



# Thermal responses of two sub-Antarctic notothenioid fishes, the black southern cod *Patagonotothen tessellata* (Richardson, 1845) and the Magellan plunderfish *Harpagifer bispinis* (Forster, 1801), from southern South America

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## Abstract

The Notothenioidei are a typical example of stenothermal fishes since most species have evolved and lived in Antarctic waters, where the water temperature is low and stable. This fact enabled them to evolve physiological characteristics related to cold. Nevertheless, some species came out of Antarctic waters a few million years ago and coped with more variable thermal regimes. This work aims to determine the thermal tolerance and preference of two sub-Antarctic notothenioid species found in Southern South America, *Patagonotothen tessellata* and *Harpagifer bispinis*, adding valuable information about thermal adaptation mechanisms. Experiments were conducted after exposing their juveniles for three weeks at 4, 7, 10 and 12 °C. Their thermal tolerance limits were established using the Critical Thermal Methodology and their acute thermal preferenda, employing a horizontal thermal gradient tank. Fishes acclimated to different exposure temperatures had small to intermediate thermal tolerance polygons (*P. tessellata*: 593.85 °C<sup>2</sup>, *H. bispinis*: 475.40 °C<sup>2</sup>) and positive relationships between preferred and acclimation temperatures. The Final Temperature Preferenda were estimated to be 14.25 °C for *P. tessellata* and 13.05 °C for *H. bispinis*, allowing to characterize them as cold eurythermal species, with *P. tessellata* more tolerant to heat and *H. bispinis* more tolerant to cold. Their different thermal sensitivities are in agreement with their different thermal histories and distributions. In a climate change context, the increase of sea surface temperatures is likely to reduce the northern boundaries of their distributions. Conversely, it can potentially enhance both species' performances at their southernmost distribution limits since those environments are cooler than their maximum thermal tolerances.

**Keywords** Nototheniidae · Harpagiferidae · Patagonia · Thermal tolerance polygons · Acute thermal preferenda · Climate change

## Introduction

The Beagle Channel is a unique subpolar marine ecosystem located in the southern part of South America (Patagonia) connecting the waters of the Pacific and the Atlantic Oceans (Isla et al. 1999; Gordillo et al. 2008). Owing to its location, the geographic area hosts a mixture of marine ichthyofauna with different origins that have experienced distinct evolutionary histories (Fernández et al. 2018). The most dominant fish group found in the Beagle Channel is the suborder Notothenioidei (Lloris and Rucabado 1991;

Vanella et al. 2007). Among them, the genus *Patagonotothen* (Nototheniidae) is the second most species-rich genus with 15 species (Matschiner et al. 2015). With only one exception, all *Patagonotothen* species are found exclusively in non-Antarctic waters around the Patagonian region and Malvinas/Falkland Islands (Eastman 2005). The initial radiation of the genus has been estimated at around 3 Ma and most likely occurred in non-Antarctic waters (Ceballos et al. 2019). Drivers involved in this radiation remain unknown; however, they are unlikely to be related to the antifreeze glycoproteins (AFGPs) since the temperature of Patagonian waters is usually well above freezing point (Palma et al. 2008). Moreover, it has also been shown that some *Patagonotothen* species have secondarily lost the ability to produce AFGPs (Cheng et al. 2003; Cheng and Detrich 2007). In

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particular, the black southern cod *Patagonotothen tessellata* (Richardson, 1845) inhabits shallow subtidal areas along the Atlantic (up to 47°S) and Pacific coasts of the Patagonian region (up to 41°S) and also Malvinas/Falklands Islands, with Tierra del Fuego being its southernmost distribution limit (Nakamura et al. 1986; Lloris and Rucabado 1991; Reyes and Hüne 2012). *Patagonotothen tessellata* is very abundant in the region (Moreno and Jara 1984) and plays an essential role in the trophic webs, representing a major link between lower and higher levels of the food web (Riccialdelli et al. 2017).

The genus *Harpagifer* (Harpagiferidae) includes 10–12 species, according to different authors (Duhamel et al. 2014; Hüne et al. 2014), and is present on both sides of the Antarctic Polar Front (APF). Hüne et al. (2014) proposed that the climatic and oceanographic changes during the Pleistocene (i.e., the Great Patagonian Glaciation, Rabassa 2008) and the northward migration of the APF produced the ideal conditions for the colonization of southern South America by *Harpagifer*, from Antarctica via the Scotia Arc Islands. In particular, the Magellan spiny plunderfish *Harpagifer bispinis* (Forster, 1801) inhabits the sublittoral and intertidal zones of Tierra del Fuego Island and the Magellan region in southern South America up to 46°S (Hureau 1990; Lloris and Rucabado 1991; Reyes and Hüne 2012; Hüne and Vega 2016). It can be found in kelp forests (Cruz-Jiménez 2019) or under rocks in tide pools in the low and medium level of the intertidal zone (Hureau 1990). Living in these tide pools can be interpreted as an ecophysiological challenge, as they are usually frozen during winter and exposed to reduced salinities by the flow of small freshwater input during ice melting (Llompert et al. 2020). Pérez et al. (2003) provided histological evidence of aglomerular kidney in *H. bispinis*. They also inferred that this characteristic might be adaptive in terms of AFGPs conservation since aglomerularism is consistent with the conservation of small molecules, including the small AFGPs size isoforms. Thus, their presence might help them to cope with extreme environmental conditions. As *P. tessellata*, *H. bispinis* also plays an essential ecological role since it preys upon a wide variety of trophic niches (Hüne and Vega 2016; Riccialdelli et al. 2017), and it is consumed by higher predators (Hureau 1990).

Differences in the evolutionary histories of *P. tessellata* and *H. bispinis* could have generated substantial variations in their thermal sensitivity as well as differences in their adaptive capacities to climate change (CC) (Cussac et al. 2009). Ocean temperatures are forecasted to increase by as much as 2 °C in the next 100 years (IPCC 2014; Shultz et al. 2016). Fishes may respond to such changes in environmental temperatures by altering their physiology or their behavior, by selecting specific habitats or by shifting their distributions to keep their body temperature within physiologically acceptable ranges (Killen 2014; Speaks et al.

2012). Therefore, the study of thermal responses of fishes from southern South America (Patagonia) has great potential for understanding and assessing the effects of CC, which are appearing faster in high southern latitudes (Gille 2002).

Recent studies have highlighted the importance of determining the physiological limits of fishes to changes in certain environmental variables, such as temperature, in order to project future species distributions and productivity, based on future climate scenarios (Pörtner and Peck 2010; Burrows et al. 2011; Marras et al. 2015). The determination of the Critical Thermal Minimum (CTmin) and Maximum (CTmax) is generally employed to assess the thermal tolerance limits of fishes (Beitinger et al. 2000; Beitinger and Lutterschmidt 2011). CTmin and CTmax are the temperatures at which fishes are unable to escape conditions that will ultimately lead to thermal death (Beitinger and Lutterschmidt 2011; Pörtner and Peck 2010). Beyond these critical temperatures, organisms are unable to supply sufficient oxygen to metabolically demanding tissues (oxygen- and capacity-limited thermal tolerance) (Pörtner and Knust 2007). Determining CTmin and CTmax for organisms at different exposure temperatures provides the data needed to construct CTM-polygons (areas, °C<sup>2</sup>) of temperature tolerance at two or more exposure temperatures (Manríquez et al. 2020). These polygons are graphical representations of the thermal niche of species (Magnuson et al. 1979; Bennett and Beitinger 1997) that provide valuable information about their physiology and ecology (Eme and Bennett 2009). They also allow making comparisons of the thermal ranges of different species (Elliot 1991; Bennett and Beitinger 1997; Elliot 2010). The larger the polygonal area, the wider the range in thermal tolerance of the species (Calosi et al. 2008). Within their thermal tolerance range, organisms select a temperature in which their metabolic functions and processes operate with the highest efficiency (Schurmann et al. 1991). That behaviorally selected temperature, termed preferred temperature (PT, Fry 1947; Reynolds and Casterlin 1979), supplies the physiological framework for fishes to diminish the impact of spatial and temporal variation of water temperature, permitting them to withstand the fluctuating environment (Shuter et al. 2012). These PT 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 by the recent thermal history (Kelsch and Neill 1990; Jobling 1994). Such temperatures are also used to calculate the Final Temperature Preference (FTP), which correlates with the optimum temperature for growth, defined as the temperature at which growth rate is highest when the fish are reared under conditions of maximum or excess feeding (Jobling 1981).

Most of the studies dealing with thermal tolerance of notothenioid fishes were performed in Antarctic species (Somero and DeVries 1967; Podrabsky and Somero 2006;

Bilyk and DeVries 2011; Peck et al. 2014). However, there is not much information available on the thermal responses of sub-Antarctic notothenioid fishes. Lattuca et al. (2018) described the thermal tolerance and preference of *Eleginops maclovinus* (Cuvier, 1830) from the Beagle Channel and characterized it as a eurythermal species. This work aims to analyze the thermal responses of two sympatric sub-Antarctic notothenioid species with different evolutionary histories, *P. tessellata* and *H. bispinis*, at their southernmost distribution limit. Understanding their thermal tolerances and preferred temperatures can provide concrete data to analyze the vulnerability of these species and generate scenarios of changes in the fish community (Pörtner and Peck 2010).

## Materials and methods

### Ethics statements

*Patagonotothen tessellata* and *H. bispinis* are not protected under wildlife conservation laws (local legislations, International Union for Conservation of Nature -IUCN-, or Convención sobre el Comercio Internacional de Especies Amenazadas de Fauna y Flora Silvestre -CITES-).

Sampling protocols and experiments on *P. tessellata* and *H. bispinis* were approved by the Ethics Committee of Austral Center for Scientific Research (CIB – CADIC).

### Fish sampling and acclimation

Samplings were performed during late spring 2018 and early summer 2019 in coastal waters of the Beagle Channel. *Patagonotothen tessellata* juveniles were collected using a seine net (25 m long, 1.5 m high and 3 mm stretched mesh) in the shallower littoral zone (< 1 m depth) of Varela Bay (54°52' S, 67°16' W). *Harpagifer bispinis* juveniles were collected manually under rocks in tidal pools and during low tides periods in Tierra del Fuego National Park and adjacent bays (54° 51' S, 68° 25' W). Individuals of both species were transported in well-aerated seawater 100-L tanks to the laboratory at the Austral Center for Scientific Research (CADIC—CONICET), where the experiments were carried out.

At the laboratory, fishes were acclimatized to captivity conditions before undergoing experimental trials. For fish maintenance and throughout the experiments, filtered environmental seawater (1 µm, Hidroquil, Buenos Aires, Argentina), with a salinity of  $28 \pm 0.5$ , pH of  $8.02 \pm 0.2$  and O<sub>2</sub> concentration near saturation levels (between 8.86 and 10.70 mg L<sup>-1</sup> depending on water temperature) was used. Water quality was maintained by partial water changes (~ 50% of total volume), at the corresponding AT, every other day. Physicochemical variables were monitored using

a multiparameter meter Hanna HI9828 (Hanna Instruments SRL, RI, USA). Ammonia, nitrite, and nitrate were monitored twice a week with NH<sub>3</sub>/NH<sub>4</sub><sup>+</sup>, NO<sub>2</sub><sup>-</sup> and NO<sub>3</sub><sup>-</sup> kits (Tetra, VA, USA) and kept under 0.3, 0.8 and 12.5 mg L<sup>-1</sup>, respectively.

After a month, groups of fish of homogenous sizes of each species were selected and exposed during 3 weeks to 4 acclimation temperatures (AT = 4, 7, 10 and 12 °C) that correspond to mean winter (4 °C), mean summer (10 °C) and mean annual (7 °C) water temperatures, and another temperature 2 °C higher than mean summer value (12 °C). All aquaria were placed in a cold room set at 4 °C. Then, the appropriate AT in each aquarium was reached by increasing the temperature at a rate of 1 °C day<sup>-1</sup> using electronic aquarium heaters (Atman J-25, Yangzhou Anipet Co., Ltd., Jiangsu, China) connected to heat controllers ( $\pm 0.2$  °C, Deksor, TC6003PD, Buenos Aires, Argentina). Fishes were held at a density of 1 individual L<sup>-1</sup> in 20-L tanks containing seawater with the same characteristics described above. The light regime was 12:12 h light:dark, and it was reached at a rate of 1 h day<sup>-1</sup>. Fishes were fed with chopped hake muscle offered ad libitum every other day, and feeding was stopped 24 h in advance of experimental trials. No visual signs of stress were observed during the acclimation period.

### Thermal acclimation limits

The total thermal acclimation ranges of *P. tessellata* and *H. bispinis* juveniles were assessed by estimating their chronic upper and chronic lower temperatures limits (Dabruzzi et al. 2012; Lattuca et al. 2018). For each species, 12 fish (*P. tessellata*,  $54.49 \pm 0.45$  mm TL,  $1.29 \pm 0.06$  g BM; *H. bispinis*,  $55.78 \pm 0.50$  mm TL,  $3.79 \pm 0.18$  g BM) from the native acclimatization pool were placed individually in 20-L aquaria at  $10 \pm 0.2$  °C. The temperature was then increased ( $n = 6$ ), using electronic aquarium heaters (Atman J-25 300 W, Yangzhou Anipet Co., Ltd., Jiangsu, China), or decreased ( $n = 6$ ) employing an LKB Bromma thermoregulator (LKB Bromma 2219 Multitemp II, Sollentuna, Sweden), at a rate of 1 °C day<sup>-1</sup> until fishes stopped feeding. Fish were offered three pieces of chopped hake muscle (~ 0.15 g) daily, and the non-feeding status was determined when fish did not eat any piece of food in 24 h. The mean lower and upper feeding cessation temperatures of each species represent the chronic lower and upper temperatures (mean  $\pm$  standard error), respectively.

### Thermal tolerance

After the acclimation period, the CT<sub>min</sub> and CT<sub>max</sub> of *P. tessellata* and *H. bispinis* juveniles at different AT were determined using the Critical Thermal Methodology (CTM, Becker and Genoway 1979; Paladino et al. 1980; Beitingner

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 and Hutchison 1997; Beitinger and Lutterschmidt 2011). In the present study, a constant rate of increase or decrease temperature of  $0.3^{\circ}\text{C min}^{-1}$  was chosen, as it was recommended by Becker and Genoway (1979), Lutterschmidt and Hutchinson (1997), and Beitinger et al. (2000) for small-bodied fishes (i.e., juveniles and adults). The selected endpoint was the loss of equilibrium (LOE), defined as the failure of fish to maintain dorsoventral orientation for at least 1 min (Beitinger et al. 2000).

To determine CTmax, 15 individuals of each species from each AT (Table 1) were put individually in aerated 300-mL beakers filled with seawater at the corresponding AT. Beakers were suspended in a 50-L water bath provided with a thermoregulator Techne TU-20D (Bibby Scientific Limited, Staffordshire, UK) that allowed the constant increase of temperature inside beakers until fishes reach the selected endpoint. Similarly, to determine CTmin, 15 individuals of each species and each AT (Table 1) were put individually in aerated 300-mL beakers filled with seawater at the corresponding AT. These beakers were transferred to a freezer (GAFA HGF 3880, Rosario, Argentina), allowing them to achieve the proper cooling rate. The fishes' responses were observed by opening the freezer's door at a frequency that did not affect the cooling rate. During both CTmin and CTmax trials, a certified digital thermometer Lutron TM-917 provided with a Pt100 thermoresistance (Lutron Electronic Enterprise Co., Ltd., Taipei, Taiwan) was used to monitor the change of the temperature inside the beakers every 5 min and to record the temperature at which the LOE occurred.

Finally, fishes were measured (TL, total length  $\pm 0.1$  mm) with a digital caliper (Sylvac, S 235 PAT, Yverdon, Switzerland), weighed (BM, body mass  $\pm 0.01$  g) with a digital balance (Ohaus, TA302, NJ, USA) and then returned to the initial AT to recover. All the trials were performed between 9:00 and 14:00 local time.

The CTmin and CTmax of fish at each AT were calculated as the arithmetic mean temperature at which LOE were observed (Becker and Genoway 1979; Beitinger et al. 2000).

## Thermal tolerance polygons

The fundamental (thermal) niches of *P. tessellata* and *H. bispinis* juveniles were graphically expressed as the dynamic thermal tolerance polygons of each species (Fangue and Bennett 2003; Dabruzzi et al. 2012; Lattuca et al. 2018). Each polygon was generated plotting CTmin and CTmax values against AT values, and extrapolating the resultant regression lines outward to the chronic upper and chronic lower temperature limits (Dabruzzi et al. 2012; Lattuca et al.

**Table 1** Thermal tolerance of *Patagonotothen tessellata* and *Harpagifer bispinis* from the Beagle Channel acclimated at different temperatures (4, 7, 10 and  $12^{\circ}\text{C}$ )

Species	AT ( $^{\circ}\text{C}$ )	n	TL (mm)	BM (g)	R ( $^{\circ}\text{C min}^{-1}$ )	CTmin ( $^{\circ}\text{C}$ )	n	TL (mm)	BM (g)	R ( $^{\circ}\text{C min}^{-1}$ )	CTmax ( $^{\circ}\text{C}$ )
<i>P. tessellata</i>	4	15	55.90 $\pm$ 1.36	1.45 $\pm$ 0.11	0.29	- 1.93 $\pm$ 0.04	15	53.76 $\pm$ 0.56	1.21 $\pm$ 0.05	0.30	23.06 $\pm$ 0.12
	7	15	55.77 $\pm$ 0.91	1.36 $\pm$ 0.08	0.31	- 1.34 $\pm$ 0.04	15	55.21 $\pm$ 0.74	1.20 $\pm$ 0.04	0.33	24.18 $\pm$ 0.08
	10	15	54.20 $\pm$ 0.80	1.35 $\pm$ 0.08	0.30	- 1.06 $\pm$ 0.04	15	52.43 $\pm$ 0.54	1.17 $\pm$ 0.05	0.32	24.82 $\pm$ 0.02
	12	15	56.21 $\pm$ 1.02	1.25 $\pm$ 0.09	0.29	- 0.39 $\pm$ 0.05	15	54.54 $\pm$ 0.83	1.30 $\pm$ 0.08	0.32	26.17 $\pm$ 0.08
<i>H. bispinis</i>	4	15	50.43 $\pm$ 2.77	3.41 $\pm$ 0.53	0.30	- 1.97 $\pm$ 0.03	15	54.57 $\pm$ 1.52	3.42 $\pm$ 0.23	0.32	23.60 $\pm$ 0.10
	7	15	53.62 $\pm$ 1.78	3.64 $\pm$ 0.34	0.30	- 1.90 $\pm$ 0.04	15	54.36 $\pm$ 2.00	3.22 $\pm$ 0.30	0.31	24.28 $\pm$ 0.12
	10	15	49.88 $\pm$ 1.65	3.15 $\pm$ 0.28	0.28	- 1.72 $\pm$ 0.02	15	49.51 $\pm$ 1.96	2.37 $\pm$ 0.25	0.33	25.30 $\pm$ 0.02
	12	15	52.52 $\pm$ 1.18	3.33 $\pm$ 0.21	0.29	- 1.00 $\pm$ 0.04	15	53.42 $\pm$ 1.04	3.52 $\pm$ 0.23	0.32	25.39 $\pm$ 0.08

Acclimation temperature (AT), number of individuals (n), total length (TL), body mass (BM), constant cooling/heating rate of temperature (R), Critical Thermal Minimum/Maximum (CTmin/CTmax). Data are expressed as mean  $\pm$  standard error (SE)



2018). The total polygonal area (TPA) was expressed in areal units ( $^{\circ}\text{C}^2$ ) with a 95% confidence interval (CI) calculated using the 95% CI of each CTmin/CTmax values. According to Beitinger and Bennett (2000), the TPA was further partitioned into three distinct zones: an intrinsic tolerance zone (ITZ, i.e., tolerance independent of previous thermal acclimation history) and upper and lower acquired tolerance zones (UAZ and LAZ, respectively, i.e., thermal tolerance gained through acclimation). These areas were obtained by dividing the polygon with horizontal lines originating at the intersection of the CTM regressions with vertical lines connecting the CTmin and CTmax values at chronic upper and chronic lower temperature limits (Dabruzzi et al. 2012; Lattuca et al. 2018). Each of these areas was also expressed in  $^{\circ}\text{C}^2$  with their 95% CI. Furthermore, the CI intervals of extreme CTmin and CTmax values extrapolated from CTM values against AT were combined to generate multiple polygonal areas for each species in order to make interspecific comparisons.

### Acute thermal preferenda

The PT of *P. tessellata* and *H. bispinis* juveniles ( $n = 15$  of each species and at each AT, Table 2) were determined in a horizontal thermal gradient tank as described by Barantes et al. (2017) and Lattuca et al. (2018). This custom-built tank consisted of a white polyvinyl chloride (PVC) pipe (4-m length, 16-cm inside diameter and 10-cm wide longitudinal upper opening all along the pipe that allows a precise fish observation) filled with 65 L of seawater. The “cold” end of the tank was connected to a LKB Bromma thermoregulator (LKB Bromma 2219 Multitemp II, Sollentuna, Sweden) which cooled the water, and the “hot” end was connected to a reservoir of water which was warmed using two Haake DC5 thermoregulators (Thermo Electron Corporation, Karlsruhe, Germany). The temperature gradient was generated and maintained

by two aluminum coils (0.7-cm diameter, 2-m long each one) placed at the bottom of the tank. They extended from each end to the center of the tank, with cold and hot water from the sources previously described flowing in opposite directions. The resulting thermal gradients are shown in Table 2. Compressed air was bubbled through regularly spaced small holes in a flexible airline tubing placed at the bottom of the tank. In addition to aeration, it ensured vertical water mixing. A net prevented fish from directly contacting coils and the air tube, and use them as a shelter.

Each trial began when one single fish was introduced into the thermal gradient tank in the section corresponding to its AT. Data collection started when habituation to experimental conditions was observed (ca. 15–30 min, depending on the species). The fish was then allowed to select different PT by steadying its position within the gradient for at least 5 min. These PT were registered, avoiding disturbing the fish, with a certified digital thermometer Lutron TM-917 provided with a Pt100 thermoresistance (Lutron Electronic Enterprise Co., Ltd., Taipei, Taiwan). Individual fish were removed from the gradient and then measured and weighed as previously described. Trials lasted between 90 and 120 min and were performed between 9:00 and 14:00 local time.

The mean and modal PT of each species acclimated at different AT were calculated. Mean PT was calculated as the arithmetic mean of selected temperatures. Modal PT was estimated by grouping such temperatures by 1  $^{\circ}\text{C}$  intervals and choosing the temperature more frequently selected by a fish during trials (Fangue et al. 2009; Baird et al. 2018).

Once the PT of fish acclimated to different AT were determined, the FTP was estimated as the temperature at which the regression line of PT (constructed from modal PT values of the 15 PT records for each specimen) on AT intersects with the line of equality (PT = AT) (Jobling 1981).

**Table 2** Preferred temperatures of *Patagonotothen tessellata* and *Harpagifer bispinis* from the Beagle Channel and acclimated at different temperatures (4, 7, 10 and 12  $^{\circ}\text{C}$ )

Species	AT ( $^{\circ}\text{C}$ )	Gradient ( $^{\circ}\text{C}$ )	<i>n</i>	TL (mm)	BM (g)	Mean PT ( $^{\circ}\text{C}$ )	Modal PT ( $^{\circ}\text{C}$ )
<i>P. tessellata</i>	4	2.96–21.10	15	56.61 ± 1.32	1.54 ± 0.12	6.29 ± 0.55	5.95 ± 0.78
	7	2.80–21.67	15	56.30 ± 1.03	1.39 ± 0.10	8.70 ± 0.34	8.43 ± 0.75
	10	3.17–22.08	15	54.91 ± 0.80	1.34 ± 0.07	11.49 ± 0.24	11.37 ± 0.41
	12	3.13–22.76	15	54.57 ± 2.05	1.52 ± 0.10	11.49 ± 0.44	12.09 ± 0.74
<i>H. bispinis</i>	4	1.90–20.54	15	54.89 ± 1.74	3.54 ± 0.24	5.55 ± 0.52	5.43 ± 0.27
	7	1.94–21.09	15	53.62 ± 1.95	3.51 ± 0.36	8.98 ± 0.62	8.00 ± 0.52
	10	1.64–21.20	15	57.64 ± 1.54	3.52 ± 0.22	11.54 ± 0.33	11.44 ± 0.42
	12	2.12–21.55	15	54.89 ± 1.74	3.51 ± 0.20	12.21 ± 0.47	11.49 ± 0.64

Acclimation temperature (AT), number of individuals (*n*), total length (TL), body mass (BM), preferred temperature (PT)

Data are expressed as mean ± standard error (SE). Gradient range temperatures represent the low- and high-end values of the seawater in the experimental tank

## Statistical analyses

Assumptions of normality and homoscedasticity were evaluated through Shapiro–Wilk and Levene tests, respectively. Simple linear regression analysis was used to test relationships between CTmin/CTmax or PT and AT. One-way analysis of variance (ANOVA) or Kruskal–Wallis, followed by post hoc Tukey or Dunn’s tests, respectively, were used to examine differences in fish size and weight at the beginning of the trials, and intraspecific differences in CTmin, CTmax and PT. Student’s *t*-test or Mann–Whitney were used to investigate interspecific differences in CTmin, CTmax, polygonal areas, and mean and modal PT values. All statistical determinations were performed at a significance level set to 5% (Zar 1984; Sokal and Rohlf 2011), using InfoStat statistical software (version 2018, Di Rienzo et al. 2018).

## Results

### Thermal acclimation limits

The chronic lower and chronic upper temperatures of each species were  $0.50 \pm 0.22$  °C ( $n=6$ ) and  $23.00 \pm 0.00$  °C ( $n=6$ ) for *P. tessellata* and  $0.20 \pm 0.17$  °C ( $n=6$ ) and  $18.20 \pm 0.78$  °C ( $n=6$ ) for *H. bispinis*, resulting in total acclimation ranges of 22.50 °C and 18.00 °C, respectively.

### Thermal tolerance

No significant intraspecific differences were found with size (*P. tessellata*, Kruskal–Wallis,  $H_7=14.38$ ,  $p=0.065$  and *H. bispinis*, Kruskal–Wallis,  $H_7=9.26$ ,  $p=0.234$ ) and weight (*P. tessellata*, ANOVA,  $H_7=7.55$ ,  $p=0.373$  and *H. bispinis*, Kruskal–Wallis,  $H_7=11.59$ ,  $p=0.115$ ) of juveniles assigned to the different experimental groups.

After CTM trials, only 3% of individuals of each species did not recover, most likely because fishes were not promptly returned to their pretest AT when CTmin/CTmax values were reached. Thermal tolerance values of both species at each AT are shown in Table 1. CTmin of fishes acclimated between 4 and 12 °C ranged from  $-1.93$  to  $-0.39$  °C in *P. tessellata* and from  $-1.97$  to  $-1.00$  °C in *H. bispinis*. The intraspecific comparisons indicated that these values differed significantly among AT in both species (*P. tessellata*, ANOVA,  $F_{3,56}=237.79$ ,  $p<0.001$ ; *H. bispinis*, Kruskal–Wallis,  $H_3=45.39$ ,  $p<0.001$ ). Moreover, all pairwise comparisons show significantly different values in *P. tessellata* (Tukey tests,  $p<0.05$ ), but not in *H. bispinis*, as CTmin did not differ between fishes acclimated at 4 and 7 °C (Dunn’s test,  $p>0.05$ ), and 7 and 10 °C (Dunn’s test,  $p>0.05$ ). CTmax of fishes at the same experimental AT ranged from 23.06 to 26.17 °C in *P. tessellata* and from 23.60 to

25.39 °C in *H. bispinis*. Kruskal–Wallis tests for each species revealed that CTmax values differed significantly among AT (*P. tessellata*: Kruskal–Wallis,  $H_3=54.94$ ,  $p<0.001$ ; *H. bispinis*: Kruskal–Wallis,  $H_3=46.77$ ,  $p<0.001$ ). The differences in *P. tessellata* are found between groups acclimated at 4 and 10 °C, 4 and 12 °C, and 7 and 12 °C (Dunn’s tests,  $p<0.05$ ), whereas in *H. bispinis* the differences are between groups acclimated at 4 and 7 °C, and 10 and 12 °C (Dunn’s tests,  $p<0.05$ ).

Simple linear regression analysis of CTmin and CTmax with AT in both species yields the following relations:

$$\text{CTmin}_{P.tessellata} = 0.18 * AT - 2.65 \quad (n = 60, r^2 = 0.89, \\ F_{1,58} = 449.76, p < 0.001)$$

$$\text{CTmin}_{H.bispinis} = 0.11 * AT - 2.54 \quad (n = 60, r^2 = 0.66, \\ F_{1,58} = 111.51, p < 0.001)$$

$$\text{CTmax}_{P.tessellata} = 0.36 * AT + 21.55 \quad (n = 60, r^2 = 0.89, \\ F_{1,58} = 487.01, p < 0.001)$$

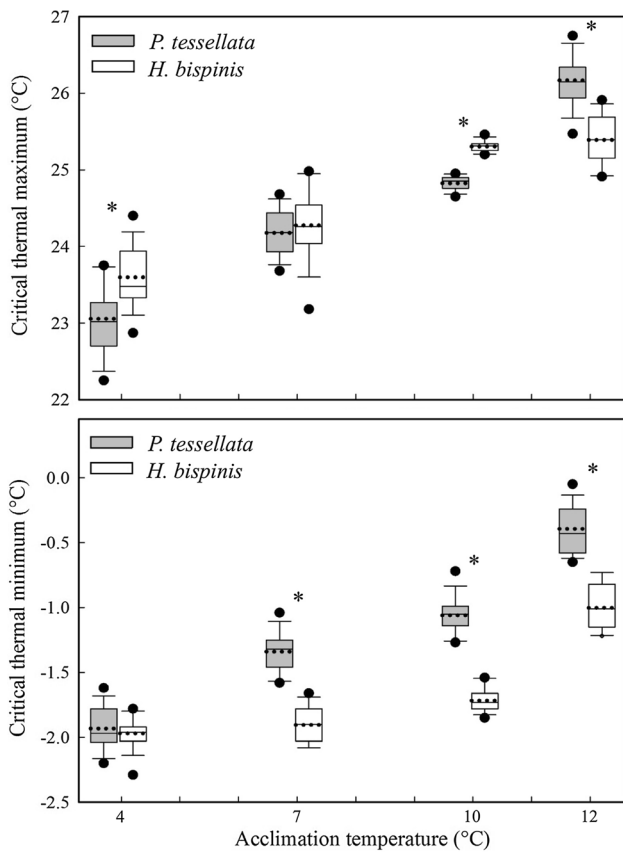
$$\text{CTmax}_{H.bispinis} = 0.24 * AT + 22.65 \quad (n = 60, r^2 = 0.80, \\ F_{1,58} = 236.89, p < 0.001)$$

These expressions suggest that *P. tessellata* gained 1.6-fold more cold tolerance and 1.5-fold more heat tolerance than *H. bispinis* for every 1 °C change in acclimation.

The interspecific comparisons of CTmin at each AT (Fig. 1) exhibited significant differences in fishes acclimated at 7 °C (*t*-test,  $t_{28}=10.54$ ,  $p<0.001$ ), 10 °C (*t*-test,  $t_{28}=15.15$ ,  $p<0.001$ ) and 12 °C (Mann–Whitney,  $U=0.00$ ,  $p<0.001$ ), with *H. bispinis* always being more cold-tolerant than *P. tessellata*. No significant differences were found when they were exposed to 4 °C (*t*-test,  $t_{28}=0.71$ ,  $p=0.48$ ). When CTmax were compared at each AT, they differed significantly at 4 °C (*t*-test,  $t_{28}=-3.53$ ,  $p=0.001$ ), 10 °C (*t*-test,  $t_{28}=-15.71$ ,  $p<0.001$ ) and 12 °C (*t*-test,  $t_{28}=6.69$ ,  $p<0.001$ ) but not at 7 °C (*t*-test,  $t_{28}=-0.70$ ,  $p=0.49$ ). At 4 and 10 °C, *H. bispinis* tolerated higher temperatures than *P. tessellata*; but at the extreme AT (12 °C) its tolerance to warming conditions waned and thus *P. tessellata* reached a higher CTmax (Fig. 1).

### Thermal tolerance polygons

The dynamic thermal polygons of *P. tessellata* and *H. bispinis* juveniles, constructed with extrapolated CTmin and CTmax values at chronic lower and upper temperatures, are shown in Fig. 2. The TPA of *P. tessellata* ( $593.85$  °C<sup>2</sup>, 95% CI =  $590.51$ – $597.87$  °C<sup>2</sup>) was larger than that of *H.*



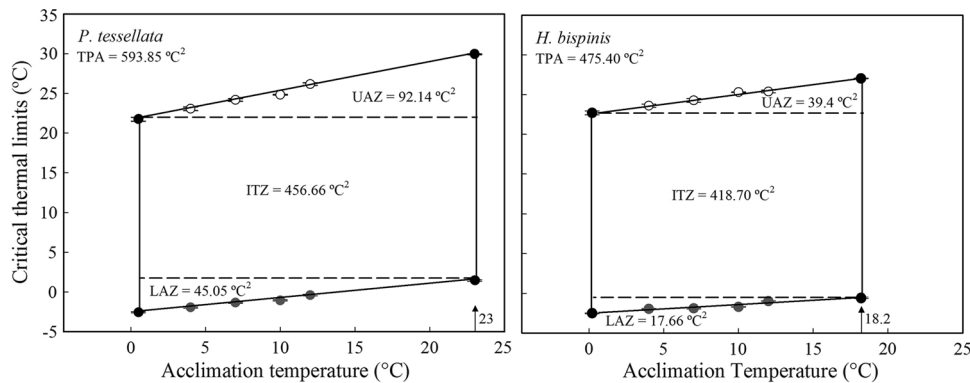
**Fig. 1** Critical Thermal Minimum (CTmin) and Maximum (CTmax) of *Patagonotothen tessellata* (grey) and *Harpagifer bispinis* (white) from the Beagle Channel acclimated at different temperatures (AT: 4, 7, 10 and 12°C). Box plots display the 25th and 75th percentiles, the median (solid lines), the mean (dotted lines), the 10th and 90th percentiles (whiskers) and outliers (dots). Asterisks indicate interspecific statistical differences on CTmin/CTmax values at the same AT

*bispinis* (475.40 °C<sup>2</sup>, 95% CI=471.56–479.43 °C<sup>2</sup>). Their ITZ were 456.66 °C<sup>2</sup> (95% CI=448.67–463.97 °C<sup>2</sup>) and 418.70 °C<sup>2</sup> (95% CI=412.58–425.16 °C<sup>2</sup>), respectively, and represented the 76.90% and 88.07% of the corresponding thermal polygon. In *P. tessellata*, the UAZ (92.14 °C<sup>2</sup>, 95% CI=88.85–95.52 °C<sup>2</sup>) and the LAZ (45.05 °C<sup>2</sup>, 95% CI=43.78–46.32 °C<sup>2</sup>) represented 15.52% and 7.59% of the TPA. The UAZ (39.04 °C<sup>2</sup>, 95% CI=37.09–40.99 °C<sup>2</sup>) and LAZ (17.66 °C<sup>2</sup>, 95% CI=17.17–17.98 °C<sup>2</sup>) of *H. bispinis* encompassed 56 °C<sup>2</sup> and represented 8.21% and 3.72% of the TPA. The statistical comparison of both polygons indicated significant differences for TPA (*t*-test, *t*<sub>4</sub> = 38.11, *p* < 0.001), ITZ (*t*-test, *t*<sub>4</sub> = 6.58, *p* = 0.003), UAZ (*t*-test, *t*<sub>4</sub> = 23.82, *p* < 0.001) and LAZ (*t*-test, *t*<sub>4</sub> = 35.64, *p* < 0.001).

**Acute thermal preferenda**

The intraspecific comparisons of size (*P. tessellata*, Kruskal–Wallis, *H*<sub>3</sub> = 1.77, *p* = 0.621 and *H. bispinis*, Kruskal–Wallis, *H*<sub>3</sub> = 4.71, *p* = 0.194) and weight (*P. tessellata*, ANOVA, *F*<sub>3,56</sub> = 1.01, *p* = 0.395 and *H. bispinis*, ANOVA, *F*<sub>3,56</sub> = 0.04, *p* = 1.000) of juveniles did not differ significantly among different experimental groups (Table 2).

According to the species’ habits, *P. tessellata* explored the thermal gradient more intensely and extensively than *H. bispinis*; however, exploratory movements of both species increased with increasing experimental temperatures. Regardless of the AT, *P. tessellata* avoided temperatures lower than 3.10 or greater than 19.10 °C. The selected temperatures by *H. bispinis* ranged between 2.10 and 19.00 °C. Mean and modal PT values for *P. tessellata* and *H. bispinis* are shown in Table 2. Because differences between mean and modal PT were not significant (*P. tessellata*, 4 °C: Mann–Whitney, *U* = 80.00, *p* = 0.18, 7 °C: Mann–Whitney, *U* = 82.00, *p* = 0.21, 10 °C: *t*-test, *t*<sub>28</sub> = 0.24, *p* = 0.81,



**Fig. 2** Thermal tolerance polygons of *Patagonotothen tessellata* and *Harpagifer bispinis* from the Beagle Channel acclimated at different temperatures (AT: 4, 7, 10 and 12 °C). Circles represent Critical Thermal Minimum (CTmin, grey), Critical Thermal Maximum (CTmax, white), and CTM values at the chronic lower and upper

temperatures (CTmin/CTmax, black) extrapolated from simple linear regressions of experimental values. Bars represent confidence intervals, and arrows indicate the chronic lower and upper temperatures. TPA total polygonal area, UAZ upper acquired tolerance zone, ITZ intrinsic tolerance zone, LAZ lower acquired tolerance zone

12 °C: Mann–Whitney,  $U = 93.00$ ,  $p = 0.43$ ; *H. bispinis*, 4 °C: Mann–Whitney,  $U = 111.00$ ,  $p = 0.97$ , 7 °C:  $t$ -test,  $t_{28} = 0.07$ ,  $p = 0.94$ , 10 °C: Mann–Whitney,  $U = 98.00$ ,  $p = 0.56$ , 12 °C:  $t$ -test,  $t_{28} = -0.63$ ,  $p = 0.53$ ), we used modal PT values for further analyses, as modes are more appropriate for describing non-normal or multimodal distributions (Baird et al. 2018). Within each species, modal PT were significantly different among AT (*P. tessellata*: Kruskal–Wallis,  $H_3 = 28.91$ ,  $p < 0.001$ ; *H. bispinis*: ANOVA,  $F_{3,56} = 32.06$ ,  $p < 0.001$ ). Pairwise comparisons indicated that these differences arose between AT that were not consecutive in *P. tessellata* (Dunn's test,  $p < 0.05$ ), and between all AT, except between groups acclimated at 10 and 12 °C, in *H. bispinis* (Tukey test,  $p < 0.05$ ).

Simple linear regressions analyses suggests positive relationships between modal PT and AT for *P. tessellata* ( $PT = 2.85 + 0.80 * AT$ ,  $r^2 = 0.47$ ,  $n = 60$ ,  $F_{1,58} = 50.54$ ,  $p < 0.001$ ) and *H. bispinis* ( $PT = 2.35 + 0.82 * AT$ ,  $r^2 = 0.60$ ,  $n = 60$ ,  $F_{1,58} = 86.80$ ,  $p < 0.001$ ) (Fig. 3).

The comparison of PT of both species at each AT did not show significant differences (4 °C: Mann–Whitney,  $U = 102.50$ ,  $p = 0.69$ , 7 °C: Mann–Whitney,  $U = 99.00$ ,  $p = 0.59$ , 10 °C:  $t$ -test,  $t_{28} = -0.11$ ,  $p = 0.91$ , 12 °C:  $t$ -test,  $t_{28} = 0.61$ ,  $p = 0.54$ ).

The FTP of *P. tessellata* and *H. bispinis* juveniles were estimated at 14.25 °C and 13.05 °C, respectively.

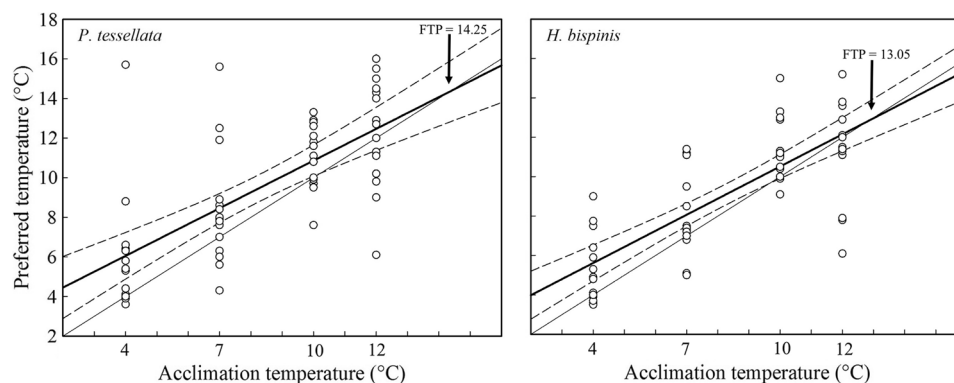
## Discussion

Understanding how environmental factors such as temperature affect the thermal physiology of fishes is fundamental to assess how future climate-driven environmental changes may cause variations in the species' distributions. In this study, we determined the thermal tolerance ranges and the

preferred temperatures of two sub-Antarctic notothenioid fishes, *P. tessellata* and *H. bispinis*, at their southernmost distribution limits, as a function of AT.

It is well known that the thermal history of fishes, especially just before testing, influences their thermal tolerance (Lutterschmidt and Hutchison 1997). Our results on CTM values indicated that southern populations of both species were able to acclimate to the selected experimental temperatures. Acclimation has also been demonstrated in some Antarctic notothenioids using different performances indicators (Seebacher et al. 2005; Strobel et al. 2012; 2013). For instance, Podrabsky and Somero (2006) and Bilyk and DeVries (2011) pointed out that, at the whole animal level, some species from the high Antarctic zone (McMurdo Sound) and the seasonal pack-ice zone (Western Antarctic Peninsula) were also capable of increasing their heat tolerance through acclimation.

With respect to cold tolerance, the CTmin of *P. tessellata* and *H. bispinis* acclimated to 4 to 12 °C were all sub-zero values. Particularly, those corresponding to the lowest AT were near the freezing point of seawater employed in the trials, with a salinity of 28. Similar CTmin values were reported by Lattuca et al. (2018) for another sub-Antarctic notothenioid from the same geographic area, *E. maclovinus* when exposed to similar AT (CTmin =  $-2.19$  and  $-1.92$  °C registered at 4 and 10 °C, respectively). Our results demonstrate high levels of cold tolerance for these sub-Antarctic species, which could be explained by their recent thermal history. The evolution of AFGPs prevents organismal freezing (DeVries 1971; Cheng and DeVries 1991) and enabled fish survival at subzero temperature. This is a remarkable example of notothenioids cold adaptation (Chen et al. 1997). There are, however, no detectable AFGPs sequences in the genome of *P. tessellata* (Cheng et al. 2003). The most parsimonious explanation for this observation is that the clade



**Fig. 3** Simple linear regression analyses (solid lines) of modal preferred temperatures (modal PT) on acclimation temperatures (AT: 4, 7, 10 and 12°C) for *Patagonotothen tessellata* and *Harpagifer bispinis* from the Beagle Channel. White circles represent modal PT calculated from the 15 PT records for each individual ( $n = 15$ ).

Dashed lines indicate 95% confidence intervals of the regression functions, and grey lines indicate the  $PT = AT$  line. Arrows indicate the final temperature preferendum (FTP), estimated as the temperature at which the regression line of modal PT on AT intersects with the line of equality (modal  $PT = AT$ )



diverged before the appearance of the AFGPs gene, although it might also have diverged after the evolution of the gene, which then went through a rapid gene loss (Cheng and Detrich 2007). In contrast, *H. bispinis* might have AFGPs in their blood (Near et al. 2012; Hüne et al. 2014), which would be consistent with its higher cold tolerance relative to *P. tessellata*.

Regarding heat tolerance, the CTmax values of *P. tessellata* and *H. bispinis* exposed to the same experimental AT were well above the temperature they are naturally exposed to in coastal areas, which generally range between 2 and 16 °C (Giménez, personal observations). Similar and even higher CTmax values were reported by Lattuca et al. (2018) for the non-Antarctic notothenioid *E. maclovinus* (27.12–30.07 °C) and other fishes from the Beagle Channel, like *Odontesthes nigricans* (Richardson, 1848) (27.53–28.67 °C) and the diadromous *Galaxias maculatus* (Jenyns, 1842) (26.17–29.16 °C) when acclimated at 4 and 10 °C, respectively. Different heat tolerances are expected among species, even when exposed to similar thermal regimes, owing to differences in their evolutionary histories and hence in their thermal sensitivities (Clarke and Johnston 1996; Cussac et al. 2009). The CTmax of *P. tessellata* and *H. bispinis* were well above the values reported by Bilyk and DeVries (2011) for Antarctic notothenioids, which were initially maintained in their natural freezing waters (11 species, 11.95 to 16.17 °C) and later acclimated to 4 °C (8 species, 15.19 to 17.39 °C).

Several studies have found a correlation between thermal tolerance and geographic range (Peck et al. 2014). Our results are consistent with this finding, as the higher tolerance of *P. tessellata* to warm waters and the higher tolerance of *H. bispinis* to cold waters correlate with the more northerly distribution of *P. tessellata* compared to *H. bispinis*. The wider thermal tolerance ranges of present sub-Antarctic species from southern South America, as compared to those of Antarctic fishes, are also consistent with the tendency for the thermal tolerance range to increase as the environmental temperature increases (Pörtner 2002). Because Antarctic notothenioids are stenothermal species (Eastman 1993; 2005; Peck et al. 2014), living near the freezing point of seawater (~ -1.9 °C), they are thought to be more susceptible to environmental perturbations, such as changes in ocean conditions, chiefly warming (Eastman 1991; Eastman and McCune 2000).

The CTM-thermal polygons of species convey more information than their thermal tolerance ranges alone, as their shape reflects the species' thermal niches (Bennett and Beitinger 1997). In addition, the areas of the polygons not only represent a useful index to compare eurythermicity between species (Bennett and Beitinger 1997) but may also be useful for understanding population fluctuations (Eme and Bennett 2009). Many studies

have reported the thermal tolerance polygons of freshwater and marine fishes (Elliot 1991; Bennet and Beitinger 1997; Beitinger and Bennet 2000, Ford and Beitinger 2005; Eme and Bennet 2009; Barrantes et al. 2017; Kir et al. 2017; Lattuca et al. 2018), with TPA ranging from 218 °C<sup>2</sup> in *Paracheirodon axelrodi* Schultz 1956 (Campos et al. 2016) to 1470 °C<sup>2</sup> in *Cyprinodon variegatus* Lacepède, 1803 (Bennet and Beitinger 1997). Except for *E. maclovinus* with a TPA of 858.69 °C<sup>2</sup> (Lattuca et al. 2018), there is no information available about thermal polygons of other notothenioid species. Compared to the polygonal areas of other fish species, particularly those inhabiting the Beagle Channel, *P. tessellata* and *H. bispinis* exhibited small to intermediate thermal polygons, with a TPA of 593.85 °C<sup>2</sup> and 475.40 °C<sup>2</sup>, respectively. Polygonal partitioning into intrinsic and acquired tolerance zones can provide an estimate of how well or poorly a fish may overcome shifts in sea temperatures that may demand readjustment in temperature tolerance (Eme and Bennet 2009). Thus, the lesser proportion of ITZ in *P. tessellata* (76.90% of TPA) compared to *H. bispinis* (88.07% of TPA) suggests that the former species has a better ability to acquire thermal tolerance through acclimation. The larger UAZ compared to LAZ in *P. tessellata* and *H. bispinis* shows that they have a better ability to acquire additional heat tolerance while still maintaining high levels of cold tolerances. Overall, these thermal polygons indicate that *P. tessellata* would be better adapted to cope with the expected rise in sea surface temperatures brought about by CC.

The thermal windows and niches of individual species are likely to influence species interactions at the ecosystem level. The resulting changes in species interactions represent crucial components of ecosystems response to CC (Pörtner and Peck 2011). This fact emphasizes the role that physiological limits and the associated species-specific dimensions of the thermal niche have in understanding climate effects on ecosystem functioning (Pörtner 2008).

Within their tolerance ranges, fishes buffer the effects of rising temperatures by selecting PTs that allow maximizing their metabolic efficiency (Kelsch and Neill 1990). In this work, the PT of *P. tessellata* and *H. bispinis* were characterized by two measures of central tendency, mean and modal PT (Reynolds and Casterlin 1979). The statistical agreement between both measures adds confidence to the results (Fangue et al. 2009; Baird et al. 2018). *Patagonotothen tessellata* and *H. bispinis* preferred warmer temperatures following exposure to warmer AT, resulting in positive relationships of modal PT with AT. Similarly, *E. maclovinus*, *O. nigricans* and diadromous *G. maculatus* at the Beagle Channel increased their PT with increasing AT (Lattuca et al. 2018). This correlation, which appears to be related to the amplitude of thermal cycles to which species have recently

been exposed, seems to be an adaptive response to changing temperature (Johnson and Kelsh 1998).

The FTP of *P. tessellata* and *H. bispinis* were also estimated based on these PT-AT relationships. Although the preference of each species at the same exposure temperature did not differ significantly, the FTP of *P. tessellata* (14.25 °C) was higher than that of *H. bispinis* (13.05 °C). The estimated values were consistent with PT values reported for fish from high latitudes (see Fig. 1 in Pörtner and Peck 2011). Jobling (1981) stated that the FTP gives a good indication of the temperatures that promote maximum growth, and these, in turn, are commonly correlated with available summer temperatures (Reynolds and Casterlin 1979). Johnson and Kelsch (1998) proposed a model based on both amplitude (FTP) and magnitude (slopes of PT-AT relationships) of thermal regimes experienced by fishes, which allows the definition of thermal guilds. According to this model, *P. tessellata* and *H. bispinis* can be included among cold eurythermal fishes, in line with their evolutionary history. *Patagonotothen tessellata* and *H. bispinis*, living in a sub-Antarctic thermally variable environment, might have acquired the advantage of adjusting their PT to increase their metabolic efficiency following temperature change (Johnson and Kelsh 1998). Their particular evolutionary origins might explain differences in their FTP. *Patagonotothen tessellata* ancestor recent radiation, estimated to be around 5 Ma, most likely occurred in non-Antarctic waters. The drivers of this radiation are unlikely to be related to the AFGPs since the temperature of Patagonian waters is regularly above the freezing point (Ceballos et al. 2019). On the other hand, the separation between *H. bispinis* and its Antarctic relative, *H. antarcticus*, is much more recent and likely occurred 1.7–0.8 Ma ago, related to a recent dispersion process from Antarctica to South America (Hüne et al. 2014). Eurythermal cold adaptation is known to cause a rise in mitochondrial density or mitochondrial aerobic capacity in fish (Guderley 1998). This process is reversed during seasonal warming. According to Pörtner (2002), it causes the standard metabolic rate to rise in relation to the degree of environmental temperature fluctuations and of the cold compensation of mitochondrial aerobic capacity and proton leakage. Further studies should be conducted in order to detect if an increase in mitochondrial density occurs in *P. tessellata* and *H. bispinis* individuals acclimated at different temperatures.

In response to CC, fishes are expected to extend their distributions poleward with warming in order to maintain their preferred temperature range (Hickling et al. 2006). Therefore, the increase of sea surface temperatures will likely reduce the available temperature ranges at the northern boundary of *P. tessellata* and *H. bispinis* distributions. On the other hand, it will generally enhance the performances of both species at their southernmost distribution limits,

considering that they are living in environments that are noticeably cooler than their CT<sub>max</sub> and FTP (Deutsch et al. 2008; Komoroske et al. 2014). Hence, one might expect populations from the Beagle Channel to be influenced by indirect consequences of CC, such as habitat degradation or changes in food chain composition (Pörtner and Peck 2011), rather than by direct temperature mortality (Eme and Bennett 2009). Other factors besides warming trends, such as hypoxia, acidification or freshening of seawater caused by ice melting, are also likely to affect sub-Antarctic organisms (Pörtner 2008; Pörtner and Peck 2011; Storch et al. 2014). Little is known about the ability of notothenioids to respond to ecologically meaningful environmental perturbations when multiple factors change simultaneously. Studies considering the effects of temperature and acidification or hypoxia conditions of seawater in the physiology of these species are needed.

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**Data availability** Data available on request from the authors

## Declarations

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Ethical approval** Sampling protocols and experiments on *P. tessellata* and *H. bispinis* were approved by the Ethics Committee of Austral Center for Scientific Research (CIB – CADIC).

## References

- Baird SE, Steel AE, Cocherell DE, Cech JJ Jr, Fangué NA (2018) Native Chinook salmon *Oncorhynchus tshawytscha* and non-native brook trout *Salvelinus fontinalis* prefer similar water temperatures. *J Fish Biol* 93:1000–1004. <https://doi.org/10.1111/jfb.13810>

- Barrantes ME, Lattuca ME, Vanella FA, Fernández DA (2017) Thermal ecology of *Galaxias platei* (Pisces, Galaxiidae) in South Patagonia: perspectives under a climate change scenario. *Hydrobiologia* 802:255–267. <https://doi.org/10.1007/s10750-017-3275-3>
- Becker CD, Genoway RG (1979) Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater fish. *Environ Biol Fish* 4:245–256. <https://doi.org/10.1007/BF00005481>
- Beitinger TL, Bennett WA (2000) Quantification of the role of acclimation temperature in temperature tolerance of fishes. *Environ Biol Fish* 58:277–288. <https://doi.org/10.1023/A:1007618927527>
- Beitinger TL, Lutterschmidt WI (2011) Measures of thermal tolerances. In: Farrell AP (ed) *Encyclopedia of Fish Physiology: From Genome to Environment*. Academic Press, San Diego, pp 1695–1702
- Beitinger TL, Bennett WA, McCauley RW (2000) Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. *Environ Biol Fish* 58:237–275. <https://doi.org/10.1023/A:1007676325825>
- Bennett WA, Beitinger TL (1997) Temperature tolerance of the sheepshead minnow, *Cyprinodon variegatus*. *Copeia* 1997:77–87. <https://doi.org/10.2307/1447842>
- Bilyk KT, DeVries AL (2011) Heat tolerance and its plasticity in Antarctic fishes. *Comp Biochem Phys A* 158:382–390. <https://doi.org/10.1016/j.cbpa.2010.12.010>
- Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel CV, Kiessling W, O'Connor MI, Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ, Richardson AJ (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334:652–655. <https://doi.org/10.1126/science.1210288>
- Calosi P, Bilton DT, Spicer JJ, Atfield A (2008) Thermal tolerance and geographical range size in the *Agabus brunneus* group of European diving beetles (Coleoptera: Dytiscidae). *J Biogeogr* 35:295–305. <https://doi.org/10.1111/j.1365-2699.2007.01787.x>
- Campos DFD, Jesus TF, Kochhann D, Heinrichs-Caldas W, Coelho MM, Almeida-Val VMF (2016) Metabolic rate and thermal tolerance in two congeneric Amazon fishes: *Paracheirodon axelrodi* Schultz, 1956 and *Paracheirodon simulans* Géry, 1963 (Characidae). *Hydrobiologia* 789:133–142. <https://doi.org/10.1007/s10750-016-2649-2>
- Ceballos SG, Roesti M, Matschiner M, Fernández DA, Damerau M, Hanel R, Salzburger W (2019) Phylogenomics of an extra-Antarctic notothenioid radiation reveals a previously unrecognized lineage and diffuse species boundaries. *BMC Evol Biol* 19:13–27. <https://doi.org/10.1186/s12862-019-1345-z>
- Chen L, DeVries AL, Cheng C-HC (1997) Evolution of antifreeze glycoprotein gene from a trypsinogen gene in Antarctic notothenioid fish. *Proc Natl Acad Sci* 94(8):3811–3816
- Cheng CHC, Detrich WH (2007) Molecular ecophysiology of Antarctic notothenioid fishes. *Philos T Roy Soc B* 362:2215–2232. <https://doi.org/10.1098/rstb.2006.1946>
- Cheng CHC, DeVries AL (1991) The role of antifreeze glycopeptides and peptides in the freezing avoidance of cold water fishes. In: di Prisco G (ed) *Life under extreme conditions*. Springer, Berlin, pp 1–14. [https://doi.org/https://doi.org/10.1007/978-3-642-76056-3\\_1](https://doi.org/https://doi.org/10.1007/978-3-642-76056-3_1)
- Cheng CHC, Chen L, Near TJ, Jin Y (2003) Functional antifreeze glycoprotein genes in temperate-water New Zealand nototheniid fish infer an Antarctic evolutionary origin. *Mol Biol Evol* 20:1897–1908. <https://doi.org/10.1093/molbev/msg208>
- Clarke A, Johnston IA (1996) Evolution and adaptive radiation of Antarctic fishes. *Trends Ecol Evol* 11:212–218. [https://doi.org/10.1016/0169-5347\(96\)10029-X](https://doi.org/10.1016/0169-5347(96)10029-X)
- Cruz-Jiménez AM (2019) Ensembles de peces en los bosques de kelp de *Macrocystis pyrifera* en el Canal Beagle, Tierra del Fuego estructura comunitaria y variación espacio-temporal. PhD Thesis, Universidad Nacional de La Plata (UNLP). Doi: <https://doi.org/10.35537/10915/79453>
- Cussac VE, Fernández DA, Gómez SE, López HL (2009) Fishes of southern South America: a story driven by temperature. *Fish Physiol Biochem* 35:29–42. <https://doi.org/10.1007/s10695-008-9217-2>
- Dabruzzi T, Bennett WA, Rummer JL, Fangue NA (2012) Thermal ecology of juvenile ribbontail stingray, *Taeniura lymma* (Forsskål, 1775), from a Mangal Nursery in the Banda Sea. *Hydrobiologia* 701:37–49. <https://doi.org/10.1007/s10750-012-1249-z>
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *P Natl Acad Sci USA* 105:6668–6672. <https://doi.org/10.1073/pnas.0709472105>
- DeVries AL (1971) Glycoproteins as biological antifreeze agents in Antarctic fishes. *Science* 172:1152–1155. <https://doi.org/10.1126/science.172.3988.1152>
- Di Rienzo JA, Casanoves F, Balzarini MG, Gonzalez L, Tablada M, Robledo CW. InfoStat version 2018. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. <http://www.infostat.com.ar>
- Duhamel G, Hulley PA, Causse R, Koubbi P, Vacchi M, Pruvost P, Vigetta S, Irisson JO, Mormède S, Belchier M, Dettai A, Detrich HW, Gutt J, Jones CD, Kock KH, Lopez LJ, Van de Putte A (2014) Biogeographic patterns of fish. In: De Broyer, C, Koubbi P, Griffiths HJ, Raymond B, Cd' Udekem d'Acoz et al. (eds), *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, pp 328–498
- Eastman JT (1991) Evolution and diversification of Antarctic notothenioid fishes. *Am Zool* 31:93–110. <https://doi.org/10.1093/icb/31.1.93>
- Eastman JT (1993) *Antarctic Fish Biology: Evolution in a Unique Environment*. Academic Press, San Diego
- Eastman JT (2005) The nature of the diversity of Antarctic fishes. *Polar Biol* 28:93–107. <https://doi.org/10.1007/s00300-004-0667-4>
- Eastman JT, McCune AR (2000) Fishes on the Antarctic shelf: evolution of a marine species flock? *J Fish Biol* 57:84–102. <https://doi.org/10.1006/jfbi.2000.1604>
- Elliott JM (1991) Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshw Biol* 25:61–70. <https://doi.org/10.1111/j.1365-2427.1991.tb00473.x>
- Elliott A (2010) A comparison of thermal polygons for British freshwater teleosts. *Freshwater Forum* 5:178–184
- Eme J, Bennett WA (2009) Critical thermal tolerance polygons of tropical marine fishes from Sulawesi, Indonesia. *J Therm Biol* 34:220–225. <https://doi.org/10.1016/j.jtherbio.2009.02.005>
- Fangue NA, Bennett WA (2003) Thermal tolerance responses of laboratory-acclimated and seasonally acclimatized Atlantic stingray, *Dasyatis sabina*. *Copeia* 2003:315–325. [https://doi.org/10.1643/0045-8511\(2003\)003\[0315:TTROLA\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2003)003[0315:TTROLA]2.0.CO;2)
- Fangue NA, Podrabsky JE, Crawshaw LI, Schulte PM (2009) Counter-gradient variation in temperature preference in populations of killifish *Fundulus heteroclitus*. *Physiol Biochem Zool* 82:776–786. <https://doi.org/10.1086/606030>
- Fernández DA, Bruno DO, Llompert FM (2018) Length-weight relationship of six notothenioid species from sub-Antarctic waters (Beagle Channel, Argentina). *J Appl Ichthyol* 35:597–599. <https://doi.org/10.1111/jai.13833>
- Ford T, Beitinger TL (2005) Temperature tolerance in the goldfish, *Carassius auratus*. *J Therm Biol* 30:147–152. <https://doi.org/10.1016/j.jtherbio.2004.09.004>
- Fry FEJ (1947) Effects of the environment on animal activity. *Univ Tor Stud Biol Ser* 55:1–62
- Gille ST (2002) Warming of the Southern Ocean since the 1950s. *Science* 295:1275–1277. <https://doi.org/10.1126/science.1065863>



- Golovanov VK (2006) The ecological and evolutionary aspects of thermoregulation behavior on fish. *J Ichthyol* 46:180–187. <https://doi.org/10.1134/S0032945206110075>
- Gordillo S, Rabassa J, Coronato A (2008) Paleoecology and paleobiogeographic patterns of mid-Holocene molluscs from the beagle channel (southern Tierra del Fuego, Argentina). *Andean Geol* 35:321–333
- Guderley H (1998) Temperature and growth rates as modulators of the metabolic capacities of fish muscle. In: Pörtner HO, Playle R (eds) *Cold Ocean Physiology*. Cambridge University Press, Cambridge, pp 58–87
- Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biol* 12:450–455. <https://doi.org/10.1111/j.1365-2486.2006.01116.x>
- Hüne M, Vega R (2016) Feeding habits in two sympatric species of Notothenioidei, *Patagonotothen cornucola* and *Harpagifer bispinis*, in the Chilean Patagonian channels and fjords. *Polar Biol* 39:2253–2262. <https://doi.org/10.1007/s00300-016-1892-3>
- Hüne M, González-Weva C, Poulin E, Mansilla A, Fernández DA, Barrera-Oro E (2014) Low level of genetic divergence between *Harpagifer* fish species (Perciformes: Notothenioidei) suggests a Quaternary colonization of Patagonia from the Antarctic Peninsula. *Polar Biol* 38:607–617. <https://doi.org/10.1007/s00300-014-1623-6>
- Hureau JE (1990) Harpagiferidae. Spiny plunderfishes. In: Gon O, Heemstra PH (eds) *Fishes of the Southern Ocean*. Grahamstown, JLB Smith Institute of Ichthyology, pp 357–363
- IPCC (2014) *Climate Change 2014: Synthesis Report*. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri RK, Meyer LA (eds)]. IPCC, Geneva
- Isla F, Bujalesky G, Coronato A (1999) Procesos estuarinos en el canal Beagle, Tierra del Fuego. *Rev Asoc Geol Argent* 54:307–318
- Jobling M (1981) Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. *J Fish Biol* 19:439–455
- Jobling M (1994) *Fish Bioenergetics*. Chapman & Hall, London
- Johnson JA, Kelsch SW (1998) Effects of evolutionary thermal environment on temperature-preference relationships in fishes. *Environ Biol Fish* 53:447–458. <https://doi.org/10.1023/A:1007425215669>
- Kelsch SW, Neill WH (1990) Temperature preference versus acclimation in fishes: selection for changing metabolic optima. *Trans Am Fish Soc* 119:601–610. [https://doi.org/10.1577/1548-8659\(1990\)119%3c0601:TPVAIF%3e2.3.CO;2](https://doi.org/10.1577/1548-8659(1990)119%3c0601:TPVAIF%3e2.3.CO;2)
- Killen SS (2014) Growth trajectory influences temperature preference in fish through an effect on metabolic rate. *J Anim Ecol* 83:1513–1522. <https://doi.org/10.1111/1365-2656.12244>
- Kir M, Sunar MC, Altındağ BC (2017) Thermal tolerance and preferred temperature range of juvenile meagre acclimated to four temperatures. *J Therm Biol* 65:125–129. <https://doi.org/10.1016/j.jtherbio.2017.02.018>
- Komoroske LM, Connon RE, Lindberg J, Cheng BS, Castillo G, Hasenbein M, Fangue NA (2014) Ontogeny influences sensitivity to climate change stressors in an endangered fish. *Conserv Physiol* 2:1–13. <https://doi.org/10.1093/conphys/cou008>
- Lattuca ME, Boy CC, Vanella FA, Barrantes ME, Fernández DA (2018) Thermal responses of three native fishes from estuarine areas of the Beagle Channel, and their implications for climate change. *Hydrobiologia* 808:235–249. <https://doi.org/10.1007/s10750-017-3424-8>
- Llompart F, Fernández DA, Aureliano D, La Mesa M (2020) Life history traits of the Patagonian spiny plunderfish *Harpagifer bispinis* (Schneider, 1801) in the Beagle Channel. *Polar Biol* 43:1643–1654. <https://doi.org/10.1007/s00300-020-02735-x>
- Lloris D, Rucabado JA (1991) Ictiofauna del Canal Beagle (Tierra de Fuego), aspectos ecológicos y análisis biogeográfico. *Publ Espec Inst Esp Oceanogr* 8:1–182
- Lutterschmidt W, Hutchison VH (1997) The critical thermal maximum: data to support the onset of spasms as the definitive endpoint. *Can J Zool* 75:1553–1560. <https://doi.org/10.1139/z97-782>
- Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. *Am Zool* 19:331–343. <https://doi.org/10.1093/icb/19.1.331>
- Manríquez PH, Jara ME, González CP, Díaz MI, Brokordt K, Lattuca ME, Peck MA, Alter K, Marras S, Domenici P (2020) Combined effect of  $p\text{CO}_2$  and temperature levels on the thermal niche in the early benthic ontogeny of a keystone species. *Sci Total Environ* 719:137239. <https://doi.org/10.1016/j.scitotenv.2020.137239>
- Marras S, Cucco A, Antognarelli F, Azzurro E, Milazzo M, Bariche M, Butenschön M, Kay S, Di Bitetto M, Quattrocchi G, Sinerchia M, Domenici P (2015) Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. *Conserv Physiol* 3:1–14. <https://doi.org/10.1093/conphys/cou059>
- Matschiner M, Colombo M, Damerau M, Ceballos S, Hanel R, Salzburger W (2015) The adaptive radiation of notothenioid fishes in the waters of Antarctica. In: Riesch R, Tobler M, Plath M (eds), *Extremophile Fishes*. Springer, Cham, pp 35–57. [https://doi.org/10.1007/978-3-319-13362-1\\_3](https://doi.org/10.1007/978-3-319-13362-1_3)
- Moreno CA, Jara F (1984) Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fuegian Islands, Chile. *Mar Ecol Prog Ser* 15:99–107
- Nakamura I, Inada T, Takeda M, Hatanaka H (1986) *Important Fishes Trawled off Patagonia*. JAMARC Publication, Tokyo
- Near TJ, Dornburg A, Kuhn KL, Eastman JT, Pennington JN, Patarrello T, Zane L, Fernández DA, Jones CD (2012) Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *P Natl Acad Sci USA* 109:3434–3439. <https://doi.org/10.1073/pnas.1115169109>
- Paladino FV, Spotila JR, Schubauer JP, Kowalski KT (1980) The critical thermal maximum: a technique used to elucidate physiological stress and adaptation in fishes. *Rev Can Biol* 39:115–122
- Palma ED, Matano RP, Piola AR (2008) A numerical study of the Southwestern Atlantic Shelf circulation: Stratified ocean response to local and offshore forcing. *J Geophys Res* 113:1–22. <https://doi.org/10.1029/2007JC004720>
- Peck LS, Morley SA, Richard J, Clark MS (2014) Acclimation and thermal tolerance in Antarctic marine ectotherms. *J Exp Biol* 217:16–22. <https://doi.org/10.1242/jeb.089946>
- Pérez AF, Calvo J, Tresguerres M, Luquet C (2003) Agglomerularism in *Harpagifer bispinis*: a subantarctic notothenioid fish living at reduced salinity. *Polar Biol* 26:800–805. <https://doi.org/10.1007/s00300-003-0551-7>
- Podrabsky JE, Somero GN (2006) Inducible heat tolerance in Antarctic notothenioid fishes. *Polar Biol* 30:39–43. <https://doi.org/10.1007/s00300-006-0157-y>
- Pörtner HO (2002) Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp Biochem Phys A* 132:739–761. [https://doi.org/10.1016/S1095-6433\(02\)00045-4](https://doi.org/10.1016/S1095-6433(02)00045-4)
- Pörtner HO (2008) Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Mar Ecol Prog Ser* 373:203–217. <https://doi.org/10.3354/meps07768>
- Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315:95–97. <https://doi.org/10.1126/science.1135471>



- Pörtner HO, Peck MA (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J Fish Biol* 77:1745–1779. <https://doi.org/10.1111/j.1095-8649.2010.02783.x>
- Pörtner HO, Peck MA (2011) Effects of Climate Change. In: Farrell AP (ed) *Encyclopedia of Fish Physiology: From Genome to Environment*. Academic Press, San Diego, pp 1738–1745
- Rabassa J (2008) Late Cenozoic glaciations in Patagonia and Tierra del Fuego. In: Rabassa J (ed), *The late Cenozoic of Patagonia and Tierra del Fuego*. Elsevier, Oxford, pp 151–204. [https://doi.org/https://doi.org/10.1016/S1571-0866\(07\)10008-7](https://doi.org/https://doi.org/10.1016/S1571-0866(07)10008-7)
- Reyes P, Hüene M (2012) *Peces del sur de Chile. Ocho Libros*. Santiago de Chile
- Reynolds WW, Casterlin ME (1979) Behavioral thermoregulation and the “final preferendum” paradigm. *Am Zool* 19:211–224. <https://doi.org/10.1093/icb/19.1.211>
- Riccialdelli L, Newsome SD, Fogel ML, Fernández DA (2017) Trophic interactions and food web structure of a subantarctic marine food web in the Beagle Channel: Bahía Lapataia, Argentina. *Polar Biol* 40:807–821. <https://doi.org/10.1007/s00300-016-2007-x>
- Schurmann H, Steffensen JF, Lomholt JP (1991) The influence of hypoxia on the preferred temperature of rainbow trout *Oncorhynchus mykiss*. *J Exp Biol* 157:75–86
- Seebacher F, Davison W, Lowe CJ, Franklin CE (2005) A falsification of the thermal specialization paradigm: compensation for elevated temperatures in Antarctic fishes. *Biol Lett* 1:151–154. <https://doi.org/10.1098/rsbl.2004.0280>
- Shultz AD, Zuckerman ZC, Suski CD (2016) Thermal tolerance of nearshore fishes across seasons: implications for coastal fish communities in a changing climate. *Mar Biol* 163:83–93. <https://doi.org/10.1007/s00227-016-2858-2>
- Shuter BJ, Finstad AG, Helland IP, Zweimüller I, Hölker F (2012) The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquat Sci* 74:637–657. <https://doi.org/10.1007/s00027-012-0274-3>
- Sokal RR, Rohlf FJ (2011) *Biometry: The Principles and Practice of Statistics in Biological Research*, 2nd edn. Freeman, New York, W. H. <https://doi.org/10.2307/2343822>
- Somero GN, DeVries AL (1967) Temperature tolerance of some Antarctic fishes. *Science* 156:257–258. <https://doi.org/10.1126/science.156.3772.257>
- Speaks JE, Randall CJ, Jimenez AG, Dabruzzi TF, Sutton MA, Pomory CM, Bennett WA (2012) Temperature tolerance comparisons among juvenile reef fishes from a beachrock nursery in Dry Tortugas National Park. *Fla Sci* 75:242–248
- Storch D, Menzel L, Frickenhaus S, Pörtner HO (2014) Climate sensitivity across marine domains of life: limits to evolutionary adaptation shape species interactions. *Glob Change Biol* 20:3059–3067. <https://doi.org/10.1111/gcb.12645>
- Strobel A, Bennecke S, Leo E, Mintenbeck K, Pörtner HO, Mark FC (2012) Metabolic shifts in the Antarctic fish *Notothenia rossii* in response to rising temperature and  $p\text{CO}_2$ . *Front Zool* 9:28–42. <https://doi.org/10.1186/1742-9994-9-28>
- Strobel A, Graeve M, Pörtner HO, Mark FC (2013) Mitochondrial acclimation capacities to ocean warming and acidification are limited in the Antarctic nototheniid fish, *Notothenia rossii* and *Lepidonotothen squamifrons*. *PLoS ONE* 8:e68865. <https://doi.org/10.1371/journal.pone.0068865>
- Vanella FA, Fernández DA, Romero MC, Calvo J (2007) Changes in the fish fauna associated with a sub-Antarctic *Macrocystis pyrifera* kelp forest in response to canopy removal. *Polar Biol* 30:449–457. <https://doi.org/10.1007/s00300-006-0202-x>
- Zar JH (1984) *Biostatistical Analysis*. Prentice-Hall International Editions, New Jersey

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