Zygote

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Effects of different temperatures on the embryonic development of the Lebranche mullet *Mugil liza*

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Research Article

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Summary

We herein investigated the influence of temperature on the embryonic development (from fertilisation to hatching) of *Mugil liza* larvae. For this purpose, oocytes (>600 µm) and sperm were obtained from breeding stock at the laboratory of marine fish culture (LAPMAR). After fertilisation, 1200 eggs were distributed in 12 cylindrical experimental units of 400 mL under four different temperatures 18, 22, 26 and 30 ºC, all in triplicate. Every 15 min until hatching, about 10 eggs were randomly sampled in each treatment. The eggs were visualized and photographed, and the classification of embryonic stages was performed. Temperature influenced the main events of the embryonic development of *M. liza*. More accelerated development was observed according to the increase in temperature until the gastrula phase. At temperatures of 22 and 26 °C, embryonic development occurred from fertilisation to hatching of the larvae. In the 18 °C treatment, it was verified that most of the embryos ceased development during the final phase of cleavage and the beginning of blastula formation, while in the 30 °C treatment patterns of embryo malformation were also verified, with erratic divisions of the blastomeres, resulting in irregular cells. Unlike what was observed at a temperature of 18 °C, none of the embryos incubated at 30 °C reached the blastopore closure phase, stopping in the gastrula. The larvae hatched in the treatments at 22 and 26 °C were viable and exhibited intense swimming, with a large amount of reserve material (yolk) and an evident drop of oil.

Introduction

Marine fish farming was the vanguard activity in Brazilian aquaculture (Cavalli and Hamilton, 2007). Despite this, until now, marine fish farming has not yet evolved into an economically important activity in Brazil (Valenti *et al.*, 2021), unlike some countries in Asia and Europe, where marine fish production is consolidated as a perennial activity (Neu *et al.*, 2019). Among the most produced diadromous species are the Atlantic salmon *Salmo salar*, the milkfish *Chanos chanos*, the Japanese eel *Anguilla japonica* and mullets of the genus *Mugil* (FAO, 2022).

Over the years, technological advances, combined with scientific developments on the biological needs of species, have contributed to increased productivity with lower production costs, making aquaculture an economically competitive source of animal protein worldwide (Asche, 2008; Silva *et al.*, 2020; Føre *et al.*, 2022; Owatari *et al.*, 2023; Kaneko *et al.*, 2023).

Currently in Brazil, the Lebranche mullet *Mugil liza* has stood out in experimental cultivations supported by scientific initiatives such as those by Angelo *et al.* (2021a) who verified that the temperature influenced the final phase of embryogenesis, initial development and survival of *M. liza* larvae, while Silva *et al.* (2020) verified the effect of feeding frequency on growth performance, blood metabolites, proximal composition and digestive enzymes of juvenile *M. liza* and recommend feeding juveniles three to five times per day. Castro *et al.* (2019) verified that the supplementation of dietary ascorbic acid between 107 and 216 mg kg^{-1} optimizes the spermatic quality in males of Lebranche mullet. Lisboa *et al.* (2015) tested different salinities and defined 24‰ as the best growth in the cultivation of mullet juveniles in relation to salinities of 0.6 and 12‰. Carvalho *et al.* (2010) determined that a diet containing 35% crude protein for juveniles resulted in greater weight gain, feed intake and higher growth rate, while Okamoto *et al.* (2006) reported that the temperature of 30 ºC is the most suitable for the growth and survival of juveniles.

The Lebranche mullet *M. liza* is a fish of the Mugilidae family that inhabits tropical and subtropical regions and is geographically distributed from Florida (USA) to Argentina (Lemos *et al.*, 2014; Mai *et al.*, 2014). In Brazil, the species has great economic importance, mainly for artisanal fisheries (Morado *et al.*, 2021). The populations are genetically distinct into two groups. One population is located to the north, above the State of Rio de Janeiro in warmer waters, while another population is located to the south, acclimatized to colder waters, even so, during the winter they migrate northwards in search of warmer waters to reproduce (Lemos *et al.*, 2014; Mai *et al.*, 2014). This behaviour of southern populations suggests a great relevance of temperature on reproduction and on the initial development of the species.

Among the various abiotic factors that affect animal physiology, temperature has a great influence, especially in ectothermic animals (Abram *et al.*, 2017). Fish, for example, are not able to maintain a constant body temperature like endothermic animals, which can affect ontogenetic development, especially in the early stages of embryogenesis (Jonsson and Jonsson, 2019).

After fertilisation of the oocytes, embryonic development begins, a sensitive phase in which successive meroblastic cell divisions occur, which in a few hours or days results in a newly hatched larva (Kucharczyk *et al.*, 1997). However, under adverse environmental conditions, where temperatures remain outside the thermal comfort range, embryonic deformation and/or infeasibility of hatching may occur, as well as larval anomaly; as observed for other marine fish species (Herbing, 2002; Donaldson *et al.*, 2008; Mendonça *et al.*, 2020; Angelo *et al.*, 2021a, 2021b; Clarkson *et al.*, 2021).

Considering that the beginning of ontogenetic development is more sensitive to abiotic conditions such as temperature (Martell *et al.*, 2005; Angelo *et al.*, 2021b), We herein investigated the influence of this parameter on the entire embryonic development of Lebranche mullet *M. liza*, from egg fertilisation to larval hatching.

Material and methods

Breeders and experimental site

The study was carried out at the facilities of the laboratory of marine fish culture (LAPMAR) of the Federal University of Santa Catarina (UFSC), located in Barra da Lagoa in Florianópolis-SC. The Lebranche mullet breeders used are part of the first Generation (F1) fish batch produced in captivity. All experiments were carried out with authorisation from the Ethics and Animal Use Committee CEUA – UFSC No. 7385251119.

Obtaining the eggs

For reproduction, the methodology described by Cerqueira *et al.* (2017) adapted to the current laboratory model, in which two male breeders were selected according to size and a female was selected according to oocyte diameter (>600 µm). Breeders were allocated in a 1000 L circular tank, with continuous water flow (salinity 33‰) from the ocean, collected at Mozambique beach Florianopolis, Brazil (27°34′02″S, 48°25′44″W), with thermostat for temperature maintenance (24.5 ± 0.7 °C).

For female specimens (length and weight of 48.0 cm and 1270.0 g), hormonal control of spawning occurred with an intramuscular application of carp pituitary extract (CPE) hormone and another application of Luteinizing Hormone-Releasing Hormone analogues (LH-RHa) (des-Gly10, D-Ala6 LH-RH ethylamid salt acetate hydrate, L4513, Sigma-Aldrich, St. Louis, USA), being a first dose with 20 mg CPE kg fish^{-1}, and after 24 h a second dose with 200 µg LH-RHa kg fish^{-1}. For the male specimens (length and weight of 28.0 cm and 270.0 g), a single dose of 100 µg kg fish^{-1} of LH-RHa was also administered intramuscularly, concomitantly with the second dose of the females (Magnotti *et al.*, 2020).

At 333.7 degree-hours, spawning and natural fertilisation occurred at a temperature of 23.7 °C. The eggs were collected automatically by a fish egg collection and harvester system for aquaculture coupled to the tank with lentic water flow, and transferred to two cylinder-conical tanks (incubators) with a useful volume of 34 L. The incubators were checked periodically (every 15 min), 3 h before the expected spawning time. As soon as the eggs appeared in the incubators, they were distributed to the experimental units.

Experimental design

To monitor the embryonic development of *M. liza* at different temperatures, 12 cylindrical experimental units with a useful volume of 400 mL were used. Each set with three experimental units was placed in a water bath inside a polyethylene tank with water at a constant temperature of 23 °C. The systems were maintained at a temperature of 23 °C until eggs were included. Then the heating thermostats were activated, and the desired temperatures were established. Hundred eggs were distributed in each experimental unit and the treatments were established in triplicate, with four temperatures, 18, 22, 26 and 30 °C.

The experiment was carried out in an acclimatized room with a constant temperature of 18 °C. In each water bath box, a heating thermostat maintained the temperature corresponding to the treatment, and an air diffuser homogenized the water, maintaining the same temperature throughout the water bath. Each of the experimental units was equipped with mild aeration to ensure oxygenation and smooth egg movement. Salinity was maintained at 33‰, pH, oxygen and temperature were measured twice daily. It is noteworthy that pH, oxygen and salinity values followed the comfort range for the species (Okamoto *et al.*, 2006).

Every 15 min until hatching, about 10 eggs were randomly sampled in each treatment. The eggs were visualized and photographed in a stereoscopic microscope (EZ4HD, Leica, Germany), coupled with a camera and software (LAZ EZ 2.1, Leica, Germany). The classification of embryonic stages was performed according to the methodology proposed by Fujimoto *et al.* (2006).

Statistical analyses

The Levene test was used to verify homoscedasticity and the Shapiro–Wilk test to verify the normality of obtained data. The data were submitted to ANOVA and Tukey's test. All tests were performed at a significance level of 5% using the STATISTICA 10.0 software.

Results

Regarding water quality, significant differences ($p < 0.05$) were observed between the treatments. The concentration of dissolved oxygen was significantly lower ($p < 0.05$) in treatments with higher temperatures (Table 1).

The temperature significantly influenced ($p < 0.05$) the events of the embryonic development of Lebranche mullet *M. liza* analyzed in the present study. A more accelerated development was observed according to the increase in temperature until the gastrula phase (Table 2).

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Table 1. Values for water quality variables (mean ± standard deviation) during incubation of Lebranche mullet *Mugil liza* eggs at different temperatures. Different letters indicate significant differences between treatments by Tukey's test

	Treatments			
Variables	18 °C	22 °C	26 °C	30 °C
Temperature (°C)	18.03 ± 0.09^{d}	21.93 ± 0.10^{c}	26.09 ± 0.09^{b}	30.09 ± 0.07^{a}
Oxygen (mg L^{-1})	8.24 ± 0.24^{a}	7.71 ± 0.20^{b}	6.83 ± 0.34^{c}	6.06 ± 0.23^{d}
pH	8.24 ± 0.04	8.29 ± 0.03	8.27 ± 0.02	8.28 ± 0.03
Salinity (‰)	35	35	35	35
Alkalinity (mg L^{-1})	≥150	≥150	≥150	≥150

Table 2. Embryonic development of Lebranche mullet *Mugil liza* subjected to different incubation temperatures. Every 15 min until hatching, about 10 eggs were randomly sampled in each treatment, visualized and photographed under a stereoscopic microscope (EZ4HD, Leica, Germany), coupled with a camera and software (LAZ EZ 2.1, Leica, Germany). Data are related to the time (in hours) for observation of events that occur during embryonic development. (NO) Non-occurrence

	Treatments				
Embryonic development	18 °C	22 °C	26 °C	30 °C	*p* value
Two cells	1.45 ± 0.05^{a}	1.00 ± 0.07^{b}	0.57 ± 0.03^{c}	0.52 ± 0.02^{c}	0.0001
Four cells	1.95 ± 0.05^{a}	1.42 ± 0.03^{b}	1.00 ± 0.03^{c}	0.90 ± 0.04^{c}	0.0001
Eight cells	2.92 ± 0.03^{a}	2.35 ± 0.04^{b}	1.92 ± 0.03^{c}	1.37 ± 0.04^{d}	0.0001
Blastulation	12.87 ± 0.04^{a}	5.87 ± 0.04^{b}	4.92 ± 0.03^{c}	4.82 ± 0.03^{c}	0.0001
Gastrulation	13.95 ± 0.06^{a}	10.37 ± 0.06^{b}	7.95 ± 0.05^{c}	6.90 ± 0.05^{d}	0.0001
Blastopore closure	14.97 ± 0.05^{a}	13.87 ± 0.05^{b}	11.15 ± 0.03^{c}	NO	0.0001
Organogenesis starting	14.87 ± 0.04^{c}	15.46 ± 0.07^{b}	17.00 ± 0.06^{a}	NO	0.0001
Embryonic axis	15.92 ± 0.05^{b}	15.90 ± 0.05^{b}	18.07 ± 0.09^{a}	NO	0.0001
Head and tail differentiation	16.95 ± 0.05^{c}	18.07 ± 0.05^{b}	19.02 ± 0.05^{a}	NO	0.0001
Appearance of somites	17.92 ± 0.05^{b}	21.17 ± 0.09^{a}	14.92 ± 0.05^{c}	NO	0.0001
Optic primordia	28.70 ± 0.10^{a}	20.95 ± 0.07^{b}	13.77 ± 0.06^{c}	NO	0.0001
Appearance of melanophores	32.77 ± 0.06^{a}	27.37 ± 0.06^{b}	15.27 ± 0.07^{c}	NO	0.0001
Heart beats	52.92 ± 0.05^{a}	37.40 ± 0.07^{b}	27.37 ± 0.06^{c}	NO	0.0001
Contraction of the embryo	54.95 ± 0.07^{a}	42.40 ± 0.05^{b}	22.90 ± 0.05^{c}	NO	0.0001
Hatching	NO	50.87 ± 0.05^{a}	36.90 ± 0.05^{b}	NO	0.0001

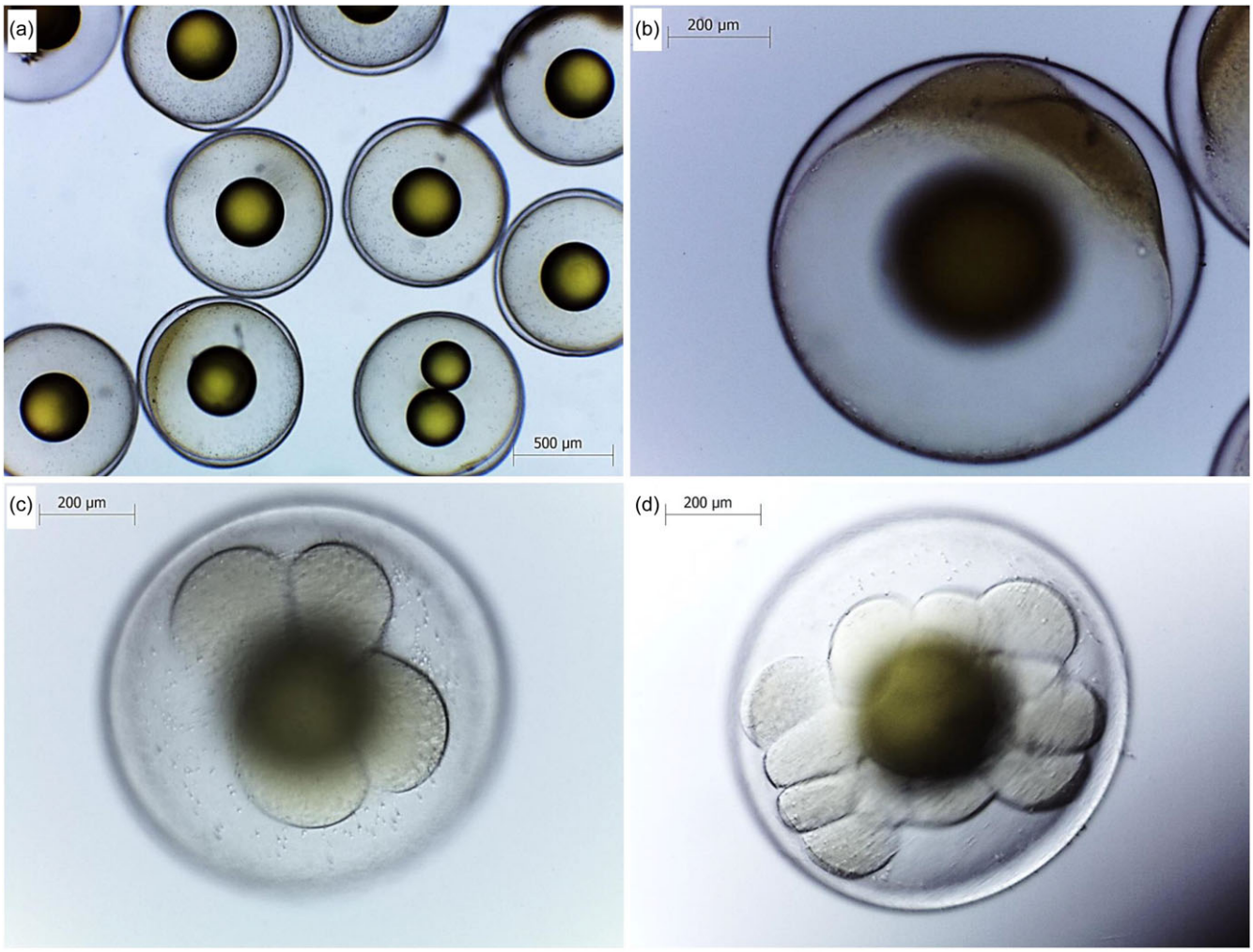

Figure 1. Eggs of Lebranche mullet *Mugil liza* during embryonic development at different temperatures of 18, 22, 26 and 30 ºC. In (a), egg in early stages collected from the incubator at 22 ºC. In (b), first cleavage. First two cell divisions under treatment at 26°C after 0.5 h. In (c), cleavage phase with four cells under treatment at 22 ºC after 1.5 h. In (d), cleavage phase with eight cells under treatment at 26 ºC after 2 h; Gastrulation occurs. Every 15 min until hatching, about 10 eggs were randomly sampled in each treatment, visualized and photographed under a stereoscopic microscope (EZ4HD, Leica, Germany), coupled with a camera and software (LAZ EZ 2.1, Leica, Germany).

At temperatures of 22 and 26 °C, embryonic development occurred from fertilisation to hatching of the larvae (Figures 1–3). In the treatment with a temperature of 18 °C, a stopping embryo development was observed during the final phase of cleavage and the beginning of blastula formation. However, in the embryos that remained in development in this treatment, an anomaly in the growth pattern was observed, presenting body impairments (Figure 4). Finally, there was total mortality of the embryos, without hatching of the eggs.

In the treatment with temperature at 30 °C, patterns of malformation of the embryos were also verified, with erratic divisions of the blastomeres, resulting in irregular cells (Figure 4). Unlike what was observed at a temperature of 18 °C, none of the embryos incubated at 30 °C reached the blastopore closure phase, stopping at the gastrula (Table 2). The larvae hatched in the treatments at 22 and 26 °C were viable and with intense swimming, with a large amount of reserve material (yolk) and an evident drop of oil. The optical system was still underdeveloped and poorly pigmented. The mouth was closed, as well as the anus.

Discussion

Environmental thermodynamics is a fundamental variable that can interfere with the chemical reactions of metabolism by increasing or reducing molecular kinetic energy in the body of ectothermic species. The consequences of temperature variation include molecular impact changes that alter the stability of chemical bonds, affecting enzymatic activity, as well as macro-level changes that can cause behavioural disturbances (Baldisserotto and Val, 2002; Motta *et al.*, 2023). During ontogenetic development, temperature is an abiotic factor that affects several fish species (Alfonso *et al.*, 2021). Indeed, in the present study, we verified that the different temperatures were fundamental for the impairments or normal embryonic development of *M. liza*. Thus, it is important

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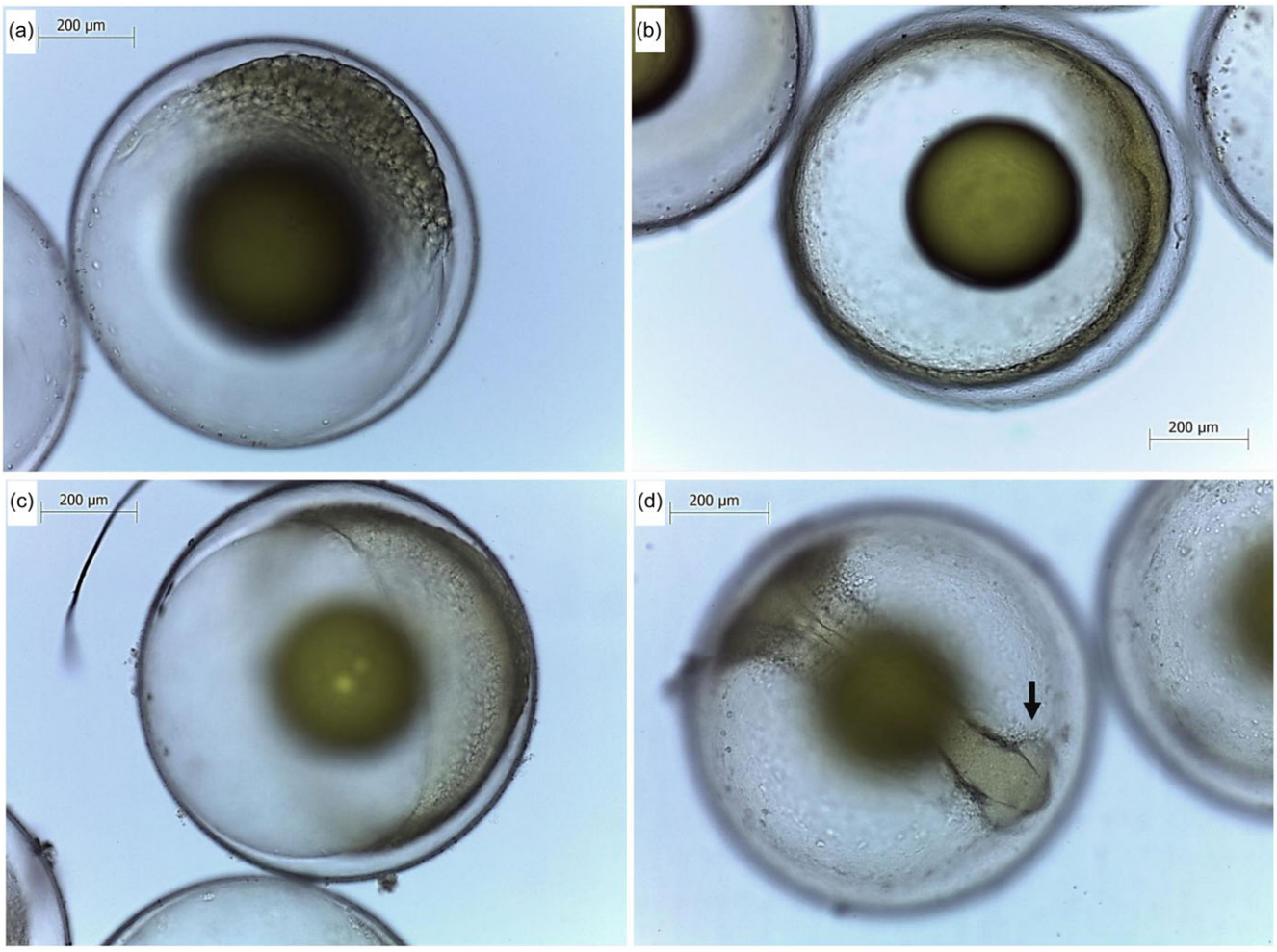

Figure 2. Eggs of Lebranche mullet *Mugil liza* during embryonic development at different temperatures of 18, 22, 26 and 30 ºC. In (a), gastrulation phase occurring with cellular movements that lead to a rearrangement of the blastula cells, resulting in the formation of an embryo, under treatment at 26°C after 8 h. In (b), blastopore formation under treatment at 26°C after 8 h. In (c), blastopore closure phase starting the organogenesis phase (differentiation of head and tail) under treatment at 22°C after 14 h. In (d), emergence of optic primordia under treatment at 26°C after 14 h. Every 15 min until hatching, about 10 eggs were randomly sampled in each treatment, visualized and photographed under a stereoscopic microscope (EZ4HD, Leica, Germany), coupled with a camera and software (LAZ EZ 2.1, Leica, Germany).

that during the embryonic development of altricial larvae such as those of *M. liza* (Whitfield, 1990; Rønnestad *et al.*, 2013), the culture environment presents ideal conditions for the development of the embryo, since at early stages of life these larvae are planktonic, with low functional capacity and unable to ingest food after hatching (Koumoundouros, 1996; Gluckmann *et al.*, 1999; Bone and Moore, 2008).

Several ecological, behavioural and physiological characteristics that emerge later in other stages of development can be influenced by temperature during embryonic development within the egg, including the rate of embryonic development, growth, reproductive distribution and migration and sex determination. Such temperature responses are probably regulated by epigenetic mechanisms, such as Deoxyribonucleic Acid (DNA) methylation, histone modification and microRNAs (Jonsson and Jonsson, 2019).

Results similar to those observed in the present study were described by Mendonça *et al.* (2020) in the pygmy angelfish *Centropyge aurantonotus*, where the incubation time was inversely proportional to the temperature, i.e., in treatments at temperatures at 22°C, egg hatching occurred in a period twice as long as at a temperature at 30°C. The best incubation temperature range was established from 24 to 28 °C to incubate *C. aurantonotus* eggs. Likewise, Petereit *et al.* (2008) when verifying the influence of temperature on the development of Baltic Sea sprat (*Sprattus sprattus*) eggs and yolk sac larvae found that egg development and hatching showed exponential temperature dependence. The authors observed that above 14.7 °C no hatching occurred and hatching success was significantly reduced below 3.4 °C. Furthermore, the time until eye pigmentation, as a proxy for mouth opening, decreased with increasing temperature from 17 days after hatching at 3.4°C to seven days at 13°C, while the larval yolk sac phase was shortened from 20 to 10 days at 3.8 and 10 °C, respectively.

When comparing the same species, Angelo *et al.* (2021a) verified after the blastopore enclosure, that temperatures between 23.2 and 23.9°C resulted in better hatching rate and larval survival of *M. liza*, with more efficient consumption of the yolk sac. However, the researchers did not assess the entire stage of embryonic development. Thus, we can infer that eggs incubated at higher temperatures can accelerate biological processes resulting in shorter incubation and hatching times. According to Boltaña *et al.* (2017), temperature variation, even when small, can generate embryos with malformations.

Several studies have reported the occurrence of malformations in embryos due to the incubation of eggs at temperatures outside

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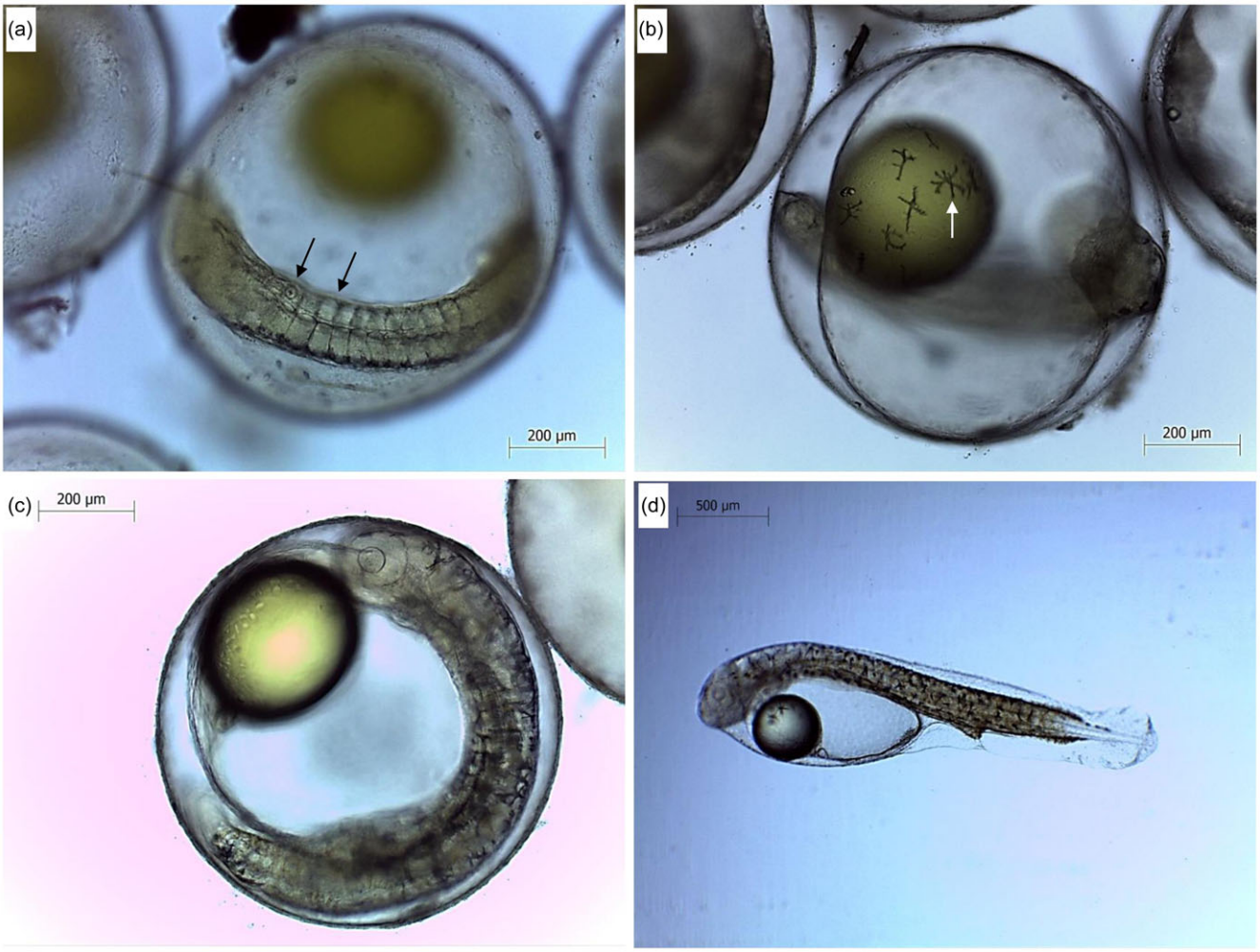

Figure 3. Eggs of Lebranche mullet *Mugil liza* during embryonic development at different temperatures of 18, 22, 26 and 30 °C. In (a), stage of organogenesis characterized by the formed somite and the presence of otolith in the treatment of 22 °C after 21 h. In (b), presence of melanophores, which are cells with a characteristic branched shape, containing melanin granules observed in the treatment at 26 °C after 15.5 h. In (c), pre-hatching larvae at 26 °C treatment. In (d), newly hatched larvae in the treatment of 26 °C after 36 h. Every 15 min until hatching, about 10 eggs were randomly sampled in each treatment, visualized and photographed under a stereoscopic microscope (EZ4HD, Leica, Germany), coupled with a camera and software (LAZ EZ 2.1, Leica, Germany).

the comfort range, both in marine and freshwater species. Okamoto (2004) observed some deformities in newly hatched larvae of Brazilian flounder *Paralichthys orbignyanus* when incubated at temperatures close to 23 °C, outside their comfort zone. The author reported that the time for hatching was inversely proportional to temperature, but the percentage of malformed larvae was higher at extreme temperatures, decreasing at temperatures 20, 23 and 26 °C.

On the other hand, Yang *et al.* (2016) verified the presence of adverse impacts in pompano *Trachinotus ovatus* embryos incubated at temperatures above 33 °C and below 23 °C. According to the authors, the growth of fish kept at 29 and 33 °C was significantly faster than those kept at 23 and 26 °C, while survival at 26 and 29 °C was greater than those kept at 23 and 33 °C. Likewise, the Ribonucleic Acid (RNA)/DNA ratio was higher at 26 and 29 °C than at 33 °C. Furthermore, jaw deformities increased significantly when the rearing temperature exceeded 29 °C, while vertebral deformities were found more frequently at 33 °C than at lower temperatures.

Herein, the malformations that were observed in the 18 °C and 30 °C treatments can be attributed to the tolerance of the species to a specific temperature range, since the temperature in the spawning incubator was set at 23.7 °C, and the most affected treatments were evidenced at 5 °C and +7 °C from this spawning temperature, negatively influencing metabolism and embryonic development.

Indeed, fish are more vulnerable to the variables of the environment in which they live during the initial stages when compared to adults (Rijnsdorp *et al.*, 2009; Ciannelli *et al.*, 2022). According to Jonsson and Jonsson (2014), the initial environment influences the later performance of the fish, i.e., the conditions that the fish face during embryogenesis can cause long-lasting deleterious effects, which can be transmitted to the offspring by the parents, mainly by the mother.

The *Mugil* species naturally spawns in specific periods, when an ideal water temperature is reached in a certain region, acting as an environmental stimulus for reproduction events (Lemos *et al.*, 2017). Thus, it was expected that thermal conditions similar to natural conditions would guarantee the best embryonic development (Karås and Klingsheim 1997). However, the planet has experienced the effects of climate change on the oceans, directly affecting fish. Ongoing climate change is estimated to directly affect aquatic

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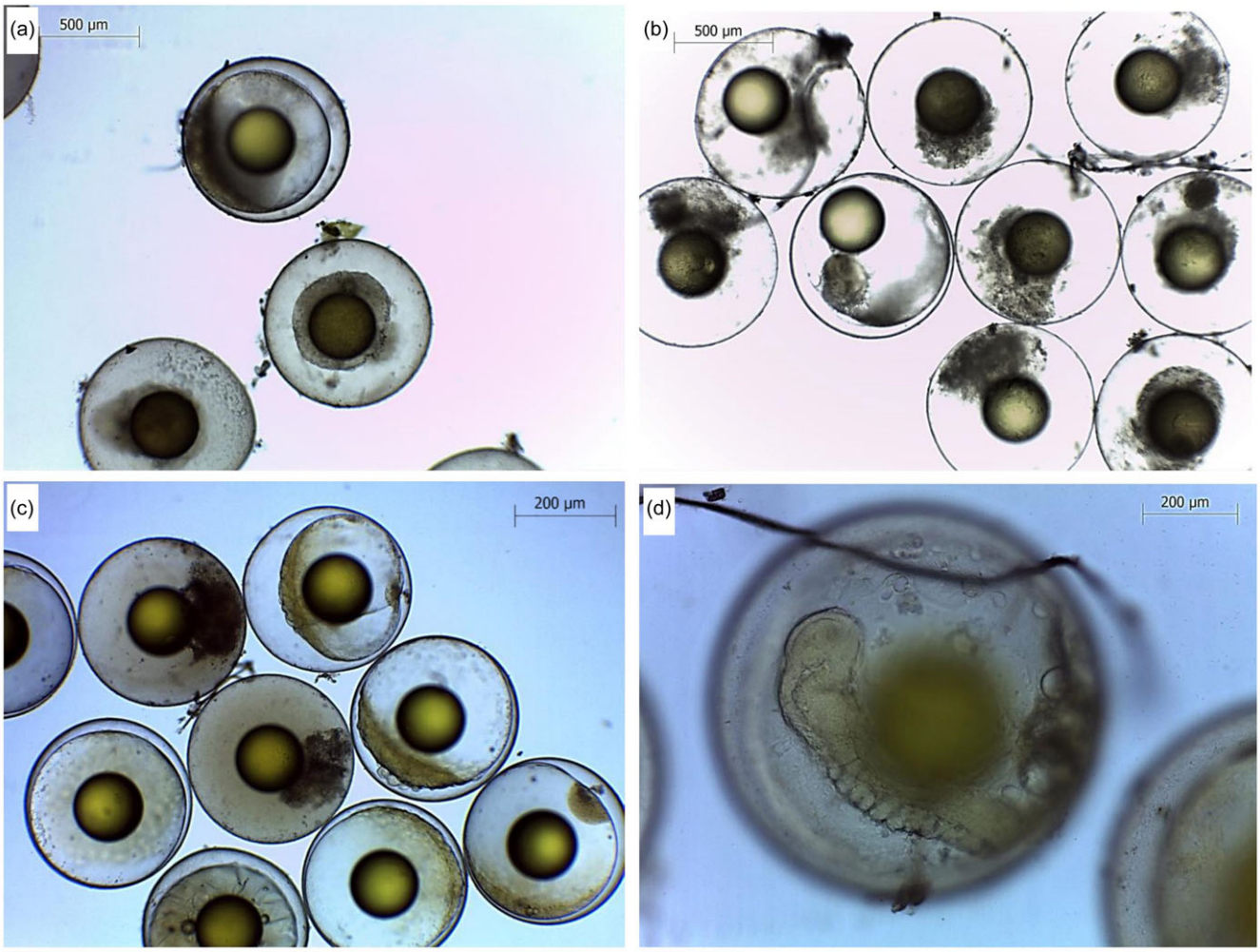

Figure 4. Eggs of Lebranche mullet *Mugil liza* during embryonic development at different temperatures of 18, 22, 26 and 30 ºC. Malformation in fish embryonic development at incubation temperatures of 18 and 30 °C. In (a), non-viable embryo during the blastula phase at 18 °C. In (b), malformed embryos at a temperature of 30 °C, during the initial cleavage phase. In (c) non-viable embryos during the blastula phase at 30 °C. In (d), malformed embryos during the organogenesis phase at 18 °C. Every 15 min until hatching, about 10 eggs were randomly sampled in each treatment, visualized and photographed under a stereoscopic microscope (EZ4HD, Leica, Germany), coupled with a camera and software (LAZ EZ 2.1, Leica, Germany).

organisms during all life stages, contributing to changes in aquatic populations and ecosystem functioning (Pörtner and Peck, 2010).

In conclusion, the temperature influenced chronologically and morphologically the embryonic development of the Mugil liza mullet, causing malformations that resulted in mortalities at temperatures of 18 and 30 °C. According to the results obtained, we recommend that the incubation of *M. liza* eggs be carried out at temperatures between 22 and 26 °C. However, at 26 °C embryogenesis was significantly faster.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0967199424000285

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Competing interests. The authors declare no conflict of interest.

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