33 and 36 °C), which were held until hatching. Sampling of eggs was carried out once the cleavage was complete, since this early development phase is not easily observed and was considered as the initial period (0 h). Eggs were sampled aseptically by gently removing a bunch of eggs from the brood pouch using sterilized forceps and separating the glycocalyx by treating eggs with trypsin (0.05%) and EDTA (400 mg L^{-1}) (Bindu and Mohanty, 2003). After each sampling, brood prawns were given a 1-min prophylactic fungus dip treatment in malachite green (5 mg L^{-1}) before being returned to incubation tanks. Embryonic stages of two brooders were rarely synchronized. Therefore, embryos were sampled at several intervals (i.e. 0, 24, 48, 72, 96, 120, 144, 168, 192, 216, 240, 264, 288, 312 h) from each brooder. Organogenesis, developmental changes and physiological processes were recorded under a light microscope equipped with computer-aided software (Motic Image version 3.1). Eggs collected from four sampling points of brood pouch (anterior to posterior) were pooled (to minimize sampling error due to position of eggs in brood pouch) and assessed the percentage mortality of fully developed embryos (from an aggregate of 20 embryos/

brooder) at the onset of hatching. Embryo dimensions (major half axis, minor half axis, area and perimeter) were measured at 48-h intervals (0, 48, 96, 144, 192 h) until total mortality or hatching occurred.

2.3. Statistical analyses

Effect of gradual acclimation on embryonic development of *M. rosenbergii* was tested using two-way





ANOVA (for comparing morphometric parameters). One-way ANOVA was used for testing the significance of duration of development and mortality at the onset of hatching. Post hoc tests in all cases were carried out using Duncan's multiple comparison procedures, if ANOVA indicated significant differences ($P<0.05$). All

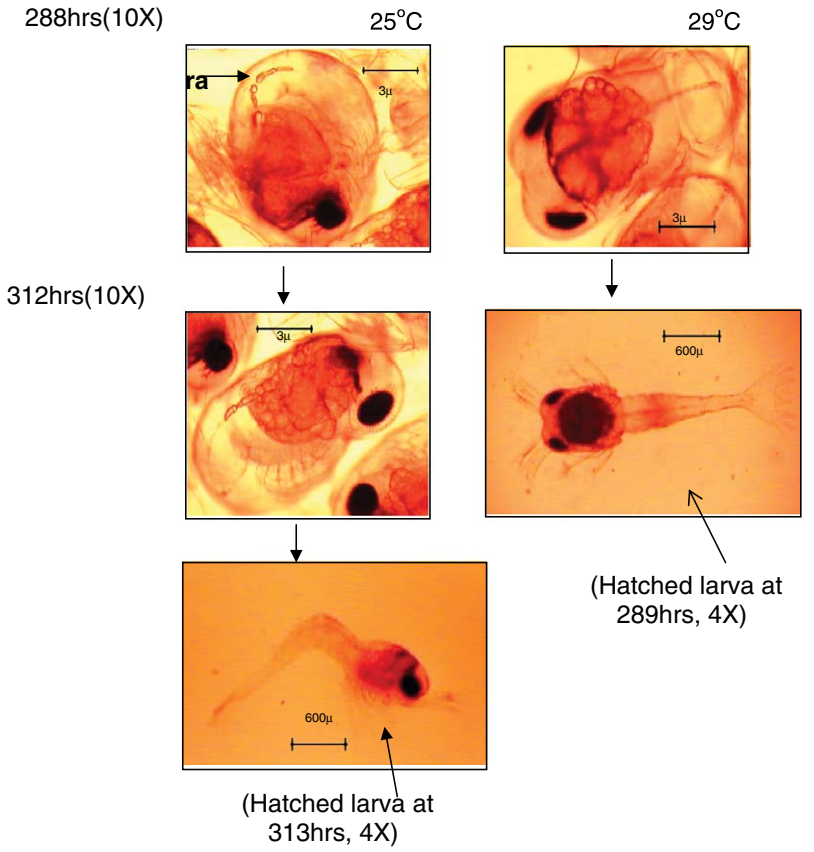


Fig. 1. Development of *M. rosenbergii* eggs incubated at four different temperatures. Sc—superficial cleavage, b—blastocyst, c—compound eye, p—protoplasmic islands, sp—star shaped protoplasmic islands, rp—round protoplasmic islands, dp—degenerated protoplasmic islands, ra—rudimentary alimentary canal, an—antennule.

the statistical analyses were performed via SPSS 11.0 for Windows.

3. Results

3.1. Organogenesis and morphophysiology of eggs

Development of *M. rosenbergii* eggs incubated at four different temperatures is represented as Fig. 1. At 0 h, eggs in all the treatments were in similar phase of development (morula stage) and primodial mesodermal and endodermal cells were visible. After 24 h, the blastocyst was visible in all the four-temperature treatments. Embryos were visible after 48 h in all treatments. However, abnormal embryonic development was evident at 36 °C. At 72 h, the primodial compound eye was visible. At 96 h, a considerable increase in length of the major axis was evident at higher temperatures (29, 33 and 36 °C). At 120 h, star shaped and round protoplasmic islands was visible at 33 and 36 °C, respectively (Fig. 1), and heartbeat was discernible at all temperature treatments. The compound eye with a visible optic lobe was visible at higher temperatures (29, 33 and 36 °C). At 144 h, star shaped protoplasmic islands appeared at lower temperatures (25 and 29 °C). Rudiments of appendages started developing at all acclimation temperatures. At 168 h, paired compound eyes were visible in all treatments. At 192 h, star shaped protoplasmic islands were visible at lower temperatures (25 and 29 °C) while at 36 °C, protoplasmic islands appeared degenerated. After 192 h, complete mortality was noticed at 36 °C (Fig. 2). At lower temperatures, rudiments of appendages were visible. The primodial digestive canal developed in segments as a dotted line in the posterior region, and appeared to originate from primodial hepatopancreas. The primodial brain was visible at the anterior part of primodial hepatopancreas. The

major half axis attained maximum length at the time of hatching. Hatching was initiated by a sudden twitching movement in the posterior region (below the compound eye) by means of the rudimentary antennule. At the time of hatching, telson (or tail) and rudiments of uropod (folded below compound eye) unfolded and the embryonic case was removed from anterior portion by straightening of abdominal segments. Embryos hatched out with a jerky movement and all the anterior appendages in the cephalothoracic region (including walking legs) started moving vigorously. Finally, larvae appeared bilaterally symmetrical (stage 1). Duration of embryonic development decreased with increasing temperatures as indicated by the negative slope in the linear regression equation, $y=-40.075x+348.75$ and $R^2=0.993$ (Fig. 3).

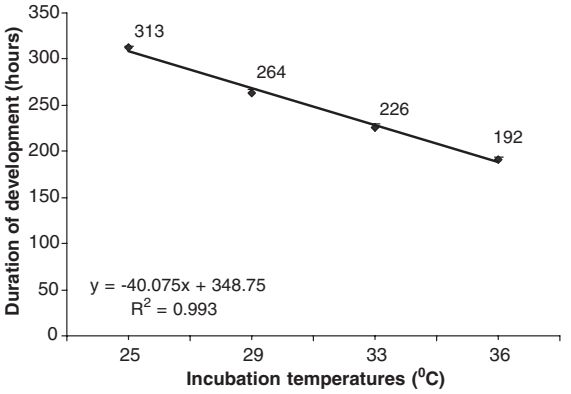


Fig. 3. Duration of embryonic development with increasing incubation temperatures (morula to hatch). Data labels against each incubation temperature indicate the actual duration of development (mean of six values).

3.2. Embryonic morphometry

Data on embryonic morphometry of *M. rosenbergii* incubated at four different temperatures (25, 29, 33 and 36 °C) are represented as Table 1. A significant increase in major axis length was evident at 29, 33 and 36 °C. However at 36 °C, size variation increased with developmental stages, indicating abnormalities until 192 h, after which total mortality was observed. A distinct ($P<0.05$) change in morphometric parameters (major half axis, minor half axis, area and perimeter) was demonstrated at higher temperatures, irrespective of the developmental duration of eggs. Length of hatched embryos increased with increasing incubation temperatures. Interestingly, a rapid rate of increase of major half axis and early hatching was observed at 33 °C.

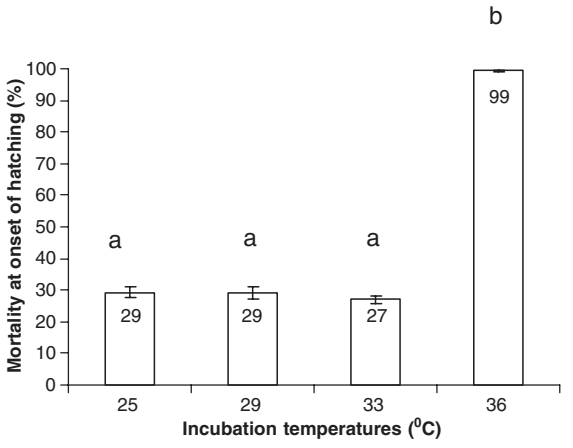


Fig. 2. Percentage mortality of fully developed embryos at the onset of hatching. Data labels inside the bars indicate the actual mortality percentage (expressed as mean of 20 values). Different superscripts (a, b) indicate significant difference amongst different incubation temperatures ($n=20$) (Duncan's multiple range test, $\alpha=0.05$).

4. Discussion

Prior knowledge on the effects of temperature on cultured aquatic organisms, especially during embryogenesis, is a prerequisite for successful hatchery operation and seed production. Embryonic development is a complex process in which cellular differentiation and proliferation occurs simultaneously but at different rates (Gould, 1977; Hall, 1922). Both organogenesis and somatic growth are controlled by enzymatic activities. Embryonic development of ectotherms mainly depends on the differential expression of certain genes and temperature (Ojanguren and Brana, 2003) and the rates of their biological functions are critically dependent on environmental temperature. The effect of temperature on developmental rate is direct and development is faster at higher temperatures. However, this increase of developmental rate of embryos at higher temperatures occurs only within tolerable thermal limits (Cossins and Bowler, 1987; Atkinson, 1996). In the present study, organogenesis and physiological responses of *M. rosenbergii* eggs incubated at different temperatures indicate that higher temperatures increase the rate of embryonic development of *M. rosenbergii* eggs. However, the data on duration of embryonic development in our study was lower than earlier reports (Ogasawara, 1984) as in our investigation; the duration of development was measured from the morula stage. Dark brownish structures appearing on the surface of embryos during the development phase of *M. rosenbergii* are known as protoplasmic islands. Morphology of

Table 1
Effect of incubation temperatures (25, 29, 33 and 36 °C) on various morphological changes (major half axis, minor half axis, area and perimeter) during embryonic development of *M. rosenbergii* eggs until hatching

Parameters	Duration of embryonic development (h)	Acclimation temperatures (°C)			
		25	29	33	36
Major half axis (μm)	0	437.8±5.61^{a}	439.9±5.35^{a}	494.9±6.20^{a}	472.9±6.23^{a}
	48	457.1±7.08^{a}	529.8±9.67^{b}	523.5±5.03^{b}	501.9±3.43^{b}
	96	532.8±6.74^{b}	546.3±6.04^{bc}	544.5±4.68^{c}	577.9±5.82^{c}
	144	535.2±8.08^{b}	618.1±6.98^{b}	585.6±4.39^{d}	619.3±3.23^{d}
	192	570.7±5.31^{c}	564.7±9.51^{c}	609.1±9.23^{e}	615.5±16.63^{d}
	Mean±SE	506.76±9.79^{A}	539.80±11.25^{B}	551.56±8.08^{C}	557.53±11.65^{C}
Minor half axis (μm)	0	414.5±9.39^{a}	407.9±6.70^{a}	423.2±6.49^{a}	450.5±5.88
	48	428.6±2.44^{a}	446.5±9.08^{b}	507.5±4.36^{b}	446.9±3.83
	96	451.1±6.26^{bc}	489.5±4.46^{c}	476.3±5.80^{c}	471.3±3.72
	144	467.3±2.44^{c}	435.1±3.21^{b}	464.9±7.08^{cd}	470.6±5.70
	192	447.5±4.14^{b}	495.6±12.05^{c}	440.8±19.75^{ad}	473.8±19.09
	Mean±SE	441.83±4.18^{A}	454.95±6.96^{B}	462.57±6.90^{B}	462.66±4.51^{B}
Area (×10^{5}) (μm^{2})	0	5.7±0.19^{a}	5.64±0.155^{a}	6.58±0.17^{a}	6.69±0.122^{a}
	48	6.15±0.14^{a}	6.15±0.144^{a}	6.15±0.14^{a}	6.15±0.144^{a}
	96	7.55±0.17^{b}	8.39±0.075^{b}	8.14±0.15^{b}	8.55±0.121^{b}
	144	7.86±0.13^{b}	8.45±0.128^{c}	8.55±0.12^{b}	9.15±0.145^{c}
	192	8.02±0.14^{b}	8.77±0.129^{c}	8.42±0.33^{b}	9.13±0.31^{c}
	Mean±SE	7.06±0.18^{A}	7.48±0.24^{B}	7.57±0.20^{B}	7.94±0.247^{C}
Perimeter (μm)	0	2678±45.91^{a}	2665±36.44^{a}	2893±37.73^{a}	2902±26.92^{a}
	48	2784±33.47^{b}	3078±56.68^{b}	3239±22.93^{bc}	2986±17.46^{a}
	96	3102±35.13^{c}	3265±15.5^{c}	3214±22.11^{b}	3397±103.94^{b}
	144	3157±30.51^{cd}	3358±28.82^{c}	3322±19.88^{cd}	3456±24.23^{b}
	192	3222±28.84^{d}	3340±22.79^{c}	3346±48.47^{d}	3458±53.34^{b}
	Mean±SE	2989±42.77^{A}	3142±50.05^{B}	3203±33.01^{C}	3240±50.75^{C}

Development at time "0 h" is considered from morula stage and parameters were observed until complete hatching or total mortality. Different superscripts (a, b, c) in the same column indicate significant difference amongst different time duration (Duncan's multiple range test, $\alpha=0.05$). Different superscripts (A, B, C) in the same row indicate significant difference ($p<0.05$) (overall mean values) between different incubation temperatures (25, 29, 33 and 36 °C). Values are expressed as mean±SE ($n=6$).

protoplasmic islands of embryos was specific at different incubation temperatures. Embryos with round, oval or star shaped protoplasmic islands demonstrated normal development until hatching. Interestingly, immediately after appearance of degenerated protoplasmic islands, complete mortality was observed at 36 °C. Future isolation and structural analysis of these protoplasmic islands may indicate a functional significance during early development of *M. rosenbergii*. It is evident that heat shock proteins are induced at early developmental phases in response to various physiological stimuli (growth factors, cell differentiation, hormonal stimulation) and under the influence of temperature (Gething and Sambrook, 1992). However, the roles of heat shock proteins and protoplasmic islands in faster development of embryos are yet to be established in *M. rosenbergii*.

Morphometric measurements (Table 1) indicated an early increase in length of the major half axis of embryos at higher temperatures. Finally, length at hatch increased with increasing temperatures and the larval major half axis was highest at 33 °C. However, complete mortality was observed at 36 °C after 17 days, which indicates that incubation at 36 °C is an upper temperature threshold for *M. rosenbergii* embryos. Earlier reports on duration of hatching in *Macrobrachium* at different temperatures indicates that eggs hatch out in 25 days at 26 °C, 20 days at 28–28.5 °C and in 17 days at 32 °C (Ogasawara, 1984). In the present study, embryonic development was assessed after acclimating the mother prawns (carrying newly released eggs in the brood chamber) at the rate of 1 °C per day to the test temperatures and maintained until hatch, as described by Beitinger et al. (2000). A negative slope in the linear regression of development time to hatching, $y=-40.075x+348.75$ ($R^2=0.99$), indicates a strong inverse relation with incubation temperature (Fig. 3).

Our study indicates a direct linear relationship between development rates of *M. rosenbergii* embryos with incubation temperature. Hence, a direct relation between organogenesis and morphological measurements and development was established. A rapid

increase in major half axis length observed at 29 and 33 °C with a concomitant rate of development and earlier hatching. Increase in larval length was observed at higher incubation temperatures indicate that such larvae may develop into dominant prawns, locally known as "shooters". Therefore, incubation temperature may prove vital in producing healthy, high quality prawn seeds for successful prawn farming, by taking advantage of "leap frog pattern" of enhanced growth and overall production. However, this hypothesis needs to be investigated by rearing freshwater prawns from embryos until adult stages at higher temperatures. Our results indicated that increasing incubation temperature reduced the hatching duration of embryos, which may be beneficial in reducing hatchery man-days and the cost of production of prawn seeds. It is evident that 29–33 °C is acceptable for *M. rosenbergii* embryonic development, which is higher than earlier reports of 29–31 °C (Sebastian, 1996). A rise in the optimum temperature for embryonic development over the years may be due to continuous warming in the test region along with a gain of adaptive capability and induced thermal tolerance over the years. This hypothesis needs to be tested at the genetic level.

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