Aquaculture Reports 2 (2015) 132–138

Contents lists available at ScienceDirect

Aquaculture Reports

journal homepage: www.elsevier.com/locate/aqrep

The effect of temperature on the embryonic development of barramundi, the Australian strain of *Lates calcarifer* (Bloch) using current hatchery practices

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ARTICLE INFO

Article history:
Received 18 April 2015
Received in revised form 22 June 2015
Accepted 18 September 2015
Available online 6 October 2015

Keywords:
Lates calcarifer
Hatch
Broodstock
Development
Egg
Temperature

ABSTRACT

Lates calcarifer (barramundi or Asian seabass) has been farmed since the 1970s, yet despite its widespread culture little has been documented on the species' embryonic development and particularly how development relates to temperature. This is particularly the case for the Australian *L. calcarifer* genetic strain. Accordingly, embryonic development of fertilised barramundi eggs incubated at 26, 28, 30, 32, 34 and 36 °C were followed from the time of incubation until hatching and the timing to reach key developmental stages and temperature-induced hatching success established. Eggs incubated at 26 and 36 °C did not survive past the first two hours post-fertilisation. Development of the Australian strain of *L. calcarifer* was observed to proceed similarly to those documented from Asia, however, differences were observed in the timing of major embryonic events among the two strains. Incubation trials showed that eggs maintained at 30 °C had the highest hatch rate (86.7%). The findings of this study are discussed and put in a commercial context with potential future research to further improve practices at the hatchery level.

1. Introduction

Barramundi (*Lates calcarifer*), also known as Asian seabass, is widely distributed in coastal rivers and inshore waters throughout the Indo-West Pacific. In Australia, and increasingly worldwide, *L. calcarifer* is of significant economic importance, supporting both capture/recreational and aquaculture fisheries (Moore, 1982; Dhert et al., 1992). *L. calcarifer* aquaculture began in Southeast Asia and Australia in the 1970s and 1980s, respectively, and has since undergone rapid expansion. The culture success of the species has been attributed to its tolerance to a wide range of culture conditions, high fecundity (300,000 eggs/kg BW), fast growth rate (up to 2 kg in 12 months), firm white flesh and the relative ease by which they can be spawned in captivity (Mackinnon, 1989; Garcia, 1990; Partridge et al., 2008). Despite the widespread culture of *L. calcarifer*, there is a lack of scientific documentation regarding the period of embryonic development from fertilisation to hatch. In particular, the timing involved in specific developmental stages have not been described in the Australian strain of *L. calcarifer*, which are known to be genetically differentiated from Asian populations (Jerry and Smith-Keune, 2013).

Few studies exist on the embryonic development of *L. calcarifer*, with existing descriptions restricted to South East Asian strains and where reports present contradictory evidence with respect to the onset of discrete developmental stages (Maneewongsa and Tattanon, 1982; Kungvankij et al., 1986). Specifically, studies show discrepancies in the timing of the reported development stages past the first cleavage, as well as the hatch time at different incubation temperatures. Such results are inconsistent with previous reports that demonstrate accelerated development of fish eggs with increasing temperature (Hamel et al., 1997). Furthermore, the broodstock used in these reports were wild caught and manually stripped to produce fertilised eggs using the "dry" method. This technique has now been replaced by hormonal treatment of domesticated broodstock, which induces the fish to naturally spawn approximately 35 h after induction (Garcia, 1990; Palmer et al., 1993). Hormonal induction is favoured over dry stripping of gametes because of the significant reduction in handling, reducing the risk of physical damage and stress to the fish and increasing the quality of a given spawn (Palmer et al., 1993; Conte, 2004; Castranova et al., 2005; Stone et al., 2008).

The absence of descriptions on the embryonic development of the Australian strain of *L. calcarifer* when reared under current

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http://dx.doi.org/10.1016/j.aqrep.2015.09.002

aquaculture spawning practices highlights the need for detailed investigation on the ontogeny of this commercially important species. The primary aim of this research was to provide insight into the embryonic development of the Australian strain of *L. calcarifer* eggs produced using commercially relevant spawning protocols. Secondly, in order to identify an optimal temperature range for hatchery culture of *L. calcarifer* we used the thermal regime employed by Maneewongsa and Tattanon (1982) and Kungvankij et al. (1986) to examine the effect of different incubation temperatures on the rate of embryonic development and hatch success of developing *L. calcarifer*. The results may be employed to improve current hatchery techniques and are specifically relevant to domesticated *L. calcarifer*.

2. Materials and methods

2.1. Broodstock maintenance

The Australian strain of *L. calcarifer* broodstock were maintained in a 15,000 L spawning tank within a 31.2 ± 0.9 ppt seawater recirculating system comprised of a bio-filter, two 50 μm bag filters, an 80 W ultraviolet filter and a protein skimmer. Temperature was maintained at 30.5 ± 0.5 °C and the photoperiod was set at 13 h light:11 h dark to mimic summer conditions in North Queensland, Australia. The spawning tank, consistently held seven broodstock, including three females, with an average weight of 7.4 ± 1.3 kg and 9.8 ± 1.9 kg for males and females, respectively. Fish were fed 2% body weight week^{-1} every 2 days at noon with 24 mm commercial feed pellets (Lansy Breed Maturation, INVE Aquaculture).

2.2. Induction and spawning

Broodstock were anaesthetised in 2‰ Aqui-S® solution to minimise handling stress and evaluated for their likelihood of successful spawning based on the following gamete condition parameters; for males, sperm motility greater than 80% once activated with sea water; females, oocytes separated with an average diameter of 400 μm or greater and uniformly spherical. Mature broodstock were then induced to spawn using a single intramuscular injection of luteinising hormone releasing hormone analogue (LHRHa; Aquatic Diagnostic Services International Pty., Ltd.).

2.3. Egg collection and incubation

Fertilized eggs, which are positively buoyant, were collected using a 100 mm PVC pipe, halved lengthways and situated in the spawning tank. The pipe directed the buoyant fertilized eggs into a 200 L egg collector tank containing a 250 μm net. For the description of the normal development of the Australian strain of *L. calcarifer* eggs (see below), the eggs remained at a density of 2000 eggs/L in the egg collector within the broodstock system (30.5 ± 0.5 °C) to not disturb the development of the embryos. For the temperature trial, the eggs were transferred to 1.5 L conical incubator tanks provided with gentle aeration to allow eggs to stay in suspension. Three incubators were allocated per treatment and were held in a water bath composed of a Styrofoam box filled with freshwater maintained at temperature using electric bar heaters with digital thermostat (±0.2 °C) and/or cold water flow. The temperature treatments under which embryonic development was evaluated were 26, 28, 30, 32, 34 and 36 °C. Two thousand eggs were transferred from the egg collector to each of the conical incubator tanks. To reduce initial thermal shock, the eggs were transferred together with 1 L of seawater from the egg collector. The required temperature for each treatment was achieved within 10 min.

2.4. Observations

The developmental stages of eggs were recorded for a single spawn and temperature trials were performed on three consecutive spawns, each one month apart and all hormonally induced as described above. Eggs were sampled every 5 min (n = 50) from each replicate. Eggs were viewed under an Olympus BX53 transmission light microscope fitted with Olympus DP73 camera to record changes in development. All photographs and observations were performed in vivo with a maximum delay of 5 min from sample collection to observation.

2.5. Statistical analysis

The effect of the different incubation temperatures on the time to reach key developmental stages and hatch success was analysed by analysis of variance (ANOVA), which was carried out using Statistica 7.0 (Statsoft Ltd., 2014). Difference between treatment means for the various developmental stages and hatch rates were considered significant at p-value of <0.05. All data was presented as mean ± standard error (SE).

3. Results

3.1. Newly released eggs

The newly released eggs had a diameter of 796 ± 4.3 μm (n = 50) and contained an oil globule with a diameter of 264 ± 2.4 μm. Individual eggs appeared clear, but had a pale orange tint when in mass. The majority of eggs contained multiple oil globules immediately after being released (Fig. 2c), with an average of three oil globules/egg (max. 17) which in some eggs later fused to form one large oil droplet (Fig. 1p).

3.2. Initial development

Ten minutes after fertilisation, the cortical cytoplasm streamed towards the animal pole and formed the blastodisc (Figs. 1a and 2a,b). The one cell stage was reached 30 min post fertilisation (mpf). Although difficult to observe in unfertilized or newly fertilized eggs, the perivitelline space was visible 20 mpf and persisted until time of hatch (Fig. 2a).

3.3. Cleavage period

The first cleavage commenced from one side of the blastodisc (Fig. 1b) and gave rise to two blastomeres of equal size (Fig. 1c). The primary cleavage axis passing between the two blastomeres can be used as a reference line for the next divisions which will operate following an alternation of perpendicular and parallel divisions to the first. The second cleavage, separated in half the first two blastomeres via an axis perpendicular to the first to produce a 2 × 2 equally voluminous arrangement (Fig. 1d). This alternation of cleavage plane was visible until the 32-cell stage (Fig. 1g).

3.4. Blastula period

The conclusion of the seventh cleavage with the 128-cell stage signalled the beginning of the blastula period, which refers to the ball shape of the blastodisc when observed in the animal polar view (Fig. 1h,i). At the 256-cell stage, one and a half hour post-fertilisation (hpf), the yolk syncytial layer (YSL) was discernible between the periblast and the edge of the blastodisc and was clearly visible at the 512-cell stage (Fig. 2j,k).

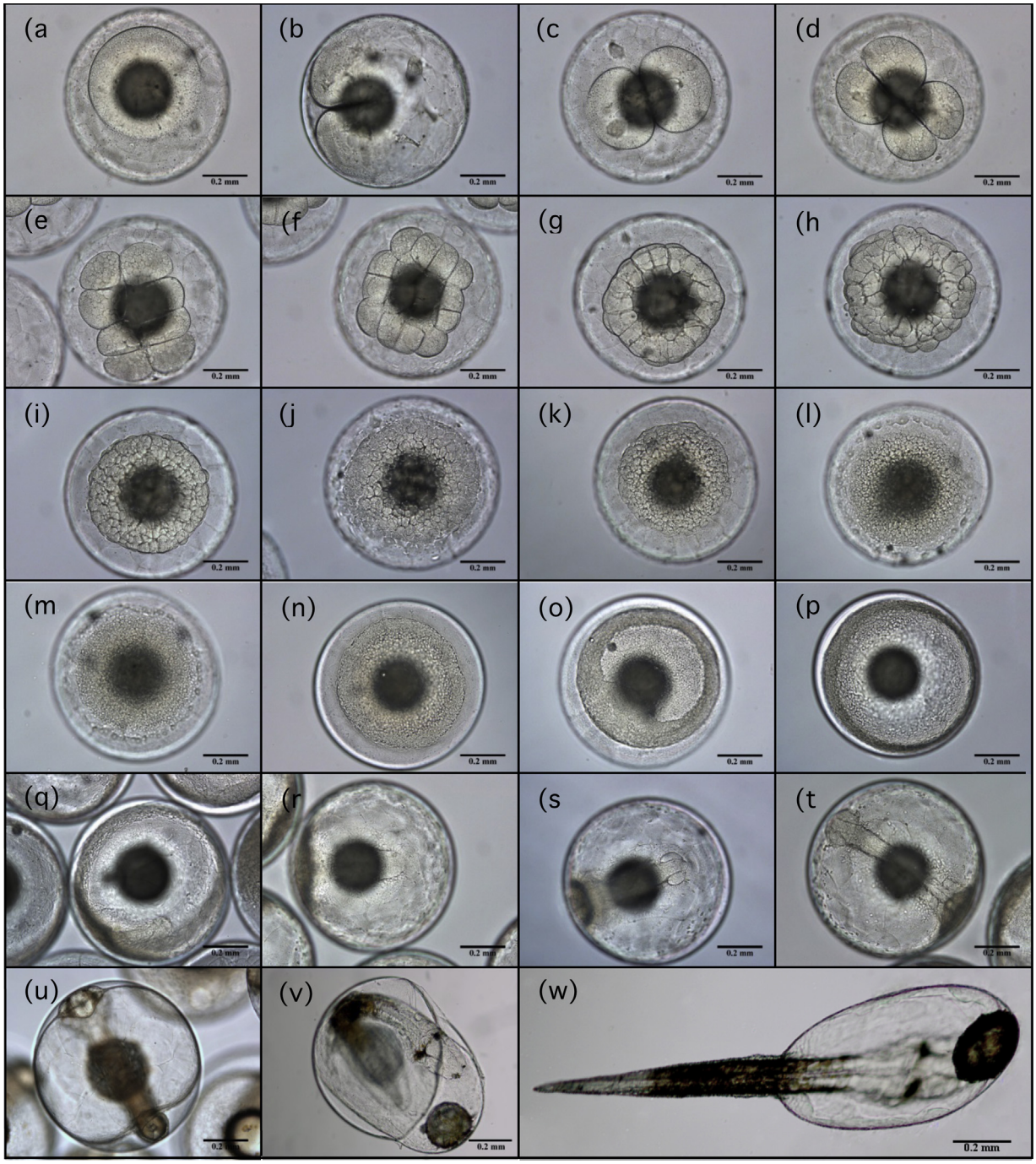

Fig. 1. Developmental stages of the Australian strain of *L. calcarifer* from fertilized egg to newly hatched larvae (top view; developmental time taken from fertilisation): (a) pre-cleavage (29 min); (b) mid first cleavage (37 min); (c) 2-cell (39 min); (d) 4-cell (42 min); (e) 8-cell (51 min); (f) 16-cell (60 min); (g) 32-cell (1 h 09 min); (h) 64-cell (1 h 09 min); (i) 128-cell (1 h 20 min); (j) 256-cell (1 h 31 min); (k) 512-cell (1 h 55 min); (l) 1k-cell (2 h 09 min); (m) high (2 h 39 min); (n) germ ring (3 h 21 min); (o) shield (3 h 36 min); (p) 50% epiboly (4 h 51 min); (q) blastoderm extension (5 h 14 min); (r) embryo elongation (5 h 35 min); (s) optic lobes (5 h 57 min); (t) 15 somites (7 h 10 min); (u) heartbeat (9 h 51 min); (v) hatching (11 h 15 min); (w) newly hatched larvae (1 h post hatch).

3.5. Gastrula period

At 30% epiboly, the rate at which the blastoderm encompassed the yolk cell dramatically slowed to a point that no evolution was visible. This marked the commencement of gastrulation with the germ ring, which appeared once the blastoderm marginal ring thickened by folding in on itself (Figs. 1n and 2l). Approximately 20 min after the formation of the germ ring, convergent morphogenetic cell movements created a localised cell; the shield (Figs. 1o and 2m). This progression in the development of an embryo allows for the primary determination of the anterior–posterior and dorsal–ventral axis. At a stage between 75 and 85% epiboly the length of the embryo equated the diameter of the egg (Fig. 2n–p).

3.6. Segmentation period

The apparition of the first somite furrow marked the transition towards the segmentation period. The rate at which the somite appeared was rapid at first, 6 somites h^{-1}, but slowed down to 4–5 somites h^{-1} once the embryo reached 10 somites (Fig. 2r).

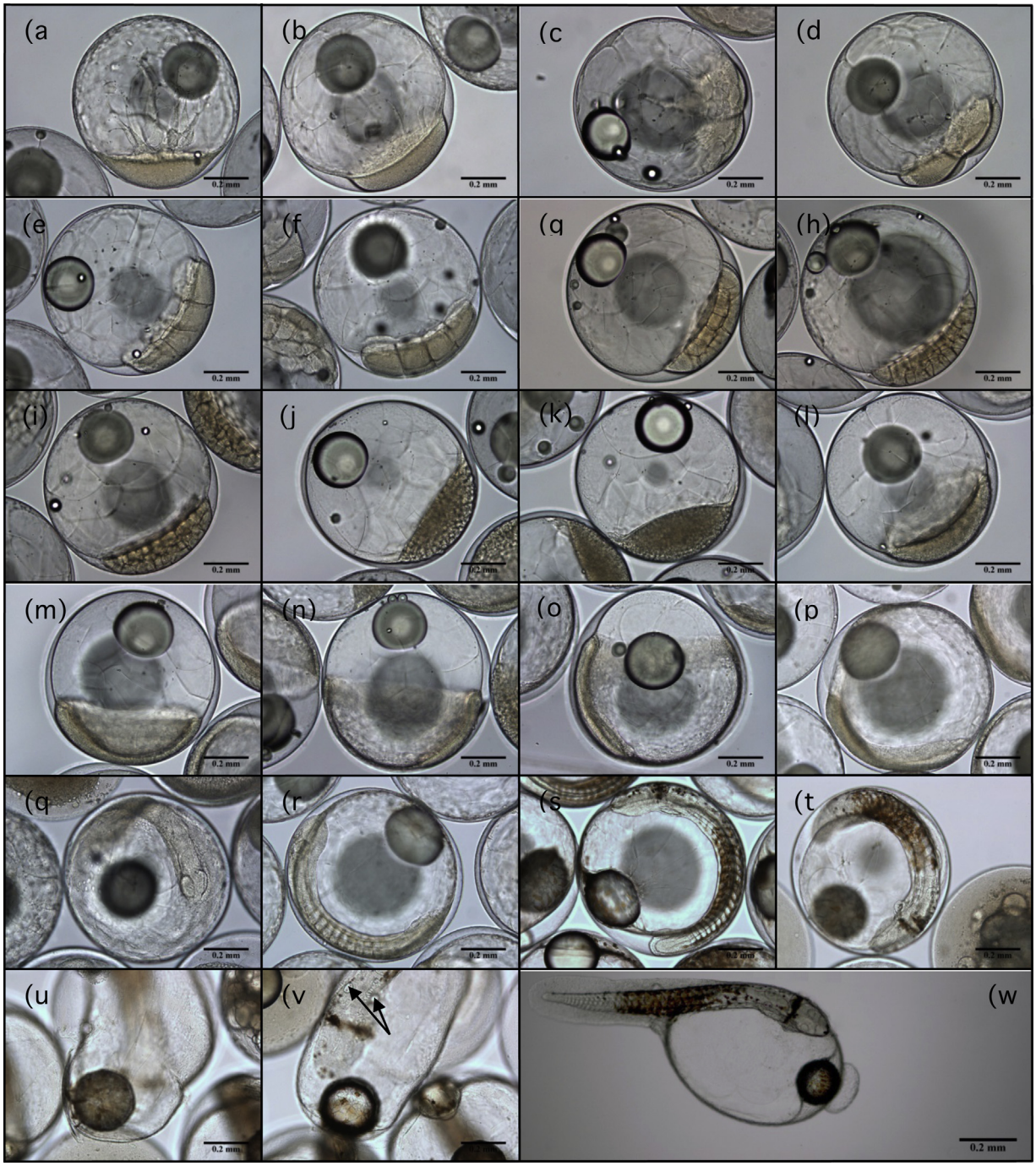

Fig. 2. Developmental stages of the Australian strain of *L. calcarifer* from fertilized egg to newly hatched larvae (side view; the developmental timing is as per Fig. 1): (a) pre-cleavage; (b) mid first cleavage; (c) 2-cell; (d) 4-cell; (e) 8-cell; (f) 16-cell; (g) 32-cell; (h) 64-cell; (i) 128-cell; (j) 512-cell; (k) dome; (l) germ ring; (m) 30% epiboly/shield; (n) 50% epiboly; (o) 80% epiboly; (p) 90% epiboly; (q) blastoderm extension; (r) embryo elongation; (s) optic lobes; (t) 15 somites; (u) hatching; (v) otic vesicles; (w) newly hatched larvae with hatching gland still present.

3.7. Hatching period

At 10 hpf, embryos had developed 20 somites and had a heartbeat of approximately 45 beats^{-1} (Fig. 2s). At this stage the otoliths were distinguishable inside the otic vesicle (Fig. 2v). The heart rate followed a sustained increase to reach 130–150 beats min^{-1}, moments before the embryo hatches. The first embryonic movements began to occur at irregular intervals between 2 and 5 min and were represented by abrupt twitches localised to the posterior part of the embryo. The twitching movements increased in intensity and frequency until facilitated by the chorionase hatching enzyme released from granules within the hatching gland (Fig. 2w), the embryo successfully pierced the weakened chorion (Fig. 2u).

Although in most cases the hatch gland degenerates as the embryo hatches, its retention within the first minutes after hatching was observed on rare occasions (Fig. 2w). The newly hatched larvae drift upside down due to the large buoyant yolk sac and oil globule. At this stage the jaws are locked and prevent any exogenous feeding, thus the yolk sac and oil globule are the only source of nutrition. The oil globule was located anteriorly to the yolk sac (Fig. 2w). The average total length of the newly hatched larvae was 1583 ± 55 μm, with an oil globule diameter of 264 ± 16 μm

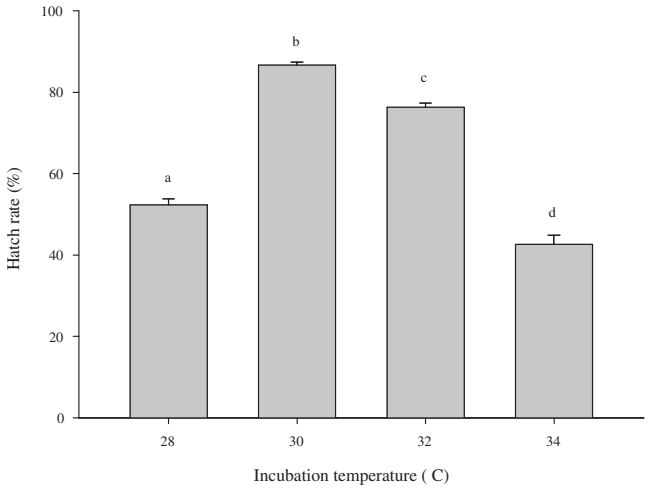

Fig. 3. Hatch rate of the Australian strain of *L. calcarifer* eggs incubated at four temperatures (mean ± SE; $n = 50$). Different superscripts denote significant difference ($p < 0.05$).

and a yolk sac length and height of 981 ± 47 μm and 458 ± 40 μm, respectively.

3.8. Effect of temperature on developmental rate

Cleavage failed to occur in eggs incubated at 26 and 36 °C and resulted in 0% hatch rate; thus the two treatments were excluded from Table 1 and Fig. 3. Incubation temperatures lead to significant differences in time to hatch, with duration of 15:51, 11:57, 10:36 and 10:20 (h:min) for eggs incubated at 28, 30, 32 and 34 °C, respectively (Table 1). No difference in developmental stage was observed between treatments until the 32-cell stage ($p > 0.05$), by which time the 28 °C treatment showed significantly slower development ($p < 0.05$). From the 32-cell stage until the hatching period, the 28 °C treatment induced significantly slower developmental rate in the developing embryo compared to all other treatments ($p < 0.05$). No difference was found between the 30 and 32 °C treatments in time to reach developmental stages that lie between fertilisation and 50% epiboly ($p < 0.05$, Table 1). Other than for the germ ring stage, the eggs incubated at 32 and 34 °C did not show any differences in developmental timing ($p > 0.05$) until the heart beat stage ($p < 0.05$, Table 1). From the heart beat stage through twitching and onwards to hatching, all treatments induced significantly different developmental rates ($p < 0.05$) with the developmental rate positively correlated to the increasing incubation temperature.

3.9. Hatching rate

The hatch rate of the Australian strain of *L. calcarifer* eggs was influenced by temperature, showing a significant difference between all treatments ($p < 0.05$). The lowest hatch rates were recorded for the extreme temperature treatments, with 42.6% and 52.3% for 34 °C and 28 °C treatments, respectively (Fig. 3). The 30 °C treatment resulted in the highest hatch rate of 86.6%, followed by the 32 °C treatment with a hatch rate of 76.3% (Fig. 3).

4. Discussion

The aims of this study were firstly to describe the key embryonic developmental stages of eggs produced by domesticated broodstock of the Australian strain of *L. calcarifer*, and secondly, to examine the influence of different incubation temperatures on the time to reach specific stages of embryonic development. As expected, embryogenesis in the Australian strain of *L. calcarifer* closely resembled that described in Asian sea bass (Maneewongsa and Tattanon, 1982; Kungvankij et al., 1986), although development of the Australian strain of *L. calcarifer* appears to occur faster at similar temperature than that of Asian strains, particularly past the 8-cell stage. In our study, the Australian strain of *L. calcarifer* eggs incubated at 28 °C hatched just under 16 h post-fertilization, compared to 18 and 17.5 h for the Asian strain of *L. calcarifer* incubated at 28-30 °C and 27 °C, respectively (Maneewongsa and Tattanon, 1982; Kungvankij et al., 1986). Interestingly, the Asian strain of *L. calcarifer* eggs incubated at 28–30 °C (Kungvankij et al., 1986) developed slower past the first cleavage compared to when incubated at 27 °C (Maneewongsa and Tattanon, 1982). It is unclear why the eggs developed slower at higher temperature but this could have been influenced by multiple factors including fluctuating temperature during egg incubation and gamete quality of the broodstock used for stripping (Palmer et al., 1993; Castranova et al., 2005; Stone et al., 2008).

The time to reach the 2-cell and 4-cell stage in Kungvankij's et al. (1986) study was 2–8 min faster than for the eggs incubated at 28, 30 and 32 °C in our study. Although, past the 4-cell stage Kungvankij's et al. (1986) reported much slower developmental rate to reach key stages compared to our study. The 2-cell stage was reached even earlier in the study conducted by Maneewongsa and Tattanon (1982) compared to Kungvankij's et al. (1986). Although this fast developmental rate was lost past the first cleavage with occasionally some stages being reached faster compared to Kungvankij's et al. (1986) observations. Another difference between the two previous studies was that regardless of the incubation temperature, the cleavages until the 32-cell stage occurred at regular intervals. The irregularities in cleavage timing were previously observed when the incubation temperature was not adequately maintained in the incubators (personal observation). Eggs and larvae of fish are highly sensitive to fluctuations in water temperature and tend to have narrower thermal tolerance ranges in comparison to their adult stages (Das et al., 2006). The retardation and acceleration effects on embryonic development in fish using low and high temperature treatments, respectively, is well established in many species (Kinne and Kinne, 1962; Pepin, 1991; Hart and Purser, 1995; Hamel et al., 1997) and was also observed in our study.

Although the high and low temperature treatments lead to fast and slow embryonic development, the extreme temperature treatments also resulted in lower observed hatch rates. Similar deleterious effects of incubation temperatures have been reported for multiple fish species, and are thought to occur when temperature treatments that lie outside a species' thermal tolerance range are applied (McCormick et al., 1977; Herzig and Winkler, 1986; Morehead and Hart, 2003; Yang and Chen, 2005). Although *L. calcarifer* can tolerate a wide thermal range (14–40 °C), this species tends to be cultured in water ranging from 22 to 35 °C (Tucker et al., 2002). Katersky and Carter (2005) found that the optimal range of *L. calcarifer* for growth was 27–36 °C. Understanding the effect of temperature during the incubation of the Australian strain of *L. calcarifer* egg on their development is critical for successful hatchery production. Although the factor of interest on development rate in this study was temperature, other abiotic factors including dissolved oxygen, pH may also have significant effects on the organogenesis and somatic growth of fish (Kinne and Kinne, 1962; Johnston et al., 1995; Das et al., 2006; Dhiyebi et al., 2013).

Temperature, especially in ectothermic species, remained one of the main ways to influence embryonic development on a commercial scale and could be a potential tool for hatchery personnel to accelerate or retard the hatching of the Australian strain of *L. calcarifer* eggs. Although, this should be done cautiously because in our study eggs did not survive the 26 and 36 °C treatments and lower hatch rate was observed at 28, 32 and 34 °C compared to

Table 1
Effects of temperature on the rate of development (min) of the Australian strain of *L. calcarifer* embryos from 2-cell stage until hatch (mean ± SE, $n = 50$). Because the eggs incubated at 26 and 36 °C did not survive past 2 hpf, they were not included in the table.

Developmental stage	28 °C	30 °C	32 °C	34 °C
2-cell	40.2 ± 0.0^{a}	39.0 ± 0.0^{a}	39.6 ± 0.0^{a}	37.2 ± 0.0^{a}
4-cell	48.0 ± 0.0^{a}	43.8 ± 0.0^{a}	45.6 ± 0.6^{a}	43.2 ± 0.0^{a}
8-cell	58.8 ± 0.0^{a}	51.6 ± 0.0^{a}	54.6 ± 0.6^{a}	52.8 ± 1.2^{a}
16-cell	72.0 ± 0.0^{a}	63.0 ± 0.6^{a}	61.8 ± 0.0^{a}	60.0 ± 0.6^{a}
32-cell	84.6 ± 0.0^{c}	73.2 ± 0.0^{b}	$70.8 \pm 0.0^{a,b}$	68.4 ± 0.6^{a}
64-cel	103.8 ± 0.6^{c}	82.2 ± 0.0^{b}	$81.0 \pm 0.0^{a,b}$	76.2 ± 0.6^{a}
Germ ring	237.0 ± 0.6^{c}	207.6 ± 1.2^{b}	199.8 ± 0.0^{b}	190.2 ± 0.6^{a}
Shield	317.4 ± 0.0^{c}	223.2 ± 1.2^{b}	$213.6 \pm 0.0^{a,b}$	205.8 ± 0.0^{a}
50% epiboly	355.8 ± 1.2^{c}	298.2 ± 1.8^{b}	$291.6 \pm 0.6^{a,b}$	280.8 ± 1.2^{a}
Optic vesicle	489 ± 1.2^{c}	373.8 ± 1.8^{b}	343.2 ± 0.6^{a}	331.8 ± 0.6^{a}
3 somites	552.6 ± 1.2^{c}	418.2 ± 1.2^{b}	378.0 ± 1.2^{a}	367.8 ± 1.2^{a}
Otic vesicle	762.0 ± 0.6^{c}	585.0 ± 1.2^{b}	535.8 ± 0.6^{a}	530.4 ± 1.2^{a}
Heart beat	822.0 ± 1.2^{d}	621.0 ± 0.6^{c}	567.0 ± 1.2^{b}	550.8 ± 2.4^{a}
Twitching	838.8 ± 1.2^{d}	631.2 ± 0.6^{c}	607.8 ± 0.6^{b}	577.8 ± 1.8^{a}
Hatching	951.6 ± 1.2^{d}	717.0 ± 0.6^{c}	620.4 ± 0.0^{b}	620.4 ± 0.0^{a}

Within the same row the superscripts a, b, c and d indicate a significant difference ($p < 0.05$) among the different treatments.

the 30 °C treatment. Notably, this is the temperature at which the broodstock tank was maintained in this study. As demonstrated for gilthead seabream, *Sparus aurata* and Mississippi silversides, *Menidia audens*, the temperature at which broodstock are held significantly influences the optimal temperature of incubation of the egg (Hubbs and Bryan, 1974; Camus and Koutsikopoulos, 1984). This may be a contributing factor for the discrepancies in the timing of development of *L. calcarifer* eggs that become apparent when comparing the results of this study with those of Maneewongsa and Tattanon, (1982); Kungvankij's et al. (1986).

5. Conclusion

This is the first study to report the effect of incubation temperature on embryogenesis and egg hatch rate in the Australian strain of *L. calcarifer*. The thermal tolerance found in this study for the Australian strain of *L. calcarifer* was 28–34 °C, although the hatch rate was significantly lower for the extreme temperature treatments. The optimal temperature of 30 °C yielded the highest hatch rate and, interestingly, was most similar to the temperature at which the induced broodstock was kept. Although the embryogenesis described in this study resembled the one described by Maneewongsa and Tattanon (1982) and Kungvankij et al. (1986), at similar temperatures, it occurred faster in the Australian strain of *L. calcarifer*. The temperature at which broodstock are kept is known to influence the optimal incubation temperature for eggs of other fish species and is thus an important consideration for future investigations in *L. calcarifer*.

Acknowledgements

The authors would like to express their sincere gratitude to James Cook University and Mainstream Aquaculture Pty., Ltd. for respectively permitting access to microscopes and for the supply of fertilised Australian *L. calcarifer* eggs. Our gratitude is extended to Alyssa Budd for proof reading and her valuable guidance during the writing process of this manuscript.

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