

Phenotypic plasticity is not a cline: Thermal physiology of an intertidal barnacle over 20° of latitude

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Abstract

1. Our understanding of the plastic and evolutionary potential of ectothermic organisms and their populational impacts in the face of rapid global change remains limited. Studies attempting on the relationship between the magnitude of thermal variability across latitude and the degree of phenotypic plasticity exhibited by marine ectotherms are inconclusive. We state that the latter arises from the narrow range of thermal variability captured by the limited span of the latitudinal gradients studied to date.
2. Using a mechanistic ecophysiological approach and a satellite-based assessment of the relevant environmental variables (i.e. temperature and food availability), we studied individuals of the intertidal barnacle *Jehlius cirratus* from seven local populations widely spread along the Humboldt current system that spanning two biogeographic regions. At the same time, we synthesized published information on the local abundance of our study species across a total of 76 sites representing 20° of latitude, and spanning from 18 to 42°S.
3. We examined the effects of latitude and environmental variability on metabolic rate plasticity, thermal tolerance (thermal breadth and thermal safety margins) and their impacts on the abundance of this widespread marine invertebrate.
4. We demonstrate that the phenotypic plasticity of metabolic rate in *J. cirratus* populations is not related to latitude. In turn, thermal breadth is explained by the temperature variability each population experiences. Furthermore, we found clinal variation with a poleward decrease of the critical thermal minimum, suggesting that episodic extreme low temperatures represent a ubiquitous selective force on the lower thermal limit for ectotherms.
5. Across our study gradient, plasticity patterns indicate that populations at the equatorial extreme are more vulnerable to a warming climate, while populations located in the biogeographic transitional zone (i.e. high environmental heterogeneity), on the centre of the gradient, display higher levels of phenotypic plasticity and may represent a genetic buffer for the effects of ocean warming. Together, our results suggest the existence of a fitness trade-off involving the metabolic cost of plasticity and population density that is evident only across the vast latitudinal gradient examined.

KEYWORDS

abundance, *Jehlius cirratus*, metabolism, ocean warming, plasticity, reaction norm, thermal breadth

1 | INTRODUCTION

Evolutionary change in variable environments allows adaptive phenotypic changes to take place over protracted time-scales (Fusco & Minelli, 2010). Yet, the rate of warming and the instability of current climate change, with extreme events unfolding continuously, are unprecedented and beyond the time-scales of phenotypic evolution for most species (Donelson et al., 2019; Harley et al., 2006). Species are limited to either migrate or use plastic phenotypic responses to cope with changing environmental conditions (Hollander et al., 2014). The former is currently taking place everywhere around the planet, particularly in the oceans (Lenoir et al., 2020). The latter, however, emerges as a key trait that can either bolster dispersal away from unfavourable conditions or support local persistence for dispersal-limited organisms (Ghalambor et al., 2006; Hadfield & Strathmann, 1996; Piersma & Drent, 2003). Thermal tolerance—the capacity of an organism to survive, grow and reproduce across a specific thermal environment—is considered as one of the main factors controlling the geographic ranges of species and populations (Angilletta, 2009; Huey et al., 2012). Hence, the close relationship between physiology, metabolism and ambient temperature, the critical temperature limits, has translated in a surge of studies assessing the vulnerability of ectotherms to global warming (Addo-Bediako et al., 2000; Calosi et al., 2008; Chown, Gaston, et al., 2004; Stillman, 2003; Sunday et al., 2019). The range of climatic variability in the ocean increases from the equator, peaks around 45° and then decreases to the poles; such canonical environmental pattern should favour the evolution of both thermal variability and thermal tolerance simultaneously (Chown, Sinclair, et al., 2004, but see Stillman, 2003). A recent meta-analysis on the relationship between thermal breadth and latitude comprising a wide range of taxonomic groups and habitats found comprehensive support for a positive relationship between thermal breadth and latitude among ectotherms (Sunday et al., 2019). Together, the evidence to date suggests that phenotypic plasticity in traits related to thermal tolerance will allow ectothermic organisms to cope with climate warming chiefly on the leading (poleward) edges of their geographic ranges as the new thermal environment will resemble the one found in their core range (Broitman et al., 2018; Donelson et al., 2019).

Our understanding on the plastic and evolutionary potential of marine organisms in the face of rapid global change remains limited and restricts our ability to predict how marine biodiversity will respond to ongoing rapid environmental changes (Munday et al., 2013; Reusch, 2014; Sunday et al., 2014; Vargas et al., 2017). Plasticity can be an important source of variation in performance between individuals, ultimately influencing short-term selection and the evolutionary trajectories of populations and species (Badyaev & Uller, 2009). Studies attempting to elucidate the relationship between the

magnitude of thermal variability across latitude and phenotypic plasticity in ectotherms are inconclusive (Rohr et al., 2018). We argue that the latter result arises from the range of thermal variability regimes captured by the breath of the latitudinal ranges studied to date: They are not broad enough to unveil differences in phenotypic plasticity among populations (Angilletta, 2009; Gunderson & Stillman, 2015; Seebacher et al., 2015). Indeed, the previous meta-analysis was based on interspecific comparisons; very few studies have focused on intraspecific variation of widely distributed populations to understand regional adaptation through phenotypic plasticity across major environmental gradients (but see Calosi et al., 2017). To understand the relationship between latitude and phenotypic plasticity, we will focus on metabolic rate (MR), an organismal trait that is directly affected by ambient temperature and food supply, and is often considered an indicator of physiological tolerance to specific thermal environments (Bozinovic et al., 2011; Ramajo et al., 2019). Moreover, as MR sets the demand for resources and the resource allocation to survival, growth and reproduction, it provides a functional link between individual and population performance (Artacho & Nespolo, 2009; Bozinovic et al., 2011).

Rocky intertidal habitats exist at the margins of both the terrestrial and marine regions; thus, marine invertebrates in this ecosystem are subject to the environmental challenges posed by both aquatic and aerial thermal regimes. As a result, rocky shore organisms may serve as early warning systems for the impacts of climate change, especially ocean warming (Harley et al., 2006; Helmuth et al., 2006; Seabra et al., 2016). Our study is focused on an intertidal invertebrate that inhabits the mid-high rocky intertidal zone along the Humboldt Current System (HCS). The HCS is a large biogeographic province, characterized by the wind-driven upwelling of cold, nutrient-rich, acidic and oxygen-poor waters along the coastline off western South America (Chavez & Messié, 2009; Vargas et al., 2017). An important biogeographic discontinuity along this broad region is located along a sector of the coastline where the regional upwelling regime is locally intensified around 30–32°S, defining a step change in upwelling seasonality and the edge of the geographic range of several marine species (Aguilera et al., 2019; Broitman et al., 2018; Hormazabal et al., 2004). The challenging physico-chemical characteristics of recently upwelled waters, involving low oxygen concentration, reduced pH and colder temperatures, which have been shown to act as a strong selective pressure for benthic invertebrates (Broitman et al., 2018; Ramajo et al., 2020). The relationship between environmental variability and phenotypic plasticity in marine ectotherms has received scant attention, despite the major ecological insights provided by the study of invertebrate thermal ecology (Bayne et al., 1976; Connell, 1961; Wetthey, 1983). The barnacle *Jehlius cirratus* is broadly distributed along the rocky shores of the Pacific coast of South America, from northern Perú to southern Patagonia; thus, it

amply spans the biogeographical transitional zone highlighted above (Brattström & Johanssen, 1983; Darwin, 1854; Ibanez-Erquiaga et al., 2018). Populations of this benthic invertebrate are dominant primary space occupiers of the mid and upper intertidal zone and a key early successional species, providing both habitat and food for a variety of mobile and sessile species, together with a settlement substratum for algal propagules (Lagos et al., 2008; Navarrete et al., 2005). Density-independent processes, such as predation and environmental stress, can be key drivers of local abundance (Navarrete et al., 2005; Shinen & Navarrete, 2010).

In the present study, we characterized the patterns of environmental variability and food supply in the coastal ocean along 20° of latitude and use *J. cirratus* individuals collected from seven local populations spread across the gradient to assess the effect of latitude and environmental variability on the magnitude of MR plasticity and thermal tolerance (thermal breadth and thermal safety margins). Then, we examine the relation of plastic physiological responses on the abundance of *J. cirratus* across the latitudinal gradient through a synthesis of data from a suite of earlier studies and long-term monitoring data. We expected that individuals from populations inhabiting the most climatically variable regime (i.e. the transitional zone) displayed the greatest metabolic plasticity and thermal breadth, while individuals inhabiting the warmest areas (i.e. northern region) would exhibit lower phenotypic plasticity and smaller safety margins since they may be near their critical maxima. Regarding the abundance of this intertidal species, our expectation was similar: A more challenging environmental regime would increase maintenance costs, reducing reproductive investment and impacting abundance patterns. Our key insight is that local ocean temperature patterns act as the main drivers of between-population differences, beyond latitude (i.e. spatial location) per se. Thus, if the mean and variance of ocean temperature drive physiological responses, populations inhabiting the transitional zones are subject to selective pressures that channel the maintenance of metabolic traits that allow them to cope with a variable thermal environment.

2 | MATERIALS AND METHODS

2.1 | Environmental characterization

Across the study gradient, the aerial thermal regime at the shoreline is relatively stable and ranges from a hyperarid coastal desert (20 and 24°S) to a transitional zone between semi-arid and mediterranean regimes (30–36°S) which is followed by a seasonal, temperate-cold marine regime (36–41°S). To quantify environmental variability and food supply for benthic invertebrates across the HCS, we used satellite-derived sea surface temperature (SST, °C) and chlorophyll-*a* concentration (CHL, mg/m³) respectively (Menge et al., 2003; Navarrete et al., 2005). We used mapped, 8-day, Level-3 (L3) night-time records from the Moderate Resolution Imaging Spectroradiometer (MODIS) using the 2003–2018 period (15 years, 736 8-day composites) that we averaged over a 12 × 12 km area immediately offshore our seven

study sites. MODIS netcdf images were downloaded from the NASA Ocean Color repository and analysed using MatLab R2014a to calculate the 15-year SST minima, maxima, mean and variance (SST_{min}, SST_{max}, SST_{mean} and SST_{var} respectively), together with the same statistics for CHL (CHL_{min}, CHL_{max}, CHL_{mean} and CHL_{var} respectively), which was log₁₀ transformed prior to analysis following the log-normal distribution of data (Table 1). Earlier studies have shown that MODIS SST underestimates the onshore cooling driven by eastern boundary coastal upwelling circulation, most of the latitudinal range encompassed by our study (Meneghesso et al., 2020). Despite this clear bias towards warmer temperatures, the underestimation of upwelling-induced coastal cooling preserves the spatial structure of temperature variability among sites along the central part of the study region (Aravena et al., 2014; Flores Fernandez et al., 2018). On the other hand, sites located on the extremes of the study region are in areas that are less influenced by seasonal upwelling circulation (Blanco et al., 2001; Narváez et al., 2019).

2.2 | Population abundance estimates and Animal collection

In addition to our seven study sites, we compiled data from a long-term monitoring study and a suite of previous studies documenting percentage cover of *J. cirratus* on the mid-high intertidal zone along our study region totalling 74 locations, which we averaged per degree of latitude. Percent cover data and sources are presented in Table S1.

We collected live adult barnacles settled on rocky substrata or as epibionts over the shells of intertidal mussels *Perumytilus purpuratus*. Individuals were randomly collected in spring season during low tide by hand from the mid-upper intertidal zone in the upper limit of the *Perumytilus purpuratus* band at all study sites by removing small pieces of rock or mussels where the barnacles were settled (Table 1). Local populations of *J. cirratus* were selected from three regions: north (equatorward, <23°S), south (poleward, >36°S) and the transitional zone between 30 and 33°S. After field collection, individuals were kept chilled and transported to the laboratory, and maintained in a common garden in artificial seawater (ASW; 33 ppm; Instant Ocean® sea salt dissolved in distilled water) at constant temperature (14°C), a light:dark cycle of 12:12 hr, and fed with Instant Algae® three times a week.

2.3 | Phenotypic plasticity of thermal reaction norm and tolerance

A total of 169 adult barnacles were sequentially acclimated for 1 month at 14°C and then followed by a second acclimation at 20°C. The first acclimation temperature reflected the SST_{mean} and the second the SST_{max} that on average experienced all populations along the latitudinal gradient. After these metabolic rate (MR) measurements, the minimal and maximal critical thermal limits (CT_{min} and

TABLE 1 Region, names of the different study sites, their geographic coordinates (Lat, Lon), number of experimental individuals of *Jehlius cirratus* (N) from each location and the satellite-derived statistics (mean, variance, maximum and minimum values) for sea surface temperature (SST) and chlorophyll- α concentration (CHL) at each study site along the Chilean sector of the Humboldt Current System

Region	Site name	Lat (S)	Lon (W)	N	SST _{mean}	SST _{var}	SST _{min}	SST _{max}	CHL _{mean}	CHL _{var}	CHL _{min}	CHL _{max}
North	Iquique	-20.32	-70.25	28	17.70	1.97	12.42	22.49	5.14	14.44	0.24	23.83
	Antofagasta	-23.76	-70.42	31	16.94	3.48	11.46	22.93	7.19	23.99	0.39	26.12
Transitional	Talcahuca	-30.48	-71.70	10	14.22	3.34	9.37	19.53	1.04	1.42	0.20	13.28
	El Tabo	-33.45	-71.68	24	13.89	3.41	9.63	18.93	4.50	22.98	0.34	26.33
South	Lenga	-36.77	-73.17	30	12.84	2.29	9.78	17.38	6.76	30.45	0.14	28.51
	Calfuco	-39.76	-73.40	31	12.13	2.20	9.15	16.35	6.68	31.33	0.42	28.73
	Chiloé	-41.86	-74.00	15	11.49	1.43	9.10	15.67	5.34	30.89	0.29	29.16

CT_{max} respectively) of individual barnacles were evaluated. Although our study species inhabits a region dominated by a semidiurnal tidal regime (SHOA, 2020), experiencing immersion and emersion conditions twice daily, we evaluated thermal responses only under immersion conditions. Previous studies simulating the impacts of tidal cycle have shown that barnacle respiration is similar in the air and underwater at the same temperature (Clavier et al., 2009), and that thermal stress in intertidal ectotherm is more related to elevated water temperature than aerial temperature (Seabra et al., 2016).

At the end of the first acclimation period, MR was measured using a four-channel Microx optic fibre O₂-meter (Presens Inc, DE) connected to a recirculating water bath by a flow-through cell housing (Presens Inc, DE) and using a glass respirometry chamber of 113 ml. The optic fibre was calibrated in a solution saturated with Na₂O₃S (0% air saturation) and in aerated artificial seawater (100% air saturation). After calibration, oxygen consumption (% air saturation) was measured for at least 60 min (recorded every 5 s). The first and the last 5 min were discarded in order to avoid possible disturbances when the optic fibre was inserted or removed. Thus, oxygen estimations are based on the remaining 50 min of measurements which imply that oxygen saturation in the respirometry chamber always was over 85%. Furthermore, the same respirometry chambers were used as controls, but without barnacles inside, under the same experimental conditions (the control never had a reduction of the oxygen concentration higher than 3% of measurements). Each oxygen reduction due to background noise was subtracted from the individual measurements performed in the experimental chambers.

Each animal measured at 14°C was then acclimated by one additional month at 20°C, under the same feeding and photoperiod conditions, and MR measurements were performed again. The magnitude of MRs plasticity was estimated as the slope b of the thermal reaction norm ($b = [(MR_{20^\circ\text{C}} - MR_{14^\circ\text{C}})/(20 - 14^\circ\text{C})]$) (e.g. Barria et al., 2018; Liefjting et al., 2009).

After 2 weeks of recovery at 14°C, individuals were used to determine CT_{min} and CT_{max}. In our experimental trials, CT_{min} and CT_{max} were determined as the ambient temperature (below or above) in which there was a lack of movement in structures and/or appendices within a predefined time period (10 min; e.g. Castañeda et al., 2005; Lutterschmidt & Hutchison, 1997). We measured cirral activity of barnacles, that is, the rates of cirral beating change with temperature (Anderson & Southward, 1987; Foster, 1970). Cirral activity observations were performed for each barnacle at the same time of day to avoid the effects of circadian rhythm and the order of the temperature exposure trials was randomized to avoid the confounding effects of time. Barnacles were submerged in aerated seawater and placed separately in plastic chambers with six subdivisions, installed in a thermoregulated bath at constant seawater temperature ($\pm 0.5^\circ\text{C}$, LWB-122D, LAB TECH) for 30 min at each temperature assayed of the thermal gradient. Experimental temperatures for thermal performance curves were chosen between -3° and 37°C . The performance traits were measured every 2°C in the extremes of each population's tolerance range and every 3°C units inside the range

(12–25°C). First, we used a decreasing temperature ramp from 14 to –3°C to determine CT_{min} . Second, after a 2-day recovery period for all individuals, we used a thermal ramp increasing from 14 to 37°C to determine CT_{max} . Each temperature exposure lasted for 30 min (e.g. Barria et al., 2018) and individuals were allowed to recover 20 min between experimental temperatures. Through direct observations, barnacles were defined as in ‘thermal comma’, once they ceased to display cirral activity even though they were being fed with Instant Algae®. We considered two measures of thermal tolerance: (a) thermal breadth, which was estimated as the difference between CT_{max} and CT_{min} and (b) thermal safety margins as the difference between individual's CT_{max} or CT_{min} , and SST_{max} and SST_{min} , respectively, as reported for other crustaceans (e.g. Gaitán-Espitia et al., 2014). After each trial, the barnacles were sacrificed, and the total wet weight and the volume of the attachment substrate (rock or mussel shell) were measured and subtracted from the volume of the respirometry chamber. Thus, oxygen consumption (mg) was standardized by unit of time (h), volume (L) and wet weight (g) of the animal.

2.4 | Statistical analysis

We evaluated the effect of spatial distance among study sites, the biogeographic transition zone and environmental variables on thermal physiological traits of *J. cirratus*: plasticity of metabolic rates, thermal breadth, thermal safety margins and population density.

We used Mantel tests to test the matrix correlation between population-level similarity between the studied variables and spatial distance among sites (Legendre & Legendre, 1998). For metabolic plasticity and population density, we also performed quadratic regressions to examine nonlinear relationships with latitude. To assess the effect of the biogeographic zone on the studied variables, we performed general linear mixed models (GLMM) fitted by REML considering north, south and transitional zones as fixed factors and locality as random intercept. This analysis allowed us to control for non-independence of the data when it belongs to different localities, but to the same biogeographical zone. When the variance associated with the random factor was negligible, we dropped it and performed general linear models (GLM) fitted by ML. Moreover, we evaluated the effect of environmental variables related to sea surface temperature (SST) and chlorophyll concentration (CHL) using general linear models (GLM) with oceanographic variables as independent variables. For GLM models, we constructed different candidate models, and the best representing the data was selected according to the Akaike information criterion (AIC, Tables S2–S4).

When appropriate, assumptions of normality and homoscedasticity in residuals were examined with Q–Q plots and plot of residuals against fitted values respectively (Zuur et al., 2010). Since MR fits a power function with body mass (Lasiewski & Dawson, 1967), MR phenotypic plasticity measurements were log-transformed and body mass was used as a covariable in the GLM and GLMM, while

maximum safety margin was root squared transformed to meet normality assumption. All statistical analyses were performed using R software version 3.5.0 (R Core Team, 2018) and the lme4 package (Bates et al., 2015).

3 | RESULTS

3.1 | Environmental characterization

Patterns of environmental variability across the large latitudinal gradient covered by our study sites differed by their SST and CHL climatologies (long-term monthly means) and time series (Figures S1 and S2 respectively). While SST climatologies followed a smooth latitudinal gradient, CHL climatologies were rather heterogeneous across the region (Figures S1, upper panels), which was evident in the weekly time series (Figures S2). SST_{mean} was significantly different between biogeographic zones ($F_{2,136} = 3,893.9$, $p < 0.001$), all biogeographic zones were significantly different between each other (Tukey test, $p < 0.001$). While extremely low year-round CHL concentrations predominated at the sites around the centre of the latitudinal gradient, higher concentrations prevailed at the extremes of the gradient. CHL_{mean} was significantly different between biogeographic zones ($F_{2,136} = 79.93$, $p < 0.001$) being lowest at the transitional zone, but no significant differences were observed between the northern and southern sectors. In the case of climatological variances, locations towards the extremes of our study region showed reduced SST variability while sites in the centre had higher variance. An exception was the lowest latitude site, where very high variance was observed during the austral summer months (Figure S1, lower panels). SST_{var} was also significantly different between biogeographic zones ($F_{2,136} = 71.59$, $p < 0.001$), with highest values of SST_{var} at the transitional zone (Figure 1a). In the case of the climatological variance of CHL, we observed an opposite pattern, where the null variability for the Talcaruca site, around the biogeographic transition zone, was associated with reduced average CHL concentrations. Sites located around the high latitude biogeographic break showed increased year-round variance (Figure S1, lower panels). There were no significant differences between biogeographic zones in CHL_{var} .

3.2 | Phenotypic plasticity in metabolic rates

The variation in MR plasticity was not related to geographic distance (Mantel test, $p = 0.82$, Figure S3). However, a quadratic regression with latitude showed a significant parabolic pattern indicating that populations located halfway along our study region, the transitional zone, showed the largest differences in plasticity when compared with populations at the extreme of the latitudinal gradient ($R^2 = 0.11$; $p = 0.001$; Figure 1b). Indeed, populations located around the edge of the transitional zone showed the largest MR plasticity ($F_{3,130} = 4.3$; $p = 0.006$, Figure 1b; Figure S5). Model selection determined that the best model included CHL_{mean} , and the

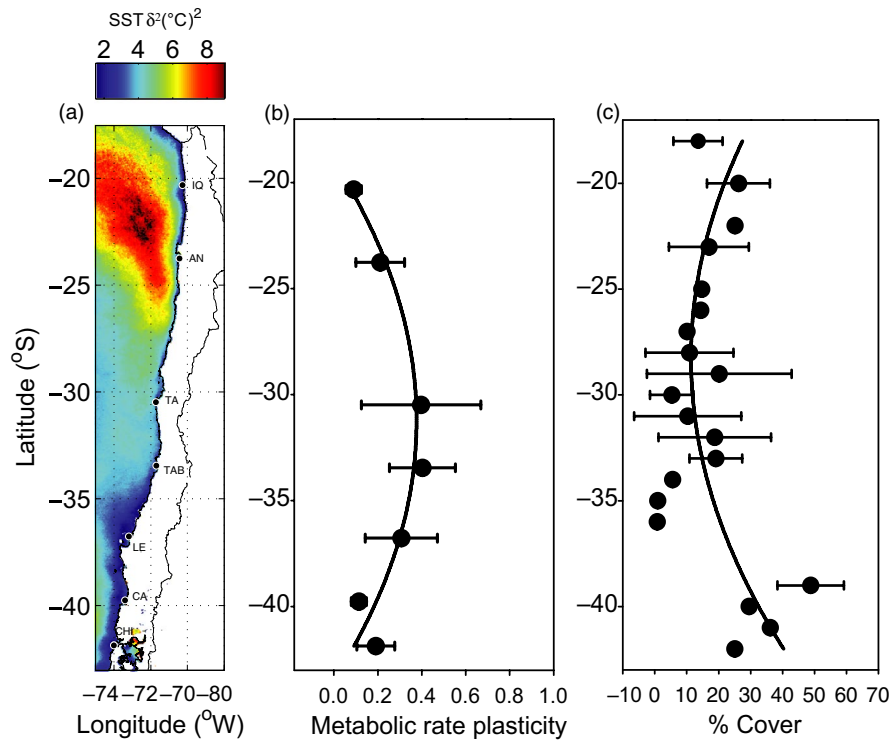


FIGURE 1 Study sites, metabolic rate plasticity and abundance of *Jehlius cirratus* along the latitudinal gradient of 3,000 km on the Chilean coast. (a) Map of the study region along north-central Chile and spatial patterns of SST variance ($^{\circ}\text{C}^2$) for the 2003–2008 period from MODIS. Black circles on the coastline indicate the location of the seven study sites long. Legends: IQ = Iquique, AN = Antofagasta, TA = Talcaruca, TAB = El Tabo, LE = Lenga, CA = Calfuco, CHI = Chiloé. (b) Latitudinal variation in metabolic rate plasticity estimated as the absolute difference between the slope in the reaction norm of *J. cirratus* individuals exposed to thermal acclimation treatments of 14 and 20°C. Mean values are indicated by black circles and error bars represent 95% confidence intervals. The black line is a significant quadratic fit of the data as: metabolic rate plasticity = $-2.08 - 0.16(\text{Latitude}) - 0.003(\text{Latitude})^2$. (c) Relationship between latitude and *J. cirratus* abundance estimated from multiple data sources, including this study (see Table S1) over each of the 20° of latitude. The mean abundance (percentage cover) for each degree of latitude is shown as black dots; error bars represent one standard deviation. The fitted line is a significant quadratic model of observations following: percentage cover = $133.6 + 8.7(\text{Latitude}) + 0.15(\text{Latitude})^2$

interaction between SST_{var} and SST_{mean} as the main explanatory variables (Tables S2 and S5).

3.3 | Thermal breadth

The variation in CT_{min} of *J. cirratus* was positively related to the geographic distance (Mantel test: coef = 0.59; $p = 0.04$, Figure 2 lower panel). Also, there was a significant effect of biogeographic zone on CT_{min} . The southern zone showed higher cold tolerance followed by the transitional and the northern zone ($F_{2,100} = 42.9$; $p < 0.001$). Model selection determined that the best model for CT_{min} included CHL_{max} , CHL_{var} and SST_{max} as explanatory variables ($F_{3,96} = 33.22$, $p < 0.0001$; Tables S3 and S5).

CT_{max} was not related to geographic distance (Mantel test: $p > 0.05$, Figure 2 lower panel), neither there was a significant effect of the biogeographic zone on this variable ($p > 0.05$). The best model for CT_{max} included CHL_{min} , SST_{mean} as explanatory variable (Table S3). Interestingly, individuals inhabiting localities with higher mean temperatures showed higher tolerance to hot temperatures ($F_{2,67} = 6.72$; $p = 0.002$, Table S5).

Differences in thermal breadth among *J. cirratus* populations were not related to geographic distance (Mantel test: $p > 0.05$, Figure 2 upper panel). An analysis by region showed no significant effect of the biogeographic zone on this physiological variable ($p > 0.05$). Finally, model selection showed that the best model included the interaction between SST_{mean} and SST_{var} as the best predictor for thermal breadth (Tables S3 and S5).

3.4 | Thermal safety margins

There was no relationship between geographic distance and the minimum thermal safety margin (Mantel test: $p > 0.05$). In contrast, there was a significant effect of the biogeographic zone, with the lowest minimum safety margin in the transitional zone compared to the other two biogeographical regions ($F_{2,100} = 10$; $p = 0.007$). Model selection showed the best model included the interaction between CHL_{var} and SST_{var} as the best predictor for minimum safety margin ($F_{3,96} = 9.99$; $p < 0.001$, Tables S4 and S5; Figure S4).

We found a significant relationship between maximum thermal safety margin and geographic distance (Mantel test: coef = 0.69;

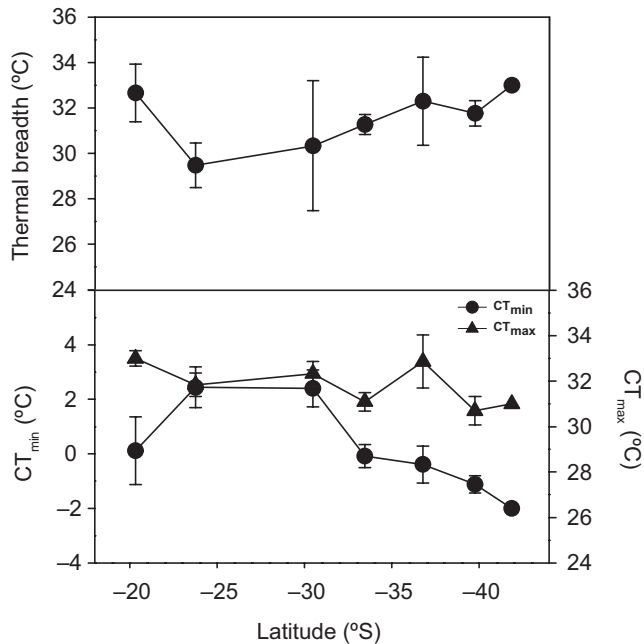


FIGURE 2 Latitudinal variation in the thermal limits of *Jehlius cirratus*. Upper panel: Thermal breadth (difference between CT_{min} and CT_{max}) for each population across the latitudinal gradient. Lower panel: Mean values for Critical Thermal minimum (CT_{min} , circles, left axis) and Critical Thermal maximum (CT_{max} , triangles, right axis), estimated in the seven populations of *J. cirratus* shown in Figure 1. Error bars represent 95% confidence intervals

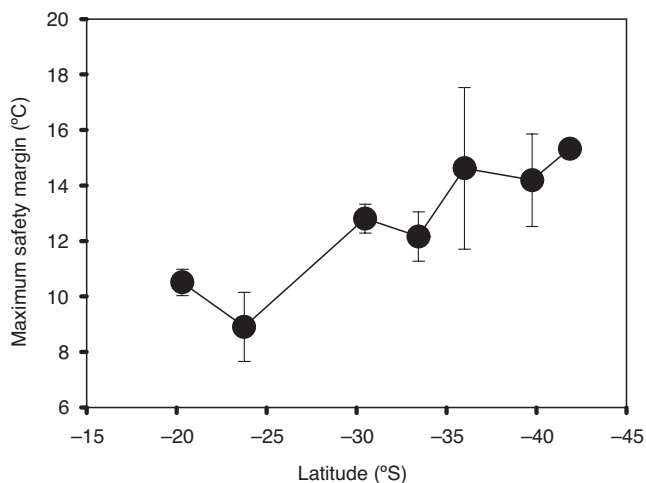


FIGURE 3 Latitudinal variation in the maximum safety margin for seven populations of *Jehlius cirratus*. Maximum safety margin (difference between T_a and CT_{max}) for each population across the latitudinal gradient. Error bars represent 95% confidence intervals

$p = 0.03$, Figure 3). Also, there was a significant effect of the biogeographic zone on this variable, showing higher values in the southern zone, followed by the transitional and the northern zone ($F_{2,70} = 16.6$; $p < 0.001$, Figure 3). The best GLM included CHL_{var} and SST_{max} as the best predictors of maximum thermal safety margin (Tables S4 and S5). Moreover, maximum safety margin was significantly lower with higher SST_{max} ($F_{2,72} = 99.1$; $p < 0.001$, Figure 3).

TABLE 2 Linear mixed model testing the effect of SST_{var} , CHL_{mean} and their interaction on barnacle abundance using Kenward–Roger's method. Data shown are degrees of freedom (df), the F values and the statistical significance (p -value) level of each fixed-factor Type III Kenward–Roger tests. Significant p values are in 'bold'

Factor	df	F	p -value
SST_{mean}	70	5.7524	0.019
CHL_{mean}	70	4.7320	0.032
$SST_{mean} \times CHL_{mean}$	70	5.2422	0.025

3.5 | Population density

We found no relationship between population density and geographic distance (Mantel test: $p = 0.08$). However, a significant quadratic relationship was found ($R^2 = 0.21$; $p < 0.001$), with the lowest densities at intermediate latitudes (Figure 1c). There was also a significant effect of the biogeographic zone on population density, with the lowest values found at the transitional zone ($F_{2,52} = 14.76$; $p < 0.001$, Figure 1c). Model selection revealed that the best GLMM included the interaction between CHL_{mean} and SST_{mean} and accounted for 25% of the variance in the data (Table 2). Although we observed similar CHL_{mean} concentrations at high and low latitudes, population densities were higher in the south (Figure 1c; Table 1). This suggests that populations exposed to higher CHL_{mean} and lower SST_{mean} reached higher abundance than those exposed to similar CHL_{mean} but higher SST_{mean} (Table 1).

4 | DISCUSSION

Sessile intertidal organisms are exposed to some of the most challenging thermal environments in the world and the ongoing increase in temperature and its extremes will strongly select for greater acclimation abilities among them (Angilletta, 2009; Gabriel et al., 2005). The symmetrical tidal regimes impose extreme conditions onto marine organisms living in the mid-high tidal level, but respiratory performance can be approached under submersed conditions (Clavier et al., 2009). The narrow window for respiration highlights the key role of seawater temperatures upon the thermal stress in ectotherms inhabiting intertidal habitats in upwelling ecosystems (see Seabra et al., 2016).

Our large-scale study revealed that there is a significant effect of biogeographical zones on MR plasticity and population densities. We found that barnacle populations inhabiting along the transitional zone (i.e. strong and continuous upwelling) showed increased MR plasticity, which is expected to impose with associated costs in other traits, and under strong directional selection (Gaitán-Espitia et al., 2017). Accordingly, our results suggest that there is a fitness trade-off between the metabolic phenotypic plasticity and the abundance of the barnacle *J. cirratus*, which provides a mechanistic underpinning for the spatial distribution

of barnacles' population densities. Note that population abundance is also linked to mesoscale oceanographic process that can limit planktonic larval arrival to the adult habitat (i.e. source-sink dynamics, Navarrete et al., 2005) and species-specific post-settlement mortality (Shinen & Navarrete, 2010). In our latitudinal gradient, strong and continuous upwelling along the centre of our study region generates a biogeographic discontinuity tightly related to regional temperature fluctuations and a reduced chlorophyll-*a* concentration (Navarrete et al., 2005). This pattern is concomitant with ongoing chemical changes in seawater (e.g. low pH/high $p\text{CO}_2$; see Gruber, 2011; Harley et al., 2006; Kroeker et al., 2016), which appears to be particularly relevant for ectotherms producing carbonate skeletons inhabiting the transitional region (Broitman et al., 2018). The kinetic dissolution of carbonates increases at low temperatures (Morse et al., 2007), which suggests that cold upwelling can also impose relevant cost for controlling calcification and mineralization of barnacle skeletons (e.g. Nardone et al., 2018). An earlier study on a mobile crustacean showed a nonlinear pattern, finding that MR plasticity was higher in populations located within the centre of our study region, around the biogeographic discontinuity at 30°S (Barria et al., 2018). The latter study, however, did not directly assess the effect of the mean and variance of both SST and CHL on the magnitude of MR plasticity nor their effects on population density. Although we did not find that within-species variation in MR plasticity was related to latitude—as some macrophysiological studies have earlier posited (Calosi et al., 2008; Gaitán-Espitía et al., 2013, 2014; Lardies et al., 2011)—our results support the idea that higher temperature variability will select for greater acclimation abilities (Angilletta, 2009; Gabriel et al., 2005). Indeed, the interaction between SST_{var} and SST_{mean} suggests that *J. cirratus* populations from 23°S, under similar SST_{var} as the transitional zone, display a slightly lower level of MR plasticity following the higher SST_{mean} at this location (see Figure 1b). Our interpretation is that to exhibit phenotypic plasticity, animals shall experience contrasting thermal environments across a range of temperatures that represent a physiological challenge, that is, conditions lying beyond their physiological optima as occurring at the transitional zone with cold oceanic temperatures (see Bennett et al., 2019). In addition, population density was related to CHL_{mean} , SST_{mean} and their interaction. The pattern was clear through the significant quadratic relationship between percentage cover (abundance) and latitude (see Figure 1c), with minimal abundance across the transitional zone, coinciding with the lowest CHL_{mean} .

In contrast with earlier studies which were based on interspecific comparisons, our results do not support a positive relationship between thermal breadth and latitude as indicated by the climatic variability hypothesis (Ghalambor et al., 2006; Sunday et al., 2011). Furthermore, the interaction between the SST_{var} and SST_{mean} that individuals experience in their habitats relates to their thermal breadth. Regarding CT_{min} , it did show a poleward decrease, which agrees with the best GLM, which showed that populations experiencing lower SST_{max} were more cold tolerant. It has been proposed

that lower thermal limits decline at a greater rate towards the poles than upper thermal limits for several taxa of ectotherms (Sunday et al., 2012). The evolution of cold tolerance has a lower bound that is related to frost damage and curtailed by the few mechanisms that invertebrates have to cope with freezing (Holmstrup et al., 2002; Murphy, 1983). Our results are in agreement with this hypothesis, considering that CT_{max} did not exhibit a latitudinal trend and did not differ among study sites while CT_{min} decreased with latitude (Araújo et al., 2013).

The maximum thermal safety margin also followed a latitudinal pattern (see Figure 3). In contrast, the minimum safety margin was not related to the latitude, but it was lower in populations that experience higher SST_{var} (Figure S4). Macrophysiological studies have shown that heat safety margins increased markedly with latitude. Hence, low-latitude species, living closer to their critical thermal maxima, might be more vulnerable to warming than high-latitude species (Deutsch et al., 2008; Huey et al., 2012; Khaliq et al., 2014; Pinsky et al., 2019; Sunday et al., 2012). *J. cirratus* individuals from our low latitude sites indeed showed lower thermal safety margins making them effectively more vulnerable to a warming climate. To date, the rate of warming of the surface ocean has been lower in the tropics (IPCC, 2018). If most physiological processes in ectotherms operate within the bounds of lethal temperature extremes, small variations in temperature may strongly affect populations at lower latitudes and they may be more susceptible to more recurrent marine heatwaves and in populations that are already warm may have large metabolic consequences (Holbrook et al., 2019; Payne & Smith, 2017; Sanford et al., 2019; Seabra et al., 2015). Temperature is arguably the most important factor determining species distributions; its effects span across all levels of biological organization, from biochemistry of molecular processes to whole-organism physiology (Pörtner et al., 2006). As expected, *J. cirratus* seems to be adapted to this wide latitudinal gradient by matching their physiological tolerances to the local thermal environment experienced along their range (Pereira et al., 2017; Sunday et al., 2012).

Phenotypic plasticity influences population dynamics and is often considered an adaptive strategy for living in predictably varying environments as long as the plastic response is sufficiently fast, accurate and not too costly (Xue & Leibler, 2018). Ongoing climate change is unravelling increased environmental stochasticity and the reliability of existing environmental cues as predictors for plastic responses will become more equivocal (Oostra et al., 2018; Reed et al., 2010). Under less predictable environmental scenarios, the energetic costs associated with plasticity—such as a lower reproductive output—might outweigh its benefits, making plastic populations more vulnerable to the increased environmental stochasticity predicted for marine environments in the future (Holbrook et al., 2019). Given that upwelling might become intensified under a warmer climate (Sydeman et al., 2014) and that these changes seem to already be taking place along the transitional zone (Wernberg et al., 2020), the elevated costs incurred through strong plasticity imply that local population extinction probability in these

regions will be high (see Reed et al., 2011). Previous studies on *J. cirratus* showed that despite the slight population structure in this species—roughly associated with the 30°S biogeographic transition zone—suggests some degree of local adaptation, there is no support for complete isolation by distance in this species. Notwithstanding, the transitional zone seems to harbour an unexpected degree of genetic heterogeneity (Guo & Wares, 2017; Haye et al., 2014). Therefore, the dispersal of the individuals able to colonize and persist in the taxing environmental conditions of transitional zones suggests its potential as genetic reservoirs under future climatic scenarios.

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AUTHORS' CONTRIBUTIONS

M.A.L. and N.A.L. conceived and designed the research; M.A.L., T.O., N.A.L., and B.R.B. performed the research; B.R.B. and N.A.L. provided cover data; B.R.B., K.M., D.F., N.R. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data associated with this publication are available on <https://doi.org/10.5061/dryad.98sf7m0j4> (Lardies et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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