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Thermal effects in rainbow trout (*Oncorhynchus mykiss*) F1 embryos (farmed female × wild thermal-resistant male)

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Abstract

The aim of this work was to investigate the response of rainbow trout embryos (*Oncorhynchus mykiss*) (*i.e.*, survival, size at hatching, time to hatching, malformations) to four incubation temperatures (5.8, 8.9, 14.0 and 16.8°C), taking into account the origin of the male parental genome and comparing pure farmed and F1 embryos (farmed female × wild thermal-resistant male). Several consequences of thermal stress were observed: lower accumulated thermal units (ATU) at hatching at high temperatures, and lower survival, shorter hatched free embryos and less-consumed yolk sac at extreme temperatures. The effect of the thermal-adapted male parental genome was shown only in the lower percentage of incompletely hatched free embryos in the F1 families. It appears that to obtain greater modification of thermal performance during early development, the adapted genome of the wild thermal-resistant population has to be included through maternal inheritance, thus producing a stabilized strain selected for domesticity, growth and thermal adaptation.

KEYWORDS
hatching, incubation temperature, malformations, size, survival, zygotic expression

1 | INTRODUCTION

High summer temperature is a problem for rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792), farming in northern Patagonia (Báez *et al*., 2011). The most commonly used incubation temperature in trout farms ranges from 9 to 11°C [Fondo Nacional de desarrollo Pesquero (FONDEPES), 2014]. Temperatures greater than 15°C affect embryonic development, increasing mortality (Aegerter & Jalabert, 2004; Babaheydari *et al*., 2016; Gray, 1928; Pankhurst *et al*., 1996; Turner *et al*., 2007). Moreover, negative thermal effects could be accentuated in trout farms by the common procedure of modifying the photoperiod in order to bring spawning forward, usually up to 3 months, thus obtaining early juveniles that can use the cages earlier in the year (Atasever & Bozkurt, 2015; Groenenberg & Cussac, 1993; Wang *et al*., 2010). Spawning is thus brought forward from early winter to the previous late summer, and so higher water temperature (near 20°C) comes into play during the incubation phase.

During early life, stress conditions have a negative effect on characteristics such as reproductive performance and growth (Estay *et al*., 1995; Jobling *et al*., 1998; Power, 1980). The incidence of skeletal anomalies could be considered an indicator of the quality of rearing conditions, as these anomalies are thought to be due to the inability of homeostatic mechanisms to compensate for environmentally induced stress (Boglione *et al*., 2014). Comparison between thermal-adapted and normal rainbow trout lines showed a better hatching rate and higher upper lethal temperature for the thermal-adapted embryos when subjected to high temperatures (Ineno *et al*., 2005). However, the creation of thermally resistant trout stocks must be carried out with caution, so as not to disturb wild population genetics by bringing about unintentional alterations to genetic lines (Crozier *et al*., 2019). Fish escapes from trout cages and their undesirable environmental effects are well documented (Cussac *et al*., 2014; Nabaes Jodar *et al*., 2017, 2020). Moreover, exotic trout and chars introduced into Northern Patagonia are in decline because of global warming (Aigo

et al., 2008, 2014), which in terms of nature conservancy is an unexpected positive side effect that should not be disturbed.

Some cases of rainbow trout adaptation to high temperature have been found in Australia (farmed strain; Molony *et al*., 2004; Chen *et al*., 2015), Northern Patagonia (Valcheta wild strain; Crichigno *et al*., 2018; Crichigno & Cussac, 2019), southwest Idaho (wild strain; Oku *et al*., 2014) and California (wild strain; Verhille *et al*., 2016; Pearse & Campbell, 2018). Severe thermal exposure in south-western Australia has produced a line of hatchery-reared *O. mykiss* (Molony *et al*., 2004; Morrissy, 1973) that swim and feed at 26°C and retain 50% of their peak aerobic capacity at 25°C (Chen *et al*., 2015). The parental populations of thermally tolerant Australian and Patagonian strains were transplanted from California at the beginning of the 20th century for recreational fishing (Crichigno *et al*., 2018; Verhille *et al*., 2016). Results from Crichigno *et al*. (2018) showed that a single pooled rainbow trout F1 stock (wild thermal-resistant Valcheta male × farmed female), reared under standard hatchery conditions (9–11°C) and selected for growth and thermal preference, presented stronger juvenile thermal preference and greater thermal tolerance than the stock currently being farmed. This cross was selected due to the availability of semen of Valcheta males in autumn and the autumn spawning of females from the Centro de Salmonicultura, Bariloche (CENSALBA). Crichigno and Cussac (2019) showed that thermal tolerance varied within unselected F1 families. When these juveniles were acclimated to 20.5°C over *c*. 109 days, them they preferred a mean temperature of 20.2 ± 0.2°C, so it appears that simple selection by growth could be all that is necessary before beginning the process of introducing these families into farmed lines. It therefore appears that thermal preference and tolerance are heritable. However, all the studied individuals (F1 and farmed) were incubated at normal temperatures (9–11°C).

The aim of this work was to determine the response of rainbow trout embryos (*i.e*., survival, size at hatching, time to hatching and malformations) to different incubation temperatures, considering the origin of the male parental genome and comparing pure farmed families with F1 (farmed female × wild thermal-resistant male) ones.

2 | MATERIALS AND METHODS

2.1 | Families

Twenty-five families (Table 1) were obtained from five 3+- and 4+-year-old females, two males from CENSALBA and three males obtained 2 years before from Valcheta stream (Crichigno *et al*., 2018). The brood-stock was fed on a commercial diet at 1% body weight per day, and all adult fish manipulation was performed under anaesthesia (0.1 g l^{-1} benzocaine).

Ova from each female were allocated to one of five groups (40–50 ml of dry ova in each) and fertilized with 0.25 ml of semen.

TABLE 1 Initial (0 ATU) number of eggs in each group, origin of mothers and fathers, and incubation temperatures

	Mothers	Fathers				
	CENSALBA	CENSALBA		VALCHETA		
Incubation temperature (°C)		M	N	O	P	Q
5.8	A	131	95	185	172	133
8.9		120	133	159	161	144
14.0		149	139	182	186	165
16.8		145	138	150	179	141
5.8	B	114	124	111	123	119
8.9		96	166	103	103	117
14.0		126	127	102	116	112
16.8		129	125	122	144	127
5.8	C	171	171	158	164	177
8.9		153	173	150	181	172
14.0		165	154	166	164	168
16.8		162	181	139	174	172
5.8	D	139	138	145	148	139
8.9		100	160	182	175	161
14.0		183	169	112	158	152
16.8		184	171	136	144	97
5.8	E	113	112	106	131	107
8.9		151	99	131	135	102
14.0		124	128	119	119	106
16.8		164	100	141	101	128

Eggs were hydrated and each family was divided into four groups and placed in bags in four 200 l aerated aquaria. The initial temperature of each aquarium (8.8°C) was maintained overnight and then modified by 1° per day until the desired temperature for each of the four treatments was reached: (a) room temperature (mean = 5.8, range 3.2–8.1°C), (b) suggested incubation temperature (mean = 8.9, range 5.1–10.9°C), (c) temperature higher than suggested (mean = 14.0, range 11.9–15.5°C) and (d) high temperature, not recommended for embryonic development (mean = 16.8, range 14.0–17.9°C) (Figure 1).

2.2 | Time to hatching

Time was considered as days after fertilization (DAF). Accumulated thermal units (ATU; *i.e.*, the cumulative product of mean daily temperature records, expressed as Celsius degrees and DAF) were considered a proxy for degree of development (Fuiman *et al.*, 1998). Ontogenetic periods, namely embryo, free embryo, alevin (larval vestige), juvenile and adult, were defined by fertilization, hatching, first feeding, metamorphosis and sexual maturation, respectively (Balon, 1990, 1999).

At 150 ATU each group was transferred from its incubation bag to a shallow tray made with a grid of rigid plastic netting (mesh size = 1 mm) in the same aquarium. Each group was randomly placed on the grid. Each 200 l aquarium had an aerator and a water circulation pump, and these devices were arranged to ensure a continuous bottom-up flow of water. In each aquarium 30% of the total volume of water was replaced every 48 h. Water quality was maintained within optimal breeding ranges (dissolved O_2 = 8.30 mg l^{-1}, pH = 7.25–7.98).

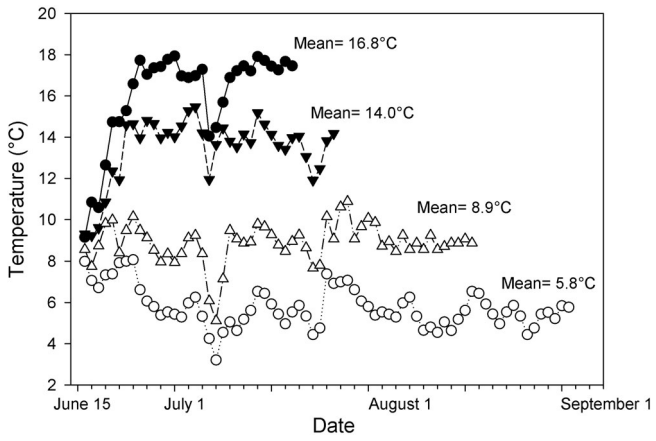

FIGURE 1 The initial temperature of each aquarium (8.8°C) was modified by 1° per day until the desired temperature for each of the four treatments was reached: room temperature (mean = 5.8, range 3.2–8.1°C), suggested temperature for incubation (mean = 8.9, range 5.1–10.9°C), temperature higher than suggested (mean = 14.0, range 11.9–15.5°C) and high temperature, not recommended for embryonic development (mean = 16.8, range 14.0–17.9°C)

2.3 | Survival, size and embryo malformations

Dead embryos and malformed free embryos were removed and counted at 150, 220, 320, 400 and 490 ATU. All deformed free embryos observed were sacrificed with an excess of benzocaine and preserved in 70% ethanol for identification of deformities under stereomicroscope (64×). The beginning of hatching was recorded for each family and treatment, and newly hatched free embryos (one per family and treatment, n = 100) were sacrificed with an excess of benzocaine, preserved in 70% ethanol and measured (standard length, depth and length of yolk sac). At 490 ATU all remaining free embryos were sacrificed with an excess of benzocaine, preserved in 70% ethanol, counted and discarded.

2.4 | Statistics

Percentage data were transformed using angular transformation ($Y = \arcsin((X \times 100^{-1})^{0.5})$) in order to satisfy normality and variance homogeneity assumptions. Homogeneity was tested with the Levene test. Analysis of variance tests (ANOVA) were performed. When normality or variance homogeneity assumptions failed, comparisons were made using the Mann–Whitney or Kruskal–Wallis tests and pairwise comparisons. Pairwise multiple comparison procedures (P < 0.05) were performed using the Holm–Sidak method for ANOVA or Dunn's method for the Kruskal–Wallis test.

3 | RESULTS

3.1 | Survival

Survival data recorded at 150, 220, 320, 400 and 490 ATU were compared between incubation temperatures, fathers and mothers (Table 2). For most of the ATU values, significant differences were observed between temperatures and between mothers, but not between fathers. Significantly lower survival for the extreme temperatures (5.8 and 16.8°C) was observed (Table 2 and Figure 2).

Time to hatching.

The time to hatching (DAF) depended on incubation temperature (ANOVA, N = 100, F = 1473.075, P < 0.001) but not on the maternal (N = 100, F = 0.088, P = 0.986) or paternal (N = 100, F = 0.192, P = 0.662) contribution to the embryo. Moreover, the relationship between time to hatching and incubation temperature (IT) was cubic ($DAF = 114.052 - 13.306IT + 0.590IT^2 - 0.009IT^3$, with P < 0.001 for each coefficient; Figure 3) and, accordingly, the number of ATU at the beginning of hatching differed significantly between incubation temperatures (Kruskal–Wallis one-way analysis of variance on ranks H = 78.964, P < 0.001). Dunn's method (P < 0.05) showed that the number of ATU at the beginning of hatching for embryos incubated at 5.8 and 8.9°C was higher than those for the embryos incubated at 14.0 and 16.8°C (Figure 3).

TABLE 2 Embryonic survival (%) at different ATU, regarding temperature incubation and origin of fathers and mothers

Survival at	Temperature (N = 4), F/P or H/P	Father (N = 2)	Mother (N = 5), F/P or H/P	N=
150 ATU	H = 8.850 with 3 degrees of freedom/P = 0.031	N.S.	H = 26.721 with 4 degrees of freedom/P = <0.001	100
	8.9 *vs.* 5.8°C			
220 ATU	N.S.	N.S.	H = 28.818 with 4 degrees of freedom/P = <0.001	100
320 ATU	H = 3.804/P = 0.013	N.S.	H = 9.442/P < 0.001	100
	14.0 *vs.* 16.8°C			
	8.9 *vs.* 16.8°C			
400 ATU	H = 3.435/P = 0.020	N.S.	H = 9.557/P < 0.001	100
	14.0 *vs.* 16.8°C			
490 ATU	H = 3.462/P = 0.019	N.S.	H = 9.490/P < 0.001	100
	14.0 *vs.* 16.8°C			

Note. Significant differences (ANOVA F or Kruskal–Wallis H) and all pair-wise multiple comparison procedures (Holm–Sidak method or Dunn's test, P < 0.05) are indicated. N.S., nonsignificant differences.

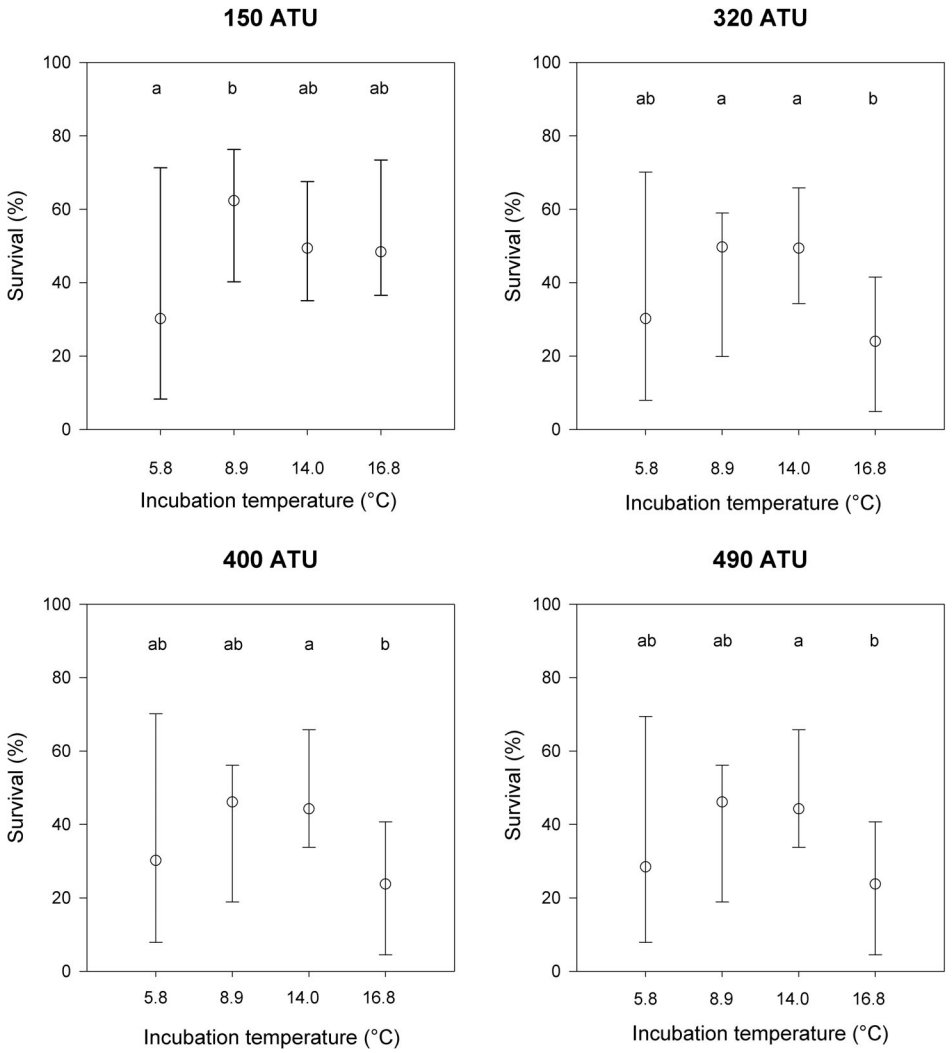

FIGURE 2 Survival (%) at 150, 320, 400 and 490 ATU (the ATU values with significant differences between incubation temperatures). Median and quartiles are indicated. Different letters imply significant differences (Table 2)

3.2 | Size of newly hatched free embryos

The standard length of newly hatched embryos varied with incubation temperature (Kruskal–Wallis H = 84.585, P < 0.001). Dunn's method showed that embryos incubated at 5.8 or 8.9°C were longer than those incubated at 14.0 or 16.8°C, and embryos incubated at 14.0°C were longer than those incubated at 16.8°C (P < 0.05; Figure 4).

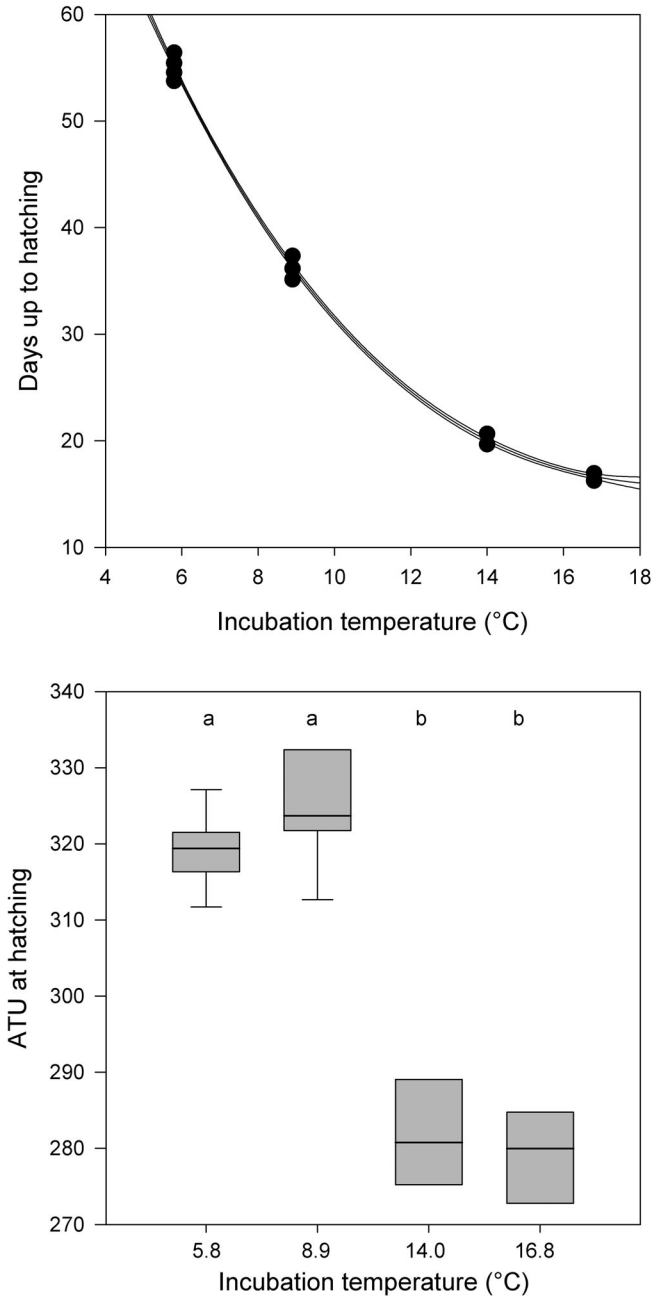

FIGURE 3 Time to hatching (DAF) *versus* incubation temperature. Grade 3 polynomial line and 95% confidence interval are indicated (top panel). ATU (day. °C) at the beginning of hatching of each family, for embryos incubated at different temperatures. Median, quartiles, 5% and 95% percentiles are indicated. Different letters imply significant differences (bottom panel)

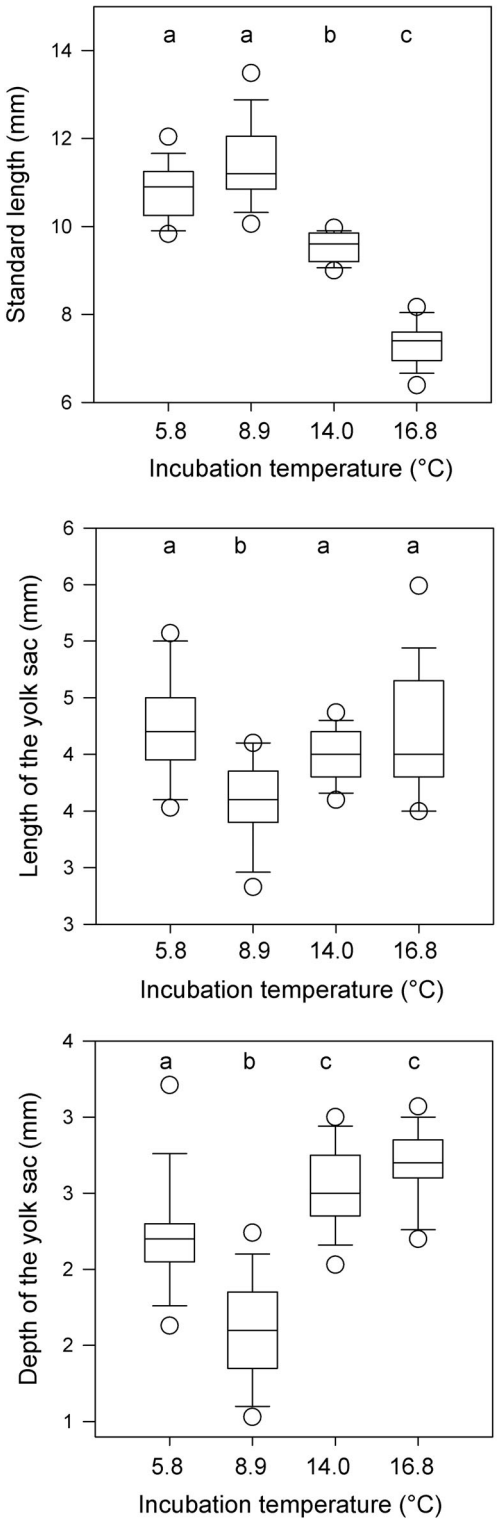

FIGURE 4 Measurements of newly hatched embryos *versus* incubation temperature: standard length (mm), length of the yolk sac (mm) and depth of the yolk sac (mm). Median, quartiles and data outside (outlier) 5% and 95% percentiles are indicated. Different letters imply significant differences

The length of the yolk sac of the newly hatched embryos presented differences between incubation temperatures (Kruskal–Wallis $H = 29.234$, $P < 0.001$). Dunn's method showed that the length of the yolk sac of newly hatched embryos incubated at 8.9°C was shorter than in those incubated at 5.8, 14.0 and 16.8°C (Figure 4).

The depth of the yolk sac of newly hatched embryos also showed differences between incubation temperatures (Kruskal–Wallis $H = 64.605$, $P < 0.001$). Dunn's method revealed that the yolk sacs of newly hatched free embryos incubated at 5.8°C were deeper than in those incubated at 8.9°C, and the yolk sacs of those incubated at 14.0°C or 16.8°C were deeper than in those incubated at 5.8 or 8.9°C ($P < 0.05$; Figure 4).

TABLE 3 Analyses of rainbow trout embryonic malformations (%) by incubation temperature and by the origin of fathers

	Malformed embryos	Micro-embryos	Broken yolk-sac	Incompletely hatched embryos	Kyphosis	Yolk-sac edema	Cyclops	Small lower jaw
Origin of male Mann–Whitney *U*				1037				
P =				0.010				
Temperature Kruskal–Wallis *H*	31.15	20.77	27.08		20.30	11.25	9.18	12.21
Degrees of freedom	3	3	3		3	3	3	3
P =	0.000	0.000	0.000		0.000	0.010	0.027	0.007

Note. Only variables with significant differences are indicated.

No significant differences were found between fathers or between mothers in terms of standard length, length or depth of yolk sac ($P > 0.05$).

3.3 | Embryo malformations

Several variables depended on incubation temperature (Table 3). It is noteworthy that for at least four variables (the percentage of malformed embryos, broken yolk-sac, kyphosis and micro-embryos) the highest temperatures (14.0 and 16.8°C) were related to a higher percentage of malformations (Dunn's method, $P < 0.05$; Figure 5).

The origin of fathers could be distinguished only slightly, but significantly, in the percentage of incompletely hatched free embryos (Mann–Whitney $U = 1037$, $P = 0.01$; Table 3), with fewer malformations in the F1 families (Figure 6). Differences between CENSALBA females regarding the percentage of Siamese twins (joined by a single yolk sac) were also found [chi-squared = 39.12, degrees of freedom (d.f.) = 24, $P = 0.027$].

4 | DISCUSSION

In this work, the hypothesis that a thermal-resistant male parental genome has a beneficial effect on rainbow trout embryos subjected to thermal stress was evaluated. Several consequences of thermal stress in rainbow trout embryos were observed here: lower survival in agreement with Ineno *et al.* (2005) and Dahlke *et al.* (2016), at extreme temperatures (5.8 and 16.8°C) which lie outside the recommended range for incubation of the species (9–11°C; FONDEPES, 2014), in agreement with Ineno *et al.* (2005) and Dahlke *et al.* (2016), a nonlinear relationship between time to hatching and incubation temperature, and, in consequence, lower ATU at hatching at higher temperatures (see Fuiman *et al.*, 1998), shorter newly hatched embryos, in agreement with Lindsey *et al.* (1984), and less-consumed yolk sac at extreme temperatures.

The highest survival rate was found at 8.9 and 14°C, the latter temperature being higher than recommended, and very close to the temperature at which several authors noted a significant decrease in survival (Aegerter & Jalabert, 2004; Babaheydari *et al.*, 2016; Gray, 1928; Pankhurst *et al.*, 1996; Turner *et al.*, 2007). A similar result was obtained by Ineno *et al.* (2005) using a strain selected for high temperature.

The nonlinear dependence of time to hatching on incubation temperature was clear. Lower ATU at hatching and shorter newly hatched free embryos were observed at higher temperatures, in agreement with Lindsey *et al.* (1984) and (Penney *et al.*, 2018), but differences regarding parental origin were not observed, in contrast to the strong maternal effects found by Penney *et al.* (2018).

Evidence of the effect of a different (wild, thermal-adapted) male parental genome can be identified here only in the lower percentage of incompletely hatched embryos in the F1 families, in agreement with the lower incidence of complex malformations in F1 than in farmed families observed by Crichigno and Cussac (2019). This difference in the percentage of incompletely hatched embryos could have several causes, *e.g.*, the functionality of the hatching enzyme, the biochemical characteristics of the vitelline envelope or embryo movement (Kunz, 2004). Underlying these causes, variations in degree of heterozygosity or specific mutations could be involved (Boglione *et al.*, 2014; Danzmann *et al.*, 1986; Gislason *et al.*, 2010). In particular, the incomplete hatching of embryos, with the head and yolk sac remaining encapsulated within the vitelline envelope, has been depicted as a consequence of acid stress by Sayer *et al.* (1993), but here a stable pH was maintained throughout the experiment. The high percentage of incompletely hatched embryos in CENSALBA families at the highest and lowest temperatures could be an indicator of thermal stress, and it is striking that F1 families, in agreement with Ineno *et al.* (2005), showed higher percentages of incompletely hatched embryos only at the lowest temperature (Figure 6). The general absence of significant differences between CENSALBA and F1 families observed here could be expected as a consequence of late zygotic genome activation (Figueroa *et al.*, 2018; Lindeman & Pelegri, 2010).

Previous studies (Crichigno *et al.*, 2018; Crichigno & Cussac, 2019) showed that both the preferred temperature and thermal tolerance of Valcheta juveniles and thermally selected F1 were significantly higher than those of CENSALBA, and the average preferred temperatures of Valcheta and selected F1 juveniles were higher than the 95% confidence interval of available reference data for rainbow trout. F1 juveniles, reared under standard hatchery conditions and selected for growth and thermal preference, presented both

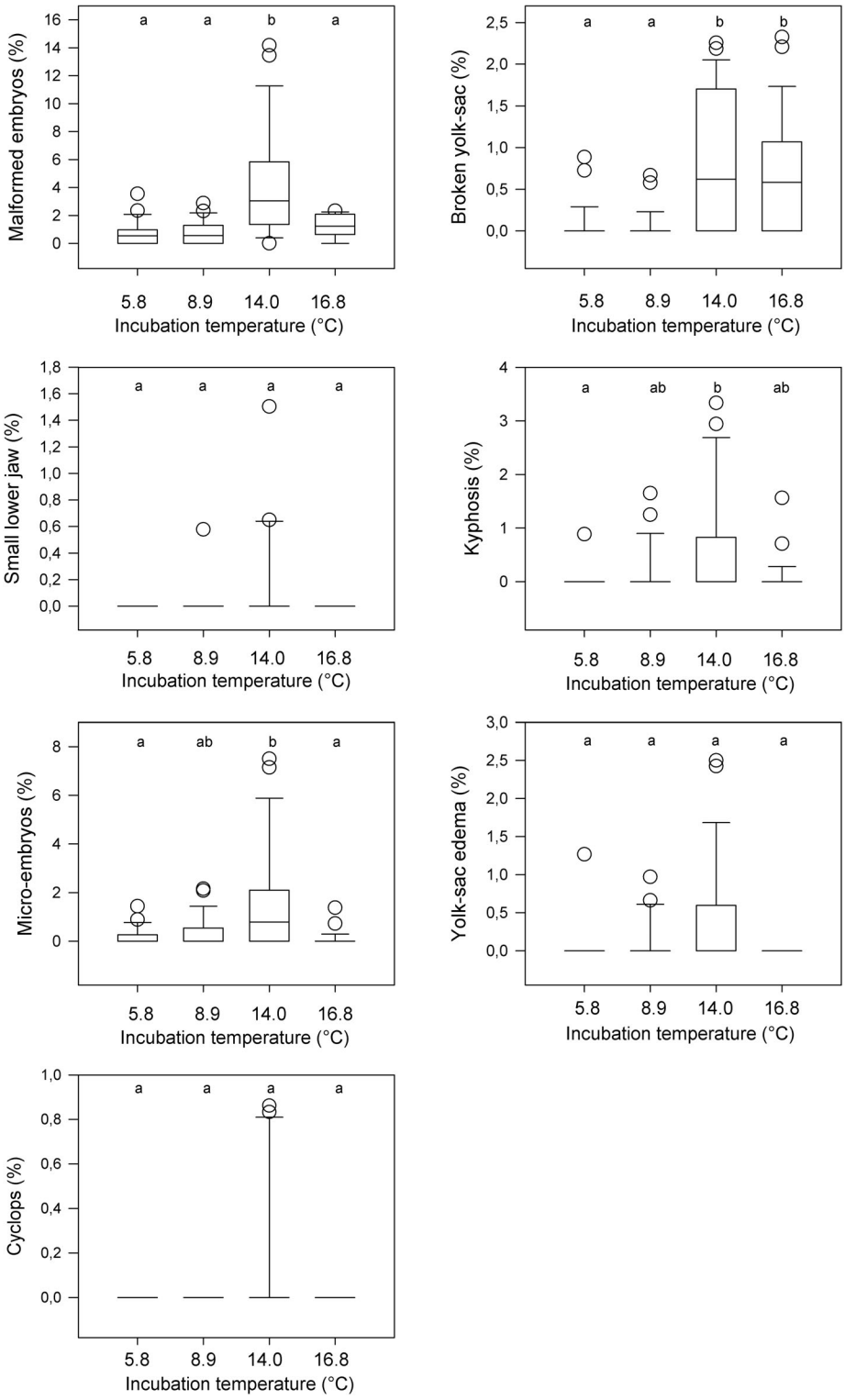

FIGURE 5 Percentage of embryos with malformations (malformed embryos, broken yolk-sac, small lower jaw, kyphosis, micro-embryos, yolk-sac edema, cyclops) *versus* incubation temperature. Median, quartiles and data outside (outlier) 5% and 95% percentiles are indicated. Different letters imply significant differences

thermal preference and thermal tolerance closer to Valcheta than to CENSALBA stock (Crichigno *et al*., 2018). F1 families showed some promising capacities; although their early survival and overall incidence of malformations at usual temperatures (5.0–8.8°C) were similar to the farmed line, they acclimated, survived, fed and grew at 20.5°C, preferred 20.2°C and tolerated up to 30.7°C. The wild origin of Valcheta males implies a lack of domesticity in F1 families (Leitritz, 1959; Tymchuk & Devlin, 2005). In this sense, the lack of difference between farmed and F1 families regarding early survival is promising (Crichigno & Cussac, 2019). It seems that in order to obtain a more profound modification of thermal performance during embryo development it will be necessary to include the adapted genome of the Valcheta population through maternal inheritance, that is, cryopreservation of "farmed" semen could enable the reciprocal F1 to

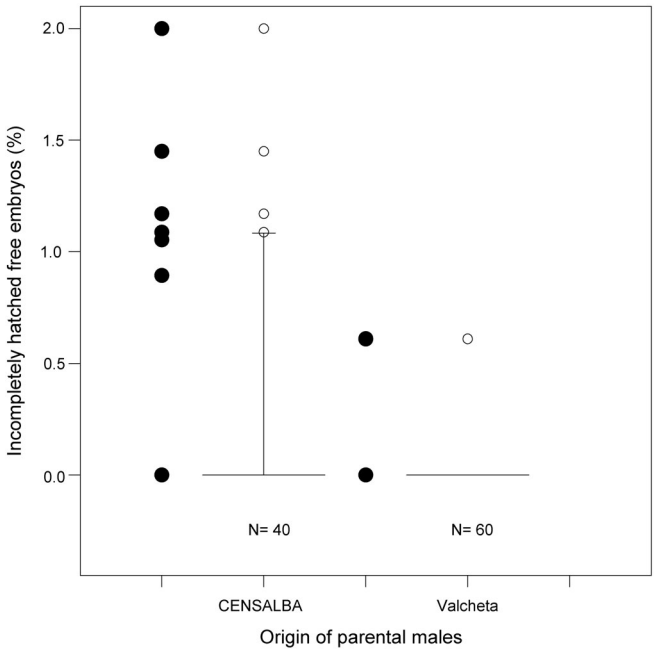

FIGURE 6 Percentage of incompletely hatched embryos *versus* the origin of fathers. Data points and median, quartiles and data outside (outlier) 5% and 95% percentiles are indicated. Note that the number of zero values is 30 of 40 for CENSALBA and 59 of 60 for Valcheta

produce a stabilized strain selected for domesticity, growth and thermal adaptation.

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AUTHOR CONTRIBUTION

S.A.C.: conceptualization, idea generation, data curation, acquisition of funds, research, experimental design, methodology, conducting experiments, keeping animals, project administration, means, validation, display, writing – original draft, writing – review and editing. M.O.: idea generation, research, experimental design, conducting experiments, keeping animals. R.L.: idea generation, research, experimental design, conducting experiments, keeping animals. G.M.: idea generation, research, experimental design, conducting experiments, keeping animals. V.E.C.: conceptualization, idea generation, data curation, acquisition of funds, research, experimental design, methodology, project administration, means, validation, display, writing – original draft, writing - review and editing.

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