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Rainbow trout adaptation to a warmer Patagonia and its potential to increase temperature tolerance in cultured stocks

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ABSTRACT

The viability of rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) culture is being challenged progressively by global warming. Previous trials with Australian and Japanese rainbow trout lines suggested that improvements in thermal performance may be possible. Here, we hypothesized that strain-related differences in physiological response to temperature exist between a north Patagonian hatchery stock (CENSALBA), a Neotropical one (Criadero Boca de Río), and a thermal stream (Valcheta) population of wild introduced rainbow trout. This was tested by comparing, at 20 °C, the thermal preference, specific metabolic rate, thermal tolerance, growth, and condition on juveniles of the three strains, and on a Valcheta stream male x CENSALBA female F1 cross. Preferred temperature (PT) and loss of equilibrium temperature (LET, a measure of thermal tolerance) of Valcheta stream and F1 were significantly higher than those of CENSALBA, and the average PTs of Valcheta stream and F1 were higher than the 95% confidence interval of available reference data for rainbow trout. These results suggest that the F1, reared under standard hatchery conditions and selected by growth and thermal preference, presents higher thermal preference and higher thermal tolerance than the current CENSALBA hatchery stock. Introduction of this naturally adapted strain to hatchery stocks would likely result in the improvement of their temperature resistance to warmer waters. Current studies on adults of this F1 generation are underway.

1. Introduction

The viability of rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) culture is being progressively challenged from temperate to tropical waters, and from high to low altitudes, which is accentuated by global warming (Ellender et al., 2016). The thermal range that lies between preferred temperature (PT) and tolerance temperature encompasses an ensemble of stressful conditions (Elliot, 1981). These may be conspicuous, such as slower growth rates and higher occurrences of diseases, or subtle, such as decreases in reproductive performance and gamete quality, e. g. partial or complete retention of oocytes in the ovary, low survival rate in ovulated oocytes (Power, 1980; Estay et al., 1995; Jobling et al., 1998), gonadal development disorders, atresia, and degeneration of oocytes (Jobling et al., 1998; Pankhurst et al., 1996).

PT is a useful indicator of temperature-related performance, as it is usually similar to, or lies within, the optimum temperature range, i.e. the range within which feeding occurs and there are no external signs of abnormal behavior (Elliot, 1981). Different populations and stocks of rainbow trout show a wide variation of PTs. In only a few cases evidence was found of adaptation to high temperature in Australia (Molony, 2001; Molony et al., 2004; Oku et al., 2014; Chen et al., 2015) and artificial selection improving heat tolerance in Japan (Ineno et al., 2005, 2008; Crozier and Hutchings, 2014). In particular, these trials with Australian and Japanese lines indicate the possibility of improving thermal performance in rainbow trout.

Summer corresponds to the gametogenesis period of rainbow trout, and Northern Patagonia, the main area of rainbow trout culture in Argentina, has been affected by a considerable increase in mean summer air temperature (MSAT, 1.0–2.5 °C from 1961 to 2015, http://www.smn.gov.ar/serviciosclimaticos/?mod=cambioclim&id=7, Báez et al., 2011). Rainbow trout eggs were first sent from the United States in 1904, probably from the McCloud River, California (Marini, 1936; Pascual et al., 2001; Riva Rossi et al., 2004), to the Centro de Salmonicultura Bariloche (CENSALBA), in order to generate a sport fishery

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(Tulian, 1908). In 1931 more eggs were sent from Chile (Marini, 1936), from fish which had originally been imported in 1905 from Hamburg, Germany (de Buen, 1959). In 1969 rainbow trout from Denmark were brought to CENSALBA (mean annual water temperature 10–12 °C, with maximum = 18 °C and minimum = 4 °C, based on daily records along 2014), from where they were extensively distributed to commercial aquaculture facilities throughout Argentina (Baiz, 1973; Macchi et al., 2008); including Criadero Boca de Río, Cordoba (mean annual water temperature 14 °C, with maximum = 20 °C and minimum = 10 °C).

The Valcheta stream belongs to the endorheic basin of Curicó pond in Northeastern Patagonia, with thermal (20–26 °C) headwaters (Menni and Gómez, 1995; Ortubay et al., 1997) and lower reaches with temperatures ranging from 8 to 10 °C. The founding stock of *O. mykiss*, a lot of 600 individuals stocked in 1941 for sport fishery purposes (Ortubay, 1998), were provided by the CENSALBA hatchery (Macchi et al., 2008). Rainbow trout prey on *G. bergii* when they swim upstream during the winter to the thermal headwaters (Ortubay and Cussac, 2000). Kacoliris et al. (2015) have reported a progressive upstream expansion of *O. mykiss* distribution.

We hypothesized that strain-related heritable differences in physiological response to temperature exist between CENSALBA, Criadero Boca de Río and Valcheta stream rainbow trout. As a first step this was tested by comparing, at a high acclimation temperature (20 °C), thermal preference, specific metabolic rate, thermal tolerance, growth, and condition on the three strains, and on a Valcheta stream male x CENSALBA female F1 cross.

2. Materials and methods

2.1. Fish stock data collection

Oncorhynchus mykiss juveniles were obtained from two hatcheries: Centro de Salmonicultura Bariloche (CENSALBA, 41°07′37″S, 71°25′14″W, 800 m a.s.l.; mean annual air temperature (MAAT) 1981–2010 = 8 to 10 °C; mean summer air temperature (MSAT) = 14 to 16 °C) and Criadero Boca de Río (Córdoba, 31°54′47″S, 65°06′48″W; 560 m asl; MAAT 1981–2010 = 16 to 18 °C; MSAT = 22 to 24 °C), and from the Valcheta stream (MAAT 1981–2010 = 14 to 16 °C; MSAT = 20 to 22 °C) (http://www.smn.gov.ar/serviciosclimaticos/?mod=elclima&id=74&clave=Temperatura-Media). Water temperature data were not equally available for comparison, so MAAT and MSAT were used (Becker et al., 2017). Individuals from Valcheta stream were captured in December 2013 by electro-fishing at three sites (Route 60 bridge, 40°43′17″S, 66°17′16″W, 237 m a.s.l.; Chipauquil, 40°54′13″S, 66°33′09″W, 401 m a.s.l.; La Horqueta, 40°56′05″S, 66°34′11″W, 421 m a.s.l.). Preferred temperature (PT), Specific metabolic rate (SMR) and a proxy of thermal tolerance, the loss of equilibrium temperature (LET), were assessed on individuals from each of the three stocks (Table 1).

2.2. Thermally selected F1 generation

In June 2014 new individuals from Valcheta stream were captured (water temperature at capture = 13.1 °C). Only mature males were obtained and sperm samples were brought to the laboratory while maintained at 3 °C.

The F1 cross was performed with 6 females from CENSALBA and 8 males from Valcheta stream to produce 48 families. Each female's brood was divided in eight 500 mL glasses (approximately 383 oocytes in each) and fertilized with 100 μL of milt from each male. Eggs were hydrated for 30 min and then distributed randomly in 6 vertical incubation trays, with 8 spacers each. At eclosion, 23 families were successful.

Selection of F1 individuals with good growth performances was carried out 85 days after first feeding. Thirty-eight individuals with a weight > 0.4 g (Fig. 1) were selected from a total of 116 surviving individuals from 16 families (founded by 6 females and 5 males). Subsequently, to select individuals with preference towards high temperature among those F1 individuals showing good growth, these 38 individuals were subjected to a shuttle-box challenge, consisting in two connected compartments (each box 17 cm in diameter × 18 cm in height, with a canal 14 cm in length × 18 cm in height, Neill et al., 1972), one at the initial water temperature (13 °C) and the other two degrees higher (15 °C), increasing or diminishing water temperature of compartments in relation to the election of the fish, always keeping a difference of 2 °C between compartments. As a result, we obtained a thermally selected F1 generation of 21 juvenile individuals belonging to 11 families (founded by the same 6 females and 5 males) that presented good growth and preferred warm water. They were reared apart in a circular fiber tank (500 L) under natural temperature and photoperiod conditions for 5 months.

Table 1
Number of juvenile individuals (*N*), weight (mean and range, g) and standard length (*SL*, mean and range, cm) in each determination of preferred temperature *(PT)*, specific metabolic rate *(SMR), and* loss of equilibrium temperature (*LET*).

Experiment Stocks	*PT*	*SMR*	*LET*
CENSALBA			
N	11	11	11
Weight	12.59 (7.83–19.24)	12.59 (7.83–19.24)	12.32 (5.61–22.93)
SL	9.45 (8.03–11.03)	9.45 (8.03–11.03)	9.04 (6.83–11.45)
Criadero Boca de Río			
N	11	10	8
Weight	14.59 (9.32–20.1)	14.63 (9.32–20.1)	25.86 (17.38–36.83)
SL	9.72 (7.94–11.07)	9.69 (7.94–11.07)	11.8 (10.08–13.12)
Valcheta stream			
N	12	11	8
Weight	10.14 (4.47–18.93)	9.34 (4.47–18.1)	12.14 (4.93–26.95)
SL	9.12 (6.96–11.65)	8.88 (6.96–11.09)	9.4 (7.21–12.36)
Selected F1			
N	18	18	16
Weight	23.02 (5.11–43.24)	23.02 (5.11–43.24)	29.24 (9.8–49.78)
SL	11.88 (7.8–13.84)	11.88 (7.8–13.84)	12.49 (8.61–14.31)

2.3. Feeding

Fish from Criadero Boca de RÍo, CENSALBA and the thermally selected F1 were fed *ad libitum* on standard commercial formulations. Valcheta individuals were fed *ad libitum* with a mix of *Daphnia* sp., *Tubifex* sp. and standard commercial formulations in an attempt to provide adequate feeding.

2.4. Acclimation

Physiological processes of fishes could depend on acclimation temperature (McNab, 2002). A high acclimation temperature (20 °C) in relation to the final temperature preferendum of rainbow trout (13.5 °C, Aigo et al., 2014) was selected in order to measure performance under a thermal condition where non adapted fish can be expected to show poor results. Juveniles from Criadero Boca de Río and Valcheta stream were taken to CENSALBA facilities in December 2013 (summer). Individuals of each stock (Criadero Boca de Río N = 79, Valcheta N = 80, and CENSALBA N = 102) were put in a circular fiber tank (250 L), with UV

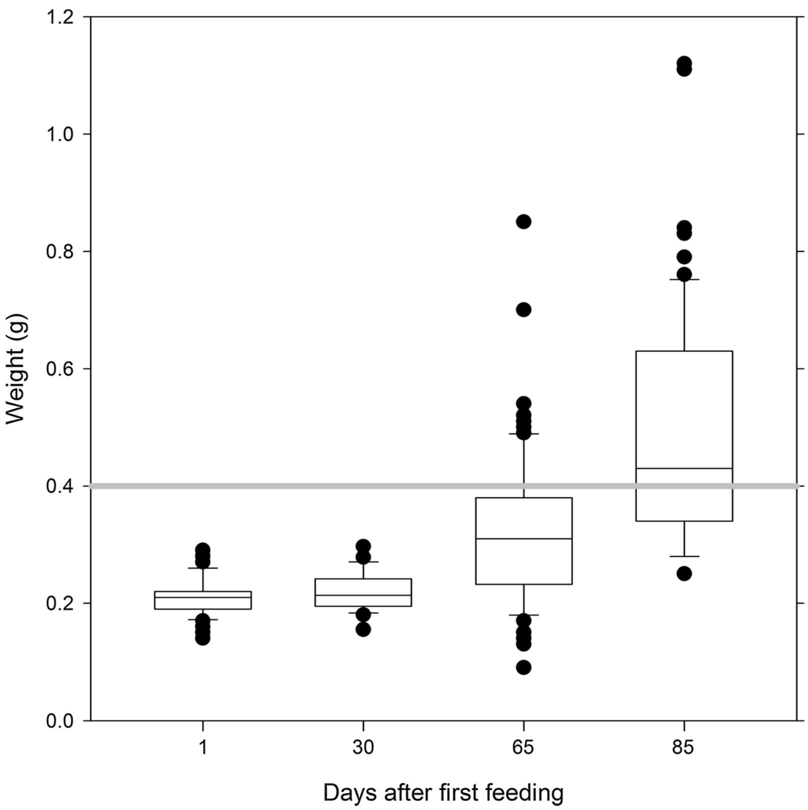

Fig. 1. Body size-based selection of the Valcheta stream (male) x CENSALBA (female) F1 generation. Individuals (38) greater than 0.4 g were selected 85 days after first feeding. Median, quartiles, data outside 5 and 95% percentiles, and 0.4 g (gray line) are indicated.

filtered (Atman 9UV) input water (1.53 L min^{-1}), and a controlled photoperiod of 12D:12N h. following Anttila et al. (2013) and Currie et al. (2013). Water temperature was increased from 13 °C by less than 1 °C per day until a controlled temperature of 18.4 °C (Min = 16.5, Max = 20.5 °C) was reached, which was then sustained for at least three months (Myrick and Cech, 2000; Pang et al., 2011; Currie et al., 2013). To decrease thermal amplitude, ten days before each experiment at least 13 individuals of each stock were put in a 200 L aquarium with aeration and controlled temperature (Mean = 20.1, Min = 19.8, Max = 20.4 °C). Every day 20% of the water in the aquarium was replaced.

In February 2015, thermally selected F1 juveniles were put into a 200 L aquarium with UV filtered (Atman 9UV) input water of 1.53 L min^{-1}, and a controlled photoperiod of 12D:12N h. Water temperature was increased by ca. 1 °C per day for at least 15 days, to reach a controlled temperature of 20 °C (range = 19.8 to 20.3 °C) that was maintained for 17 days.

2.5. Preferred temperature

After acclimation (Mean = 20.1, Min = 19.8, Max = 20.4 °C), 11–18 juvenile individuals of each origin were fasted for 24 h before temperature measurements were taken in a thermal horizontal gradient tank, similar to that used by Bettoli et al. (1985) and Aigo et al. (2014). The tank consisted of a 4 m length white polyvinyl chloride (PVC) pipe with an internal diameter of 10 cm. A longitudinal slot through the upper surface of the pipe allowed fish observation. The position of the fish was recorded indirectly with a mirror placed on the tank at a height of 1.5 m. The gradient was generated and maintained by thermal exchange with water flowing through two tubes, one (polypropylene, diameter 1.3 cm) for cold water running from the right tip to halfway along the pipe, and the other one for hot water (copper, diameter 1.9 cm), running from the left tip to halfway along the pipe, along the floor of the tank. Cold and hot water were provided by a refrigeration unit (freezer) and a water heater, respectively. The temperature extremes of the gradient ranged between 1 and 29 °C. A net prevented fish from coming into direct contact with the cold and hot pipes. At all times dissolved oxygen levels were greater than 7 ppm. Each trial began with the introduction of a single fish into the thermal gradient tank, in a position where the temperature was close to 20 °C. The temperature where the fish was located was measured with a hand-held thermocouple probe (± 0.1 °C), avoiding disturbance to the fish, after 15 min of habituation, the last in order to avoid the noise in the record due to the exploring of the new environment. Temperature recording was repeated at 5 min intervals throughout the trial (24 measurements). The PT of a given fish was taken to be the mean of the 24 records. All trials were performed during morning hours.

2.6. Specific metabolic rate

After PT measurement, juvenile individuals remained at least 48 h for recovery in a 200 L aquarium at 20.1 °C (Min = 19.8, Max = 20.4 °C), after which they were fasted for 18 h previous to oxygen consumption determination. Specific metabolic rate (SMR) of each individual was estimated using a 2 L acrylic closed respirometer with water circulation (7.78 L seg^{-1}), placed in a 100 L aquarium with a constant temperature of 20 °C maintained by an electric immersion thermocirculator (Cech, 1990; Roze et al., 2013; Chabot et al., 2016). A control measurement was taken without fish to control for consumption by bacteria and other organisms (Falahatkar et al., 2011). Each individual was placed in the respirometer (open) for a period of 1 h with aeration and water circulation. After this habituation period, the respirometer was closed and periodic measurements of oxygen concentration were made every 3 min up to loss of equilibrium (69–234 min). SMR was calculated as the ratio of the slope of the linear relationship between Oxygen concentration (mgO_2. L^{-1}) and time (h) with the respirometer volume and fish mass. In order to avoid bias, dependence on size (Jones and Randall, 1978) was eliminated by working with residuals of the regression of SMR versus standard length (measured after the O_2 recording).

2.7. Thermal tolerance

Following SMR determination, juveniles were kept for a minimum of two weeks in the 250 L circular tank (18.4 °C, Min = 16.5, Max = 20.5 °C). They were then placed in a 200 L aquarium for 10 days (20.1 °C, Min = 19.8, Max = 20.4 °C), after which they were fasted for 24 h. Upper thermal tolerance was estimated through the loss of equilibrium temperature (LET), using critical thermal maximum technique (Fry, 1971). Individuals were put in a 100 L aquarium, with aeration and a gradual increase in temperature, reaching 25 °C in 2 h, followed by increments of 0.5 °C per h, fast enough to prevent acclimation (Paladino et al., 1980; Roze et al., 2013). Individuals were constantly monitored until loss of equilibrium and were sacrificed afterward with an excess of anesthesia (benzocaine solution 1:10000).

2.8. Specific growth rate (SGR) and fulton's condition factor (CF)

On three occasions – before acclimation, after SMR determination, and after LET determination – fish were anesthetized, weighed (W, ± 0.01 g) and measured (standard length, SL, measured in cm on digital images). Assumptions (normality and homocedasticity) failed for Weight versus Date data. So, Growth rate (GR) and SGR were calculated, slope of the regression of weight versus time (=GR), SGR (=GR W^{-1}), and CF (=W SL^{-3}), were obtained for each group and time, and residuals of the regression of weight versus time were compared using Kruskal-Wallis one way ANOVA on ranks and all pairwise multiple comparison procedures (Dunn's method). A similar procedure was carried on with CF data.

3. Results

3.1. Preferred temperature

A total of 52 individuals were tested for selection of a preferred temperature within the longitudinal gradient. The preferred temperature of each group differed significantly from each other (ANOVA, $N = 52$, $F = 75.227$, $P = < 0.001$ and Tukey test, $P < 0.05$), except between both hatcheries Criadero boca de Río *versus* CENSALBA. The highest temperature chosen was for Valcheta stream ($N = 12$, mean = 21.1 °C), followed by the thermally selected F1 ($N = 18$, 19.7 °C), Criadero Boca de Río ($N = 11$, 16.6 °C) and CENSALBA ($N = 13$, 15.6 °C) (Fig. 2).

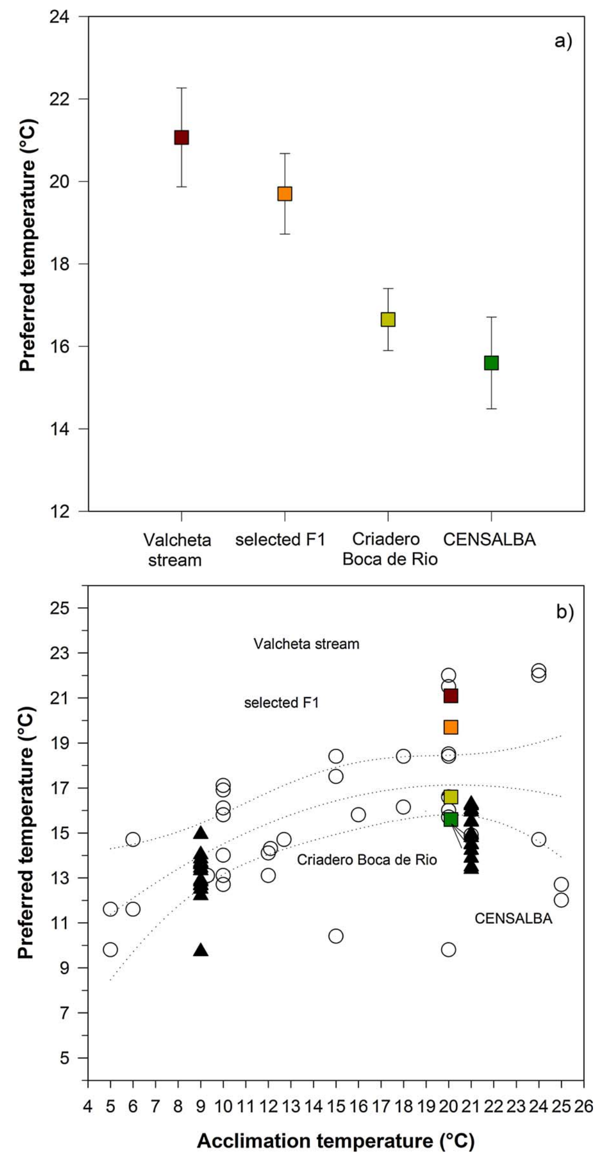

Fig. 2. a) Preferred temperature for Criadero Boca de Rio, Valcheta stream, CENSALBA, and thermally selected F1 individuals. Mean and 95% confidence intervals are indicated. b) Preferred temperature (PT) versus Acclimation Temperature. Data from Garside and Tait (1958), Javaid and Anderson (1967a, 1967b), McCauley and Pond (1971), Cherry et al. (1975, 1977), McCauley and Huggins (1975), McCauley et al. (1977), Kwain and McCauley (1978), Peterson et al. (1979), Stauffer et al. (1984), Schurmann et al. (1991), Myrick and Cech (2000) and McMahon et al. (2008) (white circles, grade 2 polynomial line and 95% confidence interval). Not included in the regression line, data from Aigo et al. (2014) for CENSALBA (black triangles). Mean PTs obtained in this work (squares) are indicated.

3.2. Specific metabolic rate

No significant differences (ANOVA, $N = 50$, $F = 1.994$, $P > 0.112$) were observed between groups (Criadero Boca de Río, Valcheta stream, CENSALBA, and thermally selected F1), either for SMR or for O_2 concentration at loss of equilibrium (ANOVA, $N = 50$, $F = 0.239$, $P > 0.915$).

3.3. Thermal tolerance

Residuals from the regression between LET and SL ($N = 43$) showed significant differences between groups (Kruskal-Wallis One Way Analysis of Variance on Ranks, $H = 17.174$ with 3 degrees of freedom, $P = < 0.001$), the LET of CENSALBA being lower than Valcheta and thermally selected F1 (Dunn's Method, $P < 0.05$) (Fig. 3).

3.4. Specific growth rate and condition factor

Residuals of the regression ($N = 369$) of weight versus time, i.e. the magnitude not explained by a growth rate common to all groups, showed significant differences in between (Kruskal-Wallis One Way Analysis of Variance on Ranks, $H = 52.668$ with 3 degrees of freedom, $P < 0.001$), being the residuals of selected F1 higher than all other groups, and CENSALBA and Criadero Boca de Río higher than Valcheta stream (Dunn's Method, $P < 0.05$). In fact, SGR showed higher values for Criadero Boca de Río and thermally selected F1 and lower values for CENSALBA and Valcheta stream (Fig. 4).

Residuals of the regression of condition factor versus time ($N = 369$) showed significant differences between groups (Kruskal-Wallis One Way Analysis of Variance on Ranks, $H = 84.431$ with 3 degrees of freedom, $P < 0.001$), being the residual condition factor of CENSALBA higher than all other groups and the residuals of Criadero Boca de Río higher than Valcheta stream (Dunn's Method, $P < 0.05$, Fig. 5).

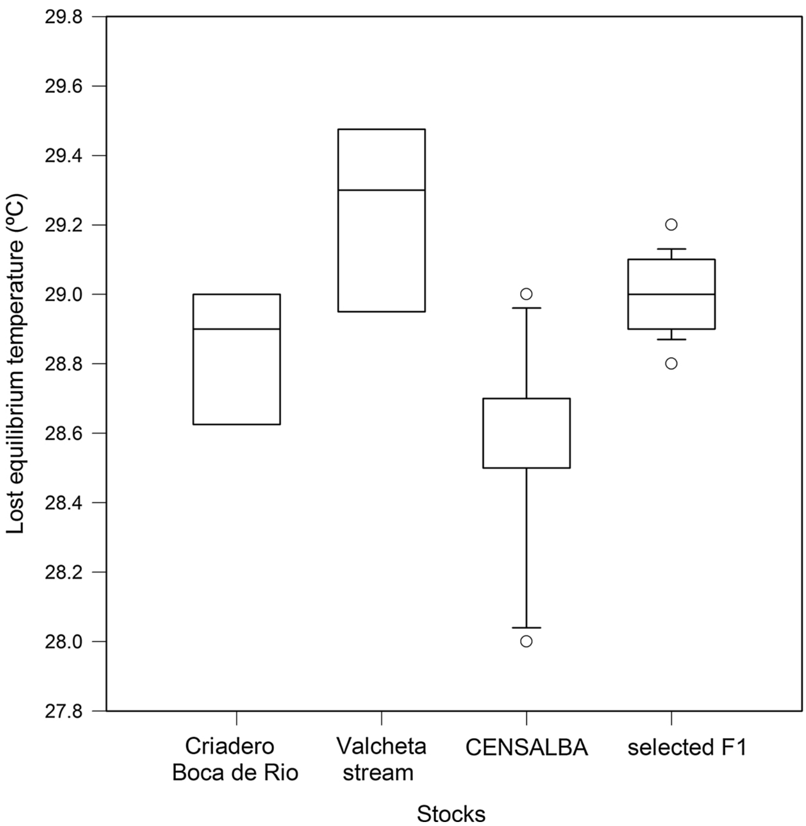

Fig. 3. Loss of equilibrium temperature for Criadero Boca de Rio, Valcheta stream, CENSALBA, and thermally selected F1 individuals. Median, quartiles and data outside 5 and 95% percentiles are indicated.

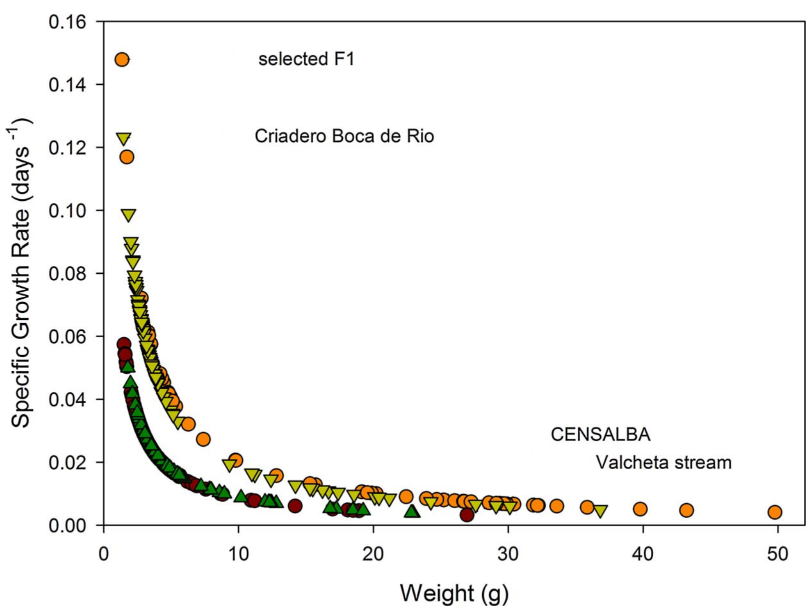

Fig. 4. Specific growth rate (days^{-1}) versus Weight (g) for thermally selected F1 (light gray triangles), Criadero Boca de Rio (Black circles), Valcheta stream (gray circles), and CENSALBA (gray triangles).

4. Discussion

Both, PTs and thermal tolerance (LET) of Valcheta stream and thermally selected F1 were significantly higher than those of CENSALBA hatchery stock, and average PTs of Valcheta stream and selected F1 lay outside the 95% confidence interval of available reference data for rainbow trout PT. These results suggest that the Valcheta (male) x CENSALBA (female) F1 generation, reared under standard hatchery conditions and selected by growth and thermal preference, presents both thermal preference and thermal tolerance closer to the Valcheta stream population than to the CENSALBA stock.

It has been established previously that thermal tolerance of rainbow trout can be selected (Ineno et al., 2005; Perry et al., 2005). The different rainbow trout lines studied here presented considerable variability in temperature performance. To our results, a portion of this variation seems to be genetically determined, for which the heritability could be estimated in further studies.

Polymorphisms at Heat Shock Proteins (HSPs, Heredia-Middleton et al., 2008; Feldhaus et al., 2010; Narum and Campbell, 2010), QTL loci (Jackson et al., 1998), and Single Nucleotide Polymorphisms (SNPs) were found associated with adaptation to elevated temperature (Narum et al., 2010). Thus, it seems plausible that the population of

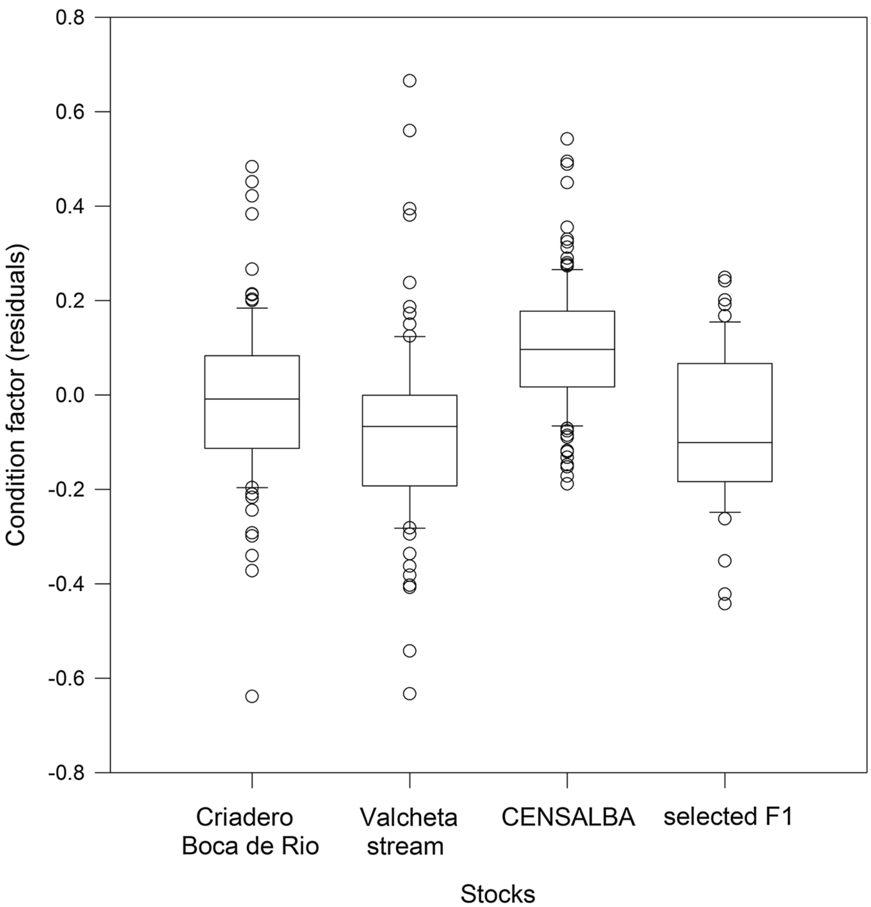

Fig. 5. Condition factor (g. cm^{-3}) for Criadero Boca de Rio, Valcheta stream, CENSALBA, and selected F1 (residuals of the regression between Condition factor and Time). Median, quartiles, data outside 5 and 95% percentiles are indicated.

Valcheta stream evolved by increasing its PTs and LETs in relation to the founding stock depicted by Ortubay (1998), Macchi et al. (2008) and Riva Rossi et al. (2004).

The lack of differences between the strains for SMR and O_2 level corresponding to loss of equilibrium, suggests effective acclimation to a common high temperature (20 °C). However, in agreement with Oku et al. (2014), growth performances at high temperature were different; the low SGR of CENSALBA and Valcheta stream could be related to the fact that the usual water temperature for CENSALBA strain is lower than the acclimation and maintenance temperature used in the experiments (20 °C), and to the wild character of Valcheta stream population and its difficult food acceptance in farm conditions.

Conversely, the similar and higher SGR of Criadero Boca de Río and the thermally selected F1 agree with a previous adaptation to warmer conditions in Criadero Boca de Río strain and with inheritance of the Valcheta stream adaptation by the latter. Present results regarding SGR and CF suggest that the introduction into cultured stocks of a thermally selected F1 generation and subsequent selection for growth and fattening in high thermal conditions, may lead to maintaining, or even enlarging the current suitable area for culture, as an important global warming countermeasure.

However, the main challenge faced by rainbow trout aquaculture in Northern Patagonia is the physiology of gametogenesis (Pankhurst et al., 1996; Pankhurst and King, 2010; Báez et al., 2011). At first, it is not obvious that this thermally selected strain will be successful as an adult performing gametogenesis under high temperature. Therefore, adult individuals of this thermally selected F1 generation are currently being studied in relation to hormonal indicators of the gametogenesis process. In addition, they are being screened for alleles at HSPs and SNPs in relation to temperature performance (Narum and Campbell, 2010) along individuals from Criadero Boca de Río y CENSALBA.

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