



Different ecophysiological responses of freshwater fish to warming and acidification

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ABSTRACT

Future climate change scenarios predict threatening outcomes to biodiversity. Available empirical data concerning biological response of freshwater fish to climate change remains scarce. In this study, we investigated the physiological and biochemical responses of two Iberian freshwater fish species (*Squalius carolitertii* and the endangered *S. torgalensis*), inhabiting different climatic conditions, to projected future scenarios of warming (+ 3 °C) and acidification ($\Delta\text{pH} = -0.4$). Herein, metabolic enzyme activities of glycolytic (citrate synthase - CS, lactate dehydrogenase - LDH) and antioxidant (glutathione S-transferase, catalase and superoxide dismutase) pathways, as well as the heat shock response (HSR) and lipid peroxidation were determined. Our results show that, under current water pH, warming causes differential interspecific changes on LDH activity, increasing and decreasing its activity in *S. carolitertii* and in *S. torgalensis*, respectively. Furthermore, the synergistic effect of warming and acidification caused an increase in LDH activity of *S. torgalensis*, comparing with the warming condition. As for CS activity, acidification significantly decreased its activity in *S. carolitertii* whereas in *S. torgalensis* no significant effect was observed. These results suggest that *S. carolitertii* is more vulnerable to climate change, possibly as the result of its evolutionary acclimatization to milder climatic condition, while *S. torgalensis* evolved in the warmer Mediterranean climate. However, significant changes in HSR were observed under the combined warming and acidification (*S. carolitertii*) or under acidification (*S. torgalensis*). Our results underlie the importance of conducting experimental studies and address species endpoint responses under projected climate change scenarios to improve conservation strategies, and to safeguard endangered freshwater fish.

1. Introduction

Earth's climate is changing at an unparalleled pace, threatening biodiversity worldwide (Field et al., 2014; Hartmann et al., 2013; Pörtner et al., 2014). In fact, air temperature is projected to increase between 2.6 and 4.8 °C (Collins et al., 2013) and atmospheric CO₂ concentration can reach values between 420 and 940 ppm by 2100 (Collins et al., 2013; Pörtner et al., 2014). Freshwater ecosystems are particularly at risk due to alterations in thermal and precipitation regimes which, in turn, will drastically change the dynamics between floods and droughts, decrease of river flow and increase of the risk of extreme events (e.g. heat waves) (Field et al., 2014; Fussler et al., 2012). Also, the increase in acid rainfall, resulting from emissions of sulfur dioxides and nitrogen oxides to the atmosphere, will contribute to the

acidification of lakes and rivers (Leduc et al., 2013; Van De Waal et al., 2010). All of this will unquestionably pose further challenges for fauna living in these habitats (Leduc et al., 2013).

Freshwater fish, as ectotherms, strongly rely on environmental temperature in order to regulate their metabolism and may have a reduced migration ability, making them prone to warming conditions (Angilletta, 2002; Berg et al., 2010). Increasing temperature is even more alarming for those species living closer to their thermal tolerance limits (Reusch and Wood, 2007; Somero, 2010; Tomanek, 2010; Hoffmann and Sgrò, 2011). Even though many studies have approached the subject of thermal stress in freshwater fish (e.g. Podrabsky and Somero, 2004; Yamashita et al., 2004; Fanguet et al., 2006; Jesus et al., 2013, 2016; Campos et al., 2017), only a few have attempted to study the effects under the context of climate change (e.g. de Oliveira and Val,

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2016; Mccairns et al., 2016; Prado-Lima and Val, 2016; Jesus et al., 2017, under review). Furthermore, the acidification of freshwater ecosystems have been poorly studied, despite the predictable effects that freshwater biota will suffer as a result of it (Leduc et al., 2013; Ou et al., 2015a). In fact, major focus has been given to ocean acidification and this process is widely known to affect many marine species physiology and behaviour (e.g. Munday et al., 2009a; Aurélio et al., 2013; Vinagre et al., 2013; Pimentel et al., 2016, 2015; Rosa et al., 2014, 2016).

The Iberian chubs, *Squalius carolitertii* (Doadio, 1988) and *Squalius torgalensis* (Coelho et al., 1998), are two closely related endemic freshwater fish species, which inhabit two distinct regions with different climatic conditions (Carvalho et al., 2010): *S. carolitertii* inhabits the northern region of Iberian Peninsula, whereas *S. torgalensis* has a restricted distribution to the Mira river basin, in the southwestern region of Portugal (Coelho et al., 1998). While *S. carolitertii* lives under milder conditions, *S. torgalensis* is exposed to higher temperatures and greater temperature fluctuations, particularly during the dry season where individuals of this species are often confined to small ponds (Coelho et al., 1998; Magalhães et al., 2003). These two distinct climates expose these species to different seasonal and even daily water temperature fluctuations, which in turn result in different life history traits such as different life span, spawning age and body size (Magalhães et al., 2003). Additionally, previous works on gene regulation of both species suggest that *S. torgalensis* seems to be better adapted to higher temperatures, presenting higher survival rates and stronger responses in gene expression under high temperatures when compared to *S. carolitertii* (Jesus et al., 2016, 2013).

When facing stressful conditions, organisms may display several physiological responses to survive under the adversities. Adjustments in metabolic pathways are amongst the most common responses and may lead to shifts in energy production (Campos et al., 2017; Mwangangi and Mutungi, 1994). The activities of citrate synthase (CS) and lactate dehydrogenase (LDH) can reflect these modifications in aerobic and anaerobic potential, respectively, and thus represent good biomarkers for these metabolic pathways (McClelland et al., 2006). Another highly common response to stressful conditions is the heat shock response (HSR) (Morris et al., 2013; Wegele et al., 2004), which consists in the synthesis of a specific group of proteins (heat shock proteins (HSP)) that are responsible for the stabilization and refold of denatured proteins as a response to increasing temperatures (Dong et al., 2008; Fangué et al., 2006; Tomanek, 2010; Yamashita et al., 2004). In addition, the production of molecules that derive from oxygen, i.e. reactive oxygen species (ROS), (e.g. superoxide anion and hydrogen peroxide) (Sevcikova et al., 2011; Sun et al., 2007) is also a good indicator of stress (Sevcikova et al., 2011; Storey and Storey, 2005; Sun et al., 2007). ROS trigger the individual's antioxidant defense system by producing antioxidant enzymes, trying to reestablish the oxidant balance. However, in excess ROS situations, several biological features of the organisms may be damaged, including cellular health and integrity due to lipid peroxidation (Sevcikova et al., 2011).

The present study aims to understand the effects of warming plus acidification on the physiology of the Iberian chubs, *S. carolitertii* and *S. torgalensis*, inhabiting different climatic regions, by using conventional stress-related biomarkers (metabolic and antioxidant responses). Particularly, we investigated the combined effects of warming (+ 3 °C) and acidification ($\Delta\text{pH} = -0.4$), in relation to summer average parameters, on the metabolic potential (CS and LDH activities), heat shock response, antioxidant enzymatic machinery [glutathione *S*-transferase (GST), superoxide dismutase activity (SOD) and catalase (CAT)] and peroxidative damage [malondialdehyde (MDA)] of these two species.

This study provides important insights on the threats of climate change, a scenario presently considered irreversible to freshwater species (Collins et al., 2013). Moreover, since *S. torgalensis* is a critically endangered species (Coelho et al., 1998), this work is of utmost importance for surveying the threats that this species may face in future,

in order to adopt proper conservation measures.

2. Material and methods

2.1. Sampling

S. carolitertii and *S. torgalensis* specimens were field collected in two river basins (Mondego: 40° 8'5.22"N–8° 8'35.06"W; Mira: 37°38'1.31"N–8°37'22.37"W), located in the west coast of Portugal. An electro-fishing device (300 V, 4A; Hans Grassl, Model EL 62) was used to perform fish collection, and the avoidance of juvenile mortality was accomplished by applying short duration pulses (3–6 ms). Organism sampling was performed during spring (May to June 2014), where water temperature and pH varied between 17.80 ± 0.67 °C and 8.08 ± 0.01 for Mondego river, and 19.50 ± 0.21 °C and 8.23 ± 0.02 for Mira river (measured with a YSI-85 handheld system). Capture procedures were performed under ICNF license (n° 263/2014/CAPT, Instituto da Conservação da Natureza e Florestas).

2.2. Experimental design

After collection, fish were transported in isothermal cases, under constant aeration conditions, to the Laboratório Marítimo da Guia (Cascais, Portugal). Subsequently, fish were progressively acclimated (2 weeks) to laboratory conditions, mimicking summer average values at the collection sites [data obtained from the national information system of water resources (<http://snirh.pt>) from 2002 to 2006] for temperature and pH under normoxic ($8 \text{ mg}\cdot\text{L}^{-1}$). After this acclimation period, each fish species (*S. carolitertii* and *S. torgalensis*) was exposed (30 days) to four different experimental conditions, under a 2×2 factorial design: i) control (19 and 23 °C, respectively, pH 6.9 and 7.3 for both species); ii) warming (22 and 26 °C, respectively, pH 6.9 and 7.3 for both species); iii) acidification (19 and 23 °C, respectively, pH 6.5 and 6.9 for both species); iv) combined warming and acidification scenario (22 and 26 °C, respectively, pH 6.5 and 6.9 for both species). Warming and acidification conditions were accomplished in order to experimentally assess the responses of each fish species to the tested climate change scenarios (temperature increase = + 3 °C; $\Delta\text{pH} = -0.4$), based on the IPCC's RCP 6.0 scenario (Field et al., 2014). During laboratory acclimation and experimental exposure, a mixture of bloodworms/white mosquito larvae (TMC Iberia, Portugal) and *Spirulina* spp. (flake food, Ocean nutrition, Belgium) was provided ad libitum to fish, on a daily basis. Light regime was set to 12 h:12 h (light/dark cycle), in accordance to prevailing natural light conditions. Monitoring of nitrate, nitrite and ammonia levels was performed daily, using colorimetric tests (Profi Test, Salifert, Holland), with abiotic parameters being kept below detectable levels, during the entire experimental procedure. Monitoring of dissolved oxygen and pH was performed through an automatic control device (Profilux 3.1N, GHL, Germany), with set point values being adjusted and monitored automatically. Individual oxygen (PL-0368, GHL, Germany) and pH (PL-0071, GHL, Germany) sensors were used. Conductivity levels were continuously (Profilux 3.1N, GHL, Germany) and individually (PL-0055, GHL, Germany) monitored, while being kept at 400 to $500 \mu\text{S}\cdot\text{cm}^{-1}$. Additional daily conductivity checks were performed, using handheld monitoring equipment (CO30, VWR, Portugal). Programmable dosing systems (Easy Dose 3, TMC Iberia, Portugal) connected to indoors-freshwater tanks (300 or $600 \mu\text{S}\cdot\text{cm}^{-1}$), allowed in-flow of freshwater to experimental tanks, in order to maintain conductivity levels within desired range (400 – $500 \mu\text{S}\cdot\text{cm}^{-1}$). Maintenance of dissolved oxygen/pH values was accomplished, as follows: injection of certified N_2/CO_2 (Air Liquide, Portugal) to down regulate values and aeration with atmospheric filtered air (soda lime, Sigma-Aldrich) to up regulate. All water parameters for the different experimental treatments are shown in Table 1.

After experimental exposure, a set number of fish ($n = 6$), derived

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