

RESEARCH ARTICLE

Thermal physiological traits and plasticity of metabolism are sensitive to biogeographic breaks in a rock-pool marine shrimp

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ABSTRACT

Populations of broadly distributed species commonly exhibit latitudinal variation in thermal tolerance and physiological plasticity. This variation can be interrupted when biogeographic breaks occur across the range of a species, which are known to affect patterns of community structure, abundance and recruitment dynamics. Coastal biogeographic breaks often impose abrupt changes in environmental characteristics driven by oceanographic processes and can affect the physiological responses of populations inhabiting these areas. Here, we examined thermal limits, performances for heart rate and plasticity in metabolic rate of the intertidal shrimp *Betaeus emarginatus* from seven populations along its latitudinal range (~3000 km). The distribution of this species encompass two breaks along the southeastern Pacific coast of Chile: the northern break is characterized by sharp discontinuities in upwelling regimes, and the southern break constitutes a major discontinuity in water conditions (temperature, pH, dissolved oxygen and nutrients), coastline topography and divergence of main oceanographic currents. For *B. emarginatus*, we found higher plasticity in metabolism at the sites sampled at the biogeographic breaks, and at the site subjected to seasonal upwelling. The variation in metabolic rate was not consistent with increasing latitude and it was not affected by breaks. The lower and upper thermal limits were lower in populations around breaks, although the optimum temperature decreased towards higher latitudes. Overall, whereas thermal limits and plasticity of metabolism are related to biogeographic breaks, metabolic rate is not related to increasing latitude or the presence of breaks in the sampled range.

KEY WORDS: Intraspecific variation, Thermal limits, Intertidal, Upwelling, Heart rate, Thermal performance curve, Reaction norm

INTRODUCTION

Because of its close relationship with physiological performance, ambient temperature (T_A) plays a key role in determining the geographic distribution of ectotherms (Pörtner, 2001; Sunday et al., 2012), as it is usually correlated with their upper and lower limits of thermal tolerance and physiological sensitivity (Sunday et al., 2011). Also, it is thought that T_A imposes selective pressure that


gradually shapes the phenotypic responses of populations of a species along geographic clines (Castañeda et al., 2004; Lardies et al., 2011), leading to intraspecific variation in physiological traits in widely distributed species inhabiting contrasting environments (Gaitán-Espitia et al., 2014; Stillman, 2002). In ectotherms, performance traits (e.g. growth, reproduction, physiology) vary with differences in T_A , and this relationship can be described by a thermal performance curve (TPC; Angilletta, 2009; Huey and Berrigan, 2001) that includes three parameters: (1) critical thermal minimum (CT_{min}), (2) critical thermal maximum (CT_{max}) and (3) optimum temperature (T_{opt}). Specifically, CT_{min} and CT_{max} represent the T_A below and above which performance is at a minimum, and T_{opt} represents the T_A at which performance is maximized. As such, TPCs have been used to mechanistically describe the variation in thermal tolerance among natural populations of ectothermic species (Kingsolver et al., 2004; Latimer et al., 2011; Schulte et al., 2011). The results of such studies indicate that the parameters of TPCs usually co-vary along geographic clines (e.g. latitude), reflecting the ability of ectotherms to adapt, at least in part, to their environments (Fangue et al., 2006; Klok and Chown, 2003; Lardies et al., 2004b).

The metabolic rate (MR) of an organism is linked to its pattern of energy use, and as such, represents a holistic measure of the 'pace of life' (Gillooly et al., 2001), and is suggested to reflect the energetic cost of adaptation to a particular thermal environment (Clarke, 2003; Clarke and Fraser, 2004). The relationship between MR and T_A also varies systematically across the ranges of ectotherms, in concert with environmental gradients (Addo-Bediako et al., 2002). Two contrasting patterns of geographic variation have been described for the MRs of ectotherms (Bozinovic et al., 2011; Burton et al., 2011). One body of evidence indicates that populations at lower latitudes, experiencing warmer temperatures throughout the year, exhibit higher MRs than their conspecifics at higher/colder latitudes (Angilletta, 2001; Barria and Bacigalupe, 2017; Lardies et al., 2004a; Peck, 2002). In contrast, the metabolic cold adaptation (MCA) hypothesis states that at equivalent T_A , the MR of ectothermic species and populations from cold climates is greater than that of their warm-climate relatives (Addo-Bediako et al., 2002; Gaston et al., 2009; Jacobsen and Brodersen, 2008). This compensation for low T_A has been thought to be a general evolutionary adaptation of ectotherms from high latitudes or altitudes (Chown and Gaston, 1999; Gaston et al., 2009). However, although some studies support the MCA hypothesis for terrestrial insects (Addo-Bediako et al., 2002; Gaston et al., 2009), other authors have failed to find an increase in metabolism at lower T_A in marine organisms (Clarke, 1991; Rastrick and Whiteley, 2011; Steffensen, 2002).

The capacity of marine intertidal ectotherms to adjust their physiological response to daily and seasonal fluctuations of environmental variables can define not only their vertical distributions, but also their geographical ranges (Pörtner, 2001;

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List of symbols and abbreviations

CT _{max}	critical thermal maximum
CT _{min}	critical thermal minimum
f_H	heart rate
MCA	metabolic cold adaptation
MR	metabolic rate
SST	sea surface temperature
T_A	environmental temperature
T_{opt}	optimum temperature
TPC	thermal performance curve

Sunday et al., 2011). Along latitudinal gradients, local adaptation to different environmental regimens can lead to differences in thermal tolerance and physiological plasticity among populations of broadly distributed species (e.g. Fangué et al., 2006; Gaitán-Espitia et al., 2013, 2014; Gardiner et al., 2010; Lardies et al., 2011; Pörtner, 2001). In general, the scope of physiological plasticity is usually proportional to the magnitude of variation in the T_A that a species experiences in their native habitat: populations inhabiting more variable thermal environments (i.e. higher latitude) are expected to have broader tolerance limits and acclimation capacities than individuals inhabiting more stable environments (Calosi et al., 2010; Chown et al., 2004; Ghalambor et al., 2006; Janzen, 1967; Naya et al., 2011; Stevens, 1989). Environmental variability increases toward higher latitudes, and it is also high in coastal ocean areas placed in biogeographic breaks, where geological, climatological and oceanographic processes have delimited abrupt changes in the environmental regimes that are concordant with the limits in the distribution of species (Bowen et al., 2016; Broitman

et al., 2018 in press). In broadly distributed species, biogeographic breaks might be contained in their range, and populations located in these areas could exhibit differences in abundance (Lancellotti and Vásquez, 1999; Sink et al., 2005), population dynamics (Broitman et al., 2001; Navarrete et al., 2008; Rivadeneira et al., 2002; Staaf et al., 2010), and also in their phenotypic response (Lardies et al., 2008; Ragionieri et al., 2009; Sanford et al., 2003). However, the environmental variability at biogeographic breaks has been poorly related to the physiological capacities and plasticity of broadly distributed species.

Two main biogeographic breaks have been reported along the range of the intertidal shrimp *Betaeus emarginatus* (H. Milne Edwards 1837) (Fig. 1) on the southeastern Pacific coast of Chile (Camus, 2001). The northern break is located around 30–32°S and is characterized by sharp discontinuities in upwelling regimes (Thiel et al., 2007). The southern break, around 42°S, where the geomorphology of the coastline changes from a continuous, almost straight line to a fragmented one, is characterized by inner seas, bays and channels, and is where the West Wind Drift over the Pacific Ocean splits into the northern Humboldt Current and the southern Cape Horn Current (Camus, 2001; Thiel et al., 2007; Montecino and Lange, 2009; Silva et al., 2009; Waters, 2008), the intensity of which varies throughout the year, inducing a higher environmental heterogeneity in this area. As such, these breaks define three biogeographic provinces: (1) the (northern) Peruvian province (from 4 to 30°S), (2) the (southern) Magellanic province (from between 41 and 43°S to 54°S) and (3) an intermediate area between both provinces (from 30°S to 41°S) (Fig. 1A). Therefore, along the range of *B. emarginatus*, we predict higher plasticity in MR in populations located near the biogeographic breaks, because of the

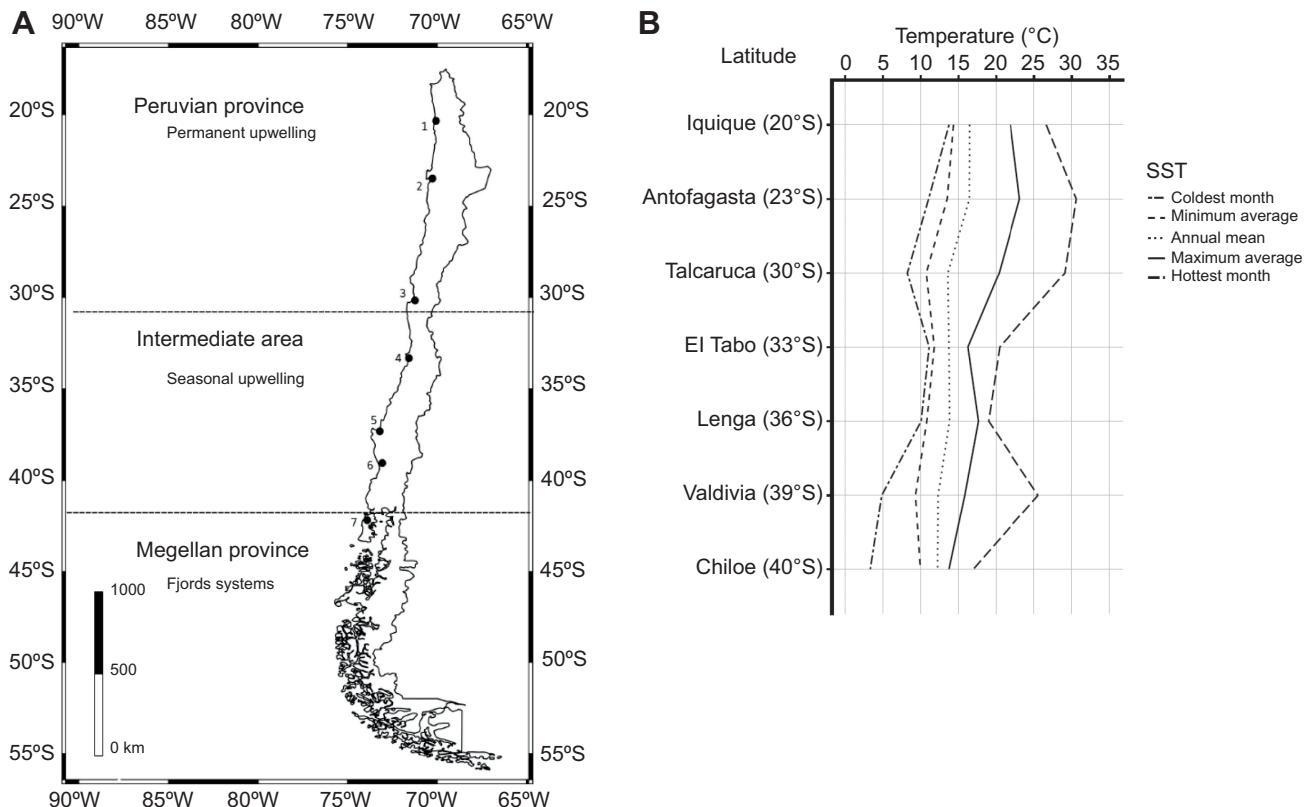


Fig. 1. Study sites and thermal regime. (A) Sampled populations across the distributional range of *Betaeus emarginatus* in Chile and (B) thermal regime according to the sea surface temperature (SST) data gathered at each sampling site.

higher environmental heterogeneity. Furthermore, we predict that in addition to an overall effect of latitude on thermal limits (CT_{\min} and CT_{\max}) and parameters of the TPC, populations at the biogeographic breaks should exhibit a stepped cline in comparison to populations further from the breaks.

MATERIALS AND METHODS

Study populations and specimen maintenance

During austral spring, *B. emarginatus* specimens were collected by hand at low tide from seven locations along the Chilean coast (ca. 3000 km), thus encompassing the majority of the species' latitudinal range (Fig. 1A). From the sampled sites, animals were taken to the laboratory at the Universidad Adolfo Ibáñez by land or air, in trips that lasted between 4 and 6 h. For transportation, individuals were placed in a plastic box (3 liter capacity), filled with humid towels with seawater from the sampling sites; this box was then placed in a plastic cooler containing ice packs to ensure that animals were at a temperature of $10 \pm 1^\circ\text{C}$. At the laboratory, individuals were maintained in common garden conditions for 1 month before the experiments were conducted, at constant temperature ($14 \pm 1^\circ\text{C}$) in artificial seawater, prepared by dissolving sea salt (Instant Ocean[®], Spectrum Brands, Blacksburg, VA, USA) in distilled water to obtain a salinity of 33 ppt. Shrimps were exposed to a light:dark cycle of 12 h:12 h and fed with Instant Algae[®] (Isochrysis 1800, Reed Mariculture, Campbell, CA, USA) and aquarium shrimp food three times a week. MR, CT_{\min} and CT_{\max} measurements were taken in animals from all of the sampled locations. However, owing to logistical limitations, TPCs from cardiac activity estimates were only measured in individuals from four populations: Antofagasta, Talcaruca, El Tabo and Valdivia. These populations, however, still encompass most of the distribution of *B. emarginatus* in Chile and the northern biogeographic break.

Physiological measurements

Metabolic rate

Oxygen consumption, here used as a proxy for MR (Brown et al., 2004), was estimated in 179 specimens that were sequentially exposed to two experimental temperatures; each temperature acclimation period lasted 30 days. The first acclimation temperature reflected the mean annual *in situ* sea surface temperature (SST; $14 \pm 1^\circ\text{C}$; Fig. 1B). The second acclimation temperature was the average maximum temperature experienced by all populations along their latitudinal range ($20 \pm 1^\circ\text{C}$; Fig. 1B). A 113 ml acrylic respirometry chamber with photosensitive, non-oxygen consumptive sensors was used for respirometric analysis. MR was measured using a temperature-compensated Microx optic fiber O_2 meter (Microx TX3, PreSens, Regensburg, Germany) connected to a recirculating water bath by a flow-through cell housing (FTCH-PSt1, PreSens) and with a stirring regime of 20–30 rpm. The optic fiber was calibrated in a saturated sodium sulfite ($\text{Na}_2\text{O}_3\text{S}$, 0% air saturation) solution and in aerated artificial seawater (100% air saturation), checking for sensor drift before and after each trial. In addition, control chambers containing only aerated artificial seawater were used to quantify background microbial oxygen consumption. After calibration, oxygen concentration (% air saturation) in the seawater was measured for 60 min (recorded every 5 s). The first and last 5 min were discarded in order to avoid possible disturbance when the fiber was inserted or removed. Thus, the oxygen estimates are averages of the remaining 50 min of measurements. Before and after each measurement, shrimp were placed briefly on a paper towel to remove excess water, and then wet body mass was recorded using an

analytical balance (AFA-180LC, Adam Equipment, Oxford, CT, USA) with ± 0.001 mg precision. The average of both body mass measurements was used in the statistical analyses. To obtain MR in units of $\text{g O}_2 \text{ l}^{-1}$, the slope of the relationship between the decrease of oxygen in the chamber and time of incubation (h) was calculated and normalized to fresh mass. Shrimp were not fed 24 h prior to physiological measurements to standardize hunger levels, because the cost of digesting and assimilating food (specific dynamic action; SDA) represents a large component of an animal's energy expenditure (Secor, 2009). In addition, to remove the possible confounding effects of sex (Valverde et al., 2009), only male shrimp of similar size were used in the experiments.

Heart rate for thermal performance curves

We estimated the heart rate (f_H) of individuals exposed to one of two thermal gradients: the full gradient included the temperatures of 2, 3, 4, 5, 6, 8, 10, 12, 14, 15, 17, 19, 21, 23, 25, 26 and 27°C , and the short gradient included only those temperatures up to and including 14°C . We measured the cardiac activity in individuals from Antofagasta ($n_{\text{Full}}=4$; $n_{\text{Short}}=1$), Talcaruca ($n_{\text{Full}}=7$; $n_{\text{Short}}=12$), El Tabo ($n_{\text{Full}}=11$; $n_{\text{Short}}=9$) and Valdivia, where all individuals were exposed to full thermal gradient ($n_{\text{Full}}=11$). Animals were individually separated in plastic chambers with six subdivisions ($200 \times 200 \times 100$ mm), where they were attached gently to the bottom of each chamber using glued tape, ensuring that they would not move during the measurements. The chambers were transferred to a thermoregulated bath (WRC-P8, Daihan, Korea), previously adjusted during one of the temperature trials. f_H was estimated using the non-invasive method described by Burnett et al. (2013), where heart beat is monitored by an infrared-light-emitting diode glued to the carapace above the pericardial sinus of each individual, from which the signal was amplified (AMP-03, Newshift Lda, Leiria, Portugal) and recorded using an oscilloscope (Handyscope HS4, TiePie Engineering, Sneek, The Netherlands). f_H signals were viewed and analyzed using TiePie Multi Channel software (version 1.0.29.0, TiePie Engineering). We recorded for 15 min, and the first and the last 5 min were discarded in order to avoid any noise or erroneous recordings generated by animal manipulation, and the results were expressed as the number of beats during 1 min (beats min^{-1} ; for details, see Gaitán-Espitia et al., 2017). Measurements of cardiac activity were performed for each shrimp at the same time of day to avoid the effects of a possible circadian rhythm of respiration. The order of the temperature trials was randomized in order to avoid the confounding effects of time.

Thermal limits

We measured the thermal limits in individuals from Iquique ($n=26$), Antofagasta ($n=26$), Talcaruca ($n=15$), El Tabo ($n=14$), Lenga ($n=8$), Valdivia ($n=28$) and Chiloe ($n=10$). The CT_{\min} and CT_{\max} were determined as the T_A below and above which the ventilatory activity (frequency of pleopods beating) ceased within 1 min (Hervant et al., 1997). Each individual was placed in a 25 ml incubation flask that was transferred to a thermoregulated bath (WRC-P8, Daihan), adjusted at a starting temperature of 8 or 24°C , to measure CT_{\min} and CT_{\max} , respectively, for 5 min. After these incubations, the temperature in the bath was decreased (or increased) at a rate of 1°C min^{-1} . To track the temperature inside the thermoregulated bath, we used a similar chamber with a HOBO data logger (model U23-003, Onset Computer Corporation, Bourne, MA, USA). Every minute or at every 1°C change in temperature, ventilatory activities were measured directly using low-energy red

light with a binocular magnifier (2.5×). When an animal was unable to beat its pleopods after 1 min, we let it recover at ambient temperature, at 20°C (CT_{min}) or in a cold chamber, at 2°C (CT_{max}).

Statistical analysis

Linear models

We used a linear mixed modeling approach to evaluate the effects of body mass, latitude, acclimation temperature (14 and 20°C), province (Peruvian, intermediate area and Magellanic) and biogeographic breaks (yes: Talcaruca and Chiloe; no: Iquique, Antofagasta, El Tabo, Lenga and Valdivia) on metabolic rate, whilst taking into account that each individual was acclimated and measured at both 14 and 20°C, and that individuals from different localities were captured and measured in different periods. Therefore, individual id and date of capture were included as random factors in the analyses. Hypothesis testing was carried out using likelihood ratio tests of nested models based on restricted maximum likelihood (REML; random factors) or maximum likelihood (ML; fixed factors). The best model was found after a series of tests that compared the full model (that include interactions) against alternative models that were simplified by the exclusion of single predictors. Body mass was log₁₀ transformed to meet the assumption of a normal distribution. Critical thermal limits were analyzed using a linear model, including body mass and latitude as covariates and province and biogeographic breaks as fixed factors. Statistical analyses were performed using the lme4 package (<https://cran.r-project.org/web/packages/lme4/index.html>) implemented in R platform 3.4.4 (<http://www.R-project.org/>).

Thermal acclimatory capacity of metabolism

We determined the variation in the capacity for acclimation of MR using two approximations. First, we estimated the mean of the slope of the reaction norm as the difference in MR in individuals exposed to 14 and 20°C along the thermal interval experienced (6°C). Differences in the slope of the reaction norm between populations were determined using a simple linear model, including population as a fixed factor and the mass of individuals as a covariate. Second, we calculated the index of phenotypic plasticity, based on maximum and minimum standardized means (Seebacher et al., 2015; Valladares et al., 2006). This index, which ranges from 0 to 1, was calculated for each population as the difference between the minimum and maximum mean values of the acclimation temperature (i.e. 6°C) divided by the maximum mean value. This broad approach was chosen given our interest in exploring the plasticity of metabolism at the interpopulation level and assuming that genetic relatedness was significantly greater within the sampled populations than among them (Gianoli and Valladares, 2012).

Thermal performance curve fitting

Cardiac activity was fitted to the Brière temperature-scaling model with four parameters (Brière et al., 1999). The Brière model is characterized by an asymmetrical, unimodal curve that provides the best description of thermal performance by allowing for a rapid drop-off of the curve beyond the thermal optimum (Shi and Ge, 2010). This model has been used to characterize the thermal dependency of the intrinsic rate of increase of terrestrial insects (Estay et al., 2014), the metabolic rate (Mertens et al., 2015) and photosynthetic activity of seagrasses (Adams et al., 2017), and metabolic and consumption rates of a sea urchin (Lemoine and Burkepille, 2012). Here, f_H was a positive function of

temperature T (°C):

$$\text{TPC}_{f_H} = aT(T - T_{\min})(T_{\max} - T)^{1/m}. \quad (1)$$

TPCs for each population were fitted using the nonlinear regression function nlsLM (this incorporates the Levenberg–Marquardt type nls.lm fitting algorithm) in the package minpack.lm (<https://cran.r-project.org/web/packages/minpack.lm/index.html>) in the R environment (<http://www.R-project.org/>). The Brière non-linear model allowed us to directly estimate the biological parameters contained in the TPC fitted for each population, where T_{\max} represents the upper threshold (CT_{max}) and T_{\min} represents the lower threshold (CT_{min}), and a and m are empirical constants. The optimum temperature (T_{opt}) in Eqn 1 depends only on T_{\max} , T_{\min} and m , and was calculated as:

$$T_{\text{opt}} = \frac{2mT_{\max} + (m+1)T_{\min} + \sqrt{(4m^2T_{\max}^2 + (m+1)^2T_{\min}^2 - 4m^2T_{\min}T_{\max})}}{4m+2}. \quad (2)$$

RESULTS

Linear models

In *B. emarginatus*, MR was negatively affected by body mass (log₁₀ scale: $b = -0.360 \pm 0.060$ s.e.; $\chi^2_1 = 30.512$, $P < 0.001$) and increased in warm (20°C) acclimated individuals ($\chi^2_1 = 39.925$, $P < 0.001$; Fig. 2). Individual ID as well as date of measurement were important factors explaining part of the variation in MR; nevertheless, MR was not affected by latitude, province or the presence of a biogeographic break (Table 1).

CT_{max} was not affected by biogeographic break ($F_{1,120} = 0.998$, $P = 0.320$) or province ($F_{2,120} = 2.685$, $P = 0.072$), but was negatively affected by body mass (log₁₀ scale: $b = -2.417 \pm 0.831$ s.e.; $F_{1,120} = 10.772$, $P = 0.001$) and latitude ($b = -0.09 \pm 0.070$ s.e.; $F_{1,120} = 6.574$, $P = 0.012$). That is, larger individuals and those inhabiting colder localities showed less tolerance to higher temperatures (Fig. 3A). CT_{min} was not affected by body mass ($F_{1,120} = 1.026$, $P = 0.313$), latitude ($F_{1,120} = 1.096$, $P = 0.297$) or biogeographic breaks ($F_{1,120} = 0.169$, $P = 0.682$), but was affected by province ($F_{2,120} = 15.223$, $P < 0.001$). In particular, individuals from the Magellanic province (Chiloe) showed a higher tolerance to colder temperatures than individuals from both the intermediate area and the Peruvian province, which did not differ in terms of tolerance to cold (Fig. 3B).

Thermal acclimatory capacity of metabolism

The slope of the reaction norm (Fig. 4) was not affected by body mass ($F_{1,169} = 2.932$, $P = 0.089$), but was affected by population ($F_{6,169} = 2.905$, $P = 0.01$). A significant higher slope of the reaction norm was found in individuals from El Tabo. The plasticity index showed that the greatest variation in MR means between temperature trials occurred in Talcaruca, El Tabo and Chiloe (Table 2, Fig. 5).

Thermal performance curve fitting

The cardiac activity (Fig. 6), fitted to the Brière model, estimated an increase in CT_{max} toward higher latitudes, while CT_{min} could not be calculated for all populations (owing to the differential degree of grouping and spacing of measurements along the temperature axis). Therefore, to estimate T_{opt} from the model, we set CT_{min} to 4°C,

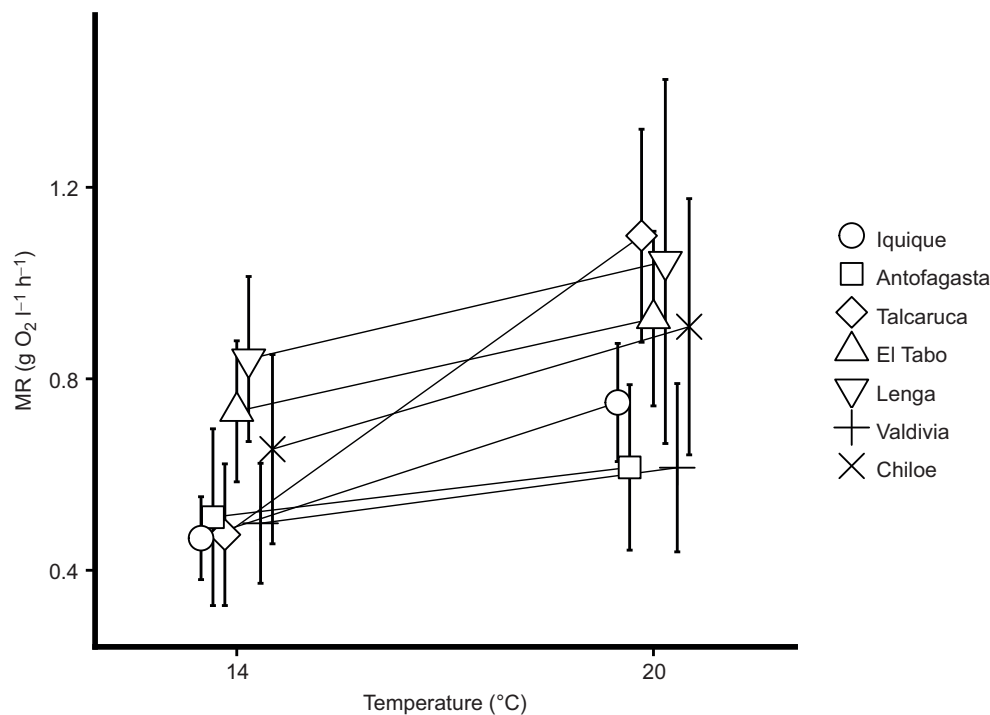


Fig. 2. Comparison of thermal reaction norms of metabolic rate (MR) of *B. emarginatus* along the latitudinal gradient on the Chilean coast.

The points on each shape-coded line represent the means for oxygen consumption measured under current environmental conditions (14°C) and the simulated future ocean-warming scenario (20°C) for each sampled location. Error bars represent 95% confidence intervals about those means.

which was the mean value found in all thermal limit experiments. The T_{opt} estimated from Eqn 2 decreased toward southern latitudes (Table 3).

DISCUSSION

It is well known that populations of broadly distributed species exhibit latitudinal variation in thermal limits and physiological plasticity (Gaston et al., 2009; Ghalambor et al., 2006; Spicer and Gaston, 1999). Although latitudinal variation in environmental temperatures has been shown to induce gradual intraspecific variation in phenotypic responses (Sunday et al., 2011), the presence of biogeographic breaks within a species' range should induce abrupt changes (stepped cline) in these parameters. In the present study, we found that (1) the MR of *B. emarginatus* did not covary with latitude, and it was not related with the presence of biogeographic breaks, nor with the province from which the individuals were sampled, but (2) we found higher plasticity of MR in populations located at the biogeographic breaks (30 and 42°S). Furthermore, (3) both measurements of plasticity (slopes of the reaction norms and plasticity index) were higher for individuals

from El Tabo, which is subjected to seasonal upwelling. Regarding the thermal limits, (4) whereas the CT_{max} decreased toward higher latitudes, the CT_{min} did not show variation in the sampled geographic range, except in Chiloe, at the southern break, where CT_{min} and CT_{max} were significantly lower. Finally, the fitted thermal performance curves showed that (5) T_{opt} decreased gradually towards higher latitudes.

Clinal patterns in physiological variation along natural environmental gradients are common in ectotherms (Bozinovic et al., 2011; Gaston et al., 2009; Lardies et al., 2004a; Sunday et al., 2011). Overall, analyses of large-scale physiological patterns can provide a powerful way to understand the causes of this variation (Chown et al., 2002; Clarke and Johnston, 1999) and its implications, given the prospects of substantial environmental change (Bozinovic et al., 2011; Gaston et al., 2009; Hoffmann et al., 2003; Sinclair et al., 2003; Somero, 2010). In terrestrial ectotherms, there is a clear pattern of broader thermal limits toward higher latitudes, but in marine species, the amplitude of this thermal window remains constant across latitudes, and thus, latitudinal trends in thermal tolerance seem to be more complex in this group (Sunday et al., 2011). Here, we found that the amplitude of the thermal window bounded by CT_{min} and CT_{max} was the same along the latitudinal gradient sampled. However, we found that CT_{min} and CT_{max} were significantly lower in shrimp taken from Chiloe, where the southern break and an important topographical breakup of the coastline occur, and individuals are subjected to high inputs of cold freshwater and cold nutrient-rich waters, saturated in CO_2 and with low dissolved oxygen and pH (Vargas et al., 2017). In contrast, T_{opt} estimated from *B. emarginatus* heart rate TPCs, decreased gradually toward higher latitudes, in accordance with previous findings of intraspecific variation in ectotherm TPC parameters (Castañeda et al., 2004; Wilson, 2001). Despite the fact that the study of variation in TPCs between populations has been cited as a fundamental tool to understand the response of ectotherms to future thermal scenarios (Bozinovic and Pörtner, 2015), very little is known about variation in T_{opt} on latitudinal scales. Here, we found

Table 1. Selection of the best model describing the variation in metabolic rate of *Betaeus emarginatus*

Metabolic rate~mass+latitude+break+province+acclimation+(1 ID)+(1 date)				
Full model	Excluded variable	χ^2	d.f.	<i>P</i>
Fixed factor	Break	1.6268	1	0.2021
	Province	1.0643	2	0.5873
	Acclimation	39.925	1	>0.001
Random factor	ID	4.4557	1	0.03479
	Date	12.575	1	>0.001
Covariates	Latitude	0.7847	1	0.3757
	Mass	30.512	1	>0.001

The full model was compared with models in which one of the variables was excluded using a chi-squared test. Bold indicates significance at $P < 0.05$.

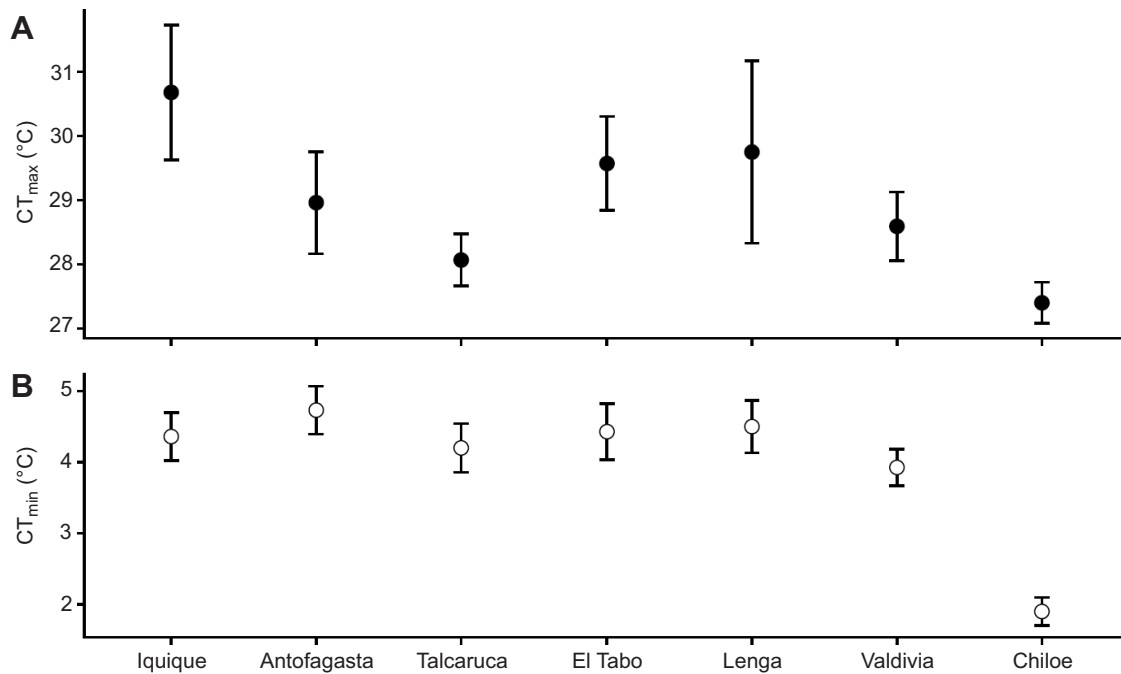


Fig. 3. Latitudinal variation in the thermal limits of *B. emarginatus*. (A) Mean values for critical thermal maximum (CT_{max}) and (B) critical thermal minimum (CT_{min}), estimated in seven populations of *B. emarginatus*. Error bars represent 95% confidence intervals.

that although T_{opt} decreases toward higher latitudes, CT_{max} values were higher in colder sites. These results highlight that individuals inhabiting warmer habitats have a reduced capacity to maintain thermal homeostasis above T_{opt} because it is closer to their upper thermal limit (see Gaitán-Espitia et al., 2014).

In coastal marine environments, species distribution patterns are often attributed to gradients or discontinuities in temperature (Somero, 2002; reviewed in Philippart et al., 2011). Such distribution patterns are influenced and maintained by ectothermic physiological and biochemical adaptations to variation in temperature across latitudes (Somero, 2002, 2010). The metabolic

rate of an organism is linked to its pattern of energy use, and is suggested to reflect the energetic cost of adaptation to a particular thermal environment (Clarke, 2003; Clarke and Fraser, 2004; see also Watson et al., 2013). The MCA hypothesis states that for broadly distributed species, an elevated metabolic rate should increase the fitness of populations at higher latitudes by allowing a higher energy uptake for growth and reproduction (Gotthard et al., 2000; Addo-Bediako et al., 2002). However, if species can compensate by growing in the next favorable season, an elevated metabolism should increase the cost of living (Clarke, 1991, 1993). Therefore, it was not likely that we would find that the metabolism

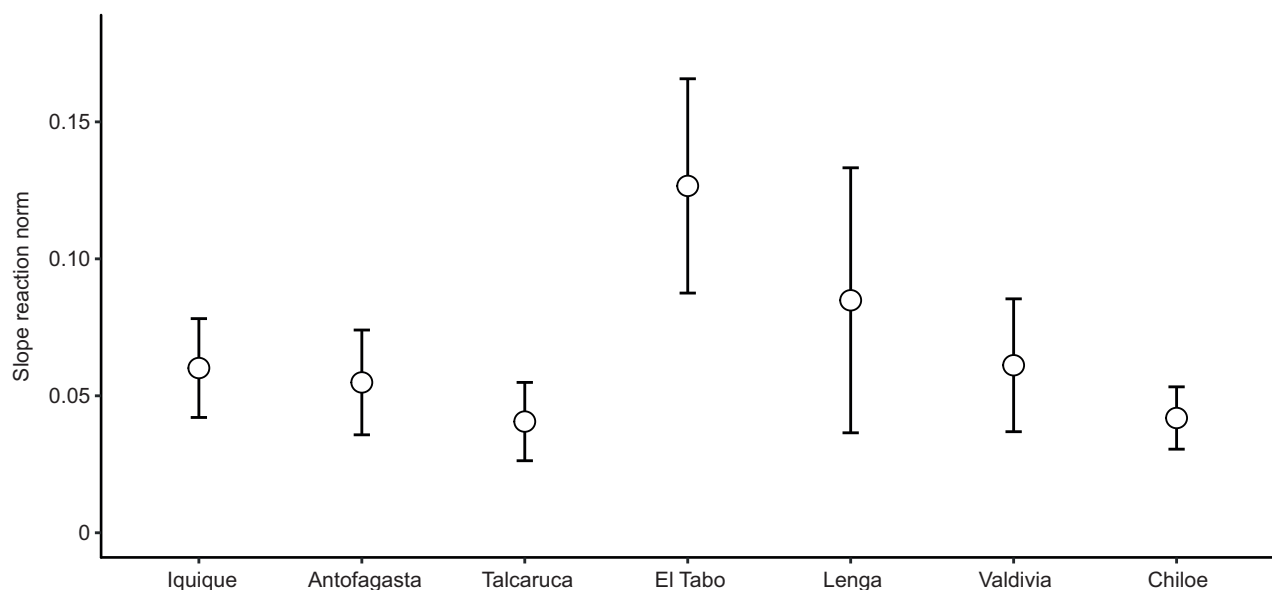


Fig. 4. Latitudinal variation in the mean slope of the reaction norm of *B. emarginatus*, estimated as the difference in metabolic rate in individuals exposed to 14 and 20°C along the thermal interval experienced. Mean values are indicated by white circles and error bars represent 95% confidence intervals.

Table 2. Measurements of plasticity [plasticity index and slope of the reaction norm (mean±s.d.)] estimated for the metabolic rate of *Betaeus emarginatus* in response to thermal acclimation treatments of 14 and 20°C

Population	Plasticity index	Slope reaction norm	N
Iquique	0.150	0.06±0.046	25
Antofagasta	0.056	0.055±0.051	27
Talcaruca	0.208	0.04±0.039	29
El Tabo	0.422	0.127±0.109	30
Lenga	0.070	0.085±0.128	27
Valdivia	0.031	0.061±0.067	29
Chiloe	0.222	0.042±0.018	10

N, number of individuals measured per population.

of an iteroparous species such as *B. emarginatus* was adjusted to the pattern of variation described by the MCA hypothesis, also because this shrimp exhibits latitudinal compensation for growth size (Conover and Present, 1990; Yamahira and Conover, 2002) and high-latitude populations exhibit larger body sizes (Lardies and Wehrmann, 1997), enhancing many aspects of organismal performance (Kingsolver and Huey, 2008). In contrast, as MR is assumed to be mechanistically dictated by temperature, according to universal temperature dependence (Gillooly et al., 2001), the latitudinal decrease in mean SST along the sampled range of *B. emarginatus* should induce a reduction in metabolism in populations at higher latitudes, because organisms are adapted evolutionarily to live at different temperatures (Clarke, 2003). Despite this, we found no evidence of a clear latitudinal pattern in MR for *B. emarginatus* between populations from different thermal environments. This could be related to larval dispersal times of approximately 3 months in Central Chile (Wehrmann and López, 2003; M. A. Lardies, unpublished observations/data). Also, it has been reported that the influence of biogeographic breaks on phenotypic variation is greater for species with shorter larval stages (Sánchez et al., 2011; Tellier et al., 2009; Zakas et al., 2009) in contrast with species with prolonged larval stages (Barria et al., 2014; Cárdenas et al., 2009; Macaya and Zuccarello, 2010). Also, the lack of a clear latitudinal pattern in the metabolism of *B. emarginatus* could be reflecting that the thermal stress that intertidal organisms experience does not increase as a simple function of decreasing latitude (Helmuth et al., 2002, 2006). Rather, local conditions of air temperature, solar radiation, substrate angle,

wave splash and fog are likely influential factors (Helmuth et al., 2006). In fact, although the annual *in situ* mean SST of marine intertidal zones in Chile is lower at higher latitudes, the difference in minimum and maximum SST at a given site varies along the range sampled here. This thus reflects local variation in solar irradiation (Broitman et al., 2001), the influence of atmospheric circulation and rainfall variability (Barros and Silvestri, 2002), and the effect of other oceanographic processes (Thiel et al., 2007).

In contrast, our results suggest that metabolic plasticity is higher in populations subjected to seasonal upwelling in the intermediate area and also in populations located near environmental discontinuities at the biogeographic breaks (for similar results, see Aravena et al., 2014; Segovia et al., 2017). Ectotherms that occupy heterogeneous thermal environments are hypothesized to have evolved greater thermal plasticity to optimize performance despite exposure to environmental variability (Angilletta, 2009; Chown and Terblanche, 2007; Ghalambor et al., 2006; Janzen, 1967). However, in intertidal zones, species are subjected to fast and frequent temperature changes that are both predictable (e.g. associated with circadian, tidal and seasonal cycles) and unpredictable (i.e. irregular short-term changes that are especially pronounced during low tide or the intensity of wind-driven upwelling). This being said, although predictable environmental variation is thought to increase thermal plasticity, unpredictable environmental variability does not favor plasticity, as environmental cues can be misleading (Berrigan and Scheiner, 2004; Kingsolver and Huey, 1998; Tufto, 2000). Despite this, both plasticity measurements used in the present study showed that individuals from El Tabo, subjected to seasonal wind-driven upwelling that intensifies during austral spring and summer, and also varies according to equatorial wind events and local topographic characteristics (Aravena et al., 2014; Vargas et al., 2017) had higher plasticity compared with shrimps of the other populations. Also, when comparing the index of phenotypic plasticity among populations, we found that populations of *B. emarginatus* located near the biogeographic breaks had higher plasticity of metabolic rates.

Intraspecific variation in physiological trait means and plasticity are of increased importance in the context of climate change (Bozinovic et al., 2011; Somero, 2010). So far, to address their response to future environmental scenarios, species are usually treated as if individuals from all populations in the species' range respond equally to environmental pressures (Banta et al., 2012; Kawecki, 2008), but there is ample evidence that within a species,

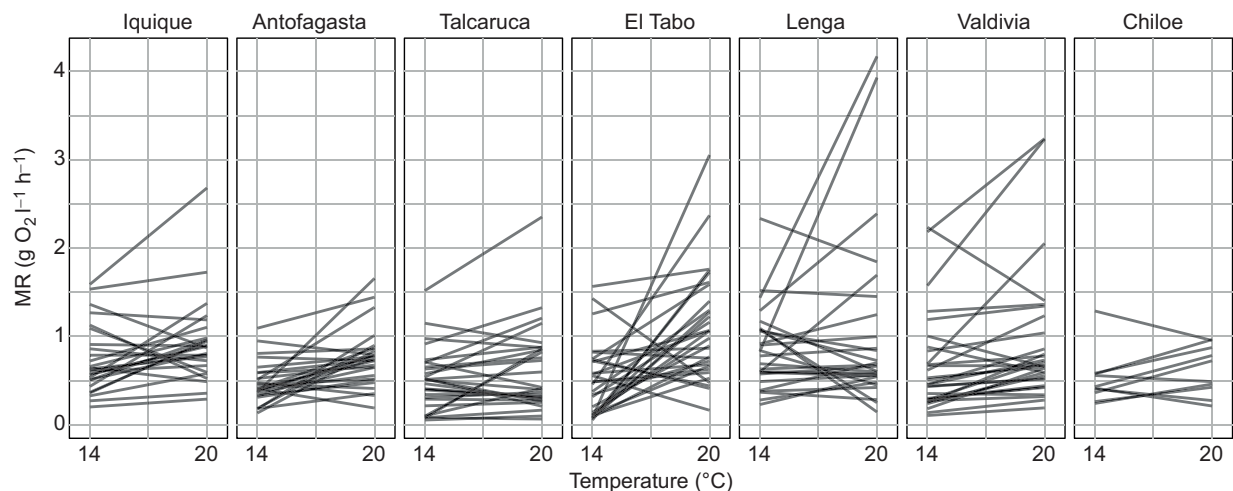


Fig. 5. Latitudinal variation in the reaction norms of the metabolic rate per individual, measured at 14 and 20°C in seven populations of *B. emarginatus*.

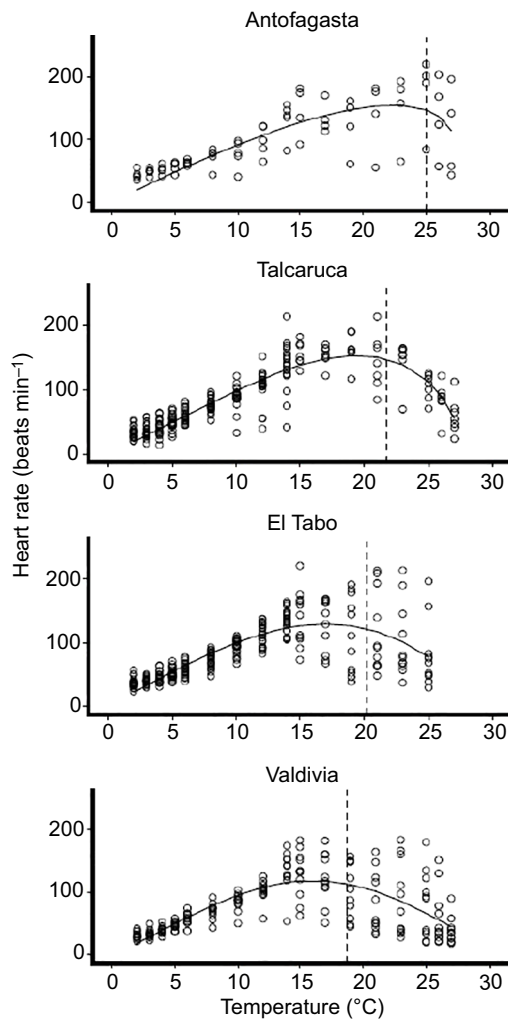


Fig. 6. Thermal performance curves of cardiac activity measured in four populations of *B. emarginatus*. Solid lines show the adjusted curve fitted to the Briere model and vertical dashed lines indicate the optimum temperature (T_{opt}) estimated for each population.

populations have distinct phenotypic responses to environmental conditions (Chown et al., 2004; Chown and Gaston, 1999; Gaston et al., 2009; Stillman, 2002). Populations that experience a wide degree of variability in environmental conditions are expected to be most plastic in traits adaptive in those conditions (Sultan and Spencer, 2002; Van Tienderen, 1991). In the face of climate change, plasticity may play a key role in enabling the persistence of populations (Chevin et al., 2010); thus, plasticity of populations along the latitudinal gradient that the range of a species encompasses will influence species' responses to the changing

Table 3. Coefficients obtained from the Briere model fitting of heart rates of four populations of *Betaeus emarginatus*

Population	m	T_{opt}	$CT_{max,Briere}$	CT_{min}	CT_{max}
Antofagasta	4.28	24.98	27.64	4.73±0.87	28.96±2.07
Talcaruca	1.65	21.76	27.69	4.20±0.67	28.07±0.79
El Tabo	1.01	20.25	29.13	4.43±0.76	29.75±1.39
Valdivia	0.6	18.69	32.35	4.11±1.17	28.54±1.43

Optimum temperature (T_{opt}) and $CT_{max,Briere}$ (critical thermal maximum determined by Briere model fitting) were also calculated. Means±s.d. for the measured thermal limits, CT_{min} and CT_{max} , are also shown.

climate and will be important for determining species distributions in novel climatic landscapes. Specifically, these responses could provide a buffer period during which niche evolution (i.e. adaptive niche expansion or shift) might occur (Chevin et al., 2010). Finally, this kind of study is required to make the necessary link between ecological physiology and macroecology and to help develop a global understanding of organismal responses in marine systems to variations in thermal environment.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.B., N.A.L., M.A.L.; Methodology: L.B., M.A.L.; Software: M.A.L.; Validation: N.A.L.; Formal analysis: A.B., L.B., M.A.L.; Investigation: L.B., M.A.L.; Resources: M.A.L.; Writing - original draft: A.B., M.A.L.; Writing - review & editing: A.B., L.B., N.A.L., M.A.L.; Supervision: A.B., L.B., M.A.L.; Project administration: M.A.L.; Funding acquisition: N.A.L., M.A.L.

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