1 **Geographic variation in thermal physiological performance of the intertidal**

2 **crab *Petrolisthes violaceus* along a latitudinal gradient**

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21 **RUNNING TITLE**: Geographic variation in thermal physiology

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22 **ABSTRACT**

23   Environmental temperature has profound implications on the biological

24 performance and biogeographical distribution of ectothermic species. Variation of this

25 abiotic factor across geographic gradients is expected to produces physiological

26 differentiation and local adaptation of natural populations depending on their thermal

27 tolerances and physiological sensitivities. Here, we have studied geographic variation in

28 whole-organism thermal physiology of seven populations of the porcelain crab

29 *Petrolisthes violaceus* across a latitudinal gradient of 3000 km, characterized by a cline of

30 thermal conditions. Our study found that populations of *P. violaceus* exhibit a lack of

31 differences in the limits of their thermal performance curves and a negative correlation of

32 their optimal temperatures with latitude. Additionally, our findings showed that high

33 latitude populations of *P. violaceus* exhibited broader thermal tolerances, which is

34 consistent with the Climatic Variability Hypothesis. Interestingly, under a future scenario

35 of warming oceans, the thermal safety margins of *P. violaceus* indicate that lower latitude

36 populations can physiologically tolerate the ocean warming scenarios projected by the

37 IPCC for the end of the twenty-first century.

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43   **INTRODUCTION**

44   For ectotherms, environmental temperature (T_a) is perhaps the most important

45   abiotic factor that affects their body temperature (Hochachka and Somero, 2002; Young

46   et al., 2011) influencing a variety of organismal processes (Angilletta et al., 2002) with

47   profound implications on their performance, physiology and fitness (Cano and Nicieza,

48   2006; Huey and Berrigan, 2001; Kingsolver and Huey, 2008). T_a also influences large

49   scale process such as the biogeographical distribution and the habitat preferences of many

50   ectothermic species (Hofmann and Todgham, 2010; Pörtner, 2002; Sunday et al., 2010),

51   depending on their thermal tolerances and physiological sensitivities (Schulte et al., 2011;

52   Sunday et al., 2014). Most physiological processes in ectotherms, operate within the

53   bounds of lethal temperature extremes, with the performance of a physiological trait

54   gradually increasing with T_a from a critical minimum (CT_{min}) to an optimum (T_{opt}) before

55   dropping precipitously as T_a approaches a critical maximum (CT_{max}) (Kingsolver, 2009;

56   Wilson, 2001). This effect of T_a on performance is usually described by a continuous

57   nonlinear reaction norm (i.e., thermal performance curve, TPC) (Huey et al., 1999).

58   Variation in the parameters of the TPCs (i.e., T_{opt}, CT_{min}, CT_{max}, maximum performance,

59   and thermal breadth) has been used to describe mechanistically the variation of thermal

60   sensitivities among natural populations of diverse ectothermic species (see Gaitán-Espitia

61   et al., 2013; Kingsolver and Gomulkiewicz, 2003; Lachenicht et al., 2010). The evidence

62   indicate that these parameters usually covary with geographic clines (e.g., latitude),

63   reflecting at least partial adaptation of ectotherms to their environments (Castañeda et al.,

64   2004; Gaitán-Espitia et al., 2013).

65   Phenotypic plasticity and/or local adaptation to thermal clines can cause different

66   patterns of thermal performance across the geographic range of an ectothemic species

67   (Gardiner et al., 2010; Huey and Kingsolver, 1989; Knies et al., 2009; Schulte et al.,

68   2011; Yampolsky et al., 2014). These patterns can be explained by at least four

69   theoretical models of thermal evolution (Angilletta et al., 2002; Gardiner et al., 2010).

70   The basis of these models contain implicit assumptions about the existence of

71   evolutionary trade-offs acting on thermal physiology as a result of negative genetic

72   correlations between performance and T_a (Angilletta et al., 2002; Huey and Kingsolver,

73   1993). For instance, the counter-gradient variation model explains that populations from

74   cooler environments (high latitudes) tend to exhibit higher maximum performance (μ_{max})

75   than those from warmer environments (low latitudes) at all temperatures. This pattern is

76   predicted when genetic and environmental influences on performance are negatively

77   associated across the thermal gradient (Angilletta, 2009; Gardiner et al., 2010). Contrary

78   to this, if genetic and environmental influences on performance are positively associated,

79   the pattern of thermal performance would be related to the co-gradient variation model in

80   which populations from warmer environments (low latitudes) tend to exhibit higher μ_{max}

81   and T_{opt} than populations from cooler environments (high latitudes) (Conover et al.,

82   2009; Gardiner et al., 2010). On the other hand, the local adaptation model states that if

83   thermodynamic constraints do not limit adaptation to temperature, then adaptation to

84   warmer and colder environments is expected to result in equal μ_{max} in their corresponding

85   T_{opt} (Angilletta, 2009). Finally, if populations do not acclimate to the local thermal

86   environment and high gene flow between populations restricts local adaptation to a

87   thermal gradient, then it would be expected no differences in TPCs among populations

88   (Gardiner et al., 2010).

89   In addition, theory suggests that thermal tolerances and sensitivities of many

90   organisms are proportional to the magnitude of T_a variation they experience (Addo-

91   Bediako et al., 2000; Calosi et al., 2010; Gaitán-Espitia et al., 2013), a characteristic of

92   climate that also increases with latitude (Ghalambor et al., 2006; Janzen, 1967; Naya et

93   al., 2011). Therefore, it is expected that individuals at higher latitudes require broader

94   tolerance ranges (i.e., greater physiological plasticity) than individuals inhabiting lower

95   latitudes (i.e., Climatic Variability Hypothesis, CVH; Chown et al., 2004; Ghalambor et

96   al., 2006; Janzen, 1967; Naya et al., 2011; Stevens, 1989). This is particularly interesting

97   in the case of organisms that inhabit highly variable habitats, such as the rocky intertidals,

98   because these habitats are characterized by a wide range of thermal conditions due to the

99   tidal cycle (Helmuth and Hofmann, 2001; Helmuth et al., 2002). During low tide, the

100   intertidal exhibits a steep thermal stress gradient which increases with the shore height

101   (Helmuth et al., 2006). In these habitats, intertidal invertebrates experience temperatures

102   at or above their heat tolerance limits during times when low tide occurs simultaneously

103   with a heat wave (Helmuth et al., 2002; Helmuth et al., 2006; Stillman, 2003).

104   Under this context, here we investigated the geographic variation in thermal

105   sensitivity and thermal tolerance of physiological traits among seven populations of the

106   intertidal crab *Petrolisthes violaceus* (Guerin, 1831) spanning a latitudinal gradient of ca.

107   3,000 km in the Chilean coast. Our central question was: *Do the individuals of low*

108   *latitude populations effectively live closer to their thermal limits compared with*

109   *populations of central or high latitudes*? Thus, the objectives of this study were: (i) To

110   characterize the TPCs at the intraspecific level in seven local populations of *P. violaceus*

111   along a latitudinal gradient of ca. 3,000 km in the Chilean coast; (ii) To determine the

112   geographic variation in their thermal physiology and organismal performance.

113

114   **RESULTS**

115   **Latitudinal variability of *in situ* seawater temperature**

116   The high-resolution monitoring program of intertidal temperature evidenced a

117   clear latitudinal cline in annual mean and absolute minimum *in situ* seawater temperature

118   (SST) along the Chilean coast (Figure 1A-C). Lower values and greater variation (ca. 5

119   ºC) of annual *in situ* mean and absolute minimum SST were observed at high latitudes

120   (Figure 1B and C). Annual absolute minimum and maximum *in situ* SST showed two

121   marked thermal breaks at 30ºS and 40ºS (Figure 1B and C). These breaks were also

122   evident for the coefficient of variation of daily mean *in situ* SST (Figure 1D). On the

123   other hand, there were not latitudinal trends for heating/cooling days (i.e., days where

124   exposure was over/under the CT_{max} and CT_{min} respectively). Signals of heating days were

125   evidenced only for Antofagasta and Talcaruca at low latitude, whereas cooling days were

126   detected only in Chiloe, at high latitude (Supplementary Table 1).

127

128   **Thermal performance curves**

129   The best-fit models used to describe the thermal performance curves (TPC) of *P.*

130   *violaceus* populations (Table 1), revealed the typical left-skewed TPC shape (Figure 2).

131   The upper and lower limits of temperature at which the heart rate (HR) decreased (CT_{min}

132   and CT_{max}) were similar among populations (Table 2), without statistical differences

133   along the latitudinal gradient (One-way ANOVA, CT_{min}: $F_{6,94}=2.09$, P= 0.06; CT_{max}:

134    $F_{6,94}=1.37$, P= 0.23). However, there were detected differences in the thermal optimum

135   (T_{opt}), thermal breadth (T_{br}) and maximal performance (μ_{max}) among populations (Table

136   2; One-way ANOVA, T_{opt}: $F_{6,94}$=17.26; T_{br}: $F_{6,94}$=7.63; μ_{max}: $F_{6,94}$=8.35, P< 0.05).

137   Overall, critical thermal limits showed no signature of latitude across the

138   geographic range of the species (CI 95 for latitude: CT_{max} = -0.047, 0.096; CT_{min} = -

139   0.016, 0.021) (Figure 3D and E). In addition, neither the height of the TPCs (CI 95 for

140   latitude: μ_{max} = -2.34, 0.791) nor their amplitude (CI 95 for latitude: T_{br} = -0.550, 0.019)

141   changed across latitude (Figure 3B and C). Similar results were evidenced for these four

142   TPC parameters when the climatic variables related to *in situ* SST (mean, maximun,

143   minimum, coefficient of variation and heating/cooling days) were included in the analysis

144   (results not shown). On the other hand, T_{opt} was negatively influenced by the geographic

145   gradient (CI 95 for latitude: T_{opt} = -0.543, 0.130, b = -0.335 ± 0.108 SE) (Figure 3A).

146

147   **Critical thermal resistance**

148   Chill and heat coma (Critical thermal resistances), using roll over speed as a proxy

149   of the relationship between organismal performance and environmental temperature,

150   exhibited differences among populations in the latitudinal gradient (Kruskal-Wallis test,

151   Chill coma: H_6= 78.03; Heat coma: H_6= 57.05, P<0.05). From these indexes of thermal

152   tolerance, only the critical thermal resistance to low temperatures (CTR_{min}) was

153   influenced by latitude (Figure 4A; CI 95 for latitude: CTR_{min} = -0.543, 0.130, b = -0.063

154   ± 0.01 SE).

155

156   **Warming tolerances and thermal safety margins**

157   Although warming tolerance (WT) and thermal safety margin (TSM) evidenced

158   differences among populations (One-way ANOVA, WT: $F_{6,94}=11.79$; TSM: $F_{6,94}=7.02$,

159   P< 0.05), both indexes showed opposite trends along the latitudinal gradient (Table 2).

160   WT of the species increased towards higher latitudes (CI 95 for latitude: WT = 0.142,

161   0.332; b = 0.237 ± 0.05 SE) whilst TSM showed no clear pattern with latitude (CI 95 for

162   latitude: TSM = -0.319, 0.073) (Figure 5A and B).

163

164   **DISCUSSION**

165   In this study, we assessed the geographic variation in whole-organism thermal

166   physiology of seven populations of the porcelain crab *P. violaceus* across a latitudinal

167   gradient of ca. 3000 km, characterized by different local thermal conditions. Our study

168   found that populations of *P. violaceus* exhibit differences in thermal sensitivities (i.e.,

169   different patterns of thermal performance curves) and thermal tolerances. These findings

170   are consistent with the Climatic Variability Hypothesis, in which populations at higher

171   latitudes exhibit broader tolerance ranges than populations inhabiting lower latitudes with

172   more stable environments (Janzen, 1967; Levinton, 1983; Naya et al., 2011). The strong

173   association between latitude and climate does not permit separation of these factors to

174   establish to what extent higher physiological tolerance at higher latitudes is due to the

175   direct effect of climatic variability or to other factors associated with latitude (Ghalambor

176   et al., 2006).

177

178   **Latitudinal variation in habitat thermal conditions**

179   The marine intertidal zone along the Chilean coast is characterized by a thermal

180   gradient with lower values of annual *in situ* mean and absolute minimum seawater

181   temperature (SST) at high latitudes. This clinal change of SST along the southestearn

182   Pacific is related to a conspicuous gradient in solar irradiation (Broitman et al., 2001), the

183   influence of atmospheric circulation and rainfall variability (Barros and Silvestri, 2002)

184   and the effect of other oceanographic processes (Thiel et al., 2007). Our results revealed

185   that *in situ* SST was much variable at higher latitudes (30ºS - 42ºS) than at lower latitudes

186   (20ºS - 24ºS), something that has also been shown in previous studies along the Chilean

187   coast (Broitman et al., 2001; Lagos et al., 2005).

188   In the southeastern Pacific coast of Chile, there are two biogeographic breaks

189   located in areas with sharp discontinuities in upwelling regimes (30–32°S) and with

190   strong influence of the Antarctic Circumpolar Current (40°S-42°S) (Camus, 2001; Thiel

191   et al., 2007). These geographic breaks are in accordance with the thermal breaks that we

192   found at 30ºS and 40ºS for all of the variables related to *in situ* SST (mean, maximun,

193   minimum and coefficient of variation). Some authors have shown that these

194   environmental discontinuities influence the temporal and spatial dynamics of benthic and

195   pelagic communities (Rivadeneira et al., 2002; Thiel et al., 2007), the species

196   composition (Meneses and Santelices, 2000), the larval dispersal and gene flow of many

197   marine species (Brante et al., 2009; Haye et al., 2014; Sánchez et al., 2011; Thiel et al.,

198   2007) and the phenotypic (co)variation of fitness-related traits (Barria et al., 2013).

199   However, in the case of the intertidal crab *P. violaceus*, the evidence indicates that these

200   biogeographic breaks do not affect the gene flow and genetic structure of its populations

201   probably as a result of its long dispersal capacity (larvae spend 15 or more days in the

202   water column) (Haye et al., 2014).

203

Thermal physiological variation in natural populations

According to theoretical models of thermal evolution, the absence of genetic

structure and high gene flow between populations may constrain local adaptation to a

thermal gradient (Angilletta, 2009; Gardiner et al., 2010). This in turn would be reflected

in a lack of differences in all of the parameters of the thermal performance curves (TPCs)

among populations (Gardiner et al., 2010). Our results offer partial support to this idea.

Overall, *P. violaceus* populations along the latitudinal gradient exhibited differences in

their thermal sensitivities that are explained by three parameters of the TPCs (Optimal

temperature, T_{opt}; thermal breadth, T_{br}; and maximal performance, μ_{max}). Nonetheless,

our results indicate that the upper and lower limits of temperature at which the heart rate

(HR) decreased (CT_{max} and CT_{min}) are similar among populations, without an effect of the

climatic variables or the geographic gradient. These findings are possibly explained by

the limited capacities of ectotherms to adapt the CT_{min} and CT_{max} in the face of T_a

variation (Faulkner et al., 2014; Hoffmann et al., 2013; Stillman, 2003). Moreover, it has

been documented that the upper and lower critical temperatures are controlled by

biophysical and thermodynamic constraints (Hoffmann et al., 2013; Somero, 2005) that

influence the shape and limits of the TPCs (Angilletta, 2009). Our critical temperatures

for HR were on average beyond maximum and minimun *in situ* SST along the Chilean

coast, and are closed to the limits of the ranges described for other species of porcelanid

crabs of the genus *Petrolisthes* (CT_{max} from 28.4 - 41.7°C and CT_{min} from -1.3 - 11.3 8C)

(Stillman, 2003). In these species, inter-population differences in the thermal cardiac

performance are evidenced between seasons and across latitudinal gradients in

226   accordance with their habitat temperature differences (Stillman and Tagmount, 2009) and

227   their local thermal microhabitat conditions (Stillman, 2003; Stillman, 2004). For

228   example, porcelanid crabs from warmer habitats exhibit higher CT_{max} compared to

229   species from cooler habitats, whereas the opposite pattern is described for CT_{min}

230   (Stillman, 2003).

231   From the three TPC parameters that differed among populations of *P. violaceus*,

232   only T_{opt} showed signals of geographic influence (negative correlation with latitude).

233   This pattern of thermal performance follows some of the expectations of the co-gradient

234   variation model in which populations from warmer environments (low latitudes) tend to

235   exhibit higher μ_{max} and T_{opt} than populations from cooler environments (high latitudes)

236   (Conover et al., 2009; Gardiner et al., 2010). The analyses of μ_{max} and T_{br} between the

237   most extreme populations of *P. violaceus* in Chile are consistent with this model of

238   thermal evolution. However, the effect of the geographic and climatic gradient on these

239   TPC parameters is eroded by the values of μ_{max} and T_{br} in populations that inhabit close

240   to the southern limit of the thermal and biogeographic break located between 30–32°S.

241   For some porcelanid species in the northern hemisphere, the evidences suggest that in

242   addition to latitude, the habitat temperature range or fluctuation is a more important

243   environmental factor in setting thermal performance than mean habitat temperature

244   (Stillman and Tagmount, 2009). This pattern was not consistent with our findings

245   probably due to the lower differences in the temperature ranges along the latitudinal cline

246   in the Chilean coast compared to the northern hemisphere.

247

248   **Thermal tolerances and thermal safety margins**

249   Thermal tolerances are closely related to the biogeographic distribution of marine

250   especies along latitudinal and vertical clines in coastal ecosystems (Pörtner, 2002;

251   Somero, 2005). It is known that heat-tolerance limits of ectothermic species vary little

252   with latitude whereas cold-tolerance limits decline steadily with increasing latitude

253   (Sunday et al., 2014). In our study, populations of *P. violaceus* along the Chilean coast

254   differed in their critical thermal resistances to high (CTR_{max}) and low (CTR_{min})

255   temperatures. However, from these indexes of thermal tolerance, only the CTR_{min}

256   evidenced a geographic influence that may suggests adaptation to local environmental

257   conditions (Somero, 2005) in which the lower CTR_{min} exhibited by crabs form high

258   latitude populations is perhaps the result of natural selection favoring a more cold-

259   adapted populations, which has been observed in other ectotherms (Keller and

260   Seehausen, 2012; Pörtner et al., 2000; Stitt et al., 2014).

261   In addition to the cold-tolerance findings, the average amount of environmental

262   warming that populations of *P. violaceus* can tolerate before performance drops to fatal

263   levels (i.e., warming tolerance) (Deutsch et al., 2008a), points out the existence of a

264   positive correlation of this thermal tolerance index with latitude. This pattern has been

265   described for other ectotherms suggesting that at low latitudes rising T_a, associated to

266   global warming, is likely to have the most deleterious consequences because ectothermic

267   species in these geographic areas are relatively sensitive to temperature change and are

268   currently living very close to their T_{opt} (Deutsch et al., 2008a; Stillman, 2002; Sunday et

269   al., 2014). Interestingly, our results about thermal safety margins (the differential

270   between organism's T_{opt} and its current T_a) (Deutsch et al., 2008a) of *P. violaceus* crabs,

271   that are the first in marine ectotherms, indicate that populations at high latitudes are

272   closer to their physiological optima than those populations from low latitudes. These

273   results may suggest that low latitude populations of *P. violaceus* might be able to

274   physiologically tolerate the increase in temperature projected by the IPCC for the end of

275   the twenty-first century (ca. 4 °C in the RCP8.5 scenario) (IPCC, 2013). Nonetheless, in

276   the case of the southeastern Pacific, it has been described a departure of the the general

277   ocean warming trend described by the IPCC (Aravena et al., 2014; Falvey and Garreaud,

278   2009). Indeed, recent studies have found a SST cooling (ca. -0.2°C/decade) along the

279   Chilean coast related to a Niña-like intensification of the South Pacific Anticyclone

280   (Aravena et al., 2014; Falvey and Garreaud, 2009). This SST cooling might play an

281   important role in the geographic variation of the thermal resistances to low temperatures

282   (CTR$_{min}$) that we found in our study.

283   In summary, because the geographical range of *P. violaceus* covers a broad

284   latitudinal gradient of climate conditions, we expected to find signals of physiological

285   differentiation of natural populations as well as adaptation to local T$_a$ (Ghalambor et al.,

286   2006; Janzen, 1967; Kuo and Sanford, 2009; Levinton, 1983). Indeed, we observed

287   differences in their thermal sensitivities that are explained by partial combination of two

288   models of thermal evolution characterized by the lack of differences in the limits of the

289   TPCs and the negative correlation of T$_{opt}$ with latitude. Additionally, high latitude

290   populations of *P. violaceus* exhibited broader thermal tolerances which is consistent with

291   the Climatic Variability Hypothesis (Ghalambor et al., 2006; Janzen, 1967). Finally,

292   under a furure rising T$_a$ scenario, our findigs about the TSM indicate that lower latitude

293   populations can physiologically tolerate future warming, at least that one projected by the

294   IPCC for the 2100.

295

MATERIAL AND METHODS

Study populations and sites

Petrolisthes violaceus is a free-living porcellanid crab commonly found in the rocky

intertidal low zone of the south-eastern Pacific (Vargas et al., 2010; Viviani, 1969) and

distributed in a latitudinal gradient along the Chilean coast, characterized by large and

meso-scale variations in the intensity of coastal upwelling (Thiel et al., 2007; Torres et

al., 2011), as well as spatial variation in sea surface temperature (SST) and air

temperature (Figure 1) (Lagos et al., 2005). Animals were collected randomly by hand on

low tides during 2011 and 2012 from the rocky intertidal area of Iquique (20º19' S,

70º15' W), Antofagasta (23º46' S, 70º40' W), Talcaruca (30º29' S, 71º41' W), El Tabo

(33º27' S, 71º66' W), Lenga (36º45' S, 73º10' W), Valdivia (39º46' S, 73º23' W) and

Chiloé (40º52' S, 73º59' W). These seven locations along the southeastern coast of Chile

(ca. 3,000 km), encompass much of the species' latitudinal range (Figure 1). To remove

possible confounding effects of sex, only male crabs were used in the experiments and

physiological measurements. Individuals were chilled and transported to the laboratory at

the Universidad Adolfo Ibañez, where they were mainteined in common garden

conditions, at constant temperature (14°C) in artificial seawater (ASW; 33 ppm; Instant

Ocean© sea salt dissolved in distilled water) for one month. Crabs were exposed to a

light/dark cycle of 12/12 h and fed with Instant Algae® and aquarium shrimp food three

times a week.

    A high-resolution monitoring program of intertidal temperature was developed

along the latitudinal gradient in the Chilean coast. Trends in intertidal temperature (SST;

318 annual and daily mean and variance) and other environmental variables such as

319 heating/cooling days (i.e., days where exposure was over/under of the CT_{max} and CT_{min}

320 respectively) were monitored between 2011 and 2013. Temperature loggers (TibdiT®,

321 Onset Computer Corp. MA, USA) were deployed in the low intertidal level (ca. 0.2 – 0.3

322 m above mean lower low water, MLLW) of each location. Intertidal logger records both

323 seawater and air temperature (during extreme low tides), which are significantly

324 correlated (Menge et al., 2008). Thus, recording overall fluctuations in temperature

325 experienced by the species model at each local intertidal habitat.

326

327 **Thermal performance curves**

328 Thermal effects on physiological performance were estimated for populations of

329 *P. violaceus* along the latitudinal gradient in the Chilean coast. Here we used heart rate

330 (HR; cardiac activity) and rollover speed (RS; the speed at which animals change form

331 the inverse to the upright position) as proxies of the relationship between organismal

332 performance and T_a (Bruning et al., 2013; Gaitán-Espitia et al., 2013; Schulte et al.,

333 2011). A total of 210 adult individuals (30 crabs for each population) were selected for

334 analyzes of thermal sensitivities (i.e., thermal performance curves, TPCs). TPCs for HR

335 were described in terms of four parameters: (1) the optimal temperature (T_{opt}); (2) the

336 thermal breadth (T_{br}); (3) the maximal performance (μ_{max}); and (4) the upper and lower

337 limits of temperature at which the HR decrease (CT_{min} and CT_{max}) (Angilletta, 2009). At

338 each temperature, animals were exposed separately in plastic chambers with six

339 subdivisions (200 x 200 x 100 mm), installed in a thermo-regulated bath at constant sea

340 water temperature (±0.5 °C, LWB-122D, LAB TECH), for 30 min. We randomized the

341 order of temperature trials for each individual and ensured at least 24 h of rest between

342 trials. Experimental temperatures for TPCs were chosen between 0 and 31 ℃. In

343 extreme temperatures of the thermal treatment (i.e., 0 to 6 ℃ and 26 to 31 ℃) HR was

344 measured every 1 ℃, whereas at intermediate temperatures (i.e., 6 to 26 ℃) it was

345 measured every 2 ℃. HR was estimated using a heartbeat amplifier AMP 03 (Newshift

346 Lda®) connected to an oscilloscope and the results were expressed in beats min^{-1}.

347 Measurements of cardiac activity were performed at the same period of the day to cancel

348 the effects of a possible circadian and tidal rhythm of respiration.

349   The mean HR for each crab at each experimental temperature was calculated with

350 the aim of estimating the TPCs for each population. We used the TableCurve2D curve-

351 fitting software (version 5.01; Systat Software, Inc.) for model fitting. TPC parameters

352 (μ_{max}, T_{opt} , CT_{min} and CT_{max}) were extracted from the best models (see below for details).

353 The ecophysiological characteristics of critical thermal maximum (CT_{Max}) and minimum

354 (CT_{Min}) were derived numerically as the intersection points of the resulting thermal

355 performance curve with the temperature axis ($\mu=0$). Temperature breadth (T_{br}) for each

356 population was calculated with the mean values of HR for each experimental temperature

357 using the following equation (Gilchrist, 1996):

358
$$T_{br} = \sqrt{\sum_{i=1}^{N}\left[\frac{\mu_i\left(T_i - T_{opt}\right)}{\mu_{max}}\right]^2}$$

359 where N equals the number of temperatures and μ_i is the mean HR at temperature T_i.

360

361 **Thermal coma and thermal tolerances**

362   Critical thermal resistances to high and low temperatures (CTR_{min} and CTR_{max})

363 were estimated in a total of 185 adult individuals of *P. violaceus* using the thermal coma

364 methodology (see Gaitán-Espitia et al., 2013). Overall, thermal comas were defined as

365 the lack of ability to achieve an upright position, or lack of movement of structures and/or

366 appendices within a pre-defined time period (e.g., Bacigalupe et al., 2007; Castañeda et

367 al., 2005; Gaitán-Espitia et al., 2013; Lutterschmidt and Hutchison, 1997). This measure

368 is sub-lethal and is useful for a broad range of ectothermic invertebrates and large sizes

369 samples (Huey et al., 1992). Animals were exposed separately in plastic chambers with 6

370 subdivisions (200 x 200 x 100 mm), installed in a thermo-regulated bath at constant sea

371 water temperature ($\pm$0.5 ºC, LWB-122D, LAB TECH), for 30 min. In the last 15 minutes,

372 crabs were turned over and if an individual was not in a thermal coma, it responded by

373 returning to an upright position. At extreme temperatures, some individuals had zero

374 performance. Those animals that exhibited a complete loss of righting response under

375 extreme temperatures were considered to be in a thermal coma (e.g., Castañeda et al.,

376 2005; Gaitán-Espitia et al., 2013; Lutterschmidt and Hutchison, 1997). Tolerance ranges

377 were determined experimentally *a priori*.

378

379 **Warming Tolerance and thermal safety margin**

380   At the collection sites of *P.violaceus*, mean habitat temperature (T_{hab}) and

381 variance (σ_t) were extracted from high-resolution temperature data-logger as the mean

382 and standard deviation of monthly sea surface temperature (SST). Theoretically,

383 seasonality (variance) is a strong predictor of warming tolerance (WT = CT_{max} - T_{hab}) and

384 also of thermal safety margins (TSM=T_{opt} - T_{hab}) (for details see Deutsch et al., 2008b).

385 These correlations simply reference the position of performance curves to local climate

386 conditions.

387

Statistical anslyses

389   Prior to analyses, we tested for normality and homoscedasticity for all variables

390 using the Lilliefors and Levene tests, respectively. Data was transformed either by $\log_{10}$

391 or by square root to fulfil the requirements for parametric tests. The fit of several

392 functions (e.g., Gaussian, Lorentzian, Weibull) that could describe organismal

393 performance as a function of temperature was analized using the Akaike Information

394 Criterion (Angilletta, 2006). The AIC represents a balance between the likelihood

395 explained by the model and the number of model parameters, with the best model

396 minimizing AIC (Kingsolver and Massie, 2007). Thermal physiological traits obtained

397 from the TPCs (i.e., μ_{max}, T_{opt}, T_{br}, CT_{min} and CT_{max}) and WT and TSM indexes were

398 analysed using a mixed modelling approach, with locality as a random grouping factor.

399 The effect of latitude (fixed effect) was evaluated through confidence intervals computed

400 from the likelihood profile (Bates et al., 2013). Critical thermal resistances (i.e., thermal

401 comas) were analyzed using Kruskal-Wallis test. In all cases, when differences in the

402 means were significant at the $P < 0.05$ level, they were also tested with a posteriori

403 Tukey's test (HSD). Statistical analyses were performed with R 3.0.2 software and the

404 package lme4 (Bates et al., 2013).

405

415

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640

FIGURE CAPTIONS

Figure 1. Geographic and environmental gradient along the southeastern Pacific. (a) Study sites along the Chilean coast; (b) Latitudinal variability in SST (mean ± SD) from 18 to 46°S estimated using 5 years historical record from July 1999 to July 2004 (Data available at http:www.podacc.gov); (c) Latitudinal variability of annual *in situ* SST (mean ± SD) recorded at the low intertidal level of the rocky shore platform in the study sites. (d) Coefficient of variation of daily mean *in situ* SST. Absolute maximum (solid line) and minimum (dashed line) *in situ* SST values recorded for the corresponding time period are also showed in each graph.

Figure 2. Thermal sensitivities of the intertidal crab Petrolisthes violaceus. (A) Latitudinal comparison of thermal performance curves; TPC for populations of (B) Iquique (20°S), (C) Antofagasta (23°S), (D) Talcaruca (30°S), (E) El Tabo (33°S), (F) Lenga (36°S), (G) Valdivia (39°S) and (H) Chiloé (40°S).

Figure 3. Latitudinal variation in the temperature optimum (A); maximum performance (B); thermal breadth (C); critical minimum (D) and critical maximum (E) of the intertidal crab Petrolisthes violaceus. The effect of latitude (fixed effect) was evaluated through confidence intervals computed from the likelihood profile (Bates et al., 2013).

Figure 4. Latitudinal variation in thermal comas (A, Chill coma; B, Heat coma). The effect of latitude (fixed effect) was evaluated through confidence intervals computed from the likelihood profile (Bates et al., 2013).

Figure 5. Geographic variation in (A) warming tolerance (WT) and (B) thermal safety margins of the intertidal crab Petrolisthes violaceus along a latitudinal gradient of ca. 3000 km in the Chilean coast.

670 Table 1. Comparison of functions used to describe the thermal performance curves of *P.*
671 *violaceus* populations across the latitudinal gradient, using Akaike's information criterion
672 (AIC). The function with the lowest AIC is the one that best describes the data. K =
673 number of parameters in the function, λ_i = difference between a given model's AIC and
674 the lowest AIC, w_i = Akaike weight. Models in boldface were selected for analyses.
675

Population	Function	K	AIC	λ_i	w_i	r^2
Iquique						
	Gaussian	4	51.22	0.00	0.48	0.96
	Lorentzian	4	51.43	0.21	0.43	0.96
	Weibull	5	54.51	3.29	0.09	0.96
Antofagasta						
	Gaussian	4	55.36	0.00	0.38	0.87
	Lorentzian	4	55.38	0.02	0.37	0.87
	Weibull	5	56.21	0.85	0.25	0.90
Talcaruca						
	Lorentzian	4	38.52	0.04	0.47	0.97
	Gaussian	4	38.47	0.00	0.48	0.97
	Weibull	5	43.20	4.73	0.05	0.96
El Tabo						
	Weibull	5	32.88	0.00	0.78	0.99
	Lorentzian	4	36.72	3.84	0.11	0.98
	Gaussian	4	36.86	3.99	0.11	0.98
Lenga						
	Gaussian	4	38.13	0.00	5.24	0.98
	Lorentzian	4	38.14	0.01	5.20	0.98
	Weibull	5	41.44	3.31	1.00	0.98
Valdivia						
	Weibull	5	39.07	0.00	0.44	0.98
	Gaussian	4	39.94	0.87	0.28	0.96
	Lorentzian	5	39.94	0.87	0.28	0.96
Chiloé						
	Gaussian	4	44.87	0.56	0.40	0.89
	Lorentzian	4	44.31	0.00	0.53	0.90
	Weibull	5	48.25	3.93	0.07	0.90

676
677

678 Table 2. Parameters of thermal performance curves in populations of the porcellanid crab *P. violaceus*. Thermal optimum (T_{opt}),
679 thermal breadth (T_{br}), maximal performance (μ_{max}), critical temperatures (CT_{min} and CT_{max}), warming tolerance (WT) and thermal
680 safety margin (TSM). (Mean ± S.E.M).
681

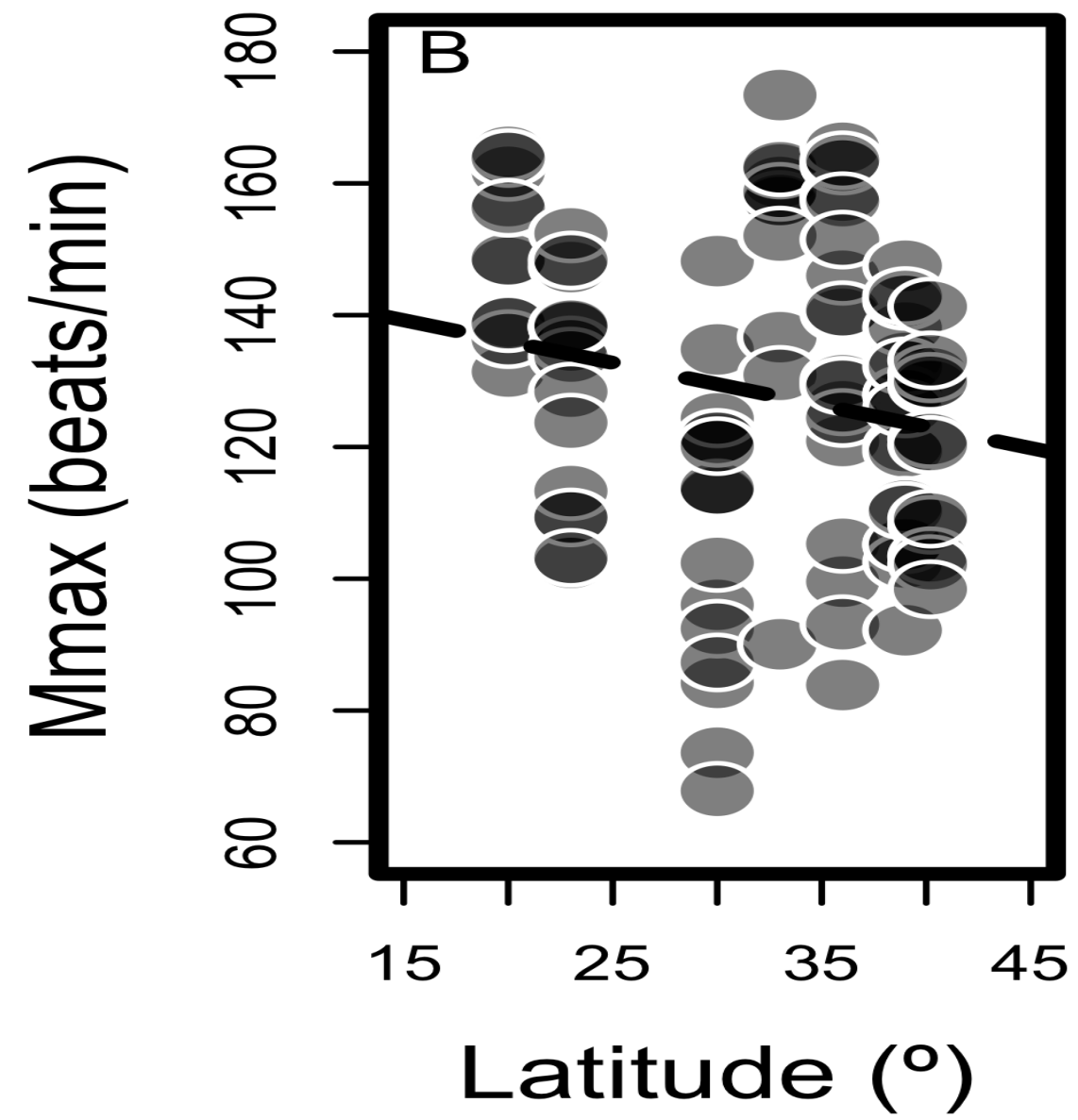| Population	Latitude	CT_{min} (ºC)	CT_{max} (ºC)	T_{opt} (ºC)	μ_{max}	T_{br}	WT	TSM
Iquique	20º19' S, 70º15' W	-0.74 ± 0.33	32.31 ± 0.74	24.43 ± 0.87	149.93	28.74	15.49	7.61
Antofagasta	23º46' S, 70º40' W	-0.75 ± 0.24	33.46 ± 0.75	19.08 ± 0.46	127.51	27.81	17.06	2.69
Talcaruca	30º29' S, 71º41' W	-0.68 ± 0.18	32.90 ± 0.68	18.34 ± 0.27	100.85	26.89	17.39	2.83
El Tabo	33º27' S, 71º66' W	-1.13 ± 0.27	31.99 ± 0.74	18.43 ± 0.27	148.18	21.22	17.15	3.59
Lenga	36º45' S, 73º10' W	-0.84 ± 0.21	34.23 ± 0.82	18.98 ± 0.23	133.24	27.51	19.54	4.29
Valdivia	39º46' S, 73º23' W	-0.52 ± 0.13	34.31 ± 0.52	16.98 ± 0.36	118.31	26.59	21.72	4.39
Chiloé	40º52' S, 73º59' W	-0.68 ± 0.17	34.38 ± 0.52	13.32 ± 0.40	118.52	19.65	22.12	1.06

682
683
684
685

(a)   (b)   (c)   (d)

SST (°C)

Annual in situ SST (°C)

CV of daily in situ SST (%)

Iquique

Antofagasta

Talcaruca

El Tabo

Lenga

Valdivia

Chiloe

Latitude (°S)

50°S

68°W