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Metabolic and reproductive plasticity of core and marginal populations of the eurythermic saline water bug *Sigara selecta* (Hemiptera: Corixidae) in a climate change context

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1 Metabolic and reproductive plasticity of core and marginal populations of the
2 eurythermic saline water bug *Sigara selecta* (Hemiptera: Corixidae) in a climate change
3 context.

4

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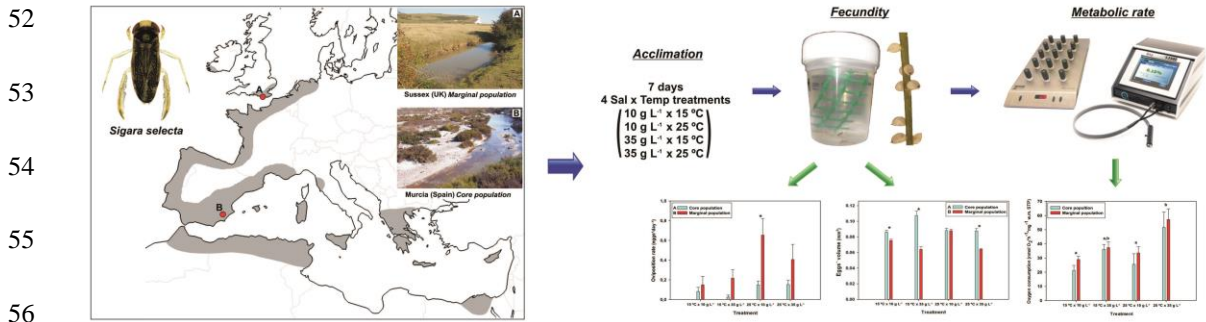
26 ABSTRACT

27 Ongoing climate change is driving dramatic range shifts in diverse taxa worldwide, and
28 species responses to global change are likely to be determined largely by population
29 responses at geographical range margins. Here we investigate the metabolic and
30 reproductive plasticity in response to water temperature and salinity variation of two
31 populations of the eurythermic saline water bug *Sigara selecta*: one population located
32 close to the northern edge of its distribution, in a relatively cold, thermally stable region
33 (SE England – ‘marginal’), and one close to the range centre, in a warmer and more
34 thermally variable Mediterranean climate (SE Spain – ‘core’). We compared metabolic
35 and oviposition rates and egg size, following exposure to one of four different
36 combinations of temperature (15 and 25 °C) and salinity (10 and 35 g L⁻¹). Oviposition
37 rate was significantly higher in the marginal population, although eggs laid were smaller
38 overall. No significant differences in oxygen consumption rates were found between
39 core and marginal populations, although the marginal population showed higher levels
40 of plasticity in both metabolic and reproductive traits. Our results suggest that
41 population-specific responses to environmental change are complex and may be
42 mediated by differences in phenotypic plasticity. In *S. selecta*, the higher plasticity of
43 the marginal population may facilitate both its persistence in current habitats and
44 northward expansion with future climatic warming. The less plastic core population
45 may be able to buffer current environmental variability with minor changes in
46 metabolism and fecundity, but could be prone to extinction if temperature and salinity
47 changes exceed physiological tolerance limits in the future.

48

49 **KEYWORDS:** Ecophysiology, range margins, metabolic rate, fecundity, trade-offs,
50 global change.

51 GRAPHICAL ABSTRACT



57

58 HIGHLIGHTS

- 59
- Metabolic and reproductive traits of core vs marginal populations of *Sigara selecta*.
- 60
- Population responses to climate change are mediated by phenotypic plasticity.
- 61
- Marginal population shows higher metabolic and fecundity plasticity.
- 62
- Marginal population may increase its fitness and expand its range northwards in the
- 63
- future.
- 64
- Core population could be more prone to extinction with climate warming.

65

66 1. INTRODUCTION

67 The vulnerability of a species to global warming largely depends on its capacity to

68 maintain present populations (species persistence) and to shift its geographical range to

69 suitable future environments (Parmesan, 2006; Williams et al., 2008), factors heavily

70 influenced by population responses at range margins (Kirkpatrick and Barton, 1997;

71 Hampe and Petit, 2005; Gaston, 2009). The persistence of populations will depend on

72 their ability to adapt to and tolerate novel conditions, i.e. on physiological tolerance

73 limits, as well as the potential to shift these limits *via* plastic and adaptive changes

74 (Chown et al., 2007; Gaston et al., 2009; Hoffmann, 2010).

75

76 The adaptive ability of marginal populations can be limited because they are typically
77 less diverse genetically than those close to the range centre (the “centre-periphery
78 hypothesis” of Mayr, 1963), since they tend to occur in less favorable habitats at lower
79 and more variable densities, and often experience stronger genetic drift (Lawton, 1993;
80 Vucetich and Waite, 2003; Hampe and Petit, 2005). However, phenotypic plasticity, or
81 the capacity of a single genotype to exhibit a range of phenotypes in different
82 environments (Whitman and Agrawal, 2009), might compensate for a lack of adaptive
83 ability and precede, or even favor, adaptive changes (Charmantier et al., 2008; Lardies
84 and Bozinovic, 2008). Physiological plasticity can confer resilience to climate change
85 (Chevin et al., 2010, Seebacher et al., 2015); for example, thermal plasticity appears to
86 be inversely related to vulnerability to climate change in a range of taxonomic groups
87 (e.g., Stillman, 2003; Calosi et al., 2008, 2010; Donelson et al., 2011; Arribas et al.,
88 2012a). Ultimately, physiological plasticity should promote the establishment of a
89 population in a new environment and its persistence when environmental conditions
90 change (Ghalambor et al., 2007).

91

92 Phenotypic plasticity can be viewed as an adaptive response to environmental
93 heterogeneity and predictability (Lardies & Bozinovic, 2008). Some studies have
94 suggested that physiological plasticity seems to be higher in organisms living in
95 moderately variable environments, such as temperate areas, and limited in those living
96 in very stable (Hoffmann and Harshman, 2000) or highly variable environments
97 (Sanders et al., 1991; Hofmann and Somero, 1995; Gaston et al., 2009; Arribas et al.,
98 2012b; Botella-Cruz et al., 2016), meaning that species from such stable or highly
99 variable environments may be more vulnerable to climate change than species from
100 moderately variable ones (Stillman, 2003; Tomanek, 2009; Magozzi and Calosi, 2015).

101 Other studies suggest the existence of trade-offs between absolute limits and plasticity;
102 organisms with the highest overall thermal tolerance exhibiting the lowest plasticity of
103 this tolerance (Calosi et al., 2008; Bozinovic et al., 2011; Gunderson and Stillman,
104 2015).

105

106 Although these hypotheses were originally framed in the context of between-species
107 comparisons, one could expect similar patterns in phenotypic plasticity to be found at
108 the intraspecific level (see Gaston et al., 2009). Thus, latitudinal variation in life-history
109 and metabolic traits amongst populations, often linked to climate and temperature
110 variability, are ubiquitous in ectotherms (Lardies and Bozonovic, 2008). A negative
111 relationship between mean standard metabolic rate and ambient environmental
112 temperature is a common physiographic pattern found along latitudinal clines between
113 populations of terrestrial insects (Addo-Bediako et al., 2002; Gaston et al., 2009). In
114 terms of reproduction, an increased number of eggs and higher reproductive output at
115 elevated latitudes have also been observed in some invertebrate species (e.g., Van't
116 Land et al., 1999; Lardies and Bozonovic, 2008). Moreover egg size is, in general,
117 inversely linked to egg number (Fox and Czesak, 2000), although in some cases (e.g.,
118 *Drosophila melanogaster*) a positive relationship between egg size and latitude has been
119 described (Azevedo et al., 1996).

120

121 To better predict how species may respond to ongoing climate change, it is also
122 necessary to consider the combined effect of multiple stressors from a physiological
123 perspective (Gunderson et al., 2016; Hewitt, Ellis & Thrush 2016). In inland aquatic
124 ecosystems, water salinity has been predicted to fluctuate widely in association with
125 changes in temperature and precipitation patterns (Poff et al., 2002). Temperature and

126 salinity can have a synergetic or antagonist effect on species performance (Todgham &
127 Stillman, 2013). Thus, population persistence in dynamic and multivariate environments
128 greatly depends on their ability to deal with the interactive effects of different stressors
129 occurring simultaneously or sequentially over short time-scales (Gunderson et al.,
130 2016).

131

132 In the present study we explore differences in metabolic and oviposition rates and egg
133 size, and their plasticity in response to changes in water temperature and salinity,
134 between core and marginal populations of the eurythermic aquatic bug *Sigara selecta*
135 (Fieber, 1848), and go on to consider how these differences may shape population
136 responses to ongoing global change. Based on the general patterns described for
137 invertebrates, we predict that: 1) metabolic and oviposition rates will be higher in the
138 northern marginal population than in the southern core one, but that eggs size should be
139 higher in the southern core population, and 2) the northern marginal population,
140 inhabiting moderately variable habitats, would show higher plasticity in metabolic and
141 reproductive traits than the core population, from highly variable habitats.

142

143 2. MATERIALS AND METHODS

144

145 2.1. *Study species, specimen collection, and laboratory maintenance*

146 *Sigara selecta* is a eurythermic aquatic corixid that inhabits saline and brackish lentic
147 coastal water bodies (Carbonell et al., 2012). Like most corixids, it is a benthic diving
148 insect with a compressible gas gill, with a high storage capacity, which is renewed at
149 regular intervals at the water surface (Popham, 1959, 1960). It is adapted to live in water
150 bodies dominated by autotrophy (gross primary production > ecosystem respiration, see

151 Velasco et al., 2003; Gutiérrez-Cánovas et al., 2009), which show large daily and
152 seasonal variation in dissolved oxygen, from being hyperoxic during the day to anoxic
153 at night. Consequently, in nature, its gas gill is likely to be efficient at relatively low
154 dissolved oxygen concentrations. This species, distributed in Western Europe and North
155 Africa (Fig. 1 - Jansson, 1986; Aukema and Rieger, 1995), offers an opportunity to
156 examine geographic variation in phenotypic plasticity of life-history and metabolic
157 traits between core and marginal populations.

158

159 Since the experimental procedure required working with live individuals from different
160 populations, over a short period of time to reduce seasonal effects on plasticity, two
161 representative populations from different latitudes but similar longitude were selected.
162 The northern population (SE England) occupies cold and more thermally stable habitats
163 close to the northern range margin – hereafter ‘marginal population’. The southern
164 population (SE Spain) inhabits warmer and more thermally variable sites near the center
165 of the species distributional range – hereafter ‘core population’. (Fig. 1, Table 1). The
166 sampling locality of the core population has a semiarid Mediterranean climate, with a
167 mean annual air temperature of 18.1 °C and high annual variation in temperature (28.3
168 °C), with a maximum annual temperature of 33.1 °C (mean data for the last 30 years).
169 The northern locality of the marginal population is much cooler (mean annual air
170 temperature 10.3 °C), has lower annual variation in temperature (20.7 °C) and a
171 maximum annual temperature of 21.8 °C (Table 1). An increase in mean temperature
172 and water salinity, and its variation, is expected at both localities with ongoing climate
173 change (IPCC, 2013).

174

175 We collected specimens of both populations between the end of May and early June
176 2014, these specimens being adults from the first spring generation (Savage, 1989;
177 Barahona et al., 2005). Bugs were collected with a D-framed pond net with 1 mm mesh.
178 They were later transported to the laboratory inside plastic containers filled with damp
179 aquatic vegetation to prevent desiccation and mechanical damage during transport.
180 Containers were kept within thermally insulated polystyrene boxes with water ice in the
181 bottom in order to minimize thermal fluctuations as much as possible. Insects were
182 transferred to an aquarium facility 24 h after collection. Upon arrival in the laboratory,
183 individuals were maintained at 15 °C with a natural photoperiod (approx. 15 h light: 9 h
184 dark) for 24 h in a 5 L aquarium with their original water and aquatic vegetation. They
185 were fed *ad libitum* with frozen chironomid larvae.

186

187 2.2. *Experimental design*

188 To investigate the combined effects of water temperature and salinity changes on
189 metabolic and reproductive traits and their plasticity, an orthogonal experimental design
190 was used, incorporating two levels of temperature (15 and 25 °C) and salinity (10 and
191 35 g L⁻¹). Since previous laboratory experiences combining higher temperatures and
192 salinities resulted in the rapid death of individuals, we chose temperature and salinity
193 ranges representative of the habitats where the species usually lives. The two
194 temperatures tested were chosen as they correspond approximately to the summer
195 average temperature for the two sampling localities respectively ([http://climate-](http://climate-data.org)
196 [data.org](http://climate-data.org)_last accessed 1 November 2014 - see Table 1). The two salinities correspond to
197 the average point of isotonicity for aquatic insects (10 g L⁻¹; Chown and Nicolson,
198 2004; Bradley, 2009) and one at which the species normally occurs in the field (35 g L⁻¹
199 - Barahona et al., 2005; Carbonell et al., 2012), but at which hypo-osmotic regulation is

200 necessary. Water of different salinities was prepared by dissolving an appropriate
201 amount of artificial sea salt (Instant Ocean, Aquarium Systems, Sarrebourg, France) in
202 distilled water.

203

204 *2.3. Reproductive traits*

205 Male-female pairs from each population were transferred to 100 mL containers at each
206 salinity x temperature treatment (n = 15 pairs by treatment and population). Containers
207 were held inside a controlled-temperature room kept at each temperature (15 or 25 °C)
208 with L:D 12:12 h for 7 d and specimens were fed daily with frozen chironomid larvae.
209 If the male died before the end of the trial, it was replaced. A piece of plastic mesh was
210 placed in each container as an oviposition substrate. Eggs laid during the first two days
211 were not included in our estimations, to minimise the effect of females carrying eggs
212 when collected in the field; after this time egg production was monitored daily. After
213 eggs were counted, they were removed from the substrate and measured. Length and
214 width of collected eggs were immediately scored using a Leica MZ8 stereomicroscope
215 with an eyepiece micrometer (to 1 µm). Egg volume was calculated using the following
216 formula for an ellipsoid:

217

$$218 \text{ Egg volume} = \frac{4}{3} * \pi * a * b * c$$

219 where a = length / 2, b and c = width / 2

220

221 Fecundity plasticity was estimated as the change in magnitude of oviposition rate and
222 egg volume between acclimation temperatures and salinities.

223

224 *2.4. Metabolic rate determination*

225 Routine metabolic rate ($\dot{M}O_2$) was determined using closed respirometry based on
226 measures of oxygen exchange between the bug's air bubble and the surrounding water
227 (Di Giovanni et al., 1999; Kehl & Dettner, 2009). $\dot{M}O_2$ was measured after seven days
228 acclimation at each temperature x salinity treatment for the same individual females
229 after the previous oviposition period (n = 12). Each chamber (10 mL blackened glass
230 chambers, each containing one individual) was supplied with oxygen saturated water at
231 the appropriate temperature and salinity, pre-filtered (0.22 μ m vacuum filter) to remove
232 algae and bacteria to minimize background oxygen production and respiration
233 respectively. To standardize the volume of air in the bubble carried by the insects,
234 individuals were allowed to replenish their air bubble at the water surface before being
235 introduced into the chamber. In addition, to control for background fluctuations in
236 oxygen measurements, three respirometry chambers were left empty in each trial,
237 equipped with a magnetic flea and placed on a multi-channel magnetic stirrer (MIX 15
238 eco; 2mag AG, Munich, Germany) to ensure moderate mixing of water. All chambers
239 were sealed while submerged to ensure no air bubbles were present.

240

241 Oxygen levels in the chambers were measured every 2 min using a calibrated optical O_2
242 analyzer (5250i, OxySense, Dallas, TX) in combination with an external probe (101,
243 OxySense) and a fluorescent disc placed inside each chamber (Oxydot, OxySense).
244 Although preliminary tests showed that individuals remained alive for more than two
245 hours in respirometry chambers without a surface air space, $\dot{M}O_2$ was measured over the
246 first 60 minutes to avoid critical hypoxic conditions. During this first hour, variation in
247 PO_2 was linear (see Appendix S1), indicating that the critical point, at which PO_2
248 drastically declines, was not reached. During experiments bugs divided their time
249 between resting and swimming. When resting, the oar-like hind legs were moved

250 synchronously to ventilate their gas gill, this being part of the normal respiratory
251 behavior of corixids (Popham, 1960; Matthews & Seymour, 2010). Measurements were
252 undertaken inside temperature controlled rooms at the appropriate treatment
253 temperature to improve thermal stability. $\dot{M}O_2$ was expressed as $\text{nmol } O_2 \text{ h}^{-1} \text{ STP}$
254 (standard temperature and pressure) per unit wet mass (mg). To calculate $\dot{M}O_2$ the
255 volume of individuals were estimated and subtracted from the volume of the chambers
256 to determine the volume of water present during measurements. Upon completion of
257 $\dot{M}O_2$ measurements, insects were removed from the chamber, blotted dry, and weighed
258 with an electronic high-precision balance to $\pm 0.0001 \text{ g}$ (MS 1225 P, Sartorius AG,
259 Goettingen, Germany) to obtain individual wet mass.

260

261 Metabolic plasticity was determined for each population at the two studied salinities as
262 the response of metabolic rate to changing temperature, and was expressed as Q_{10} values
263 according to the formula:

264

$$265 \quad Q_{10} = K_1 / K_2^{10 / (t_1 - t_2)}$$

266 Where K_1 = the mean metabolic rate at temperature t_1 (15°C)

267 K_2 = the mean metabolic rate at temperature t_2 (25°C)

268

269 2.5. Data analysis

270 To explore how acclimation at different temperatures and salinities affected oxygen
271 consumption, oviposition rate and egg volume in *S. selecta*, we employed Generalized
272 Linear Models (GLM) with ‘population’ and ‘temperature x salinity treatment’ as fixed
273 independent factors and body mass as a covariate. We assumed a Gaussian distribution
274 and identity link function (equivalent to a 3-factor ANCOVA). Sidak's post-hoc tests

275 were implemented to identify significant differences in the response variables between
276 populations and/or treatments. In addition, to test the independent effect of temperature
277 and salinity on response variables in each population we ran GLM tests with these
278 environmental variables as fixed factors and weight as covariate, separately for reach
279 population. Possible trade-offs between metabolic and oviposition rates were analyzed
280 using Pearson's correlation tests for each temperature level and population. All
281 statistical analyses were conducted using SPSS for Windows, version 15.0.1.

282

283 3. RESULTS

284

285 3.1. Oviposition rate

286 Mean oviposition rates were higher overall in the marginal population (core: 0.104 eggs
287 day⁻¹ ± 0.021; marginal: 0.408 eggs day⁻¹ ± 0.079, $F = 6.51$, $P = 0.012$), which also had
288 heavier females (core: 0.0063 g ± 0.0001; marginal: 0.0067 g ± 0.0001; $F = 4.78$, $P =$
289 0.032). The oviposition rate of the marginal population was significantly higher than
290 that of the core, in the 25 °C x 10 g L⁻¹ treatment (Fig. 2, Table 2). Temperature had a
291 significant positive impact on the oviposition rate of both populations, with higher
292 oviposition rates at 25 than at 15 °C. In contrast, salinity did not significantly affect
293 oviposition rate in either of the two populations (Tables S2.1 and S2.2 in Appendix S2).
294 Body mass had a significant positive effect on oviposition rate in the marginal
295 population, but had no effect in the core (Tables S2.1 and S2.2 in Appendix S2). The
296 marginal population showed higher plasticity of oviposition rate between temperatures
297 than the core, at both salinities (Fig. 2, Table 3).

298

299 3.2. Egg volume

300 Significant differences in mean egg volume were found between populations in all
301 temperature x salinity treatments, except 25 °C x 10 g L⁻¹ (Fig. 3, Table 2). Core
302 population eggs were on average 27 % larger than those from the marginal population
303 (Core: 0.092 mm³ ± 0.002; Marginal: 0.072 mm³ ± 0.002) (Table 3). Salinity and
304 temperature significantly affected egg volume in both populations, but in different ways
305 (significant population x treatment interaction p<0.001, Table 2; and temperature x
306 salinity p< 0.007, Tables S2.3 and S2.4 in Appendix S2). In the core population, eggs
307 were larger at low temperatures and high salinities (Fig. 3), whilst in the marginal
308 population the opposite pattern was observed.

309

310 *3.3. Oxygen consumption rate and metabolic plasticity*

311 Mean oxygen consumption ranged between 21.4 ± 3.5 nmol O₂ h⁻¹ mg⁻¹ at 15 °C and 10
312 g L⁻¹ in the core population and 57.3 ± 7.5 nmol O₂ h⁻¹ mg⁻¹ at 25 °C and 35 g L⁻¹ in the
313 marginal population (Fig. 4). No significant differences in oxygen consumption rates
314 were found between core and marginal populations, although there were significant
315 differences across treatments (Table 2). In both populations, oxygen consumption rate
316 was significantly increased in the highest salinity and temperature treatment (Fig. 4).
317 Maximum mean ΔMO₂ was 105.94 nmol O₂ h⁻¹ mg⁻¹ in the marginal population and
318 125.53 nmol O₂ h⁻¹ mg⁻¹ in the core population between the 15 °C x 10 g L⁻¹ and 25 °C x
319 35 g L⁻¹ treatments. In the marginal population, increases in both salinity and
320 temperature produced significant increases in metabolic rate, whilst in the core
321 population only higher salinity increased metabolic rate significantly (Tables S2.5 and
322 S2.6 in Appendix S2).

323

324 Q_{10} values were higher at salinity 35 than at salinity 10 in both populations (Table 3)
325 and the marginal population showed higher Q_{10} values than those of the core at salinity
326 35. No significant relationships were found between metabolic and reproductive traits
327 (Appendix S3).

328

329 4. DISCUSSION

330 The populations that inhabit the margins of a species' distributional range are likely to
331 be critically important in determining its responses to ongoing climate change (Thomas
332 et al., 2001; Iverson et al., 2004; Travis and Dytham, 2004). Our results reveal that the
333 northern marginal population of *S. selecta* was more sensitive to changes in temperature
334 and salinity than the core population studied, showing higher phenotypic plasticity in its
335 metabolic and reproductive traits. This evidence could have positive implications when
336 coping with future environmental change.

337

338 The life history traits of aquatic insects are mainly dependent on environmental
339 temperatures (Sweeney, 1984), particularly fecundity, growth rate and adult body size
340 (Vannote and Sweeney, 1980). Fecundity typically increases with temperature up to a
341 threshold causing a shift in energy allocation away from reproduction into maintenance
342 and repair (Huang et al., 2007; Hercus et al., 2003; Massamba-N'Siala et al., 2012).
343 This positive effect on oviposition rate was seen in both populations at 25 °C,
344 particularly in the marginal population which showed greater plasticity in this trait.
345 Such a difference in fecundity plasticity between populations could reflect local
346 adaptation to environmental temperature variation, with both wider daily and seasonal
347 thermal variation, and a longer reproductive period in the core population than in the
348 northern marginal one. The northern marginal population may therefore be adapted to

349 maximize egg production in the shorter reproductive period (from May to the end of
350 summer) when temperatures are optimal (mean monthly temperature >10 °C, Barahona
351 et al., 2005). On the other hand, the core population can extend its breeding period, with
352 a lower oviposition rate, but a higher annual reproductive output overall. Such a finding
353 is in accordance with known latitudinal and climatic variation in voltinism in aquatic
354 insects (Sweeney, 1984). English corixids are typically univoltine or in some cases
355 bivoltine (Savage, 1989), whilst south-eastern Iberian populations of *S. selecta* breed
356 between March and October, with four generations a year (Barahona et al., 2005).
357 Differences in fecundity between the two populations may be partially explained by
358 weight differences between females. Those from the marginal population are
359 approximately 9 % heavier than those from the core population, probably due to a
360 longer period of nymphal development. Such larger size in colder conditions is
361 normally attained by a prolonged growth period overcompensating for slow growth at
362 low temperatures (Kozłowski et al., 2004; Gaston et al., 2009).

363

364 As expected we found an inverse relationship between the number and size of eggs,
365 with the eggs of the core population being approx. 27 % larger in volume and more
366 plastic in size in response to increases in salinity than those of the marginal population.
367 The semiarid Mediterranean climate experienced by the core population in southeast
368 Spain means that occupied water bodies are subject to frequent droughts and sudden
369 increases in salinity and/or temperature (Millán et al., 2006). In such areas larger eggs
370 may be more resistant to drought than smaller ones, since the former have more stored
371 water and a lower surface area/volume ratio (Le Lagadec et al., 1998; Lapinski and
372 Tschapka, 2014).

373

374 Contrary to expectations, no inter-population differences in metabolic rate were found
375 within the temperature and salinity ranges examined. The metabolic rates of both
376 populations increased at high temperatures and salinities. At salinities above the iso-
377 osmotic point (10 g L^{-1}), there is an increase in the cost of osmoregulation in most
378 aquatic insects (Nelson et al., 1977). However, this potential osmoregulation cost did
379 not result in a trade-off with oviposition rate under our experimental conditions. Despite
380 this, at higher temperatures and salinities (above $25 \text{ }^{\circ}\text{C}$ and 35 g L^{-1}), physiological
381 homeostasis could have negative consequences on fitness, decreasing the amount of
382 resources/energy allocated to reproduction and maintenance (Folguera et al., 2011).
383 Where such a threshold sits for this species could not be determined in our experiments,
384 however, acclimation to salinities above those employed here (e.g. $50\text{-}75 \text{ g L}^{-1}$) rapidly
385 led to the death of animals in the laboratory.

386

387 In hyperosmotic media (e.g., 35 g L^{-1}), the metabolic rate of the marginal population
388 was more sensitive to changes in temperature than that of the core, as the former
389 showed higher Q_{10} values, indicating greater metabolic plasticity (Calosi et al., 2005,
390 2007). Population differences in metabolic plasticity could reflect adaptations to
391 environmental variability and predictability, as have previously been observed in
392 interspecific comparisons (Stillman, 2003; Tomanek, 2009). The marginal population
393 normally experiences narrower variation in temperature (see Table 1) and apparently
394 compensates for temperature change by increasing metabolism to a greater extent. In
395 contrast the core population, which experiences a wider and more unpredictable range
396 of temperatures, appears to be less sensitive to changes in temperature. Our results are
397 in accordance with the general pattern observed in terrestrial animals, with the
398 metabolic rates of species from warm environments being less sensitive to temperature

399 variation than those from cooler areas (Seebacher et al., 2015). It seems that this air-
400 breathing aquatic bug behaves more like a terrestrial than an aquatic organism in this
401 regard, in line with its terrestrial evolutionary origin (Pritchard et al., 1993; Bozinovic et
402 al., 2011).

403

404 Although there is no clear intra-specific pattern between metabolic acclimation ability
405 and climate or latitude, the low metabolic and reproductive plasticity found in the core
406 population is similar to the low plasticity observed in the upper thermal limit of other
407 saline insects such as aquatic Coleoptera (Arribas et al., 2012b; Botella-Cruz et al.,
408 2016). The higher plasticity in metabolic and reproductive traits seen in the marginal
409 population of *S. selecta* may provide resilience against the effects of ongoing climate
410 change. Core populations, which currently experience more extreme and variable
411 temperatures, but show lower plasticity, might be more resistant to environmental
412 changes within their tolerance ranges. Outside such tolerance ranges, however, these
413 populations will be more vulnerable to global warming.

414

415 The implications of the patterns we uncover for population persistence or range
416 expansion in this species could be profound. An increase of mean temperature at the
417 northern edge of the distributional range of *S. selecta* is likely to increase the degree of
418 climatic suitability or habitat quality in both currently occupied and new locations. Our
419 results suggest that warming in these northern areas could increase oviposition rate and
420 extend the oviposition period, increasing reproductive output, and allowing both
421 persistence and range expansion. Such increases in temperature could incur a metabolic
422 cost, but this does not lead to an apparent trade-off with fecundity, at least below 25 °C.
423 In addition, higher temperatures may lead to an increase in dispersal flights in this insect

424 (Kirkpatrick et al., 1997; Thomas et al., 2001), further facilitating range expansion.
425 Whether the plastic responses seen in our study could be sustained in the long term,
426 considering potential costs associated with them remains unclear, however. In marked
427 contrast to those close to the northern range edge, core populations, despite being more
428 resistant to environmental fluctuations, might be more sensitive to rapid and intense
429 warming events, perhaps driving a northward retreat of the species southern range limits
430 (Hughes, 2000; Parmesan, 2006).

431

432 5. CONCLUSIONS

433 The population-specific responses of *S. selecta* to environmental change are complex
434 and may be mediated by differences in phenotypic plasticity related to the
435 environmental variability experienced in nature. When comparing the studied
436 populations of *S. selecta* at the center and edge of its geographical range, the northern
437 marginal population showed higher oviposition rates, smaller eggs and higher levels of
438 metabolic and fecundity plasticity than the core population. The higher plasticity of the
439 marginal population may increase its fitness in current habitats and facilitate its
440 expansion northwards with climate warming. Whilst the core population seems less
441 sensitive to changes in temperature and salinity it could be prone to extinction in current
442 localities if temperature and salinity changes exceed physiological tolerance limits,
443 leading to a northward retreat of the species southern range limits. Further extension of
444 this experimental study, considering several populations of *S. selecta* in the marginal
445 and core areas within the species geographical range are of special concern to
446 corroborate the generality of the pattern found.

447

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726

727 **SUPPORTING INFORMATION**

728

729 Metabolic and reproductive plasticity of core and marginal populations of the
730 eurythermic and saline water bug *Sigara selecta* (Hemiptera: Corixidae) in a climate
731 change context.

732

733 J.A. Carbonell, D.T. Bilton, P. Calosi, A. Millán, A. Stewart & J. Velasco

734

735 *Journal of Insect Physiology*

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737 **Appendix S1.** Changes in PO₂ along experiments for the marginal and core populations
738 at the four temperature x salinity treatments.

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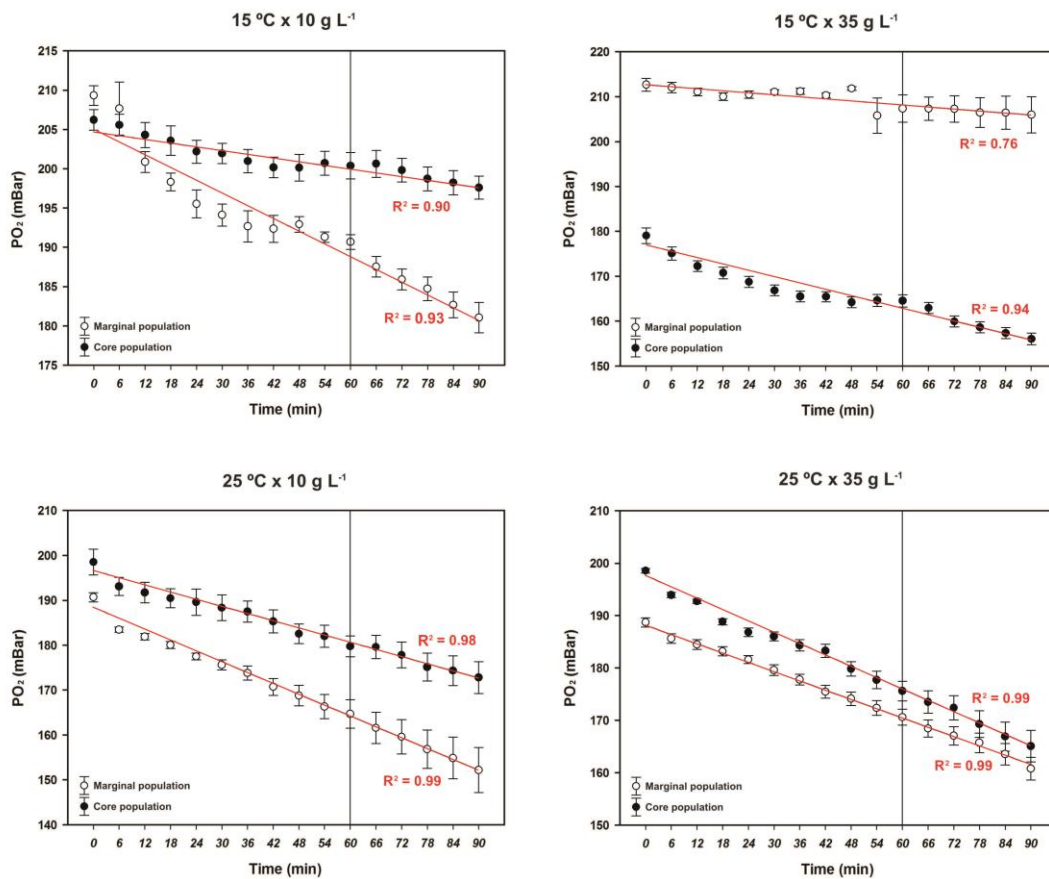
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752 **Appendix S2.** GLM results at population level. GLM assuming Gaussian distribution
 753 and identity link function.

754

755 **S2.1.** Effects of temperature, salinity and their interaction on oviposition rate for the
 756 core population of *S. selecta*.

757

Effect	SS	df	F	P
Full model	0.153	4	2.012	0.110
Intercept	0.022	1	1.171	0.285
Weight (cov)	0.063	1	3.323	0.075
Temperature	0.096	1	5.082	0.029
Salinity	0.170	1	0.876	0.354
Temperature x salinity	0.005	1	0.245	0.623
Error	0.816	43		

758

759

760 **S2.2.** Effects of temperature, salinity and their interaction on oviposition rate for the
 761 marginal population of *S. selecta*.

762

Effect	SS	df	F	P
Full model	5.962	4	7.854	< 0.001
Intercept	2.409	1	12.696	0.001
Weight (cov)	3.399	1	17.914	< 0.001
Temperature	2.644	1	13.934	0.001
Salinity	0.002	1	0.008	0.929
Temperature x salinity	0.314	1	1.656	0.205
Error	8.160	43		

763

764

765 **S2.3.** Effects of temperature, salinity and their interaction on eggs volume for the core
 766 population of *S. selecta*.

767

Effect	SS	df	F	P
Full model	0.003	3	7.112	0.001
Intercept	0.342	1	2384.413	< 0.001
Temperature	0.001	1	5.582	0.024
Salinity	0.001	1	7.411	0.010
Temperature x salinity	0.001	1	8.341	0.007
Error	0.005	36		

768

769 **S2.4.** Effects of temperature, salinity and their interaction on eggs volume for the
 770 marginal population of *S. selecta*.

771

Effect	SS	df	F	P
Full model	0.004	3	27.308	< 0.001
Intercept	0.213	1	4536.798	< 0.001
Temperature	0.000	1	8.261	0.007
Salinity	0.003	1	65.324	< 0.001
Temperature x salinity	0.000	1	8.338	0.007
Error	0.002	36		

772

773

774

775 **S2.5.** Effects of temperature, salinity and their interaction on oxygen consumption rate
 776 for the core population of *S. selecta*.

777

Effect	SS	df	F	P
Full model	6585.627	4	2.946	0.030
Intercept	3745.880	1	6.703	0.014
Weight (cov)	1057.905	1	1.893	0.178
Temperature	219.456	1	0.393	0.535
Salinity	3065.139	1	5.485	0.015
Temperature x salinity	232.374	1	0,416	0.523
Error	18999.763	34		

778

779

780

781 **S2.6.** Effects of temperature, salinity and their interaction on oxygen consumption rate
 782 for the marginal population of *S. selecta*.

783

Effect	SS	df	F	P
Full model	1019.602	4	5.182	0.003
Intercept	1899.266	1	9.653	0.004
Weight (cov)	558.252	1	2.837	0.104
Temperature	1027.307	1	5.222	0.030
Salinity	1667.542	1	8.476	0.007
Temperature x salinity	250.740	1	1274.000	0.269
Error	196.744	27		

784

785

786 **Appendix S3.** Pearson product-moment correlation coefficients between metabolic
787 rates and oviposition rates for core and marginal populations of *S. selecta* at each
788 studied temperature.

789

	15 °C		25 °C	
	Cor. Pearson	Sig.	Cor. Pearson	Sig.
Core population	-0.105	0.866	0.320	0.439
Marginal population	-0.698	0.190	-0.184	0.636

790

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792