

*Susceptibility of native perca (Percichthys trucha) and exotic rainbow trout (Oncorhynchus mykiss) to high temperature in Patagonia: different physiological traits and distinctive responses*

**Juana Aigo, María Eugenia Lattuca & Víctor Cussac**

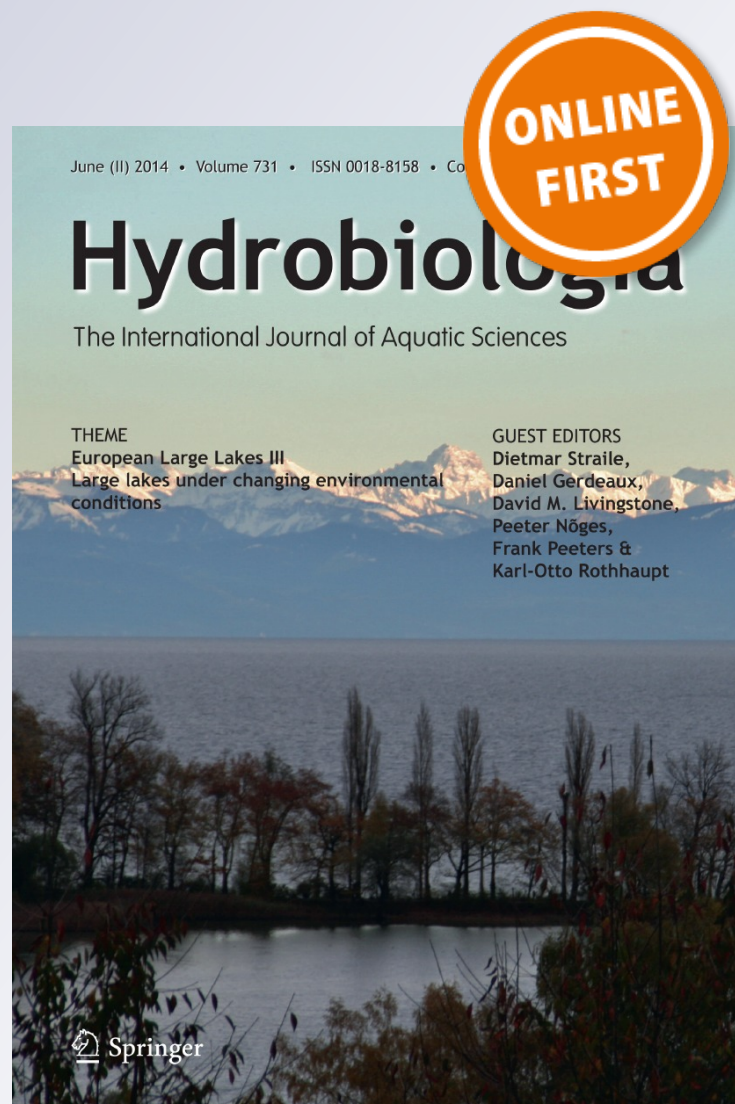
**Hydrobiologia**

The International Journal of Aquatic Sciences

ISSN 0018-8158

Hydrobiologia

DOI 10.1007/s10750-014-1888-3



**Your article is protected by copyright and all rights are held exclusively by Springer International Publishing Switzerland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Susceptibility of native perca (*Percichthys trucha*) and exotic rainbow trout (*Oncorhynchus mykiss*) to high temperature in Patagonia: different physiological traits and distinctive responses

Juana Aigo · María Eugenia Lattuca ·  
Víctor Cussac

Received: 19 November 2013 / Revised: 9 April 2014 / Accepted: 10 April 2014  
© Springer International Publishing Switzerland 2014

**Abstract** The aim of this work was to explore for the existence of a physiological basis for the apparent exclusion of salmonid fish from the littoral zone of lakes in Patagonia in response to increasing water temperature, to the benefit of the native perca (*Percichthys trucha*). We conducted experiments on the thermal preferences of juvenile perca and rainbow trout collected in three sites of Northern Patagonia. We characterized the relationship between preferred and acclimation temperature (PT, AT) for perca and trout and analyzed between-sites variations in PTs. Both species responded with increasing PT to higher AT, but with differences in overall PT for perca from different sites (lower PTs for fish from cooler lake). In general, rainbow trout displayed lower PT and a narrower range of PT than perca. Our results provide the first comparative view of PTs of one important

native fish and the main sport fish species of Patagonia. Native perca may be better equipped to cope with warmer waters than exotic rainbow trout, in agreement with their geographic distribution. Also, perca may have an advantage at the local level, particularly in littoral areas of lakes, through the alleviation of predation by and trophic competition with trout.

**Keywords** Preferred temperature · Acclimation · Global warming · Patagonia

## Introduction

Fish are ectothermic poikylotherms and their physiology is greatly influenced by their thermal environment (Abrahams, 2006). Because water temperature varies widely in space and time, it constitutes a critical variable limiting the geographical and seasonal distribution of fishes. For this reason, the study of preferred temperatures (PTs) provides key information to interpret fish distribution, analyze the vulnerability of different species, and generate predictions for community change (Pörtner & Peck, 2010). In temperate ecosystems, not all fish species have the same optimal temperature and may respond differentially to temperature changes (Magnuson & De Stasio, 1996). As a consequence of climate change, species extinctions and distributional shifts are expected to occur, but data to validate these predictions are relatively scarce (Sinervo et al., 2010).

---

Handling editor: M. Power

---

J. Aigo (✉) · V. Cussac  
Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Universidad Nacional del Comahue (UNCO) – Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Quintral 1250, San Carlos de Bariloche, 8400 Río Negro, Argentina  
e-mail: juanaaigo@gmail.com

M. E. Lattuca  
Centro Austral de Investigaciones Científicas (CADIC), CONICET, Ushuaia, Argentina

Elevated water temperatures increase vulnerability of fish to predation by sub-lethal heat shocks (Coutant, 1973; Yokum & Edsall, 1974) and reduce the availability of littoral thermal habitats (Jansen & Hesslein, 2004). For instance, salmonid fishes have been regarded as highly vulnerable to the potential effects of increasing temperature (Keleher & Rahel, 1996; Carveth et al., 2006), through direct mortality or physiological/ecological impairment, as compared to other species adapted to warmer water temperatures (Bear et al., 2007). Some of the effects reported on reproduction in salmonids have been lack of ovulation, atresia, and partial or total absence of spawning during the breeding season (Pankhurst & King, 2010). In a context of rising water temperature, fish may be exposed to a trade-off regarding the access to different resources necessary for survival (Matthews & Berg, 1997), having to choose between habitats providing optimal thermal conditions and those offering better foraging opportunities (Li et al., 1994; Spina, 2007).

Behavioral thermoregulation is an important factor influencing the distribution of fish in heterothermal environments (Magnuson et al., 1979). Within their tolerance range, individual fish select certain temperatures known as PTs, where their functions and metabolic processes operate with maximum efficiency (Elliot, 1981; Schurmann et al., 1991). These preferences are not only determined in part by the evolutionary history of the species and the population (Golovanov, 2006), but can also be modulated by environmental factors such as food, light, oxygen, and the distribution of competitors and predators (Jobling, 1996). The PTs are also modified by the recent thermal experience of the individual (Kelsch & Neill, 1990). Many species can tolerate certain temperatures in a condition of slow change, which may otherwise be lethal. This is accomplished through biochemical compensation during a gradual change to a new temperature, i.e., acclimation (Hill et al., 2006). Therefore, mechanisms of acclimation result in changes in temperature preference following exposure to different temperatures (Kelsch & Neill, 1990). The relationship between PT and acclimation temperature (AT) varies among fish species, and can be positive, negative, or independent (Johnson & Kelsch, 1998). The understanding of PTs, therefore, requires considering several components, including population and AT.

The freshwater fish fauna of Patagonia is made up by a small and unique group of native species and

several exotic fishes (Pascual et al., 2007). Native species include fishes of Gondwanan origin, marine dispersants, and oceanic elements of local origin. Today, perca *P. trucha* (Valenciennes, 1833), Patagonian pejerrey *Odontesthes hatcheri* (Eigenmann, 1909), small puyen *Galaxias maculatus* (Jenyns, 1842), big puyen *Galaxias platei* Steindachner, 1898, and peladilla *Aplochiton zebra* Jenyns, 1842 are common in lakes and reservoirs. Exotic fish are mostly salmonids, with the geographically dominant rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792), brown trout, *Salmo trutta* Linnaeus, 1758, and brook trout, *Salvelinus fontinalis* (Mitchill, 1814).

Temperature appears to be an important factor in shaping fish communities along the climatic gradient of southern Argentina (Quirós, 1991; Cussac et al., 2009), with some species limited in their southward distribution by low temperatures and others limited in their northward distribution by high temperatures (Gonçalves et al., 2010). However, knowledge about the thermal requirements of Patagonian native fishes, the environmental constraints to their distributions, or their relative vulnerability to climate change is still limited (Gómez, 1990; Ortubay et al., 1997; Gómez et al., 2007; Cussac et al., 2009; Gonçalves et al., 2010). Meanwhile, a significant literature exists on salmonids from elsewhere. Rainbow trout and brown trout are the species with most restricted thermal requirements, but can tolerate a broad range of other physical and environmental variables (Jobling, 1996; Hillman et al., 1999; Molony, 2001; Sauter et al., 2001; Milaja, 2006; Ficke et al., 2007; Spina, 2007).

In any case, understanding temperature preferences of both native and exotic fishes, may be instrumental in explaining their distributions at the geographic scale (Quirós, 1991; Liotta, 2006), as well as the local scale within lakes (Aigo et al., 2008; Lattuca et al., 2008; Aigo, 2010). An important difference between salmonid and native fish species relies on the breeding habitat, streams for salmonids, and the vegetated lake littoral area for most of Patagonian native fishes. In consequence, it is in the lake littoral where trophic interactions between native fish preys and both native and exotic predators take place (Macchi et al., 2007). The exclusion of salmonid fish from the littoral zone due to an increase in water temperature at lake shores (Jansen & Hesslein, 2004) seems to have occurred in Patagonia during the last decades, to the benefit of perca (Aigo et al., 2008). In particular, the low

capacity for acclimation (sensu Stillman, 2003) of salmonids limits their resistance to large annual temperature changes, determining their habitat choice (Carveth et al., 2006). This is consistent with the geographic distribution of salmonids in Patagonia with respect to those of the native *P. trucha* and *O. hatcheri* (Liotta, 2006), with the seasonal abundance of salmonids and native species in the lake littoral (Aigo et al., 2008; Aigo, 2010), and with the negative correlation between the relative abundance of salmonid species and the mean annual air temperature, throughout Patagonia (Quirós, 1991).

In this paper, we conduct an experimental study on the thermal preferences of juveniles of perca, one of the most conspicuous native species in Patagonia and juveniles of rainbow trout, the most conspicuous exotic species, to generate a first comparative portrayal of their responses to temperature. In particular, we (1) characterize the relationship between PT and AT for perca, and rainbow trout and (2) analyze variations in PTs responses of fish coming from different sites.

## Materials and methods

### Fish collection and general experimental framework

The Limay River watershed extends from northwest to southeast, covering part of Northwestern Patagonia (Argentina). The overall weather is cold temperate, with a mean annual air temperature ranging between 14 and 9°C and surface water temperature in lakes ranging between 6 and 22°C (Wicki & Luchini, 2002; Báez et al., 2011). Fish were collected from three different sites in the Limay River Watershed, two headwater locations and one downstream location (Table 1). The two headwater sites were located in colder, higher, western locations within the temperate *Nothofagus* forest: the Huechulafquen Lake and a hatchery center near Bariloche city. This hatchery (Centro de Salmonicultura Bariloche, CSB) draws water from the Gutiérrez Stream which flows into the Nahuel Huapi Lake. The downstream site, the Alicura Reservoir, is located eastward, on the main-stem Limay River, in the warmer, lower, semiarid transition zone between the steppe and the forest. Mean temperature is 18°C in January and 4°C in July. The

average monthly water temperature during the summer is around 20°C, with extreme values above 24°C (Báez, 2007; Báez et al., 2011).

The two species were not available for all three sites: juveniles of both rainbow trout and perca were collected from Lake Huechulafquen, only rainbow trout juveniles from the hatchery, and only perca juveniles from Alicura (Table 1). In the Alicura Reservoir and Huechulafquen lake sites, fish were collected by seine nets and electrofishing (Smith-Root Inc., Vancouver, WA, USA) from the littoral zone, between 0.3 and 1.5 m depth during the spring and summer of years 2006 and 2007. Water temperature was recorded with a single measurement at the time of fish collection ( $\pm 0.1^\circ\text{C}$ ; Table 1). All fish were carried alive to the laboratory (CSB, Universidad Nacional del Comahue) and kept in aquaria with aeration and natural photoperiod during the acclimation period (rate =  $1^\circ\text{C day}^{-1}$ ). During this period (a minimum of 10 days), they were fed with artificial food until 24 h prior to determination of thermal parameters.

### Preferred temperatures

The tests of PTs were conducted at the CSB hatchery center. Treatments consisted of certain combinations of species and collection site (fish group), and AT (Table 2). Between 10 and 15, individual fish were tested for each treatment. Note that only two of the fish groups, perca from Alicura and rainbow trout from the CSB hatchery, were exposed to contrasting ATs (Table 2). The other two fish groups, rainbow trout and perca from Lake Huechulafquen, were tested for a single AT.

The PT of individual fish was measured in a custom-built thermal horizontal gradient tank (Fig. 1), similar in design to that described by Bettoli et al. (1985). The tank consisted of a covered, 4-m length pipe made of white polyvinyl chloride (PVC) with an inside diameter of 10 cm. A longitudinal slot through the upper surface of the pipe allowed the fish observation. A gradient was generated and maintained by thermal exchange with water running through two polypropylene tubes (diameter 1.9 cm) along the floor of the tank, i.e., a dual, counter-current heat exchanger with refrigerated and heated water flowing in opposite directions. The components of the system external to the tank were a 50 liters reservoir, a refrigeration unit (freezer), a centrifugal pump, and a water heater

**Table 1** Geographical and environmental characteristics of the sites of capture of juvenile fish: name, location, altitude, mean summer air temperatures (MSAT, °C), mean summer water

(epilimnion) temperatures (MSWT, °C), water temperatures at capture (CT, °C) and species collected from each site

Sites	Latitude (°S)	Longitude (°W)	Altitude <sup>a</sup> (m a.s.l.)	MSAT (°C)	MSWT (°C)	CT (°C)	Species
Alicura Reservoir	40°40'	71°00'	698	15.4	20–24	18.4	<i>P. trucha</i>
CSB	41°07'	71°25'	801	14.0	14.02	12	<i>O. mykiss</i>
Lake Huechulafquen	39°46'	71°20'	895	14.2	15.3	12.5	<i>O. mykiss</i> <i>P. trucha</i>

CSB Centro de Salmonicultura Bariloche, Universidad Nacional del Comahue

<sup>a</sup> Source [earth.google.com](http://earth.google.com)

Source MSAT, °C—[www.worldclim.org](http://www.worldclim.org); MSWT, °C—Báez et al. (2011), Báez (2007), and Shimizu et al. (1997)

**Table 2** Summary of the thermal parameters determined for *P. trucha* and rainbow trout

Species	Sites	N	AT (°C)	Mean TL (mm)	Mean W (g)	PTs (°C)
<i>O. mykiss</i>	CSB	15	21.0	63.1	2.0	14.9 (13.4–16.3)
	CSB	15	9.0	64.5	2.2	13.0 (9.7–14.9)
	Lake Huechulafquen	12	12.0	38.8	0.4	13.0 (11.0–15.2)
<i>P. trucha</i>	Alicura Reservoir	12	12.6	39.5	0.6	17.8 (12.5–21.2)
	Alicura Reservoir	13	21.0	32.2	0.6	21.2 (18–24.4)
	Lake Huechulafquen	10	12.0	30.3	0.3	12.9 (10.9–15.9)

Species, sites, number of fish (N); acclimation temperatures (AT, °C); mean total length (TL, mm), mean body weight (W, g), and preferred temperatures (PTs, °C; mean and range into brackets) are indicated

CSB: Centro de Salmonicultura Bariloche, Universidad Nacional del Comahue

(Fig. 1). The temperature extremes of the gradient offered to the fish ranged between 4 and 31°C. A net prevented fish from directly contacting the cold and hot tubes. Compressed air was bubbled through regularly spaced holes to ensure aeration and vertical water mixing.

Each trial began with the introduction of a single fish in the thermal gradient tank, in a position with temperature close to the fish's AT. The temperature where the fish were located was measured with a hand-held thermocouple probe ( $\pm 0.1^\circ\text{C}$ ), avoiding to disturb the fish, at 5-min intervals throughout the trial. The fish were allowed to select its PT by steadying its position within the tank for at least 10 min. Trials lasted from 30 to 60 min, though most ended after 50 min. Our measure of PT for a given fish was the mean value of the temperatures recorded during the trial. All tests were performed during morning hours.

Minimum and maximum tank temperatures were routinely recorded over the course of each trial and adjustments in hot and cold water were made to maintain desired gradients. The gradient was generally consistent within trials, whereas adjustments between

trials to stabilize the gradient were conducted as needed by controlling the flow of cold and hot water.

### Statistical analysis

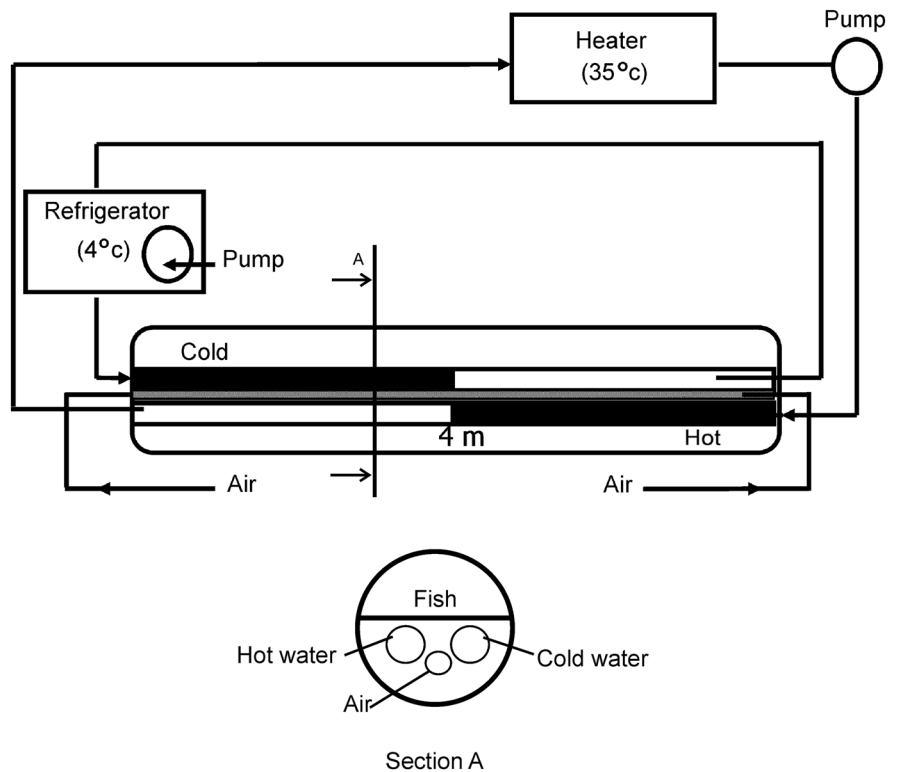
We modeled PT as a function of species, AT, and site by fitting a multiple linear regression model to the whole dataset. PT was modeled as a linear response variable of one continuous variable, AT, and two categorical variables, namely species (perca or rainbow trout), and site (Alicura Reservoir or Lake Huechulafquen for perca and Lake Huechulafquen or CSB hatchery for rainbow trout; Table 2). The general model was

$$PT = \alpha_{s,p} + \beta_{s,p} AT + \varepsilon, \tag{1}$$

where “s” indexes species, “p” indexes site, and “ $\varepsilon$ ” is a normal random variable with zero mean and constant variance (standard assumption of residuals, normally distributed and with homogeneous variance).

The significance of the response of PT to AT, and deviations from the general response associated to species and site of origin were analyzed through the statistical assessment of models of varying

**Fig. 1** Schematic representation of the thermal horizontal gradient tank (*top view, above*) and a cross-sectional view (section A) of the tank (*below*). The components of the system external to the tank were a refrigeration unit (freezer), two centrifugal pumps, and a water heater (see text for details)



complexity. To this end, a backwards stepwise model selection process was performed, where alternative models were assessed by likelihood ratio tests (Hilborn & Mangel, 1997). We started by fitting the most complex possible model, where each of the four fish groups (two for each species) had its own PT–AT relationship (i.e., its own  $\alpha$  and  $\beta$  in Eq. (1), an eight parameters model). We then tested alternative simplifications of this model to evaluate the significance of the relationship between PT and AT and to evaluate differences in this relationship associated to species and sites.

We favored a regression approach over an ANCOVA in recognition of the fact that not all fish groups were exposed to contrasting ATs, or to the same ATs (Table 2). A regression approach allowed us to measure PT responses along the gradient of AT (a continuous variable) as a linear response function, incorporating species and site as categorical variables. Also, and because only one level of AT was available in experiments with perca and rainbow trout from Lake Huechulafquen (Table 2), we did not attempt testing for the whole temperature response in this species-site combinations. Rather, we incorporated

them in the general regression model to investigate whether Lake Huechulafquen fish of each of the two species conform to the general PT patterns displayed by the same species from alternative sites.

Model's fitting and selection through likelihood ratio tests were performed on a custom-made Excel spreadsheet (M. Pascual, Centro Nacional Patagónico, CONICET, Puerto Madryn, Argentina). Assumptions of normality and homocedasticity were evaluated through normal plots and a Kolmogorov–Smirnov test (SPSS; Norusis, 1986).

## Results

### Preferred temperatures

The model fitting to the data of PT experiments with perca and rainbow trout (Table 2) revealed a number of patterns associated to species and site-specific responses to AT (Table 3; Fig. 2). The most complex model we fitted considered specific responses of PT to AT for each of the four fish groups (Model 1 in Table 3). We rejected a simple model which consisted

**Table 3** Models of varying complexity fitted to the response of PT to AT of perca and rainbow trout

Model definition	Model assessment					
	SSQ	Parameter	Contrast	Likelihood ratio	df	P value
1. Full: different slope and intercept by species and populations	193.51	8				
2. Simplest: same slope & intercept for species and populations	631.99	2	vs. Model 1	88.77	6	0.00000
3. Slope for perca = 0	265.48	6	vs. Model 1	23.72	2	0.00001
4. Slope for rainbow trout = 0	219.80	6	vs. Model 1	9.55	2	0.00843
5. Slope rainbow trout = slope perca	212.80	5	vs. Model 1	7.12	3	0.06802
6. Perca (A) = perca (H) (both slope and intercept)	305.87	6	vs. Model 1	34.34	2	0.00000
7. Rainbow trout (H) = rainbow trout (C) (both slope and intercept)	195.01	6	vs. Model 1	0.58	2	0.74831
8. Slope rainbow trout = slope perca; rainbow trout (H) = rainbow trout (C) (both slope and intercept)	213.23	4	vs. Model 1	7.28	4	0.12194

Species (perca and rainbow trout) and population of origin (A Alicura Reservoir; H Huechulafquen and C CSB: Centro de Salmonicultura Bariloche, Universidad Nacional del Comahue) are indicated

of a universal response of all groups to AT (i.e., same slope and intercept, Model 2 in Table 3,  $P < 0.001$ ), indicating that significant heterogeneities exist among the groups analyzed (Fig. 2).

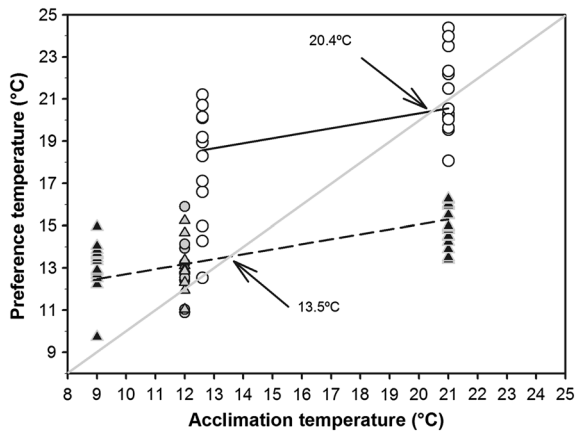
Then, we evaluated alternative models to identify what those significant heterogeneities were. Initially, we rejected models with slopes equal to 0 for perca (Model 3,  $P < 0.001$ ) and with slopes equal to 0 for rainbow trout (Model 4,  $P = 0.008$ ), indicating that PT responded positively to AT in both species (Fig. 2). A model with the same slope for both species (same rate of response to AT) but with different intercepts (more than 5°C higher for perca) was not rejected at a 5% alpha level (Model 5,  $P = 0.068$ ). Overall, this first set of tests provides a strong statistical support to a significant positive relationship between PT and AT for both species, with similar slope for all fish groups, but heterogeneities in the PT by species (trout PT ranged from 9.7 to 16.3°C and perca PT from 10.9 to 24.4°C, Table 2).

We then proceeded to test for deviations from this general pattern of fish from different sites. Site-specific PTs were significantly different for perca (Model 6,  $P < 0.001$ ), but such differences were not significant for rainbow trout (Model 7,  $P = 0.748$ ). Because only one level of AT was available in experiments with perca and rainbow trout from Lake Huechulafquen (Table 2), these last two models do not allow testing for the whole

temperature response by site, but they do inform us about deviations of these two groups from the general pattern displayed by their conspecific from other sites. In this regard, perca from Lake Huechulafquen showed a significant preference for lower temperatures than those from Alicura Reservoir for very similar AT, whereas temperature preferences by rainbow trout did not differ between sites (Table 2).

Finally, we tested a model which combines the same slope for both species and differences in intercepts for perca from different sites (Model 8) and the two simplifications from the full model that could not be rejected in individual tests (Models 5 and 7, respectively). This model was not rejected ( $P = 0.122$ ), providing the best representation of the data ("best model", fitted in Fig. 2). This model indicates that both species respond in similar fashion to AT, but with perca from Alicura Reservoir preferring significantly higher temperatures than rainbow trout, as well as than perca from Lake Huechulafquen. In fact, though PTs of perca and rainbow trout from Lake Huechulafquen were not significantly different ( $P = 0.178$ ). Over the ATs of 9–21°C, rainbow trout PTs ranged from 12.5 to 14.5°C and perca PTs from 18 to 20°C; Fig. 2). It must be noted that when final temperature preferences (FTP, Jobling, 1981) are interpolated, FTP = 13.5°C for rainbow trout and FTP = 20.4°C for perca are obtained (Fig. 2).

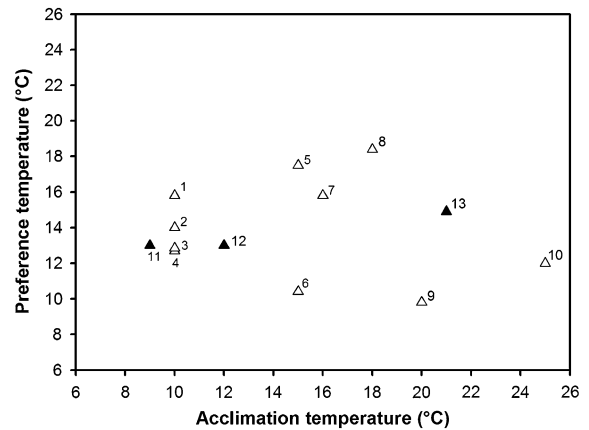




**Fig. 2** PTs as a function of AT for all fish in the experiments. Symbols indicate species: *P. trucha* (circles) and *O. mykiss* (triangles); and sites: Alicura Reservoir (open), Huechulafquen Lake (gray) and CSB hatchery (black). The two lines represent the PT-AT regression model fit (“Best” model 8 in Table 3) for *P. trucha* from Alicura Reservoir (solid line) and the two *O. mykiss* populations (dashed line). Intersections with  $Y = X$  gray line indicate (arrows) the Final Temperature Preferendum (Jobling, 1981)

## Discussion

In this paper, we provide novel information on PTs of perca and exotic rainbow trout in Patagonia. This information constitutes the first published record for individual species in the region, as well as a comparative view among species. The PTs of perca and rainbow trout were positively related with AT. We found inter-specific differences in the PT values, with perca from Alicura Reservoir preferring higher temperatures than rainbow trout. Particularly, it should be noted the great difference between the FTP (the “temperature around which all individuals will ultimately congregate, regardless of their thermal experience before being placed in the gradient” Jobling, 1981) of rainbow trout (13.5°C) and perca (20.4°C). We also found significant differences in the PT values between perca from different sites. This population-specific difference in PT is consistent with the temperature of their native environments (Table 1), suggesting that this species may have a larger plasticity and greater capacity for acclimation as compared to rainbow trout. Whether this difference is the expression of phenotypic plasticity or has a genetic basis requires further study. Nevertheless, and considering that only one level of AT was available for one of the



**Fig. 3** PTs as a function of AT for *O. mykiss*. Comparison data of previous studies (open triangles) and our data (black triangles). References: 1: Javaid & Anderson (1967), 2: McMahon et al. (2008), 3: Kwain & McCauley, 1978, 4: McCauley et al. (1977), Myrick & Cech (2000), 5: McCauley et al. (1977), 6: Javaid & Anderson (1967), 7: McMahon et al. (2008), 8: McCauley & Pond (1971), 9: McCauley et al. (1977), 10: McCauley et al. (1977), Myrick & Cech (2000); 11–13: this paper (see Table 2)

sites, substantiating the existence of population-specific differences would require further testing. Ideally, fish collected from several environments with contrasting water temperatures should be tested for standardized levels of ATs.

The PTs registered for rainbow trout agree with world-wide information on the thermal requirements of salmonids (Fig. 3). In Patagonia, rainbow trout has been a very successful invader and is today widely distributed (Pascual et al., 2002; Macchi et al., 2008). Simulations to test the effect of temperature on growth efficiency of rainbow trout based on a fixed diet show that waters 2–4°C warmer than the PTs found for rainbow trout (12–14°C) decrease growth efficiency, indicating that temperatures above a certain level generate a metabolic cost that is not compensated by consumption of a more energy-rich diet (Juncos et al., 2011). High water temperature is known to affect farmed rainbow trout in the region, resulting in low survival rates at hatching and first feeding in Alicura Reservoir (Báez et al., 2011).

Thermal requirement data provide a gateway to analyze the risks for native species associated to an increase of littoral water temperature. Frequently, species live and are captured under thermal ranges that match their PTs (Johnson & Kelsch, 1998). In this

way, rainbow trout and perca were captured at temperatures consistent with their PTs (Table 1). The wide PT range of perca is in agreement with their wide latitudinal distribution (Baigún & Ferriz, 2003; Liotta, 2006). *Percichthys* has a geographically extensive fossil record, extending as far north as Bolivia and Brazil (Cione & Báez, 2007). In the fossil record, *Percichthys* is associated with the Brazilian fish fauna (Loricariidae, *Corydoras*, *Callichthys*, and *Pimelodella*). Particularly, perca is today captured in Andean lakes, reservoirs, and steppe shallow lakes. This species are particularly abundant in shallow lakes, such as the Blanca lake (Ortubay et al., 2006), where summer air and water temperatures are high (Aigo, 2010).

These records of low PT for salmonids, together with their low relative abundances with respect to perca in littoral zones of Patagonian lakes (Aigo et al., 2008; Aigo, 2010) suggest that salmonids species are more sensitive to warming than perca. The higher tolerance of some native species would provide them the advantage of using warmer, shallow environments, with important thermal fluctuations and provision of refuge, a particularly important advantage during the juvenile period.

A non negligible aspect of the fate of rainbow trout populations introduced elsewhere in Patagonia is the case of shallow lakes of Patagonian plateau. Hydrological variability in Patagonia during the last 13.0 Ka (Piovano et al., 2009) led to the formation of great number of fishless shallow lakes. Some of these lakes were stocked with rainbow trout and native fishes (*P. trucha* and *O. bonariensis*) during the twentieth century, with verified effects on the structure of plankton communities (Reissig et al., 2006). Nowadays, the absence of a deep thermal refuge for salmonid fishes suggests that appreciable changes can be expected again in these lakes.

## Conclusions

Present results constitute the first comparative view of PT of rainbow trout and perca in Patagonia. We propose that under warming conditions, perca would obtain an advantage, particularly in the littoral zone of Andean–Patagonian lakes, through the alleviation of predation by and trophic competition with salmonids. We identify PT as a tool for assessing the vulnerability

of native fish species and exotic salmonids in Patagonian lakes to global warming. Thus, correlative observations of Quirós (1991), Ortubay et al. (2006), and Aigo et al. (2008), regarding the decrease of trout and the increase of perca relative abundances in relation to increasing temperature would be rooted in the thermal physiology of these species. However, while PT patterns can give the first approximation of the effects of increasing temperatures, we recommend a cautious and integrated assessment with other biotic, abiotic, ecological, and anthropogenic factors as the primary basis for any analysis concerning the management of freshwater fish communities of Patagonia.

**Acknowledgements** We thank to Universidad Nacional del Comahue and CONICET (Argentina) for supporting previous and present research. We would like to thank Drs. M. Pascual, D. Milano, J. P. Barriga, and J. Kuroda for assistance and suggestions that improved this work.

## References

- Abrahams, M., 2006. The physiology of anti-predator behaviour: what you do with what you've got. In Sloman, K. A., R. W. Wilson & S. Balshine (eds), *Behaviour and Physiology of Fish*. Elsevier, San Diego, CA: 79–108.
- Aigo, J., 2010. Interacción entre peces nativos y salmónidos en Patagonia: su vulnerabilidad frente al cambio climático, Doctoral Thesis, Universidad Nacional del Comahue, Bariloche, Argentina.
- Aigo, J., V. Cussac, S. Peris, S. Ortubay, S. Gómez, H. López, M. Gross, J. P. Barriga & M. Battini, 2008. Distribution of introduced and native fish in Patagonia (Argentina): patterns and changes in fish assemblages. *Reviews in Fish Biology and Fisheries* 18: 387–408.
- Báez, V. H., 2007. Cría intensiva y rendimiento del cultivo de trucha de arroyo (*Salvelinus fontinalis* (Mitchill)) a partir de ejemplares silvestres norpatagónicos. Tesis de Maestría. Facultad de Agronomía, Universidad de Buenos Aires.
- Báez, V. H., J. Aigo & V. E. Cussac, 2011. Climate change and fish culture in Patagonia: present situation and perspectives. *Aquaculture Research* 42: 787–796.
- Baigún, C. & R. Ferriz, 2003. Distribution patterns of native freshwater fishes in Patagonia, Argentina. *Organisms, Diversity & Evolution* 3: 151–159.
- Bear, E. A., T. E. McMahon & A. V. Zale, 2007. Comparative thermal requirements of West slope Cutthroat trout and Rainbow trout: implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society* 136: 1113–1121.
- Bettoli, P. W., W. H. Neill & S. W. Kelsh, 1985. Temperature preference and heat resistance of grass carp, *Ctenopharyngodon idella* (Valenciennes), bighead carp, *Hypophthalmichthys mobilis* (Gray), and their F1 hybrid. *Journal of Fish Biology* 27: 239–247.

- Carveth, C. J., A. M. Widmer & S. A. Bonar, 2006. Comparison of upper thermal tolerances of native and nonnative fish species in Arizona. *Transactions of the American Fisheries Society* 135: 1433–1440.
- Cione, L. A. & A. M. Báez, 2007. Peces continentales y anfibios cenozoicos de Argentina: los últimos cincuenta años. *Publicación Especial 11. 50° aniversario. Ameghiniana*: 195–220.
- Coutant, C. C., 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. *Journal of the Fisheries Research Board of Canada* 30: 965–973.
- Cussac, V. E., D. A. Fernández, S. E. Gómez & H. L. López, 2009. Fishes of southern South America: a story driven by temperature. *Fish Physiology and Biochemistry* 35: 29–42.
- Elliot, J. M., 1981. Some aspects of thermal stress on freshwater teleosts. In Pickering, A. D. (ed.), *Stress and Fish*. Academic Press, London: 209–246.
- Ficke, A. D., A. Christopher, A. E. Myrick & L. Hansen, 2007. Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries* 17: 581–613.
- Golovanov, V. K., 2006. The ecological and evolutionary aspects of thermoregulation behavior on fish. *Journal of Ichthyology* 46: 180–187.
- Gómez, S. E., 1990. Some thermal ecophysiological observations on the catfish *Hatcheria macraei* (Girard, 1855) (Pisces, Trichomycteridae). *Biota* 6: 89–95.
- Gómez, S. E., R. C. Menni, J. Gonzalez Naya & L. Ramirez, 2007. The physical–chemical habitat of the Buenos Aires pejerrey, *Odontesthes bonariensis* (Teleostei, Atherinopsidae), with a proposal of a water quality index. *Environmental Biology of Fishes* 4: 234–239.
- Gonçalves, R. J., M. S. Souza, J. Aigo, B. Modenutti, E. Balseiro, V. E. Villafañe, V. E. Cussac & E. W. Helbling, 2010. Responses of plankton and fish from temperate zones to UVR and temperature in a context of global change. *Ecología Austral* 20: 129–153.
- Hilborn, R. & M. Mangel, 1997. The ecological detective. Confronting models with data. In: *Monographs in Population Biology*. Princeton Academic Press, Princetown: 315 pp.
- Hill, R. W., A. G. Wyse & M. Anderson, 2006. *Fisiología Animal*. Editorial Médica Panamericana S.A. Madrid, España.
- Hillman, T. W., M. D. Miller & B. A. Nishitani, 1999. Evaluation of seasonal-cold-water temperature criteria. *BioAnalysts, Inc. Criteria*. Idaho Division of Environmental Quality, Boise, ID: 1–48.
- Jansen, W. & R. H. Hesslein, 2004. Potential effects of climate warming on fish habitats in temperate zone lakes with special reference to Lake 239 of the experimental lakes area, north western Ontario. *Environmental Biology of Fishes* 70: 1–22.
- Javald, M. Y. & J. M. Anderson, 1967. Thermal acclimation and temperature selection in Atlantic salmon, *Salmo salar*, and rainbow trout, *S. gairdneri*. *Journal of Fish Research Board Canadian* 24: 1507–1513.
- Jobling, M., 1981. Temperature tolerance and the final preference-rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology* 19: 439–455.
- Jobling, M., 1996. *Environmental Biology of Fishes*. Fish and Fisheries Series. Chapman & Hall, London: 476 pp.
- Johnson, J. A. & S. W. Kelsch, 1998. Effects of evolutionary thermal environment on temperature-preference relationships in fishes. *Environmental Biology of Fishes* 53: 44–458.
- Juncos, R., D. Milano, P. J. Macchi, M. F. Alonso & P. H. Vigliano, 2011. Response of Rainbow trout to different food web structures in Northern Patagonia: implications for growth, bioenergetics, and invasiveness. *Transactions of the American Fisheries Society* 140: 415–428.
- Keleher, J. C. & F. J. Rahel, 1996. Thermal limits to salmonid distributions in the Rocky Mountain Region and potential habitat loss due to global warming: a geographic information system (GIS) approach. *Transactions of the American Fisheries Society* 125: 1–13.
- Kelsch, S. W. & W. H. Neill, 1990. Temperature preference versus acclimation in fishes: selection for changing metabolic optima. *Transactions of the American Fisheries Society* 119: 601–610.
- Kwain, W. & R. W. McCauley, 1978. Effects of age and overhead illumination on temperatures preferred by underyearling rainbow trout, *Salmo gairdneri*, in a vertical temperature gradient. *Journal of the Fisheries Research Board of Canada* 35: 1430–1433.
- Lattuca, M. E., M. Battini & P. J. Macchi, 2008. Trophic interaction among fishes in a northern Patagonian oligotrophic lake. *Journal of Fish Biology* 72: 1306–1320.
- Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait & J. C. Buckhouse, 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. *Transactions of the American Fisheries Society* 123: 627–640.
- Liotta, J., 2006. Distribución geográfica de los peces de aguas continentales de la República Argentina. *ProBiota. Serie Documentos 3*. Universidad Nacional de La Plata: 701 pp.
- Macchi, P. J., M. A. Pascual & P. H. Vigliano, 2007. Differential piscivory of the native *Percichthys trucha* and exotic salmonids upon the native forage fish *Galaxias maculatus* in Patagonian Andean lakes. *Limnologia* 37: 76–87.
- Macchi, P. J., P. H. Vigliano, M. A. Pascual, M. Alonso, M. A. Denegri, D. Milano, M. Garcia Asorey & G. Lippolt, 2008. Historical policy goals for fish management in northern continental Patagonia, Argentina: a structuring force of actual fish assemblages? *American Fisheries Society Symposium* 49: 331–348.
- Magnuson, J. J. & B. T. De Stasio, 1996. Thermal niche of fishes and global warming. In Wood, C. M. & D. G. McDonald (eds), *Global Warming – Implications for Freshwater and Marine Fish*. SEB Seminar Series. Cambridge University Press, Cambridge: 377–408.
- Magnuson, J. J., L. B. Crowder & P. A. Medvick, 1979. Temperature as an ecological resource. *American Zoologist* 19: 331–343.
- Matthews, K. R. & N. H. Berg, 1997. Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. *Journal of Fish Biology* 50: 50–67.
- McCauley, R. W. & W. L. Pond, 1971. Temperature selection of rainbow trout (*Salmo gairdneri*) fingerlings in vertical and

- horizontal gradients. *Journal of Fish Research Board Canadian* 28: 1801–1804.
- McCauley, R. W., J. R. Elliot & L. A. A. Read, 1977. Influence of acclimation temperature on preferred temperature in the rainbow trout *Salmo gairdneri*. *Transactions of the American Fisheries Society* 106: 362–365.
- McMahon, T. E., E. A. Bear & A. V. Zale, 2008. Use of an annular chamber for testing thermal preference of west slope cutthroat trout and rainbow trout. *Journal of Freshwater Ecology* 23: 55–63.
- Milaja, N., 2006. Effects of temperature and feeding regime on compensatory growth of rainbow trout, *Oncorhynchus mykiss*. M.S. Thesis. University of Jyväskylä, Heinäkuu.
- Molony, B., 2001. Environmental requirements and tolerances of rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) with special reference to Western Australia: a review. *Fisheries Research Report* 130: 1–28.
- Myrick, C. A. & J. J. Cech, 2000. Temperature influences on California rainbow trout physiological performance. *Fish Physiology and Biochemistry* 22: 245–254.
- Norusis, M. J., 1986. SPSS/PC+ Advanced Statistics. SPSS Inc., Chicago, Illinois: 481 p.
- Ortubay, S. G., S. E. Gómez & V. E. Cussac, 1997. Lethal temperatures of a Neotropical fish relic in Patagonia, the scale-less characinid *Gymnocharacinus bergi* Steindachner 1903. *Environmental Biology of Fishes* 49: 341–350.
- Ortubay, S., V. Cussac, M. Battini, J. Barriga, J. Aigo, M. Alonso, P. Macchi, M. Reissig, J. Yoshioka & S. Fox, 2006. Is the decline of birds and amphibians in a steppe lake of northern Patagonia a consequence of limnological changes following fish introduction? *Aquatic Conservation* 16: 93–105.
- Pankhurst, N. W. & H. R. King, 2010. Temperature and salmonid reproduction: implications for aquaculture. *Journal of Fish Biology* 76: 69–85.
- Pascual, M. A., V. Cussac, B. Dyer, D. Soto, P. Vigliano, S. Ortubay & P. Macchi, 2007. Freshwater fishes of Patagonia in the 21st century after a hundred years of human settlement, species introductions and environmental change. *Aquatic Ecosystem Health and Management* 10: 212–227.
- Pascual, M., P. Macchi, J. Urbanski, F. Marcos, C. Riva Rossi, M. Novara & P. Dell'Arciprete, 2002. Evaluating potential effects of exotic freshwater fish from incomplete species presence–absence data. *Biological Invasions* 4: 101–113.
- Piovano, E. L., D. Ariztegui, F. Córdoba, M. Cioccale & F. Sylvestre, 2009. Hydrological variability in South America below the tropic of Capricorn (Pampas and Patagonia, Argentina) during the last 13.0 Ka. In: Vimeux, F. et al. (eds), *Past Climate Variability in South America and Surrounding Regions*, *Developments in Paleoenvironmental Research* 14. Springer, Dordrecht. doi:10.1007/978-90-481-2672-914.
- Pörtner, H. O. & M. A. Peck, 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology* 77: 1745–1779.
- Quirós, R., 1991. Factores que afectan la distribución de salmonidos en Argentina. COPESCAL, FAO, Documento Técnico 9: 163–173.
- Reissig, M., C. Trochine, C. Queimaliños, E. Balseiro & B. Modenutti, 2006. Impact of fish introduction on planktonic food webs in lakes of the Patagonian Plateau. *Biological Conservation* 132: 437–447.
- Sauter, S. T., J. McMillan & J. Dunham, 2001. Salmonid Behavior and Water Temperature. U.S. Environmental Protection Agency Report EPA-910-D0-01-001: 1–27.
- Schurmann, H., J. F. Steffensen & J. P. Lomholt, 1991. The influence of hypoxia on the preferred temperature of rainbow trout *Oncorhynchus mykiss*. *Journal of Experimental Biology* 157: 75–86.
- Shimizu, I., A. Espinos, R. Gader & C. Gonzalez, 1997. Calidad de agua y productividad primaria y secundaria del sistema del lago Huechulafquen. VII Conferencia Internacional sobre Conservación y Gestión de Lagos – Lacar'97. ILEC – INAA – UNC – San Martín de los Andes, Neuquén, Argentina.
- Sinervo, B., F. Méndez de la Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagran-Santa Cruz, R. Lara-Resendiz, N. Martínez-Méndez, M. L. Calderon-Espinosa, R. Nelsi Mesa-Lázaro, H. Gadsden, L. J. Avila, M. Morando, I. J. De la Riva, P. Victoriano Sepulveda, C. F. Duarte Rocha, N. Ibarzüengoytía, C. Aguilar Puntriano, M. Massot, V. Lepetz, T. A. Oksanen, D. Chapple, A. Bauer, W. Branch, J. Clobert, & J. W. Sites, Jr., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328: 894–899.
- Spina, A. P., 2007. Thermal ecology of juvenile steelhead in a warm-water environment. *Environmental Biology of Fishes* 80: 23–34.
- Stillman, J. H., 2003. Acclimation capacity underlies susceptibility to climate change. *Science* 301: 65.
- Wicki, G. A. & L. Luchini, 2002. Evaluación del potencial para acuicultura en la región del Comahue (Provincias de Neuquén y Río Negro). *Información Básica*, Secretaría de Agricultura, Ganadería, Pesca y Alimentos (SAGPyA), BuenosAires, Argentina: 52 pp.
- Yokum, T. G. & T. A. Edsall, 1974. Effect of acclimation temperature and heat shock on vulnerability of fry of lake whitefish (*Coregonus clupeaformis*) to predation. *Journal of the Fisheries Research Board of Canada* 31: 1503–1506.