

# Contrasting environments shape thermal physiology across the spatial range of the sandhopper *Talorchestia capensis*

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**Abstract** Integrating thermal physiology and species range extent can contribute to a better understanding of the likely effects of climate change on natural populations. Generally, broadly distributed species show variation in thermal physiology between populations. Within their distributional ranges, populations at the edges are assumed to experience more challenging environments than central populations (fundamental niche breadth hypothesis). We have investigated differences in thermal tolerance and thermal sensitivity under increasing/decreasing temperatures among geographically separated populations of the

sandhopper *Talorchestia capensis* along the South African coasts. We tested whether the thermal tolerance and thermal sensitivity of *T. capensis* differ between central and marginal populations using a non-parametric constraint space analysis. We linked thermal sensitivity to environmental history by using historical climatic data to evaluate whether individual responses to temperature could be related to natural long-term fluctuations in air temperatures. Our results demonstrate that there were significant differences in the thermal response of *T. capensis* populations to both increasing/decreasing temperatures. Thermal sensitivity (for increasing temperatures only) was negatively related to temperature variability and positively related to temperature predictability. Two different models fitted the geographical distribution of thermal sensitivity and thermal tolerance. Our results confirm that widespread species show differences in physiology among populations by providing evidence of contrasting thermal responses in individuals subject to different environmental conditions at the limits of the species' spatial range. When considering the complex interactions between individual physiology and species ranges, it is not sufficient to consider mean environmental temperatures, or even temperature variability; the predictability of that variability may be critical.

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## Introduction

Biologists have long sought to understand macroscale patterns of ecological traits, a central aspect of many ecological and biogeographical questions (Brown 1995; Gaston

2003). The factors determining the size of the geographical ranges of organisms are, however, still poorly understood, mainly because variation in range-size potentially results from the interactions of multiple physical, ecological, physiological and evolutionary processes (Gaston 2003; Holt 2003; Parmesan et al. 2005; Chown and Gaston 2008). The fundamental niche breadth hypothesis (Brown 1984) assumes that the geographical extent of a species is a reflection of its ecological niche. From this perspective, populations that live within the centre of distribution should experience better conditions than those at the limits of the distributional range (Sagarin and Gaines 2002). Hence, the Abundant Centre Hypothesis (ACH), which predicts higher numbers of individuals at the centre of their spatial distribution compared to the periphery, has been tested in many taxa (Sagarin and Gaines 2002; Samis and Eckert 2007; Tuya et al. 2008; Rivadeneira et al. 2010; Virgós et al. 2011; Fenberg and Rivadeneira 2011; Baldanzi et al. 2013). In addition to abundance, a variety of comparisons have been used to test the predictions of the ACH, including life history traits and size (Gilman 2006; Lester et al. 2007; Rivadeneira et al. 2010; Baldanzi et al. 2013).

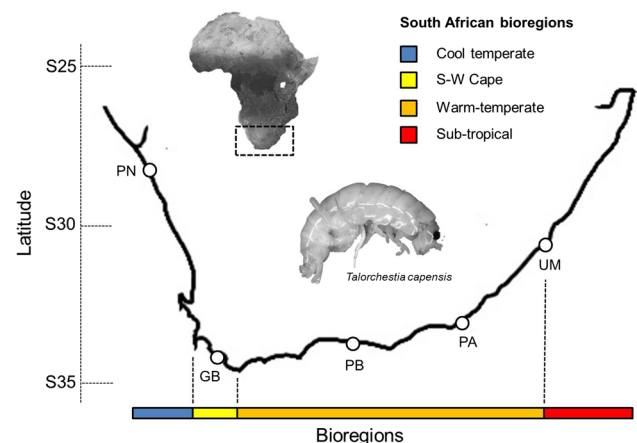
Integrating physiological traits and the extent of a species range is a powerful tool for evaluating the success of species in their respective landscape (Spicer and Gaston 1999; Calosi et al. 2007). In particular, knowledge of thermal physiology would contribute to a better understanding of the potential consequences of climate change (Pörtner and Knust 2007; Khaliq et al. 2014). Temperature is one of the main climatic variables affecting biological functions, from molecules to ecosystems (Clarke 2004; Kasahn et al. 2009; Somero 2010), as well as an essential abiotic factor governing the distribution and abundance of species (Schulte et al. 2011; Bozinovic et al. 2011). Natural fluctuations in environmental temperatures, especially but not necessarily across a latitudinal gradient, have been demonstrated to positively affect the thermal tolerance of ectotherms (Sunday et al. 2011). This Climatic Variability Hypothesis (CVH; see review by Pither 2003 for a detailed definition) relates to latitude based on the fact that higher latitudes usually exhibit greater variations in temperature and thereby select for more eurythermal species (Stevens 1989; Mermillod-Blondin et al. 2013). The time scale of temperature variation is also important, as demonstrated in an annual killifish (*Austrofundulus limnaeus*) in which changes in the transcriptome were found to differ between long-term acclimation and responses to diurnally cycling temperatures (Podrabsky and Somero 2004). Even in the absence of a latitudinal gradient, however, according to Jensen's Inequality Theory, temperature variability should reduce the thermal sensitivity of species (Ruel and Ayres 1999; Fischer and Karl 2010). The effect of temperature variability on the thermal physiology of ectotherms

has been only recently been demonstrated (Folguera et al. 2009; Williams et al. 2012; Paaajmans et al. 2013), and the need to consider not only the mean temperature but also the variability in temperature when forecasting the effects of climate change on species distribution and persistence has been recommended (Schulte et al. 2011; Williams et al. 2012). For example, Paaajmans et al. (2013) showed that mosquitoes were sensitive to daily fluctuations in temperature as these reduce key factors of thermal sensitivity, including thermal safety margins.

Physiological responses to temperature become particularly interesting in the case of organisms which live at the interface between sea and land since they are constantly exposed to extreme daily environmental fluctuations and are therefore potentially best poised to cope with high variability (Helmuth et al. 2006).

To test the relationships between physiological traits and position within a species' range, we used a supralittoral amphipod, the sandhopper *Talorchestia capensis*, which is found on the coasts of South Africa. Since respiration is a critical dimension of a species' thermal niche, we investigated the effects of temperature on the metabolic rate (estimated as oxygen consumption) and the thermal tolerance of populations from different biogeographic provinces spread across the limits of the species' distributional range (Fig. 1).

We hypothesised that populations of *T. capensis* would show a geographical pattern in their thermal physiology (thermal tolerance and thermal sensitivity) as physiological traits are known to constrain species' boundaries (Spicer and Gaston 1999; Sunday et al. 2010). We expected higher



**Fig. 1** Map of the sites of collection and image of a female *Talorchestia capensis*. PN Port Nolloth, GB Gansbaai, PB Plettenberg Bay, PA Port Alfred, UM Mngazana. Colour-coded bar The four bioregions along the South African coasts, with the colour code as given on the figure. PN and UM are the western and eastern limits of the geographic range, respectively; PB and GB are within the centre of the distribution; PA lies between the centre and the eastern limit of distribution. Between GB and PN there is a gap in the spatial distribution of *T. capensis* (Baldanzi et al. 2013)

thermal tolerance at collection sites where the environmental temperatures are more variable, as suggested by the CVH while, conversely, more variable environmental temperatures should lower the thermal sensitivity as predicted by Jensen's Inequality Theory (Ruel and Ayres 1999).

To test these predictions, we compared the population thermal tolerance and individual thermal sensitivity of central and marginal populations using a non-parametric constraint space analysis of the goodness of fit of five hypothetical models. Subsequently, to potentially gain further insight into the role of local climate variability in the ecology of populations, we evaluated whether variation in individual thermal sensitivity is related to long-term (multi-generational) fluctuations in environmental temperatures and the predictability of such variation.

## Materials and methods

### Model organism, collection, maintenance and acclimation

The sandhopper *Talorchestia capensis* is widely, but patchily distributed along the South African coast (Griffiths 1976; Baldanzi et al. 2013). Its distribution is mainly driven by the morphodynamic conditions of the shore and does not follow the assumptions of the Abundance Centre Theory (Baldanzi et al. 2013). Nonetheless, its distribution does encompass four different biogeographic regions (defined by Lombard 2004) which are strongly affected by ocean currents with contrasting temperature regimes, suggesting that there may be differences in thermal physiology among populations (Baldanzi et al. 2013). Little is known about the biology of *T. capensis*, but these sandhoppers should have a life-span of about 1 year, with two main reproductive peaks, although females can carry eggs all year around (Van Senus 1988). Specimens were collected from five geographically separated populations, covering approximately 1800 km of coastline within the distributional range of *T. capensis* (Fig. 1): Port Nolloth (PN, S29.28002; E16.87979), Gansbaai (GB, S34.5636; E19.35), Plettenberg Bay (PB, S34.0524; E22.377), Port Alfred (PA, S33.89336; E26.29815) and Mngazana (UM, S31.6836; E29.4372). Sites were sandy shores of similar morphodynamic type (Baldanzi et al. 2013) chosen on the basis of their relative position within the geographical range of *T. capensis*. Animals were collected during a single survey of 15 days, from March to April 2013. One hundred adults of similar size (sex was not considered at this stage) were collected by hand from each population and transported to the laboratory in cool boxes containing sand and kelp, which helped keep humidity and temperature constant (maximum travel time 24 h). In all experiments,

females and males were equally distributed among the replicates, thereby avoiding any confounding effect of sex. Animals were maintained under common controlled conditions (7 days in 20-l aquaria partially filled with humidified sand, fed ad libitum at 18 °C and 12/12 h photoperiod) before the experiments were performed in order to re-set metabolic stability, as suggested by Calosi et al. (2007).

### Collection of climatic data

Historical data (from January 1990 to July 2013) for air temperature were collected from meteorological stations for each site (South African weather service; <http://www.weathersa.co.za>). Historical data for Mngazana were not available over a long-term period due to its remote location; consequently, data were collected from the closest location available [Port Edward (PE), approximately 80 km farther east, S31.03222; E30.23677]. To avoid confusion this dataset is referred to as Mngazana (UM).

### Upper and lower critical thermal limits experiments

After the period of common controlled conditions, 40 animals of similar size were selected from each aquarium and placed individually in 4-ml plastic tubes. Uniformity of size was ensured using a microbalance (size range 0.03–0.05 g), as there is a high correlation between size of sandhoppers and their upper thermal tolerance (Morritt and Ingolffson 2000). Twenty animals each were used to assess the upper thermal limit (UTL) and lower thermal limit (LTL), respectively. Humidity was controlled, and food was provided as desiccation and starvation can significantly affect the metabolism of an animal during long-term experiments (Terblanche et al. 2011). Tubes containing animals were kept in a water bath (GP 200; Grant Instruments®, Cambridge, UK) at 18 °C for 2 h in the dark before the start of temperature ramping, following Morritt and Ingolffson (2000). The water bath was pre-set to increase or decrease at a rate of 1 °C/h, as slow rates of change in temperature are more likely to reflect natural conditions (Terblanche et al. 2011). In addition, the average rate of change in temperature between maximum and minimum daily temperature for the five locations was 0.8 °C h<sup>-1</sup>. Mortality was examined hourly by monitoring movement of the sensory antennules, mouthparts and other appendages. Animals which did not show any active movement were gently stimulated using the thermocouple probe. The thermal limits were calculated following a similar approach to that of Stillman and Somero (2000), using the LT50 method, the temperature at which 50 % of animals from a sample die, at which point the experiment was terminated. These experiments were used to define the thermal range (UTL – LTL) within which we performed the oxygen consumption

experiments. This thermal range is used as proxy of thermal tolerance (TT).

### Oxygen consumption experiments

Experiments for thermal performance were conducted in air only, as sandhoppers generally live in water-saturated sand, but do not experience immersion (Morritt 1988). Oxygen consumption ( $MO_2$ ) was measured using an oxygen meter (Fibox 3 LCD; PreSens Precision Sensing GmbH, Regensburg, Germany) able to detect the air saturation of a closed environment through a sensor spot installed in the respirometer chamber (2-ml glass vial). Thirty-two animals of similar size were assessed; each animal was gently placed inside a chamber, one animal per chamber, close to the sensor spot area. The chambers were too small to allow active movement. The entire system (vial and tube) was filled with gas-inert, toroid-shape beads (outer diameter approx. 3 mm), in order to minimise the volume of air inside the chambers and to allow for a better detection of the oxygen saturation of the air. Temperatures were increased/decreased at a rate of  $1\text{ }^\circ\text{C h}^{-1}$ , according to Terblanche et al. (2007). The temperature ramps used ranged between  $3^\circ$  below and three above the LTL and UTL, respectively (values retrieved from the LT50 experiments), allowing investigation of oxygen consumption within and beyond the sandhoppers' thermal range. This experimental design allowed us to make a rough comparison of the thermal limits using two different experimental techniques. After 4 h at  $18\text{ }^\circ\text{C}$  in the dark, 16 animals were individually exposed to an increasing ramp of temperatures, and 16 were exposed to decreasing temperatures.  $MO_2$  was recorded at two time intervals every  $3^\circ$  with both increasing and decreasing temperatures. Between the two readings the tubes were clamped for approximately 3 h, creating a closed environment in which the decrease of oxygen at a specific temperature was due to the animal's respiration. After every measurement the vials were refilled with normoxic air to avoid hypoxia (Schurmann and Steffensen 1997). Oxygen probes were calibrated prior to each experiment in air-saturated (100 %) and oxygen-free distilled water, following the instruction manual. After each ramp, the vials and tubes were sterilised with 100 % ethanol overnight to avoid growth of bacteria. To check for bacterial growth during ramping, especially at high temperatures, sterilised control chambers with no animals were used in preliminary experiments. An oxygen decrease of 0–0.5 % was detected only at  $40\text{ }^\circ\text{C}$ .

### Data analysis

At the end of the experiments on oxygen consumption, the total volume of air available in each chamber for

each animal was calculated from the difference between the total volume of the chamber minus the volume occupied by the beads and the animal. The live mass of each animal was also determined using a precision balance and expressed in grams. The percentage of oxygen saturation of air was converted to oxygen concentration  $[O_2]$  and consequently to millimoles per minute per gram body weight ( $\text{mmol}\cdot\text{min}^{-1}\cdot\text{g}^{-1}$ ). All of the analyses described in the following sections were performed separately for increasing and decreasing ramps. In order to compare the overall trend of oxygen consumption among populations (the slopes of the curves), we performed analysis of covariance (ANCOVA) with temperature and size as the covariates and population as the predicting factor. If variation in size was found not be significantly related to our response variable, ANCOVA were performed with temperature only as covariate. Not all replicates survived during ramping, and we included only values retrieved from healthy replicates (minimum of 8). The resulting curves therefore ranged between  $6$  and  $27\text{ }^\circ\text{C}$ . Analyses were carried out on linearised data, using Arrhenius plots (natural logarithm of metabolic rate as a function of inverse temperature in degrees Kelvin).

A post hoc analysis (Tukey HDS test) was carried out on population effects to investigate different responses to temperature. Data were analysed using STATISTICA (ver. 10; StatSoft Inc., Tulsa, OK).

Thermal sensitivity (TS) of populations was assessed by calculating the  $Q_{10}$  factor from the Arrhenius plots for each individual, within the reduced range of  $6$ – $27\text{ }^\circ\text{C}$ , in all populations. Two sets of  $Q_{10}$  were obtained, one for increasing ( $Q_{10i}$ ) and one for decreasing ramps ( $Q_{10d}$ ). The formula used to calculate the  $Q_{10}$  was:

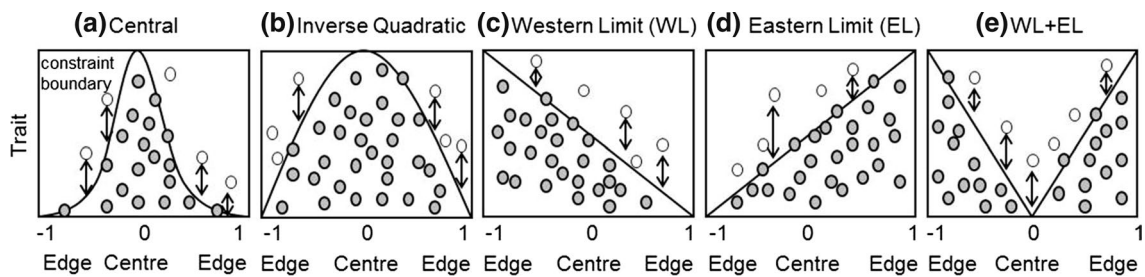
$$Q_{10} = (R_2/R_1) \exp [10/(T_2 - T_1)],$$

where  $R_1$  and  $R_2$  are the individual  $MO_2$  values (calculated between  $6$  and  $15\text{ }^\circ\text{C}$  for  $Q_{10d}$  and between  $18$  and  $27$  for  $Q_{10i}$ ), and  $T_1$  and  $T_2$  are the temperatures at which  $R_1$  and  $R_2$  were calculated. Temperature range, variability and predictability (dT, COV and  $P$ , respectively; see following sections) were introduced into the simple linear regression analyses as predictors, with  $Q_{10}$  as the dependent variable, to investigate the thermal sensitivity of the animals to the variability and predictability of climatic conditions experienced over the past 23 years.

### Non-parametric constraints space analyses

To test whether the TS (both  $Q_{10i}$  and  $Q_{10d}$ ) and TT of *T. capensis* differed between central and marginal populations, we used a non-parametric constraint space analysis, following procedures similar to those used by Enquist et al. (1995) and Sagarin and Gaines (2002). Even though these models have been developed to describe patterns





**Fig. 2** Five hypothetical models proposed for explain the patterns of distribution of thermal tolerance (TT) and thermal sensitivity (TS) along the geographical range of *T. capensis* (modified from Sagarin and Gaines 2002; Fenberg and Rivadeneira 2011). **a** Central model, **b** Inverse Quadratic model, **c** Eastern Limit model (EL), **d** Western

Limit model (WL), **e** WL + EL model. We calculated the residual sum of square deviations (RSS, deviations indicated by arrows) for the observed data that exceeded the constraint boundary (open dots). Grey dots Analysed trait values after creating  $10^6$  randomised values

of abundance of species throughout their ranges (Sagarin and Gaines 2002; Sagarin et al. 2006), they can be used to investigate spatial patterns in size, life history traits and physiological constraints (Rivadeneira et al. 2010; Baldanzi et al. 2013). In our study, we used these models to describe the spatial distribution of physiological data, such as the distribution of TS and TT. For each population, TS (both  $Q_{10i}$  and  $Q_{10d}$ ) values were calculated for each animal by dividing each  $Q_{10}$  by the maximum  $Q_{10}$  value found at any site within the range. Relative  $Q_{10}$  values were named as RTSi and RTSd for increasing and decreasing values, respectively. Relative values of TT (RTT) were also calculated by dividing each TT by the maximum TT value found at any site. Relative values of TS and TT were calculated to allow reasonable comparisons among sites, as suggested by Sagarin and Gaines (2002). To evaluate whether RTSi, RTSd and RTT varied with position within the distributional range, a range index (RI) was calculated using the expression proposed by Brown (1995) and Sagarin and Gaines (2002) and adapted to South African coasts by Baldanzi et al. (2013). The RI index ranges between  $-1$  and  $1$ ; in ours study, sites with values close to  $0$  were considered to be near the centre of distribution and values close to  $-1$  and  $+1$  were considered to be near the western and eastern edges, respectively.

The spatial distributions of TS and TT were evaluated statistically against the predictions of five hypothetical models (see Fig. 2 for a description of the models). The same models have previously been used to test abundance, size and sex ratio data in *T. capensis* (Baldanzi et al. 2013) and have been applied to other species (Sagarin and Gaines 2002; Gaston 2003; Sagarin et al. 2006; Rivadeneira et al. 2010; Fenberg and Rivadeneira 2011). The degree of fit of each model to the observed data was evaluated by calculating the residual sum of squared deviations (RSS) for sites exceeding the constraint boundaries generated by each model. The significance of the observed RSS values was evaluated by generating  $10^6$  randomised values of

RTSi, RTSd and RTT. The fit of the model was considered to be significant when the observed RSS value was  $<5$ th percentile of the randomised distribution. The degree of support for each model was evaluated by calculating the Akaike's Information Criterion, selecting all models with Akaike weights of  $>0.25$  (Rivadeneira et al. 2010; Baldanzi et al. 2013). Analyses were carried out using a routine in R Development Core Team 2007), slightly modified from Rivadeneira et al. (2010).

#### Analyses of climatic dataset

To confirm the relationship between temperatures from weather stations and microhabitat conditions, we performed a preliminary test using temperature dataloggers at Port Nolloth over 2 days (14–17 April 2013). We deployed three dataloggers placed 10 cm deep in the sand, the average depth to which these sandhoppers burrow (bottom, B) and three on the surface (S). Temperature was recorded every 5 min for a total of 48 h [see Electronic Supplementary Material (ESM) 1 for the entire dataset], and the collected data were then plotted to check for linearity between B and S temperatures. Significant positive linearity between B and S (see ESM 2) suggested that any variation in the temperature at the surface should positively and linearly reflect variation in temperatures at the bottom. Although slopes were  $<1$ , indicating that a variation of  $1^\circ\text{C}$  in surface temperature corresponds to less variation at the bottom, we considered the data from weather stations to be a valid proxy of variability/predictability in microhabitat conditions.

Differences between maximum and minimum daily temperatures were averaged for each calendar month and shown as mean monthly range (dT,  $^\circ\text{C}$ ). Data were plotted against time (year). To test for differences in the dT among sites where the populations were found, one-way permutational ANOVA (PERMANOVA; Anderson et al. 2008) was performed on the dT dataset with population as a fixed

factor. To assess temperature variability, a coefficient of variation (COV, %) was calculated for the dT values [multiplying the standard deviation (SD) by 100 and dividing it by the mean]. COV gives an indication of the reliability of the average: the higher the COV, the less reliable the average (Hasanean 2004). Predictability of dT (P, the certainty regarding the values of a fluctuating variable at a given time) was assessed using the mathematics of information theory on climatic datasets (Colwell 1974). Colwell's calculations are based on the fact that a certain variable can be predictable, either because its values are constant with time or because they vary on a known time scale. Consequently, Colwell's predictability is the sum of constancy and contingency (equal to seasonality) calculated for the whole time series of dT at each site. Thus, for each site and for each of 23 years, frequency tables were built by specifying how many monthly ranges for each of the 12 months (the columns of the table) fell into 12 equal categories of thermal range (states, i.e. the rows of the table) from the highest to the lowest dT values for all sites. Once constructed, it was possible to use these tables to calculate the predictability, which is maximal when there is absolute certainty that all dT values for each month will fall in only one state; that is, when for each column there is only one non-zero value (Colwell 1974).

## Results

The UTL, LTL and TT retrieved from the LT50 experiments for the five populations are reported in Table 1. Port Nolloth and Gansbaai, to the north and west, had a wide range of tolerance (PN = 39 °C; GB = 37 °C), followed by Port Alfred and Mngazana (PA = 30.5 °C; MN = 30.5 °C), which lie to the east. The central Plettenberg Bay population showed a narrow range of tolerance (PB = 27.5 °C).

MO<sub>2</sub> for the five populations was calculated individually, and all the populations showed an increase of MO<sub>2</sub> with temperature (Fig. 3). Variation in size did not show a significant effect on the response variable, although there

was a significant interaction between size and population (data not shown). The analysis of covariance showed a significant overall effect of population on the responses to both increasing (ANCOVA,  $F_{(4,238)} = 8.460$ ,  $p < 0.0001$ ) and decreasing (ANCOVA,  $F_{(4,182)} = 5.826$ ,  $p < 0.001$ ) temperatures. Responses did not follow an apparent geographical pattern (Tukey HSD test), although for both increasing/decreasing temperatures the eastern populations (PA, UM) were separated from the rest (Table 2).

When linearised following the Arrhenius equation, the MO<sub>2</sub> of Gansbaai, Plettenberg Bay, Port Alfred and Mngazana were significantly related to temperature, whether increasing or decreasing, while Port Nolloth did not show linearity between MO<sub>2</sub> and increasing temperature (Table 2).

The climatic data showed differences among all sites in terms of dT, COV and P. The mean monthly range was significantly different among locations (PERMANOVA,  $F = 159.87$ ,  $df = 4$ ,  $p = 0.0001$ ), and the pairwise comparisons showed that all locations differed from each other (mean and SD are reported in Table 1). For predictability of dT, 12 states equal in size from the lowest (1.45 °C for October 1992 in PN) to the highest dT value (15.03 °C for July 2008 in PA) were defined and used to build the frequency tables. A weakly significant negative relation ( $r^2 = 0.085$ ;  $p < 0.05$ ) was found for  $Q_{10i}$  and COV, with a weak positive relation ( $r^2 = 0.079$ ,  $p < 0.05$ ) for  $Q_{10i}$  and P. No significant regressions were found for  $Q_{10d}$  and the climatic variables (Fig. 4).

The non-parametric constraint space analyses showed that both RTS and RTT followed a geographical pattern of distribution (Table 3; ESM 3). Particularly, for RTSi and RTSd the best degree of fit was a ramped pattern (Eastern Limit model, Table 3), while for RTT it was a double ramp pattern (Western + Eastern Limits model, Table 3).

## Discussion

Previous studies have reported a positive relationship between latitude and thermal physiology in ectotherms,

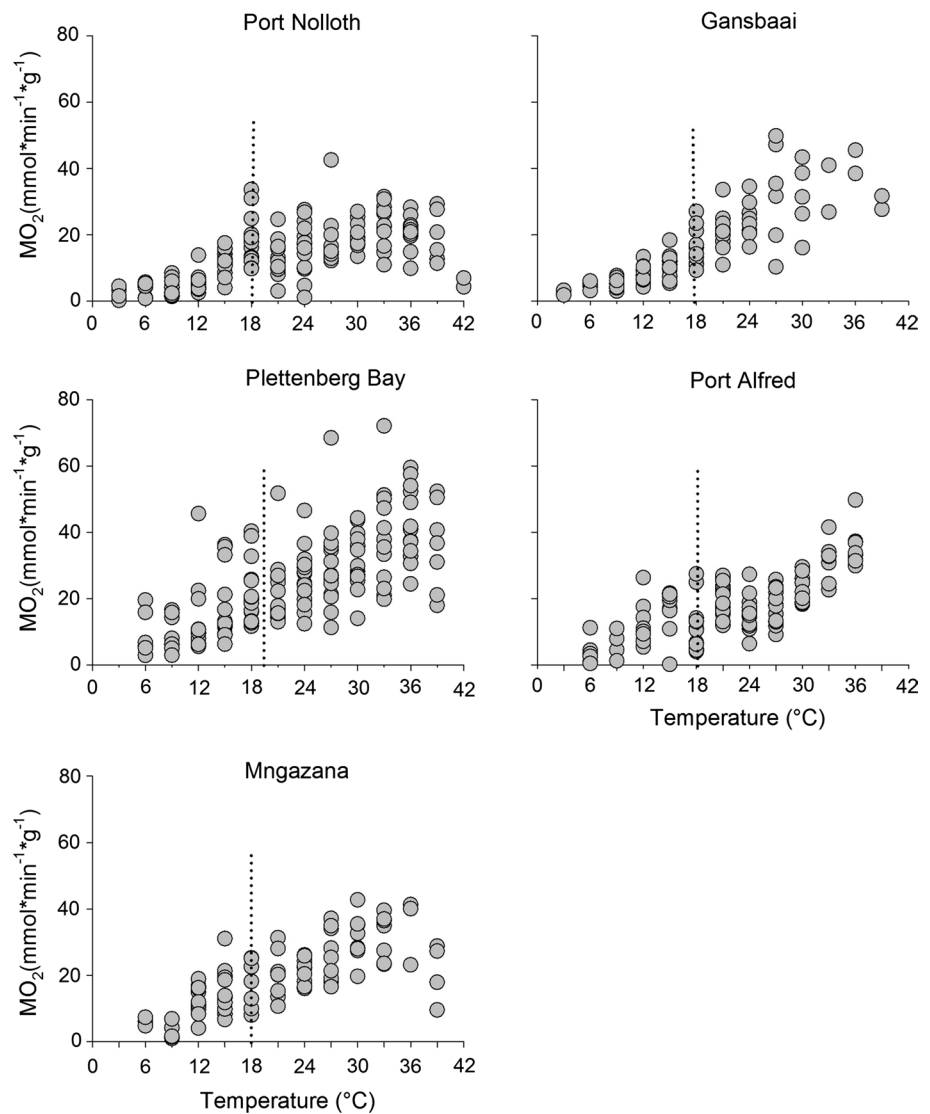
**Table 1** Thermal tolerance and climatic variables of the individual populations

Population <sup>a</sup>	UTL (°C)	LTL (°C)	TT (°C)	dT (°C)	COV (%)	P
PN	39	0	39	8.26 ± 1.76	21.3	0.40
GB	37	0	37	6.96 ± 0.60	8.69	0.68
PB	33	5.5	27.5	7.24 ± 0.96	13.3	0.65
PA	36	5.5	30.5	9.19 ± 2.09	22.3	0.43
MN	36	5.5	30.5	6.34 ± 1.38	21.75	0.69

UTL, Upper thermal limit; LTL, lower thermal limit; TT, thermal tolerance (UTL – LTL); dT, mean monthly range [±standard deviation (SD)]; COV, coefficient of variation for dT; P, predictability. See Sect. "Analyses of climatic dataset" for explanation of variables

<sup>a</sup> See Fig. 1 for explanation of populations/sampling sites

**Fig. 3** Oxygen consumption ( $MO_2$ ) curves for the five populations of *T. capensis*. All replicates are shown in the graphs (grey dots). Vertical dotted line Temperature at which individuals had been acclimated (18 °C). From that value of temperature, increasing and decreasing ramps of temperature were performed



with greater tolerances at higher latitudes, often related to a concurrent increase in climate variability (see Sunday et al. 2010). Although latitude is often used as a proxy for temperature, in our study we can exclude the effects of latitude per se as the study area is dominated by two major current systems with very different temperature regimes. The west coast is dominated by the cool Benguela Current, while the coastal waters of the east coast are strongly affected by the much warmer Agulhas Current. Therefore, although it spans less than 5° of latitude, the study area includes subtropical (Mngazana) to cool temperate (Port Nolloth) conditions, with sites at the same latitude having completely different temperature conditions on the west and east coasts. Consequently, we were able to relate the physiological responses observed directly to variability and predictability in temperature (as well as to the mean values), with no potentially confounding effects associated with latitude. We showed that geographical patterns in the response of

populations of *T. capensis* to increasing or decreasing temperature differed across the spatial range in terms of both thermal tolerance and thermal sensitivity. Sandhoppers had higher tolerance at the edges than at the centre of distribution, while their thermal sensitivity increased when moving from the western to the eastern edge.

The slow rate of increase/decrease in temperature used was chosen to mimic changes in temperature under natural conditions and was close to the natural rate averaged over our five locations. Long ramps can lead to several confounding effects which can increase or decrease the thermal limits (Terblanche et al. 2011; Ribeiro et al. 2012), and while we avoided starvation and desiccation, we could not eliminate other potential factors, such as daily cycles of thermal limits, as has been reported for the frog *Rana clamitans* (Willhite and Cupp 1982).

According to the fundamental niche breadth hypothesis (Brown 1984), variation in physiological traits is

**Table 2** Linear regression analyses on the Arrhenius<sup>a</sup> plots for each of the five populations

Population <sup>b</sup>	<i>n</i>	Slope	Intercept	<i>R</i> <sup>2</sup>	<i>p</i> value	Tukey HSD <sup>c</sup>
Port Nolloth						
I	66	10.084	6.143	0.007	N.S	a
D	43	12.878	46.939	0.436	***	a
Gansbaai						
I	40	50.356	20.091	0.305	***	b, c
D	44	7.651	28.850	0.476	***	a, c
Plettenberg Bay						
I	69	43.018	17.371	0.144	***	a, b
D	30	15.541	56.543	0.283	***	a, c
Port Alfred						
I	73	34.203	14.699	0.171	***	c
D	40	6.808	26.299	0.177	***	d
Mngazana						
I	49	43.688	17.915	0.194	***	c
D	31	14.275	52.262	0.392	***	c, d

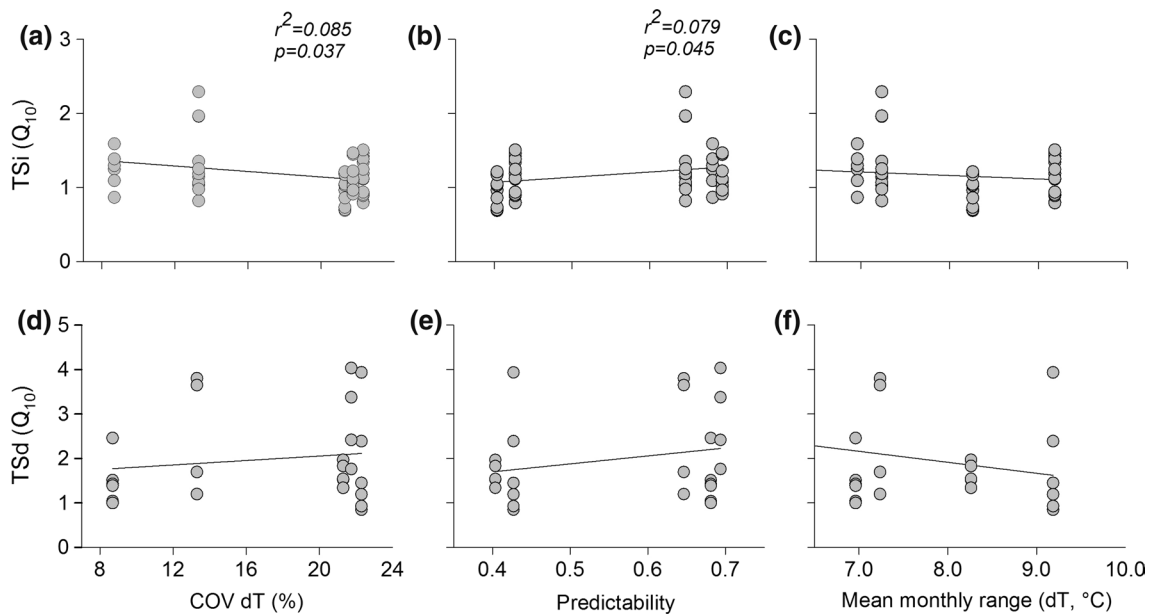
\*\*\* Significant *p* values at  $p < 0.0001$ ; N.S., not significant

*n*, Number of samples; *R*<sup>2</sup>, coefficient of determination

<sup>a</sup> Arrhenius equation ( $\ln O_2 = \ln a - Ea/k \times 1/T$ ) where  $O_2$  is the oxygen consumption,  $\ln a$  is the intercept,  $Ea/k$  is the slope and  $T$  is temperature

<sup>b</sup> I increasing ramps, D decreasing ramps

<sup>c</sup> Same lowercase letters indicate similar groups among populations after post hoc comparison following analysis of covariance (ANCOVA; see text for details on analysis)



**Fig. 4** Regression plots of TS and climatic variables [*COV dT* coefficient of variation for *dT* (%), *dT* mean monthly range in temperature (°C), predictability]. *TS<sub>i</sub>* Thermal sensitivity for increasing values,

*TS<sub>d</sub>* thermal sensitivity of decreasing values,  $Q_{10}$   $Q_{10}$  factor as calculated from the Arrhenius plots (see text). *R*<sup>2</sup> and *p* values are reported only for significant linear relationship (**a**, **b**)

considered to be critical in determining the extent of a species' range, and widespread species should show greater variability in the range of tolerances and in physiological

plasticity (Spicer and Gaston 1999). Logistic constraints on the numbers of animals we could use prevented the use of methodologies such that proposed by Gilchrist (1996)



**Table 3** Degree of fit of each model for relative thermal sensitivity and thermal tolerance

Model <sup>a</sup>	RSS	5th percentile	AIC	AICwt
<b>RTSi</b>				
C	7.27*	7.55	26.9	0.00
IQ	4.41*	4.73	39.4	0.00
WL + EL	2.68	1.38	47.83	0.02
WL	5.40	4.57	34.3	0.00
<b>EL</b>	<b>2.30*</b>	<b>2.32</b>	<b>55.64</b>	<b>1.00**</b>
<b>RTSd</b>				
C	3.77	2.66	43.3	0.00
IQ	2.51	1.52	53.5	0.00
WL + EL	1.51	0.87	62.2	0.00
WL	3.38	1.79	46.1	0.00
<b>EL</b>	<b>0.78*</b>	<b>0.79</b>	<b>80.35</b>	<b>1.00**</b>
<b>RTT</b>				
C	1.58	1.18	65.1	0.00
IQ	1.51	1.11	66.1	0.00
<b>WL + EL</b>	<b>0.30*</b>	<b>0.31</b>	<b>103.3</b>	<b>1.00**</b>
WL	0.876	0.78	79.8	0.00
EL	1.02	0.68	76.0	0.00

\* Significant values for RSS, \*\* higher degree of support for each model (AICwt >0.25)

RTS Relative thermal sensitivity, RTT thermal tolerance, *i* increasing ramps, *d* decreasing ramps; RSS, residual sum of square, AIC Akaike Information Criterion, AICwt AIC weight

<sup>a</sup> Models: *C* Normal, *IQ* Inverse Quadratic, *WL* Western Limit, *EL* Eastern Limit, *WL + EL* Western and Eastern Limits. Models in bold font: fitted models

or the estimation of thermal limits using recovery time from heat/chill coma (e.g., Gaitán-Espitia et al. 2013), and we based our estimation of thermal tolerance on the simple difference between upper and lower thermal limits (UTL – LTL). Nonetheless, our models (calculated through randomisation of the available data) revealed that thermal tolerance was lower at the centre of distribution than at the edges, while thermal sensitivity gradually increased from one edge to the other (from the western to the eastern limit). Relatively long-term data (covering multiple generations of this short-lived animal) showed that environmental temperatures were more variable at the edges of the species' distribution than at the centre and that such fluctuation could explain the “edge to centre” pattern of decreasing thermal tolerance. The CVH, which postulates an increase in thermal tolerance with increasing latitude and/or temperature fluctuation (Stevens 1989; Pither 2003), can be applied to variation in thermal tolerance within a single species characterised by a wide distributional range (Sanford and Kelly 2011). We showed a negative correlation between the variability of the environmental temperature and thermal tolerance, suggesting that more unstable

conditions at the edges of the distributional range of *T. capensis* may have allowed animals to be more tolerant to temperature fluctuations. This indicates that widespread species can show a range of physiological responses to temperature that differs among populations (Fusi et al. 2015), depending on the thermal variability they experience over time. This result has important implications for understanding the evolution of species that exist as separated populations with relatively low gene flow, such as Talitroids (Pavesi et al. 2013). Further investigations on the population genetic of *T. capensis* should bring more light on whether differences in physiology among populations can be attributed either to phenotypic variation or genetic variability.

The results also have important implications for understanding the effects of climate change. Predictions based on the overall species thermal tolerance that ignore differences among populations, would fail to predict extinctions in locally adapted populations with a narrow range of tolerances (Kelly et al. 2012). For example, populations of *T. capensis* at the edges of the species' distribution should cope better with changing environmental temperatures, as they presented wider thermal tolerances than the population near the centre.

Interestingly, such an “edge to centre” pattern in thermal tolerance did not apply to thermal sensitivity, suggesting that, in contrast to thermal tolerance, individual thermal sensitivity differed between the two edges of distribution. Thermal sensitivity to both increasing and decreasing temperature showed a ramped pattern of distribution (EL model). Essentially, individuals were more sensitive to increasing/decreasing temperatures if they originated from a location that experiences predictable variation of temperature over time. At the western limit (high variability, low predictability), individuals lowered their metabolic responses and therefore their thermal sensitivity, as predicted by Jensen's Inequality Theory. At the other edge of the geographical range (Eastern limit: high variability, high predictability), individuals did not show the expected low sensitivity to temperature change, but rather exhibited high thermal plasticity, in disagreement with Jensen's theory. Thus, our results show that where temperature variability is more predictable, sandhoppers are more sensitive to increasing/decreasing temperatures. When environmental conditions fluctuate constantly (with a certain degree of prediction), an individual can continuously adjust its phenotype to match prevailing conditions (Huey et al. 1999) and even tolerate variation in environmental conditions among seasons. In the case of environments that show unpredictable variability, acclimatisation can come at a high cost (Pigliucci 2005), and this scenario applies to individuals from our western edge. Furthermore, the ability to anticipate future conditions and adjust the

phenotype accordingly can be weakened by stochastic variations in environmental conditions, explaining why many organisms fail to acclimatise to such change (reviewed by Angilletta 2009).

Jensen's Inequality Theory states that high thermal fluctuation will induce lower thermal sensitivity and behavioural thermoregulation (Ruel and Ayres 1999; Fischer and Karl 2010). In nature, sandhoppers burrow into the top 10 cm of sand to avoid heat and desiccation during the day, burrowing deeper in summer than in winter (Tsubokura et al. 1997), and emerge to migrate across the shore during the night (Williams 1995; Morritt 1998). Such behavioural thermoregulation was not possible in our experiments, and we recognise that this potentially represents a limitation to our interpretation of natural responses. Nonetheless, comparing individuals from different populations under identical conditions in the laboratory elucidates their physiological responses when they cannot avoid or minimise temperature variability.

In our study, linear regressions between climatic data and thermal sensitivity showed that the  $Q_{10}$ I significantly decreased as temperature variability (COV) increased, but that it was positively related to temperature predictability (P). These regressions need to be interpreted cautiously given the extremely low, though significant, values of  $R^2$ . However, when similarly variable environments show different levels of predictability (the case of PN and MN at the western and eastern limits of our study area, respectively), the expected negative effect of temperature variability on thermal sensitivity is annulled by the concurrent positive effect of its prediction. Hence, individuals show higher sensitivity. Our measure of temperature variability is based on dT (the simple difference between maximum and minimum daily averages) and therefore is not affected by the absolute values. We recognise that absolute values, especially extremes, can have important effects on the thermal physiology of ectotherms (Angilletta 2009), but we found no relationships between the thermal sensitivity of *T. capensis* and the absolute values of minimum and maximum daily temperatures from which dT was calculated.

Generating predictions by means of correlative approaches that link an ecological factor to an environmental variable is a common strategy, and this approach finds its support in the ecological niche concept (Hutchinson 1959; Brown 1984). Such simple models are, however, unlikely to provide realistic predictions if climatic variables do not actually shape a species' distribution of abundance (Kearney 2006). For example, applying a distanced-based linear model to *T. capensis* demonstrated that the distribution of abundance was shaped by site-specific conditions of the shore rather than climatic variables (Baldanzi et al. 2013). Our linear relationship between thermal sensitivity

and climatic variables showed that simple linear regressions alone may not be sufficient to predict the effect of environmental variables on a physiological trait. By combining the results from linear regressions and the constraint space analyses on thermal tolerance and thermal sensitivity, however, we showed that variability and predictability of environmental temperatures are important factors in shaping the physiology of *T. capensis*.

Estimating variation in thermal sensitivities among populations is an important tool for evaluating adaptation to local conditions (Angilletta 2009; Angilletta et al. 2010; Schulte et al. 2011). Our experiments were intended to test biogeographical/macrophysiological, rather than evolutionary hypotheses, but the results may have important evolutionary implications. For example, sandhoppers showed differences in physiological traits which are considered to be critical when the aim is to investigate population adaptation to local conditions (Angilletta et al. 2010). In our study, subjecting all individuals to homogeneous conditions before starting the experiments allows us to link observed phenotypic differences directly to the source population (Gianoli and Valladares 2012). Phenotypic plasticity, defined as the capacity of a single genotype to produce alternative phenotypes under different environments (Pigliucci 2001), is better examined when an individual genotype is tested (Gianoli and Valladares 2012). Given that, we showed that individuals responded differently to increasing and decreasing temperature ramps and that this plasticity showed a geographic pattern, with eastern populations being more plastic than the western ones. Differences in thermal sensitivity among individuals of *T. capensis* inhabiting distant locations characterised by contrasting levels of predictability in temperature variation is likely to have led to local adaptation to those conditions.

## Conclusions

Investigating variation in the physiological ecology of a species over large geographical scales is fundamental to evaluating the likelihood that a species can maintain itself in the landscape (Calosi et al. 2008; Chown and Gaston 2008). Our analyses demonstrate that there are intra-specific differences among populations of *T. capensis* in terms of both thermal tolerance (thermal range) and metabolic rate (oxygen consumption). Our data showed a geographical pattern in the distribution of thermal tolerance and thermal sensitivity that can be attributed to differences in aspects of local temperatures other than their absolute values. Temperature variability was associated with lower thermal plasticity at the western limit, supporting the Jensen's Inequality Theory, while greater predictability in the

variability of temperature at the eastern limit was linked to greater sensitivity to changes in temperature. Our results highlight the importance of including physiological data in biogeographical studies, particularly when testing how local environment may shape and influence ecologically the interactions between physiological traits and the limits of a species' range. This study confirms the importance of temperature fluctuation when investigating the effect of climate change on species distribution and indicates that the predictability of such fluctuations can be critical when forecasting the ecological responses of local populations to climate change.

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**Author contribution statement** SB, FP and MF conceived the ideas. SB and MF designed and performed the experiments. SB, NFW, MF, SC analysed the data. SB, NFW, CDM and FP wrote the manuscript.

#### Compliance with ethical standards

**Conflict of interest** The authors declare no competing financial interests or any other form of conflict of interest

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