

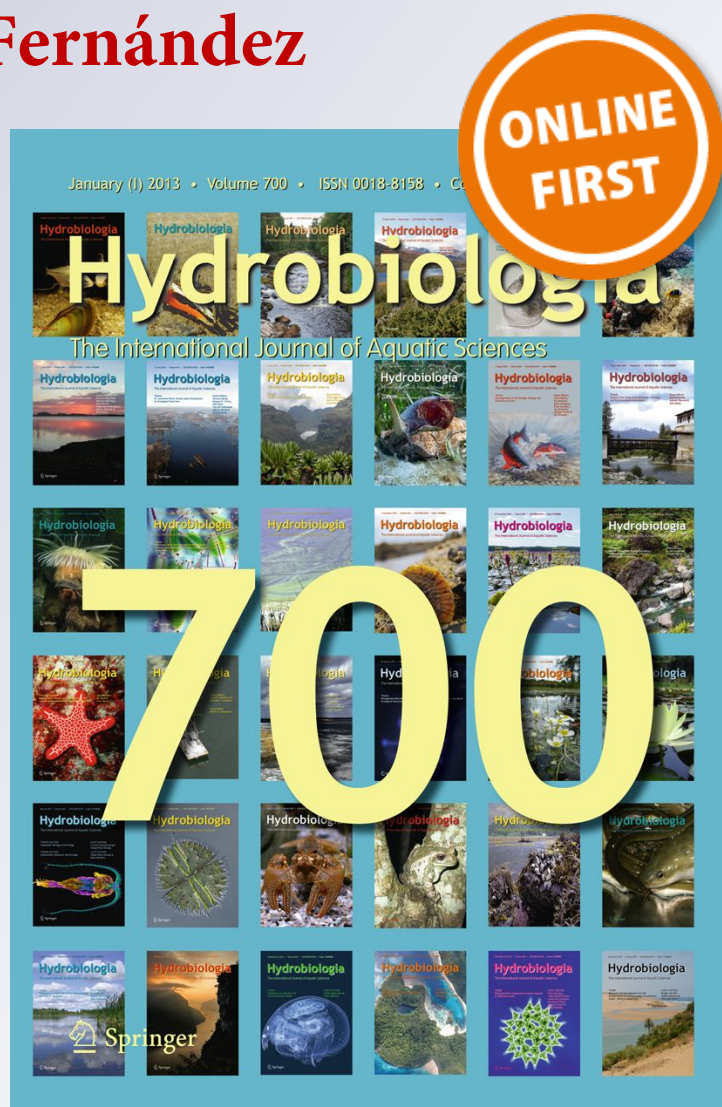
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# Thermal responses of three native fishes from estuarine areas of the Beagle Channel, and their implications for climate change

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**Abstract** The aim of this work was to analyze the thermal responses of *Odontesthes nigricans*, *Eleginops maclovinus* and diadromous *Galaxias maculatus*, key species in estuarine areas of the Beagle Channel (Tierra del Fuego, Argentina), under a climate change scenario. We hypothesized that in the southernmost limit of the species' distribution,

individuals are more likely to be affected by indirect consequences of climate change rather than direct temperature mortality. Their thermal tolerance limits were assessed using the Critical Thermal Methodology and their preferred temperatures, using a thermal gradient. Additionally, the Fulton's condition factor and the energy density of individuals were analyzed as a proxy of the condition of fishes acclimated to different temperatures. Results showed that species analyzed have the ability to acclimate to the different temperatures, intermediate to large tolerance polygons and positive relationships between preferred and acclimation temperatures, indicating their eurythermic nature. Thus, *O. nigricans*, *E. maclovinus* and diadromous *G. maculatus* populations from Tierra del Fuego could experience enhanced performances because of moderate warming being and, as it was hypothesized, be influenced by indirect consequences of climate change (habitat degradation or changes in trophic structure) since they are living in environments that are widely cooler than their maximum tolerance.

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## Introduction

Ongoing climate change is considered one of the main threats to biodiversity and the structure and functioning of ecosystems (McCarthy et al., 2001). The increase in global average temperature by about 0.6°C over the past century (Houghton et al., 2001; Hulme et al., 2002) is a clear indicator of this phenomenon. Furthermore, marine temperatures are expected to increase by as much as 2°C in the next 100 years (IPCC, 2013; Schultz et al., 2016). Since fish are ectotherms, their physiology is strongly influenced by water temperature (Lutterschmidt & Hutchison, 1997; Abrahams, 2006; Beitinger & Lutterschmidt, 2011) which is highly variable, both in space and time, in turn influencing the geographical and seasonal distribution of these organisms. For this reason, the study of temperature tolerance and behavioural thermoregulation provide data to understand fish distribution in heterothermal environments (Magnuson et al., 1979). Within its tolerance range, fish select certain temperatures known as preferred temperature, in which their functions and metabolic processes operate with greater efficiency (Schurmann et al., 1991). These preferred temperatures are determined in part by the evolutionary history of the species and populations (Golovanov, 2006), but can also be modulated by different environmental factors and the recent thermal history (Kelsch & Neill, 1990; Jobling, 1994). Knowledge of preferred temperatures and thermal tolerance ranges can provide concrete elements to analyze the vulnerability of different species and produce scenarios for changes in the fish community (Pörtner & Peck, 2010).

A possible effect of global warming is that the water temperatures would increase to levels that are suboptimal or lethal for fishes (Ficke et al., 2007). When exposed to temperatures within the suboptimal range, fishes could reallocate energy to adjust to changing environmental conditions, affecting their ability to grow, reproduce and maintain homeostasis (Sogard & Spencer, 2004). Thus, the energy density of fish can be used to assess the potential response (individual/population) to changes in the environment (Paine, 1971; Ludsin & DeVries, 1997; Madenjian et al., 2000). It provides an approximation to physiological status of individuals, and therefore their condition to face situations of high energy

demand, such as processes of environmental/climate change, migrations, reproduction, among others (Rotiers & Tucker, 1982; Shearer, 1994; Ludsin & DeVries, 1997). A decrease in the energy density indicates that the energy obtained (food) is not sufficient to support metabolic demands, and evidence a stress situation at the organism level.

To date, there is practically no information related to thermal responses and the energetic condition, with the exception of Fernández et al. (2009), of most marine or diadromous fishes from southern Patagonia. Particularly, some of the most widespread species found in estuarine areas of the Beagle Channel (Tierra del Fuego) are *Odontesthes nigricans* (Richardson, 1848), *Eleginops maclovinus* (Cuvier, 1830) and diadromic *Galaxias maculatus* (Jenyns, 1842). The 'pejerrey' *O. nigricans* has been reported along the Atlantic Ocean from Orense (39°S, Buenos Aires Province) down to Cabo de Hornos (56°S) (Dyer, 2000). The 'róbalo' *E. maclovinus* shows an extended bioceanic distribution, being found from Valparaiso in the Pacific Ocean (Chile, 33°S) and from San Matías Gulf in the Atlantic Ocean (Argentina, 40°S) down to the Beagle Channel (55°S) (Pequeño, 1989; Cousseau & Perrota, 2000). Both 'pejerrey' and 'róbalo' are of considerable economic importance to sport and artisanal fisheries (Lattuca et al., 2015), with an average of 12.5 ton landed annually in the last 5 years in Tierra del Fuego. The 'puyen chico' *G. maculatus* has a wide distribution in the southern hemisphere, being present in South America, New Zealand, Australia, Tasmania and Chatham Island (McDowall, 1970; Waters & Burridge, 1999; Cussac et al., 2004) with both landlocked and diadromous populations. The most updated synthesis about its distribution in South America is that of Cussac et al. (2004). Environmental conditions associated with latitude (e.g., low temperatures, lower food resources in fresh water compared to sea water) in southern Patagonia seem to have favoured the expression of the diadromous behaviour (Boy et al., 2009, 2017) while northern Patagonian population of *G. maculatus* are landlocked (Cussac et al., 2004; Zattara & Premoli, 2005; Carrea et al., 2013). Populations of *O. nigricans*, *E. maclovinus* and *G. maculatus* in Tierra del Fuego represent, therefore, peripheral populations within each species' ranges.

The interest in studying such peripheral populations is that they are more likely to be imperilled than



central populations. They tend to occur in less suitable environments and are often isolated from more central and continuous populations, being more prone to local extirpation. However, distinct traits found in peripheral populations may also be crucial to the species, allowing adaptation in the face of environmental changes. Therefore, peripheral populations will often have high value for conservation (Lesica & Allendorf, 1995).

At high latitudes, where peripheral populations inhabit, temperature affects their viability either through constraints to body size imposed by winter starvation conditions (Shuter & Post, 1990) or directly by lethality (Fry, 1971). Moreover, current climate change is expected to have both direct and indirect effects on individual organisms (Munday et al., 2008; Eme & Bennet, 2009), thereby impacting populations, communities, and the functioning of ecosystems (Pörtner & Peck, 2011). Available data also suggest that fish have different thermal windows (e.g., the difference between upper and lower lethal temperatures), thus influencing their interactions within an ecosystem. In general, species coexist where their thermal windows overlap; but these thermal windows are not necessarily identical. This would explain why climate sensitivity differs among species and may be one of the principal reasons for climate-induced changes in community composition and food-web interactions (Pörtner & Peck, 2011).

In this context, the aim of this work was to perform an overall analysis of thermal responses of three key fish species inhabiting the Beagle Channel, southernmost limit of their distribution. In particular, the thermal tolerance limits were established, the relationship between acclimation and preferred temperature was characterized and the energy content was quantified. In a context of climate change, the study of thermal responses of fish assemblages can provide concrete elements to analyze the vulnerability of different species and generate scenarios for community change (Pörtner & Peck, 2010).

## Materials and methods

### Collection, maintenance and acclimation of fish

Field work was carried out in Varela Bay (54°52'S, 67°16'W) during 2011–2014. During 2011–2013 and

prior to experimental trials, water temperature was recorded, at 1 m depth with data loggers (iButton-TMEX, Maxim Dallas Semiconductors, Dallas, TX, USA) every 2 h, in order to assess the range of temperature to which fish are exposed to.

*Odontesthes nigricans*, *E. maclovinus* and diadromous *G. maculatus* juveniles were collected during spring 2014 by means of a seine net and electrofishing (Smith-Root Inc., Vancouver, WA, USA). Fish were transported to the laboratory into aerated 100 l tanks containing either seawater (*O. nigricans* and *E. maclovinus*) or freshwater (*G. maculatus*). In the laboratory, marine species were transferred to aquaria containing seawater with salinity of  $28 \pm 2$  and at  $10 \pm 0.2^\circ\text{C}$  and *G. maculatus* to aquaria containing freshwater at  $10 \pm 0.2^\circ\text{C}$ . Oxygen was maintained near saturation conditions (seawater:  $8.91 \pm 0.22$  mg/l; freshwater:  $11.12 \pm 0.14$  mg/l) in each aquarium. They were left to acclimatize for 2 weeks to captivity conditions before undergoing experimental acclimation and 'thermal tolerance' or 'thermal preference' trials. Then, groups of fish of homogeneous sizes of each species (Table 1) were selected and held at a density of 1 individual  $\text{l}^{-1}$  for 3 weeks at different acclimation temperatures (AT). Four different AT were selected, which corresponded to extreme (2 and  $16^\circ\text{C}$ ) and mean (4 and  $10^\circ\text{C}$ ) winter and summer water temperatures of the Beagle Channel, Tierra del Fuego, respectively. Different AT and experimental diel photoperiod (12:12 h L:D) were reached at a rate of  $1^\circ\text{C day}^{-1}$  and  $1 \text{ h day}^{-1}$ , respectively. During the acclimation period, the feeding regime consisted of chopped hake muscle offered ad libitum every 3 days; however, fishes were not fed 24 h in advance of, or during experimental trials. Water quality was maintained by changing water (20–25% of total volume) every other day. Nitrogen wastes were measured twice a week and ammonia ( $\text{NH}_3/\text{NH}_4^+$ ), nitrite ( $\text{NO}^-2$ ) and nitrate ( $\text{NO}^-3$ ) levels were kept under 0.25, 0.8 and  $12.5 \text{ mg l}^{-1}$ , respectively. No visual signs of stress were observed during the acclimation period.

### Thermal acclimation limits

The total thermal acclimation range of each species was estimated from chronic upper and chronic lower temperatures measurements, as indicated in Dabruzzi et al. (2012). For this purpose, 12 juveniles of each

**Table 1** Summary of experimental results on Critical Thermal Maxima/Minima (CTmax/CTmin, °C, mean  $\pm$  SD) for *O. nigricans*, *E. maclovinus* and *G. maculatus* from Varela Bay (Beagle Channel, Patagonia)

Species	AT	<i>n</i>	TL	BM	CTmin	<i>n</i>	TL	BM	CTmax
<i>O. nigricans</i>	2	20	98.98 $\pm$ 7.35	4.54 $\pm$ 2.37	- 2.09 $\pm$ 0.19	20	91.40 $\pm$ 7.43	3.40 $\pm$ 0.73	27.13 $\pm$ 0.64
	4	20	97.95 $\pm$ 7.52	4.14 $\pm$ 4.14	- 2.20 $\pm$ 0.31	20	101.96 $\pm$ 8.19	4.32 $\pm$ 1.40	27.53 $\pm$ 0.76
	10	20	94.38 $\pm$ 4.43	4.04 $\pm$ 4.30	- 1.53 $\pm$ 0.28	20	107.48 $\pm$ 5.87	4.51 $\pm$ 1.73	28.67 $\pm$ 0.41
	16	20	94.10 $\pm$ 7.16	3.81 $\pm$ 3.09	- 1.37 $\pm$ 0.21	20	96.15 $\pm$ 8.36	4.26 $\pm$ 0.93	32.30 $\pm$ 0.25
<i>E. maclovinus</i>	2	20	89.57 $\pm$ 6.65	4.97 $\pm$ 1.73	- 2.10 $\pm$ 0.34	20	91.00 $\pm$ 6.84	4.69 $\pm$ 1.69	25.20 $\pm$ 0.54
	4	20	84.03 $\pm$ 5.21	3.90 $\pm$ 0.71	- 2.19 $\pm$ 0.24	20	83.93 $\pm$ 6.03	3.87 $\pm$ 0.88	27.12 $\pm$ 0.56
	10	20	80.96 $\pm$ 5.36	3.52 $\pm$ 0.84	- 1.92 $\pm$ 0.44	20	80.61 $\pm$ 7.45	3.74 $\pm$ 0.91	30.07 $\pm$ 0.48
	16	20	91.32 $\pm$ 6.68	4.53 $\pm$ 0.97	1.70 $\pm$ 1.96	20	91.97 $\pm$ 7.01	4.57 $\pm$ 1.03	30.69 $\pm$ 0.50
<i>G. maculatus</i>	2	20	68.82 $\pm$ 3.44	1.21 $\pm$ 1.21	0	20	68.71 $\pm$ 3.01	1.15 $\pm$ 0.23	24.53 $\pm$ 0.75
	4	20	69.66 $\pm$ 3.14	1.13 $\pm$ 1.13	0	20	70.23 $\pm$ 2.99	1.23 $\pm$ 0.23	26.17 $\pm$ 0.24
	10	20	68.99 $\pm$ 2.84	1.24 $\pm$ 1.23	0	20	69.07 $\pm$ 2.97	1.16 $\pm$ 0.22	29.16 $\pm$ 0.29
	16	20	68.56 $\pm$ 2.85	1.31 $\pm$ 1.31	0.33 $\pm$ 0.25	20	69.20 $\pm$ 2.36	1.46 $\pm$ 0.21	31.17 $\pm$ 0.29

Acclimation temperature (AT, °C), number of individuals (*n*), total length (TL, mm, mean  $\pm$  SD) and mean body mass (BM, g, mean  $\pm$  SD) of fishes are also indicated

species (*O. nigricans*: 84–89 mm mean total length (TL), *E. maclovinus*: 68–91 mm TL, *G. maculatus*: 69–74 mm TL) were placed individually into 20 l tanks at  $10 \pm 0.2^\circ\text{C}$ , fed daily, and the temperature was increased ( $n = 6$ ) or decreased ( $n = 6$ ) at a constant rate of  $1^\circ\text{C day}^{-1}$  until fish stopped feeding. The mean upper and lower feeding cessation temperatures were considered as the upper and lower chronic temperatures, respectively.

### Thermal tolerance

Thermal tolerance values of juvenile *Odontesthes nigricans*, *E. maclovinus* and *G. maculatus* at each experimental AT were estimated as Critical Thermal Maximum (CTmax) or Critical Thermal Minimum (CTmin) temperatures, and were derived using the Critical Thermal Methodology (CTM) originally described by Cowles & Bogert (1944), and later adapted for fish (Becker & Genoway, 1979; Paladino et al., 1980; Beitinger et al., 2000). This methodology involves fish being initially acclimated at a predetermined temperature and then subjected to a continuous dynamic temperature change until the point at which a predefined sub lethal endpoint is reached (Lutterschmidt & Hutchison, 1997; Beitinger & Lutterschmidt, 2011). In this work, the loss of equilibrium (LOE), defined as the inability of fish

to maintain dorso-ventral orientation for at least 1 min (Beitinger et al., 2000), was chosen as the endpoint of the experimental trials. The temperature change during the trials proceeded at a constant rate of  $0.3^\circ\text{C min}^{-1}$ , as is recommended for small-bodied fishes by Becker & Genoway (1979) and Beitinger et al. (2000), and similar to rates used with other species (Lutterschmidt & Hutchison, 1997; Currie et al., 1998; Chattherjee et al., 2004; Currie et al., 2004; Carveth et al., 2006; Beitinger & Lutterschmidt, 2011; Bilyk & DeVries, 2011).

For CTmax trials, juvenile fish ( $n = 20$  for each species and each AT, Table 1) were placed individually into 300 ml plastic enclosures, filled with water at appropriate AT, and suspended within a 50 l plastic test chamber. This chamber was provided with moderate aeration to prevent thermal stratification. Water in the test chamber was then heated by means of a Techne TU-20D (Bibby Scientific Limited, Stone, Staffordshire, UK), in such a way that temperature inside plastic enclosures increased at a constant rate of  $0.3^\circ\text{C min}^{-1}$  until LOE was observed in each fish.

For CTmin trials, juvenile fish ( $n = 20$  for each species and each AT, Table 1) were introduced, one each, into 300 ml plastic enclosures, filled with water at the appropriate AT. A constant cooling rate of  $0.3^\circ\text{C min}^{-1}$  was achieved within the enclosures by

placing them inside of a refrigeration unit (freezer). Water temperature change continued until LOE was observed in each fish.

When LOE was observed in both CT<sub>max</sub> and CT<sub>min</sub>, water temperature of experimental chambers was registered with a certified digital thermometer Lutron TM-917 provided with a Pt100 thermo resistance Luftman 3636 (Lutron Electronic Enterprise Co., Ltd., Taipei, Taiwan), each fish was measured (TL, mm  $\pm$  0.1 mm), weighed (body mass, BM, g  $\pm$  0.1 mg) and then returned to acclimation temperatures to assess survival after 24 h. Temperature changes continued until LOE was observed in all test fishes. All trials were performed during morning hours.

The CT<sub>max</sub> and CT<sub>min</sub> of juvenile fishes at each AT were calculated as the arithmetic mean temperature at which LOE was observed (Becker & Genoway, 1979; Beitinger et al., 2000).

The thermal tolerance niches of the species were quantified by means of dynamic thermal tolerance polygons (Bennett & Beitinger, 1997; Fangué & Bennett, 2003; Eme & Bennett, 2009; Dabruzzi et al., 2012). These thermal tolerance polygons were constructed by plotting CT<sub>max</sub> and CT<sub>min</sub> on AT and extrapolating the resulting regression lines outward to the chronic upper and chronic lower temperature limits. The resulting figures were expressed quantitatively using the areal units of °C<sup>2</sup>. Total polygonal areas were further divided into an intrinsic tolerance zone (i.e., thermal tolerance independent of previous thermal acclimation) as well as upper and lower acquired tolerance zones (i.e., thermal tolerance gained through acclimation) by dividing the polygon with horizontal lines originating at the intersection of the CT<sub>min</sub> and CT<sub>max</sub> regressions at their respective upper and lower chronic temperatures (Dabruzzi et al., 2012).

#### Acute thermal preferenda

The preferred temperatures (PT) of juvenile *O. nigricans*, *E. maclovinus* and *G. maculatus* ( $n = 20$  for each species and each AT), were measured in a custom-built thermal horizontal gradient chamber following Bettoli et al. (1985) and Aigo et al. (2014), with some modifications. This preference chamber consisted of a covered, 4 m length pipe made of white polyvinyl chloride (PVC) with an inner diameter of

160 mm. A longitudinal slot through the upper surface of the pipe allowed for fish observation. The chamber contained 65 l of water when in use.

The temperature gradient was established and maintained by thermal exchange with heated (40°C) and refrigerated ( $-2^{\circ}\text{C}$ ) water, that ran through two winding pipes (70 mm diameter and 2 m length each) along the floor of the chamber, originating from 'hot' and 'cold' extremes of the chamber, respectively. Heated water entered the chamber through the 'hot' extreme from a reservoir provided with two Haake DC5 thermoregulators (Thermo Electron Corporation, Karlsruhe, Germany) and refrigerated water entered through the 'cold' extreme from a LKB Bromma thermoregulator (LKB Bromma, Sollentuna, Sweden). The temperature extremes of the gradient ranged between 1 and 29°C (Table 2). Compressed air was bubbled through regularly spaced holes to ensure aeration and vertical water mixing. A net prevented fish from directly contacting the pipes.

For each trial, a single juvenile fish (Table 2) was placed into the preference chamber at a temperature close to the fish's AT. Data collection started when habituation to experimental conditions was observed. The juvenile fish was then allowed to select different PT, identified as a steady position within the tank for at least 5 min. The temperatures selected were monitored with a certified digital thermometer Lutron TM-917 provided with a Pt100 thermo resistance Luftman 3636 (Lutron Electronic Enterprise Co., Ltd., Taipei, Taiwan), in such a way as to disturb the fish as little as possible. Trials lasted from 90 to 120 min and were all performed during morning hours. Measure of PT for a given fish was the mean value of the preferred temperatures recorded during the trial.

#### Body condition

The condition of juvenile *O. nigricans*, *E. maclovinus* and *G. maculatus* individuals ( $n = 20$  for each species and each AT) held for 3 weeks at different AT, was analyzed through the Fulton's condition factor and the energy density (ED). Fulton's condition factor was calculated as  $K = [\text{BW}(\text{TL}^3)^{-1}]100$  (Ricker, 1975) and the ED was determined following Boy et al. (2009). The same fishes tested for thermal preference were sacrificed with deep anaesthesia after

**Table 2** Summary of experimental results on preferred temperatures (PT, °C, mean  $\pm$  SD) for *O. nigricans*, *E. maclovinus* and *G. maculatus* from Varela Bay (Beagle Channel, Patagonia)

Species	AT	Gradient	n	TL	BM	PT
<i>O. nigricans</i>	2	1.20–11.00	20	82.76 $\pm$ 5.11	2.50 $\pm$ 0.51	2.07 $\pm$ 0.43
	4	1.90–13.00	20	79.07 $\pm$ 8.99	2.10 $\pm$ 0.68	3.27 $\pm$ 0.75
	10	2.20–23.00	20	84.47 $\pm$ 8.26	2.75 $\pm$ 0.61	7.34 $\pm$ 1.73
	16	2.30–27.00	20	95.99 $\pm$ 7.30	2.47 $\pm$ 0.55	10.42 $\pm$ 2.10
<i>E. maclovinus</i>	2	1.50–14.00	20	85.90 $\pm$ 8.15	4.55 $\pm$ 1.35	2.63 $\pm$ 0.52
	4	1.70–15.00	20	84.91 $\pm$ 8.16	4.25 $\pm$ 1.19	4.93 $\pm$ 1.23
	10	2.30–23.00	20	83.39 $\pm$ 9.06	2.24 $\pm$ 1.47	10.75 $\pm$ 2.60
	16	2.30–28.00	20	81.97 $\pm$ 9.39	3.64 $\pm$ 1.52	17.90 $\pm$ 2.89
<i>G. maculatus</i>	2	1.60–14.00	20	68.97 $\pm$ 2.53	1.09 $\pm$ 0.24	3.18 $\pm$ 1.65
	4	1.90–14.00	20	69.55 $\pm$ 3.51	1.20 $\pm$ 0.29	3.97 $\pm$ 1.70
	10	2.50–22.00	20	68.25 $\pm$ 3.22	1.21 $\pm$ 0.21	8.19 $\pm$ 4.08
	16	2.90–27.00	20	69.14 $\pm$ 2.49	1.50 $\pm$ 0.35	14.71 $\pm$ 3.09

Acclimation temperature (AT, °C), gradient of temperature offered (°C), number of individuals (n), total length (TL, mm, mean  $\pm$  SD) and body mass (BM, g, mean  $\pm$  SD) of fishes are also indicated

each trial, measured (TL, mm  $\pm$  0.1 mm) and weighed (BM, g  $\pm$  2 mg). The dry body mass (DBM, g) of each fish was determined after drying at 70°C to a constant mass. Dry samples for calorimetric determinations were ground and pellets were made with a press (Parr 2812, Parr Instruments Company, Moline, IL, USA). The caloric content of each fish was obtained by burning pellets of 20–200 mg in a micro-bomb calorimeter (Parr 1425, Parr Instruments Company, Moline, IL, USA). The values obtained were corrected for ash and acid content and expressed as kJ/g AFDW (energy density, ED). Benzoic acid calibrations were carried out periodically.

#### Statistical analyses

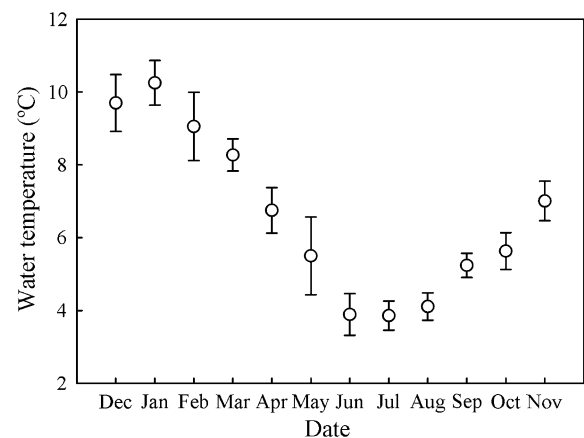
Simple linear regression analyses were performed to model the relationship of CTmax, CTmin, PT and DE on AT for each species. Statistical comparisons of CTmax, CTmin, PT, K condition factor and DE within and among species were made with one-way analysis of variance (ANOVA) or Kruskal–Wallis one-way analysis of variance on ranks (Kruskal–Wallis), followed by pairwise multiple comparison procedures (Tukey test or Dunn's test). Assumptions of normality and homoscedasticity were evaluated through Shapiro–Wilks and Levene

tests, respectively. All statistical decisions were based on  $\alpha = 0.05$  (Zar, 1984; Sokal & Rohlf, 1995).

## Results

### Varela Bay thermal profile

The thermal profile at 1 m depth in Varela Bay during 2011–2013 (Fig. 1) showed that mean monthly water temperatures had a maximum seasonal change of 6.39°C with highest values in January and lowest in



**Fig. 1** Mean ( $\pm$  SD) monthly water temperatures from Varela Bay recorded during 2011–2013



July. However, it is worth mentioning that in coastal areas where juveniles of the species are usually captured, extreme temperatures lower as 2°C and higher as 16°C were also registered (Lattuca, personal observations).

### Thermal acclimation limits

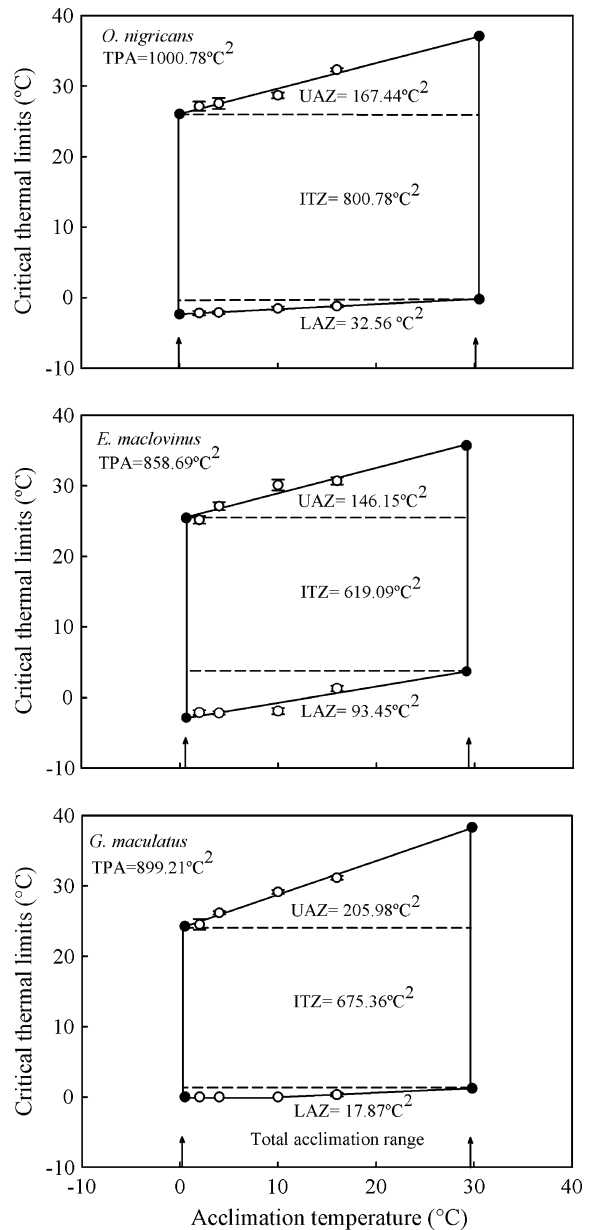
The thermal acclimation limits of each species were 30.50° and 0°C for *O. nigricans*, 29.20° and 0.70°C for *E. maclovinus* and 29.80° and 0.50°C for *G. maculatus*; thus, establishing their acclimation ranges in 30.50°, 28.50° and 29.30°C, respectively (Fig. 2).

### Thermal tolerance

In CTM trials, 2.7% of total fish tested did not recovered after 24 h; mortality probably occurred because fishes were not removed promptly after LOE was reached.

The CTmax and CTmin values obtained for juvenile *O. nigricans*, *E. maclovinus* and *G. maculatus* acclimated at 2, 4, 10 and 16°C are shown in Table 1. All fishes exhibited CTmax greater than 24.50°C and CTmin less than 1.70°C, regardless of the AT. While *O. nigricans* and *E. maclovinus* showed the higher CTmax values, 28.91 ± 2.35 and 28.27 ± 2.59°C (mean ± SD) respectively, *G. maculatus* tolerated water reaching 0°C during most of the CTmin trials and individuals only reached the LOE temperature when they were acclimated to 16°C (0.33 ± 0.25°C) (Table 1). As the absolute lowest temperature tolerated by many fish in freshwater may be lower than the freezing point, it is usually reported as 0°C owing to difficulties in achieving sub-0°C temperatures in freshwater (Beitinger & Bennett, 2000). Taking this in account, the CTmin of *G. maculatus* at 2, 4 and 10°C would be referred as 0°C from now on; however, these data will not be used for comparative purposes due to the difficulties in interpreting the importance of these temperatures in the life of *G. maculatus*.

Regression analyses found highly significant relationships between CTmax values and AT of each species; which were defined by the following equations:  
*O. nigricans*:  $CT_{max} = 0.36 \cdot AT + 26.05$ ,  $R^2 = 0.86$ ,  $n = 80$ ,  $P < 0.0001$   
*E. maclovinus*:  $CT_{max} = 0.36 \cdot AT + 25.19$ ,  $R^2 = 0.86$ ,  $n = 80$ ,



**Fig. 2** Thermal tolerance polygons for *O. nigricans*, *E. maclovinus* and *G. maculatus* from Varela Bay (Beagle Channel, Patagonia). Polygons were constructed from CTmax/CTmin values (white circle) (mean ± SD) measured across species' acclimation ranges and CTmax/CTmin values at extreme acclimation temperatures (black circle) extrapolated from regression analyses of CTmax/CTmin values on AT. The total polygonal area (TPA) is divided into an intrinsic tolerance zone (ITZ) and upper and lower acquired tolerance zones (UAZ, LAZ). Arrows indicate the total acclimation range for each species

$P < 0.0001$ . *G. maculatus*:  $CT_{max} = 0.48 \cdot AT + 24.03$ ,  $R^2 = 0.95$ ,  $n = 80$ ,  $P < 0.0001$ .

In the same way, regression analyses of  $CT_{min}$  values on AT showed significant relationships and were defined as: *O. nigricans*:  $CT_{min} = 0.07 \cdot AT - 2.34$ ,  $R^2 = 0.74$ ,  $n = 80$ ,  $P < 0.0001$ . *E. maclovinus*:  $CT_{min} = 0.23 \cdot AT - 3.01$ ,  $R^2 = 0.73$ ,  $n = 80$ ,  $P < 0.0001$ . *G. maculatus*:  $CT_{min} = 0.06 \cdot AT - 0.57$ ,  $R^2 = 0.53$ ,  $n = 40$ ,  $P < 0.001$ .

These regression analyses revealed that *G. maculatus* gained more heat tolerance for every 1°C change in acclimation than marine species. On the contrary, *E. maclovinus* gained 3.3 and 3.8-fold more cold tolerance for every 1°C change in acclimation than *O. nigricans* and *G. maculatus*, respectively.

Differences in CTM values obtained at different AT were analyzed within and among species. For all the species,  $CT_{max}$  values increased with increasing AT. When comparing  $CT_{max}$  values within each species, *O. nigricans* showed significant differences among different AT (Kruskal–Wallis,  $P < 0.0001$ ). However, pairwise multiple comparison procedures did not find significant differences between 2 and 4°C (Dunn's test,  $P > 0.0001$ ). Moreover, *E. maclovinus* (ANOVA,  $P < 0.0001$ ) and *G. maculatus* (Kruskal–Wallis,  $P < 0.0001$ ) also showed a significant increase in  $CT_{max}$  values with increasing AT, being all pairwise multiple comparison significantly different for *E. maclovinus* (Tukey test,  $P < 0.0001$ ) and *G. maculatus* (Dunn's test,  $P < 0.0001$ ).

Regarding the tolerance to low temperatures, all the species increased their  $CT_{min}$  values with increasing AT.  $CT_{min}$  values for *O. nigricans* decreased significantly with decreasing AT (ANOVA,  $P < 0.0001$ ), though pairwise multiple comparison procedures did not found significant differences between 2 and 4°C (Tukey test,  $P > 0.0001$ ). *Eleginops maclovinus* showed significantly different  $CT_{min}$  values (ANOVA,  $P < 0.0001$ ), whereas only values registered at 16°C differed from those observed at 2, 4 and 10°C, when compared in pairs (Tukey test,  $P < 0.0001$ ). Conversely, *G. maculatus* tolerated water freezing during  $CT_{min}$  trials at 2, 4 and 10°C, and reached the LOE temperature with an AT = 16°C.

Comparisons of  $CT_{max}$  values at same AT exhibited significant differences among species, regardless of their thermal history (AT = 2°C, ANOVA,  $P < 0.0001$ ; AT = 4, 10, 16°C, Kruskal–

Wallis,  $P < 0.0001$ ). Pairwise multiple comparison procedures showed that all  $CT_{max}$  were significantly different when fish were acclimated to 2°C (Tukey test,  $P < 0.0001$ ) and 10°C (Dunn's test,  $P < 0.0001$ ). Whereas, neither marine species acclimated to 4°C (Dunn's test,  $P > 0.0001$ ) nor *E. maclovinus* and *G. maculatus* acclimated to 16°C (Dunn's test,  $P > 0.0001$ ) show significant different  $CT_{max}$  values.

When comparing  $CT_{min}$  values of *O. nigricans* and *E. maclovinus* registered at 2, 4 and 10°C, they only differed significantly when fishes were acclimated to 10°C (Mann–Whitney,  $P < 0.0001$ ), being the latter species more tolerant to low temperatures. At the highest AT (16°C), all species reached the LOE temperature, and the between species comparisons of  $CT_{min}$  showed significant differences (Kruskal–Wallis,  $P < 0.0001$ ), even when compared in pairs (Dunn's test,  $P < 0.0001$ ), being *O. nigricans* the most tolerant species to cold and *G. maculatus* the least tolerant.

Finally, the thermal tolerance polygon of each species was determined from  $CT_{max}$  and  $CT_{min}$  values across the range of possible acclimation temperatures. All the species exhibited intermediate to large tolerance polygons. Particularly, *O. nigricans* showed the largest polygon, with a total area of 1000.78°C<sup>2</sup>. The intrinsic thermal acclimation zone was 800.78°C<sup>2</sup> and represented 80.02% of the thermal polygon. The upper and lower acquired thermal tolerance zones represented 16.73 and 3.25% of the fish thermal niche, respectively, and comprised 200°C<sup>2</sup> of the acclimation area. The polygon of *E. maclovinus* was the smallest and had a total area of 858.69°C<sup>2</sup>. Its intrinsic thermal acclimation zone was 619.09°C<sup>2</sup> and accounted for 72.10% of the overall thermal polygon. The upper and lower acquired thermal tolerance zones encompassed 239.60°C<sup>2</sup> of the total acclimation area and represented 17.02 and 10.88% of the fish' thermal polygon, respectively. *Galaxias maculatus* showed a total polygonal area of 899.21°C<sup>2</sup>, with an intrinsic thermal acclimation zone of 675.36°C<sup>2</sup> that accounted for 75.10% of the thermal polygon. The upper and lower acquired thermal tolerance zones comprised 223.85°C<sup>2</sup> of the acclimation area and represented 22.91% and 1.99% of the fish thermal niche, respectively.

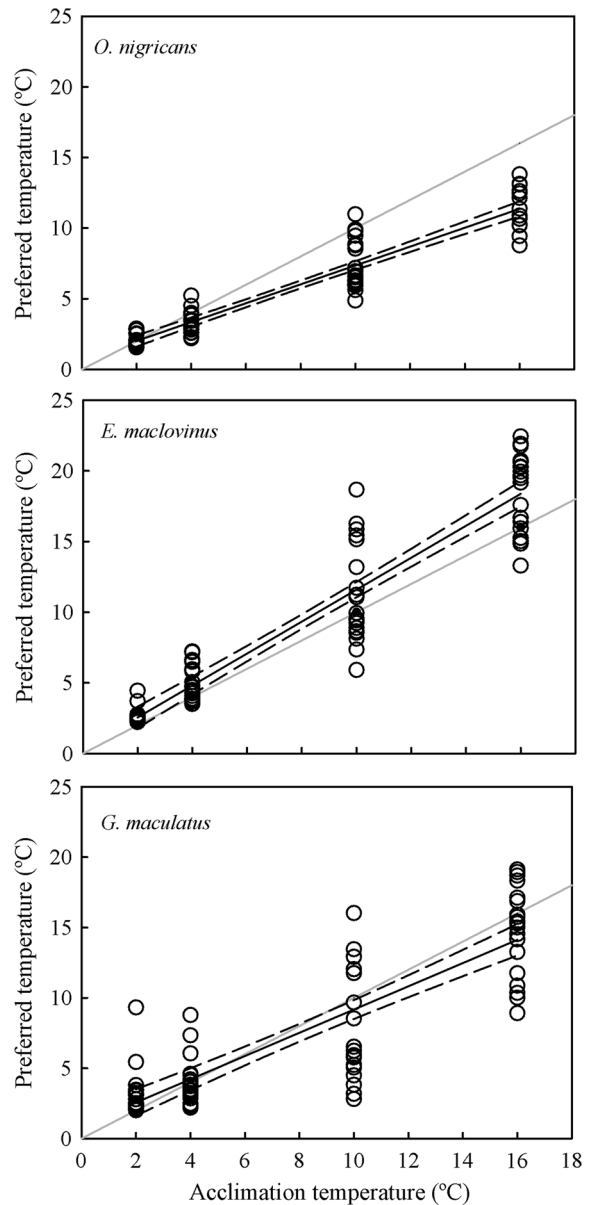
## Thermal preference

When *O. nigricans* and *G. maculatus* were placed into the thermal gradient, they moved randomly along the experimental chamber for nearly 20–30 min until they settled. Conversely, *E. maclovinus* individuals showed substantially reduced exploratory movements (5–10 min). For all species, exploratory movements along the thermal gradient increased with increasing AT.

For all the species, positive relationships between PT and AT were found. Regression analyses between PT values and AT of each species were defined as follows: *O. nigricans*:  $PT = 0.67 \cdot AT + 0.67$ ,  $R^2 = 0.86$ ,  $n = 80$ ,  $P < 0.0001$ . *E. maclovinus*:  $PT = 1.13 \cdot AT + 0.29$ ,  $R^2 = 0.94$ ,  $n = 80$ ,  $P < 0.0001$ . *G. maculatus*:  $PT = 0.83 \cdot AT + 0.91$ ,  $R^2 = 0.73$ ,  $n = 80$ ,  $P < 0.0001$ .

The individual mean values of PT for each species at different AT are shown in Fig. 3 and grand means and standard deviations of PT, calculated from the individual mean values, are shown in Table 2. Differences in PT values obtained at different AT were analyzed within and among species. The comparison of PT values within each species revealed that *O. nigricans* chose significantly different PT at different AT (Kruskal–Wallis,  $P < 0.0001$ ); however, pairwise comparisons did not show differences between PT values obtained at 10 and 16°C (Dunn's test,  $P > 0.0001$ ). For *E. maclovinus*, PT values also differed significantly (Kruskal–Wallis,  $P < 0.0001$ ), even though differences between PT values obtained at 2 and 4°C and differences between PT values at 10 and 16°C were not observed (Dunn's test,  $P > 0.0001$ ). Finally, *G. maculatus* selected different PT at different AT (Kruskal–Wallis,  $P < 0.0001$ ), too. For this species, PT values at 2 and 4°C were not statistically different (Dunn's test,  $P > 0.0001$ ).

Comparisons of PT at same AT showed significant differences among species, regardless of their thermal history (AT = 2, 4 and 10°C, Kruskal–Wallis,  $P < 0.0001$ ; AT = 16°C, ANOVA,  $P < 0.0001$ ). Particularly, when AT = 2°C, *O. nigricans* showed the lowest PT and no significant differences were found between *E. maclovinus* and *G. maculatus* (Dunn's test,  $P > 0.0001$ ). At 4°C, *O. nigricans* selected again the lowest PT but this value did not differ significantly from that of *G. maculatus* (Dunn's test,  $P > 0.0001$ ). At 10°C, these two species did not

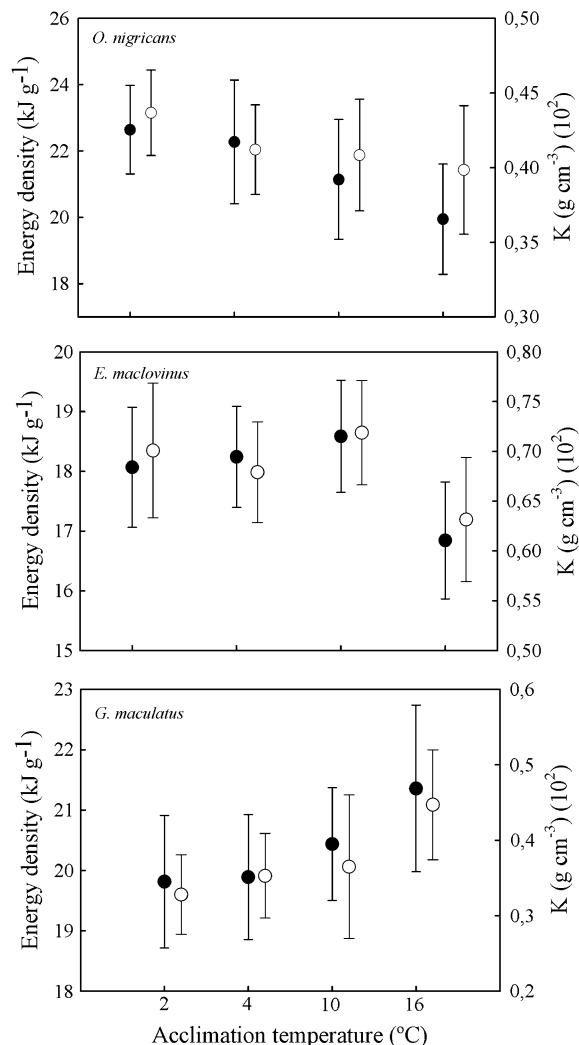


**Fig. 3** Regressions analyses of preferred temperatures (PT) on experimental acclimation temperatures (AT) for *O. nigricans*, *E. maclovinus* and *G. maculatus* from Varela Bay (Beagle Channel, Patagonia). Dashed lines indicate 95% confidence intervals. PT = AT lines (grey) are also indicated

choose significant different PT either (Dunn's test,  $P > 0.0001$ ), whereas *E. maclovinus* selected the highest PT. At the highest AT (16°C), pairwise comparisons exhibited significant differences among PT of all species (Tukey test,  $P < 0.0001$ ).

## Body condition

In terms of the Fulton's condition factor, *O. nigricans*, *E. maclovinus* and *G. maculatus* acclimated at different AT showed different patterns. *Odontesthes nigricans* significantly decreased its K values with increasing AT (ANOVA,  $P < 0,001$ , Fig. 4); but only K registered at 2°C differed from that registered at 16°C, when compared in pairs (Tukey test,  $P < 0.0001$ ). *Eleginops maclovinus* showed significantly different K (ANOVA,  $P < 0,001$ , Fig. 4), but



**Fig. 4** Mean ( $\pm$  SD) of Fulton's condition factor (K,  $\text{g cm}^{-3}10^2$ , black circle) and energy density values (ED,  $\text{kJ g}^{-1}$  AFDW, white circle) at different acclimation temperature (AT) for *O. nigricans*, *E. maclovinus* and *G. maculatus* from Varela Bay (Beagle Channel, Patagonia)

when compared in pairs only AT = 16°C was significantly lower than all the other AT (Tukey test,  $P < 0.0001$ ). *Galaxias maculatus* significantly increased its K values with increasing AT (ANOVA,  $P < 0,001$ , Fig. 4), being K registered at 16°C significantly higher than all the other AT, when compared in pairs (Tukey test,  $P < 0.0001$ ).

ED values of *O. nigricans*, *E. maclovinus* and *G. maculatus* at different AT also showed interspecific differences, but each species showed trends similar to those of the K condition factor. In particular, *O. nigricans* significantly decreased its ED with increasing AT (ANOVA,  $P < 0,001$ , Fig. 4); however, only ED registered at 2°C differed from that registered at 16°C, when compared in pairs (Tukey test,  $P < 0.0001$ ). *Eleginops maclovinus* showed significantly different ED (ANOVA,  $P < 0,001$ , Fig. 4), but when compared in pairs only AT = 16°C was significantly lower than all the other AT (Tukey test,  $P < 0.0001$ ). *Galaxias maculatus* showed increasing ED with increasing AT (ANOVA,  $P < 0.001$ , Fig. 4); whereas only ED registered at 16°C differed from those observed at 2 and 4°C, when compared in pairs (Tukey test,  $P < 0.0001$ ).

Comparisons of ED at same AT exhibited significant differences among species, regardless of their thermal history (AT = 2, 4, 16°C, ANOVA,  $P < 0.0001$ ; AT = 10°C, Kruskal–Wallis,  $P < 0.0001$ ). Moreover, pairwise multiple comparison showed that all ED were significantly different when fish were acclimated to same AT (AT = 2, 4, 16°C, Tukey test,  $P < 0.0001$ ; AT = 10°C, Dunn's test,  $P < 0.0001$ ); showing always *O. nigricans* the highest ED and *E. maclovinus* the lowest values.

## Discussion

In this study, we conducted an overall analysis of thermal responses of three key species inhabiting estuarine areas of the Beagle Channel, their southernmost limit of the distribution. Within the total thermal acclimation ranges, the thermal windows of all species were broad and, in general, increased with increasing AT. *Odontesthes nigricans* had the largest thermal window of the three species (33.67°C, AT = 16°C) while *G. maculatus* had the lowest (24.53°C, AT = 2°C). However, it must be kept in mind that diadromous *G. maculatus* showed the

ability to survive freezing temperatures and since its CT<sub>min</sub> values were reported as 0°C owing to difficulties in achieving < 0°C temperatures in freshwater (Beitinger & Bennett, 2000). Present thermal windows indicate that *O. nigricans*, *E. maclovinus* and *G. maculatus* can cope with a wide range of environmental temperatures, covering, and exceeding, the entire seasonal temperature range seen in Varela Bay (Fig. 1).

To date, no published CTM values for these species were available. Hence, present values obtained at AT of 2, 4, 10 and 16°C represent the only CTM data available for *O. nigricans*, *E. maclovinus* and *G. maculatus*. The heat tolerance of 11 Antarctic notothenioids, with CT<sub>max</sub> ranging from 9.50 to 16.17°C, was determined by Bilyk & DeVries (2011). When 8 of these species were warm acclimated to 4°C, all showed a significant increase in their CT<sub>max</sub>, with several species showing plasticity comparable in magnitude to some far more eurythermal fishes. Nevertheless, their CT<sub>max</sub> values were still well below those of the non-Antarctic notothenioid *E. maclovinus* from Tierra del Fuego. Information about CTM of galaxiid species is also scarce; the most extensive work, by Richardson et al. (1994), compiled CT<sub>max</sub> values from species of New Zealand acclimated to 16°C. They exhibited values ranging from 28°C (*Galaxias brevipinnis* Günther, 1866) to 31.70°C (*G. maculatus*) in freshwater. Cussac et al. (2004) also reported a broad tolerance, from 0°C to more than 30°C, for landlocked *G. maculatus* from northern Patagonia. Among atherinopsids, *Menidia menidia* (Linnaeus, 1766), a species from the North-Western Atlantic Ocean, displayed a linear tolerance of 1.4 to 32.60°C, see Brett (1970) in Beitinger & Bennett (2000). In addition, Strüssmann et al. (2010) reviewed the implications of climate change for the reproductive capacity and survival of the family Atherinopsidae; indicating the acceleration, shortening or overall disruption of spawning activity and also highly skewed sex ratios and partial or total loss of fertility.

The regressions of CT<sub>max</sub> and CT<sub>min</sub> on AT of each species showed indicated that marine species, *O. nigricans* and *E. maclovinus*, and diadromous *G. maculatus* (in freshwater) have the ability to acclimate to different temperatures. Within each species, slopes relating CT<sub>max</sub> to AT were remarkably larger than those relating CT<sub>min</sub> to AT, suggesting that AT

has a greater influence on tolerance to high rather than low temperatures. Slopes also indicated that *G. maculatus* gained more heat tolerance for every 1°C increase in acclimation than marine species, while *E. maclovinus* gained more cold tolerance for every 1°C drop in acclimation than *O. nigricans* and *G. maculatus*.

Attributes of thermal tolerances polygons, such as relative size, position and shape, provide important insights into fish ecology and distribution and have been used to identify temperature-related survival tactics (Bennett & Beitinger, 1997; Fangué & Bennett, 2003). In this work, the species analyzed exhibited intermediate to large thermal tolerance polygons, centrally positioned, characterizing them as eurythermal fishes. Furthermore, all the species showed moderately large intrinsic tolerances (72.10–80.02%) that allow for activity across a considerable temperature range while still preserving moderate abilities to acquire additional heat (16.73–22.90%) and small abilities to acquire additional cold (2.00–10.88%) tolerance through acclimation. In particular, higher acclimation-dependent areas were 1.56–11.45 times greater than lower acclimation-dependent areas, indicating that acclimation plays a major role in high rather than in low thermal tolerance and that these fish maintain consistently high levels of cold tolerance. Polygonal profiles of this type reflect a thermal tolerance strategy suited to environments subjected to thermal cycles of relatively high amplitude and duration, as those seen in Varela Bay. Eme & Bennett (2009) reported that overall polygon area (°C<sup>2</sup>) provides a convenient and useful comparative index of eurythermicity between species. By comparison, *O. nigricans* exhibited a larger total polygon area when compared to *M. menidia* (699°C<sup>2</sup>, Brett, 1970) in Beitinger & Bennett (2000). Additionally, among galaxiids, *Galaxias platei* Steindachner, 1898 displayed a tolerance polygon of 876.02°C<sup>2</sup> (Barrantes et al., 2017), very similar in size, shape and position to diadromous *G. maculatus* in freshwater. Regarding to notothenioid species, no data on thermal polygons are available in order to compare with *E. maclovinus*.

Whilst *O. nigricans*, *E. maclovinus* and diadromous *G. maculatus* (in freshwater) tolerate a wide range of temperatures, they selected certain PTs that were influenced by their previous thermal history. The increase of AT from 2 to 16°C shifted upward PT



values. The determination of the acute thermal preferenda of the species did not allow estimating a final temperature preferendum (temperature at which the preferred temperature is equal to the acclimation temperature), with biological meaning, that could give a good indication of the optimum temperature for growth (Fry, 1947; Jobling, 1981). However, *O. nigricans*, *E. maclovinus* and *G. maculatus* were able to experiment changes, presumably occurring at the tissue, cellular and subcellular level (Jobling, 1994), that allow them to adapt well to the different temperatures within their thermal tolerance niches.

Johnson & Kelsch (1998) have developed a model that predicts classes of temperature-preference relationships on the basis of the amplitude of environmental thermal cycles to which species have recently been exposed. Thus, the relationship between preference-temperature could be positive, negative or independent. In the present study, the positive PT–AT relationships exhibited by the three species, held at different AT for 3 weeks, could be related to the experienced naturally occurring thermal cycles of relatively high amplitude and duration (long-cycle) in the environment. According to the model, the species studied here can also be characterized as eurytherms. This arises from the prediction that because time is required for acclimation to occur, only species that evolved experiencing gradual long term temperature changes (e.g., temperate species) would have the time necessary to make metabolic changes that would result in substantial shifts in PT or ranges of tolerance.

Although the species showed positive relationships between PT and AT, some inter-specific differences in the selected PT values were observed in relation to the different AT. While *O. nigricans* preferred lower temperatures, *E. maclovinus* preferred higher temperatures and diadromous *G. maculatus* in freshwater selected either higher or lower PT, when comparing to the corresponding AT. These responses could be related to the body conditions achieved by the species at each temperature, which were analyzed through the Fulton's condition factor and the ED. The condition factor can be used for comparing the condition, "fatness", or "well-being" of fish, based on the assumption that heavier fish of a given length are in better condition (Tesch, 1968; Froese, 2006). Besides, the ED provides an approximation to their condition to face situations of high energy demand,

such as processes of climate change (Rottiers & Tucker, 1982; Shearer, 1994; Ludsins & DeVries, 1997). Extreme temperatures are known to increase metabolism and energetic demands (Hochanka & Somero, 1971), so if food supply is kept constant, as in the present study, body condition is likely then to deteriorate over time (Mora & Maya, 2006). According to this, *O. nigricans* showed a decrease in its K and ED with higher AT, promoting then the selection of lower PTs in relation to the experienced AT. On the contrary, diadromous *G. maculatus* in freshwater decreased its K and ED with decreasing AT. Urbina & Glover (2013) and Boy et al. (2017) suggested that this species has the capability to sustain the metabolic rate under a broad range of external conditions at the expense of obtaining energy from somatic reserves. However, the lowest AT appeared to be the least favourable to support the energetic demands, explaining the selection of higher PT at 2°C. Regarding *E. maclovinus*, no clear explanation could be found in this sense, as its body and energetic condition remained rather constant, or only slightly decreasing, with increasing AT.

Impacts on species of ongoing climate change is likely to vary geographically (Root et al., 2003; Thomas et al., 2004) and is predicted to increase with latitude, in parallel with the rate of warming (Gille, 2002). Particularly, the Beagle Channel hosts an ichthyofauna with diverse origins (Atlantic, Pacific and Antarctic) that has experienced different evolutionary histories. These differences could have generated strong variations in the thermal sensitivity of species (Cussac et al., 2009) and probably also differences in their adaptive capacities in the face of climate change. Nevertheless, present results revealed that *O. nigricans*, *E. maclovinus* and *G. maculatus*, despite their different evolutionary histories, exhibited similar thermal responses to changing environmental temperatures.

In general, species distributions are expected to slide increasingly poleward with warming to maintain their preferred temperature range (Hickling et al. 2006). Taking this into account, northern populations of *O. nigricans*, *E. maclovinus* and *G. maculatus* could slide their distributions southward as a consequence of increasing temperatures. Yet, in the Southern Hemisphere, species could fail to disperse southward from lower latitudes (Last et al., 2011; Wernberg et al. 2011), as there is a limit to how far

south the ranges of temperate species will be able to shift before they are blocked by the Southern Ocean (Fraser et al. 2012). However, the southernmost populations of studied species from the Beagle Channel, could still experience enhanced performances (assumed to be a proxy for fitness), because of moderate warming, as they are living in environments that are widely cooler than their CT<sub>max</sub> (Deutsch et al., 2008; Komoroske et al., 2014). Therefore, it could be suggested that these fishes are more likely to be influenced by the indirect consequences of climate change (e.g., habitat degradation or changes in trophic structure) rather than direct temperature mortality (Munday et al., 2008; Eme & Bennett, 2009).

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