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

Article (Accepted Version)

Carbonell, J A, Bilton, D T, Calosi, P, Millan, A, Stewart, A and Velasco, J (2017) Metabolic and reproductive plasticity of core and marginal populations of the eurythermic saline water bug *Sigara selecta* (Hemiptera: Corixidae) in a climate change context. *Journal of Insect Physiology*, 98. pp. 59-66. ISSN 0022-1910

This version is available from Sussex Research Online: <http://sro.sussex.ac.uk/id/eprint/66045/>

This document is made available in accordance with publisher policies and may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the URL above for details on accessing the published version.

Copyright and reuse:

Sussex Research Online is a digital repository of the research output of the University.

Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable, the material made available in SRO has been checked for eligibility before being made available.

Copies of full text items generally can be reproduced, displayed or performed and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

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

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

AUTHORS: J.A. Carbonell¹, D.T. Bilton², P. Calosi³, A. Millán¹, A. Stewart⁴ & J. Velasco¹

1. Departamento de Ecología e Hidrología, Facultad de Biología, Campus de Espinardo, 30100, Universidad de Murcia. Murcia, Spain.

2. Marine Biology and Ecology Research Centre, School of Marine Science and Engineering, University of Plymouth, Davy Building, Drake Circus, Plymouth PL4 8AA, UK.

3. Département de Biologie Chimie et Géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Québec, G5L 3A1, Canada.

4. School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex, BN1 9QG, UK.

Corresponding author: joseantonio.carbonell@um.es

23
24
25
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.

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

GRAPHICAL ABSTRACT

HIGHLIGHTS

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

1. INTRODUCTION

The vulnerability of a species to global warming largely depends on its capacity to maintain present populations (species persistence) and to shift its geographical range to suitable future environments (Parmesan, 2006; Williams et al., 2008), factors heavily influenced by population responses at range margins (Kirkpatrick and Barton, 1997; Hampe and Petit, 2005; Gaston, 2009). The persistence of populations will depend on

their ability to adapt to and tolerate novel conditions, i.e. on physiological tolerance limits, as well as the potential to shift these limits *via* plastic and adaptive changes (Chown et al., 2007; Gaston et al., 2009; Hoffmann, 2010).

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

Phenotypic plasticity can be viewed as an adaptive response to environmental heterogeneity and predictability (Lardies & Bozinovic, 2008). Some studies have suggested that physiological plasticity seems to be higher in organisms living in moderately variable environments, such as temperate areas, and limited in those living in very stable (Hoffmann and Harshman, 2000) or highly variable environments

(Sanders et al., 1991; Hofmann and Somero, 1995; Gaston et al., 2009; Arribas et al., 2012b; Botella et al., 2016), meaning that species from such stable or highly variable environments may be more vulnerable to climate change than species from moderately variable ones (Stillman, 2003; Tomanek, 2009; Magozzi and Calosi, 2015). Other studies suggest the existence of trade-offs between absolute limits and plasticity; organisms with the highest overall thermal tolerance exhibiting the lowest plasticity of this tolerance (Calosi et al., 2008; Bozinovic et al., 2011; Gunderson and Stillman, 2015).

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

To better predict how species may respond to ongoing climate change, it is also

necessary to consider the combined effect of multiple stressors from a physiological perspective (Gunderson et al., 2016; Hewitt, Ellis & Thrush 2016). In inland aquatic ecosystems, water salinity has been predicted to fluctuate widely in association with changes in temperature and precipitation patterns (Poff et al., 2002). Temperature and salinity can have a synergetic or antagonist effect on species performance (Todgham & Stillman, 2013). Thus, population persistence in dynamic and multivariate environments greatly depends on their ability to deal with the interactive effects of different stressors occurring simultaneously or sequentially over short time-scales (Gunderson et al., 2016).

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

2. MATERIALS AND METHODS

2.1. Study species, specimen collection, and laboratory maintenance

Sigara selecta is a eurythermic aquatic corixid that inhabits saline and brackish lentic

coastal water bodies (Carbonell et al., 2012). Like most corixids, it is a benthic diving insect with a compressible gas gill, with a high storage capacity, which is renewed at regular intervals at the water surface (Popham, 1959, 1960). It is adapted to live in water bodies dominated by autotrophy (gross primary production > ecosystem respiration, see Velasco et al., 2003; Gutiérrez-Cánovas et al., 2009), which show large daily and seasonal variation in dissolved oxygen, from being hyperoxic during the day to anoxic at night. Consequently, in nature, its gas gill is likely to be efficient at relatively low dissolved oxygen concentrations. This species, distributed in Western Europe and North Africa (Fig. 1 - Jansson, 1986; Aukema and Rieger, 1995), offers an opportunity to examine geographic variation in phenotypic plasticity of life-history and metabolic traits between core and marginal populations.

Since the experimental procedure required working with live individuals from different populations, over a short period of time to reduce seasonal effects on plasticity, two representative populations from different latitudes but similar longitude were selected. The northern population (SE England) occupies cold and more thermally stable habitats close to the northern range margin – hereafter ‘marginal population’. The southern population (SE Spain) inhabits warmer and more thermally variable sites near the center of the species distributional range – hereafter ‘core population’. (Fig. 1, Table 1). The sampling locality of the core population has a semiarid Mediterranean climate, with a mean annual air temperature of 18.1 °C and high annual variation in temperature (28.3 °C), with a maximum annual temperature of 33.1 °C (mean data for the last 30 years). The northern locality of the marginal population is much cooler (mean annual air temperature 10.3 °C), has lower annual variation in temperature (20.7 °C) and a maximum annual temperature of 21.8 °C (Table 1). An increase in mean temperature

and water salinity, and its variation, is expected at both localities with ongoing climate change (IPCC, 2013).

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

2.2. Experimental design

To investigate the combined effects of water temperature and salinity changes on metabolic and reproductive traits and their plasticity, an orthogonal experimental design was used, incorporating two levels of temperature (15 and 25 °C) and salinity (10 and 35 g L⁻¹). Since previous laboratory experiences combining higher temperatures and salinities resulted in the rapid death of individuals, we chose temperature and salinity ranges representative of the habitats where the species usually lives. The two temperatures tested were chosen as they correspond approximately to the summer average temperature for the two sampling localities respectively (<http://climate196data.org>_last accessed 1 November 2014 - see Table 1). The two salinities correspond to

the average point of isotonicity for aquatic insects (10 g L^{-1} ; Chown and Nicolson, 2004; Bradley, 2009) and one at which the species normally occurs in the field (35 g L^{-1} - Barahona et al., 2005; Carbonell et al., 2012), but at which hypo-osmotic regulation is necessary. Water of different salinities was prepared by dissolving an appropriate amount of artificial sea salt (Instant Ocean, Aquarium Systems, Sarrebourg, France) in distilled water.

2.3. Reproductive traits

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

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

where $a = \text{length} / 2$, b and $c = \text{width} / 2$

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 μm 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

hours in respirometry chambers without a surface air space, $\dot{M}O_2$ was measured over the first 60 minutes to avoid critical hypoxic conditions. During this first hour, variation in PO_2 was linear (see Appendix S1), indicating that the critical point, at which PO_2 drastically declines, was not reached. During experiments bugs divided their time between resting and swimming. When resting, the oar-like hind legs were moved synchronously to ventilate their gas gill, this being part of the normal respiratory behavior of corixids (Popham, 1960; Matthews & Seymour, 2010). Measurements were undertaken inside temperature controlled rooms at the appropriate treatment temperature to improve thermal stability. $\dot{M}O_2$ was expressed as $nmol\ O_2\ h^{-1}\ STP$ (standard temperature and pressure) per unit wet mass (mg). To calculate $\dot{M}O_2$ the volume of individuals were estimated and subtracted from the volume of the chambers to determine the volume of water present during measurements. Upon completion of $\dot{M}O_2$ measurements, insects were removed from the chamber, blotted dry, and weighed with an electronic high-precision balance to $\pm 0.0001\ g$ (MS 1225 P, Sartorius AG, Goettingen, Germany) to obtain individual wet mass.

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

$$Q_{10} = K_1 / K_2^{10 / t_1 - t_2}$$

Where K_1 = the mean metabolic rate at temperature t_1 ($15^\circ C$)

K_2 = the mean metabolic rate at temperature t_2 ($25^\circ C$)

2.5. Data analysis

To explore how acclimation at different temperatures and salinities affected oxygen consumption, oviposition rate and egg volume in *S. selecta*, we employed Generalized Linear Models (GLM) with ‘population’ and ‘temperature x salinity treatment’ as fixed independent factors and body mass as a covariate. We assumed a Gaussian distribution and identity link function (equivalent to a 3-factor ANCOVA). Sidak's post-hoc tests were implemented to identify significant differences in the response variables between populations and/or treatments. In addition, to test the independent effect of temperature and salinity on response variables in each population we ran GLM tests with these environmental variables as fixed factors and weight as covariate, separately for each population. Possible trade-offs between metabolic and oviposition rates were analyzed using Pearson's correlation tests for each temperature level and population. All statistical analyses were conducted using SPSS for Windows, version 15.0.1.

3. RESULTS

3.1. Oviposition rate

Mean oviposition rates were higher overall in the marginal population (core: 0.104 eggs day⁻¹ ± 0.021; marginal: 0.408 eggs day⁻¹ ± 0.079, $F = 6.51$, $P = 0.012$), which also had heavier females (core: 0.0063 g ± 0.0001; marginal: 0.0067 g ± 0.0001; $F = 4.78$, $P = 0.032$). The oviposition rate of the marginal population was significantly higher than that of the core, in the 25 °C x 10 g L⁻¹ treatment (Fig. 2, Table 2). Temperature had a significant positive impact on the oviposition rate of both populations, with higher oviposition rates at 25 than at 15 °C. In contrast, salinity did not significantly affect oviposition rate in either of the two populations (Tables S2.1 and S2.2 in Appendix S2).

Body mass had a significant positive effect on oviposition rate in the marginal population, but had no effect in the core (Tables S2.1 and S2.2 in Appendix S2). The marginal population showed higher plasticity of oviposition rate between temperatures than the core, at both salinities (Fig. 2, Table 3).

3.2. Egg volume

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

3.3. Oxygen consumption rate and metabolic plasticity

Mean oxygen consumption ranged between 21.4 ± 3.5 nmol O₂ h⁻¹ mg⁻¹ at 15 °C and 10 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 marginal population (Fig. 4). No significant differences in oxygen consumption rates were found between core and marginal populations, although there were significant differences across treatments (Table 2). In both populations, oxygen consumption rate was significantly increased in the highest salinity and temperature treatment (Fig. 4). Maximum mean Δ $\dot{M}O_2$ was 105.94 nmol O₂ h⁻¹ mg⁻¹ in the marginal population and

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 35 g L⁻¹ treatments. In the marginal population, increases in both salinity and temperature produced significant increases in metabolic rate, whilst in the core population only higher salinity increased metabolic rate significantly (Tables S2.5 and S2.6 in Appendix S2).

Q₁₀ values were higher at salinity 35 than at salinity 10 in both populations (Table 3) and the marginal population showed higher Q₁₀ values than those of the core at salinity 35. No significant relationships were found between metabolic and reproductive traits (Appendix S3).

4. DISCUSSION

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

The life history traits of aquatic insects are mainly dependent on environmental temperatures (Sweeney, 1984), particularly fecundity, growth rate and adult body size (Vannote and Sweeney, 1980). Fecundity typically increases with temperature up to a threshold causing a shift in energy allocation away from reproduction into maintenance and repair (Huang et al., 2007; Hercus et al., 2003; Massamba-N'Siala et al., 2012).

This positive effect on oviposition rate was seen in both populations at 25 °C, particularly in the marginal population which showed greater plasticity in this trait. Such a difference in fecundity plasticity between populations could reflect local adaptation to environmental temperature variation, with both wider daily and seasonal thermal variation, and a longer reproductive period in the core population than in the northern marginal one. The northern marginal population may therefore be adapted to maximize egg production in the shorter reproductive period (from May to the end of summer) when temperatures are optimal (mean monthly temperature >10 °C, Barahona et al., 2005). On the other hand, the core population can extend its breeding period, with a lower oviposition rate, but a higher annual reproductive output overall. Such a finding is in accordance with known latitudinal and climatic variation in voltinism in aquatic insects (Sweeney, 1984). English corixids are typically univoltine or in some cases bivoltine (Savage, 1989), whilst south-eastern Iberian populations of *S. selecta* breed between March and October, with four generations a year (Barahona et al., 2005). Differences in fecundity between the two populations may be partially explained by weight differences between females. Those from the marginal population are approximately 9 % heavier than those from the core population, probably due to a longer period of nymphal development. Such larger size in colder conditions is normally attained by a prolonged growth period overcompensating for slow growth at low temperatures (Kozłowski et al., 2004; Gaston et al., 2009).

As expected we found an inverse relationship between the number and size of eggs, with the eggs of the core population being approx. 27 % larger in volume and more plastic in size in response to increases in salinity than those of the marginal population. The semiarid Mediterranean climate experienced by the core population in southeast

Spain means that occupied water bodies are subject to frequent droughts and sudden increases in salinity and/or temperature (Millán et al., 2006). In such areas larger eggs may be more resistant to drought than smaller ones, since the former have more stored water and a lower surface area/volume ratio (Le Lagadec et al., 1988; Lapinski and Tschapka, 2014).

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

In hyperosmotic media (e.g., 35 g L^{-1}), the metabolic rate of the marginal population was more sensitive to changes in temperature than that of the core, as the former showed higher Q_{10} values, indicating greater metabolic plasticity (Calosi et al., 2005, 2007). Population differences in metabolic plasticity could reflect adaptations to environmental variability and predictability, as have previously been observed in 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 air400
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 et al., 2016).
408 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

climatic suitability or habitat quality in both currently occupied and new locations. Our results suggest that warming in these northern areas could increase oviposition rate and extend the oviposition period, increasing reproductive output, and allowing both persistence and range expansion. Such increases in temperature could incur a metabolic cost, but this does not lead to an apparent trade-off with fecundity, at least below 25 °C. In addition, higher temperatures may lead to an increase in dispersal flights in this insect (Kirkpatrick et al., 1997; Thomas et al., 2001), further facilitating range expansion. Whether the plastic responses seen in our study could be sustained in the long term, considering potential costs associated with them remains unclear, however. In marked contrast to those close to the northern range edge, core populations, despite being more resistant to environmental fluctuations, might be more sensitive to rapid and intense warming events, perhaps driving a northward retreat of the species southern range limits (Hughes, 2000; Parmesan, 2006).

5. CONCLUSIONS

The population-specific responses of *S. selecta* to environmental change are complex and may be mediated by differences in phenotypic plasticity related to the environmental variability experienced in nature. When comparing the studied populations of *S. selecta* at the center and edge of its geographical range, the northern marginal population showed higher oviposition rates, smaller eggs and higher levels of metabolic and fecundity plasticity than the core population. The higher plasticity of the marginal population may increase its fitness in current habitats and facilitate its expansion northwards with climate warming. Whilst the core population seems less sensitive to changes in temperature and salinity it could be prone to extinction in current localities if temperature and salinity changes exceed physiological tolerance limits,

leading to a northward retreat of the species southern range limits. Further extension of this experimental study, considering several populations of *S. selecta* in the marginal and core areas within the species geographical range are of special concern to corroborate the generality of the pattern found.

ACKNOWLEDGMENTS

We thank Susana Pallarés and Simone Guareschi for field assistance and Marie Palmer and Michael Jarrold for laboratory assistance. Wilco C.E.P. Verberk provided valuable suggestions and members of the Aquatic Ecology research group (Universidad de Murcia, Spain) and the Marine Biology and Ecology Research Centre (University of Plymouth, United Kingdom) helped at various stages of this project. This work was partially supported by funding from a predoctoral FPU grant to J.A. Carbonell. P. Calosi is supported by a NSERC Discovery Program Grant. This work was also supported by the project CGL2013-48950-C2-2-P (J.V.) (Ministerio de Economía y Competitividad).

REFERENCES

Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2002. Metabolic cold adaptation in insects: a large-scale perspective. *Functional Ecology*, 16, 332–338.

Angilletta, M.J., 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology*, 82, 3044–3056.

Arribas, P., Abellán, P., Velasco, J., Bilton, D.T., Millán, A., Sánchez-Fernández D., 2012a. Evaluating drivers of vulnerability to climate change: a guide for insect conservation strategies. *Global Change Biology*, 18, 2135–2146.

Arribas, P., Velasco, J., Abellán, P., Sánchez-Fernández, D., Andújar, C., Calosi, P., Millán, A., Ribera, I., Bilton, D., 2012b. Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *Journal of Biogeography*, 39, 984–994.

Aukema, B., Rieger C., 1995. Catalogue of the Heteroptera of the Palearctic Region. Vol. 1: Enicocephalomorpha, Dipsocoromorpha, Nepomorpha, Gerromorpha and Leptopodomorpha. Netherlands Entomological Society. Amsterdam.

Azevedo, R.B.R., French, V., Partridge, L., 1996. Thermal evolution of egg size in *Drosophila melanogaster*. *Evolution*, 50, 2338–2345.

Barahona, J., Millán, A., Velasco J., 2005. Population dynamics, growth and production

483 of *Sigara selecta* (Fieber, 1848) (Hemiptera, Corixidae) in a Mediterranean hypersaline
 484 stream. *Freshwater Biology*, 50, 2101–2113.
 485
 486 Botella-Cruz, M., Carbonell, J.A., Pallarés, S., Millán, A., Velasco, J., 2015. Plasticity
 487 of thermal limits in the aquatic saline beetle *Enochrus politus* (Küster 1849)
 488 (Coleoptera: Hydrophilidae) under changing environmental condition. *Limnetica*, 35,
 489 131–142.
 490
 491 Bozinovic, F., Calosi, P., Spicer, J.I., 2011. Physiological correlates of geographic range 492
 in animals. *Annual Review of Ecology, Evolution and Systematics*, 42, 155–179.
 493
 494 Bradley, T.J., 2009. Animal osmoregulation. Oxford University Press, U.K.
 495
 496 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a 497
 metabolic theory of ecology. *Ecology*, 85, 1771–1789.
 498
 499 Calosi, P., Bilton, D., Spicer, J., 2008. Thermal tolerance, acclimatory capacity and 500
 vulnerability to global climate change. *Biology Letters*, 4, 99–102.
 501
 502 Calosi, P., Bilton, D.T., Spicer, J.I., Votier, S.C., Atfield, A., 2010. What determines a
 503 species' geographical range? Thermal biology and latitudinal range size relationships in
 504 European diving beetles (Coleoptera: Dytiscidae). *Journal of Animal Ecology*, 79,
 194–
 505 204.
 506

507 Calosi, P., Morritt, D., Chelazzi, G., Ugolini, A., 2007. Physiological capacity and
 508 environmental tolerance in two sandhopper species with contrasting geographical 509
 ranges: *Talitrus saltator* and *Talorchestia ugoninii*. *Marine Biology*, 151, 1647–1655.

510

511 Calosi, P., Ugolini, A., Morritt, D., 2005. Physiological responses to hyposmotic stress
 512 in the supralittoral amphipod *Talitrus saltator* (Crustacea: Amphipoda). *Comparative* 513
Biochemistry and Physiology Part A: Molecular and Integrative Physiology, 142, 267–
 514 275.

515

516 Carbonell, J.A., Millán, A., Velasco, J., 2012. Concordance between realised and
 517 fundamental niches in three Iberian *Sigara* species (Hemiptera: Corixidae) along a 518
 gradient of salinity and anionic composition. *Freshwater Biology*, 57, 2580–2590.

519

520 Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E., Sheldon, B.C.,
 521 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird 522
 population. *Science*, 320, 800–803.

523

524 Chown, S.L., 2001. Physiological variation in insects: hierarchical levels and 525
 implications. *Journal of Insect Physiology*, 47, 649–660.

526

527 Chown, S.L., Nicolson, W.N., 2004. *Insect Physiological Ecology: Mechanisms and* 528
Patterns. Oxford University Press, U.K.

529

530 Chown, S.L., Slabber, S., Mcgeoch, M.A., Janion, C., Leinaas, H.P., 2007. Phenotypic

plasticity mediates climate change responses among invasive and indigenous
arthropods. *Proceedings of the Royal Society B*, 274, 2531–2537.

Clarke, A., 1993. Seasonal acclimatization and latitudinal compensation in metabolism:
do they exist? *Functional Ecology*, 7, 139–149.

Clarke, A., 2004. Is there a universal temperature dependence of metabolism?
Functional Ecology, 18, 252–256.

Clarke, A., Fraser, K.P.P., 2004. Why does metabolism scale with temperature?
Functional Ecology, 18, 243–251.

Di Giovanni, M.V., Pirisinu, Q., Giangiuliani, G., Goretti, E., Pampanella, L., 1999.
Oxygen consumption in two aquatic Coleoptera species: *Hydrous piceus* and *Dytiscus*
marginalis. *Italian Journal of Zoology*, 66, 329–332.

Donelson, J.M., Munday, P.L., McCormick, M., Nilsson, G.E., 2011. Acclimation to
predicted ocean warming through developmental plasticity in a tropical reef fish. *Global*
Change Biology, 17, 1712–1719.

Folguera, G., Bastías, D.A., Caers, J., Rojas, J.M., Piulachs, M.D., Bellés, X.,
Bozinovic, F., 2011. An experimental test of the role of environmental temperature
variability on ectotherm molecular, physiological and life-history traits: implications for
global warming. *Comparative Biochemistry and Physiology Part A: Molecular and*
Integrative Physiology, 159, 242–246.

556

557 Forsman, A., 2014. Rethinking phenotypic plasticity and its consequences for 558
individuals, populations and species. *Heredity*, 1–9.

559

560 Fox, C.W., Czesak, M.E., 2000. Evolutionary ecology of progeny size in arthropods.

561 *Annual Review of Entomology*, 45, 341–369.

562

563 Gaston, K.J., 2009. Geographic range limits of species. *Proceedings of the Royal 564 Society
of London B: Biological Sciences*, 276, 1391–1393.

565

566 Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., ... van

567 Kleunen, M., 2009. Macrophysiology: a conceptual reunification. *The American 568
Naturalist*, 174, 595–612.

569

570 Ghalambor, C.K., McKay, J.K., Carroll, S.P., Reznick, D.N., 2007. Adaptive versus

571 non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new
572 environments. *Functional Ecology*, 21, 394–407.

573

574 Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of 575
size and temperature on metabolic rate. *Science*, 293, 2248–2251.

576

577 Gunderson, A.R., Armstrong, E.J., Stillman, J.H., 2016. Multiple stressors in a changing
578 world: The need for an improved perspective on physiological responses to the dynamic
579 marine environment. *Annual Review of Marine Science*, 8, 357–378.

580

581 Gunderson, A.R., Stillman, J.H., 2015. Plasticity in thermal tolerance has limited
582 potential to buffer ectotherms from global warming. *Proceedings of the Royal Society* 583
of London B: Biological Sciences, 282, 20150401.

584

585 Gutiérrez- Cánovas, C., Velasco, J., Millán, A., 2009. Effects of dilution on the 586
functioning of a Mediterranean saline stream. *Hydrobiologia*, 619, 119–132.

587

588 Hampe, A., Petit R.J., 2005. Conserving biodiversity under climate change: the rear 589 edge
matters. *Ecology Letters*, 8, 461–467.

590

591 Hercus, M.J., Loeschcke, V., Rattan, S.I.S., 2003. Life span extension of *Drosophila* 592
melanogaster through hormesis by repeated mild stress. *Biogerontology*, 4, 149–156.

593

594 Hewitt, J.E., Ellis, J.I., Thrush, S.F., 2016. Multiple stressors, nonlinear effects and the
595 implications of climate change impacts on marine coastal ecosystems. *Global Change* 596
Biology, 22, 2665–2675.

597

598 Hoffmann, A.A., 2010. Physiological climate limits in *Drosophila*: patterns and 599
implications. *Journal of Experimental Biology*, 213, 870–880.

600

601 Hoffmann, A.A., Hallas, R.J., Dean, J.A., Schiffer M., 2003. Low potential for climatic 602
stress adaptation in a rainforest *Drosophila* species. *Science*, 301, 100–102.

603

604 Hoffmann, A.A., Harshman, L.G., 2000. Desiccation and starvation resistance in
605 *Drosophila*: patterns of variation at the species, population and intrapopulation levels.

606 Heredity, 83, 637–43.

607

608 Hofmann, G.E., Somero, G.N., 1995. Evidence for protein damage at environmental
609 temperatures: Seasonal changes in levels of ubiquitin conjugates and hsp70 in the
intertidal mussel *Mytilus trossulus*. Journal of Experimental Biology, 198, 1509–1518.

611

612 Huang, L., Chen, B., Kang, L., 2007. Impact of mild temperature hardening on
613 thermotolerance, fecundity and Hsp gene expression in *Liriomyza huidobrensis*. Journal
614 of Insect Physiology, 53, 1199–1205.

615

616 Hughes, L., 2000. Biological consequences of global warming: is the signal already
apparent? Trends in Ecology and Evolution, 15, 56–61.

618

619 IPCC, 2013. Climate change 2013: the physical science basis. Contribution of Working
Group I to the Fifth Assessment Report of the IPCC. Stocker TF, et al., editors. IPCC.

621

622 Iverson, L.R., Schwartz, M.W., Prasad, A.M., 2004. How fast and far might tree species
623 migrate in the eastern United States due to climate change? Global Ecology and
Biogeography, 13, 209–219.

625

626 Jansson, A., 1986. The Corixidae (Heteroptera) of Europe and some adjacent regions.
627 Acta Entomologica Fennica, 47, 1–94.

628

629 Kehl, S., Dettner, K., 2009. Surviving submerged–Setal tracheal gills for gas exchange
630 in adult rheophilic diving beetles. Journal of morphology, 270, 1348–1355.

631

632 Kirkpatrick, M., Barton, N. H., 1997. Evolution of a species' range. The American 633
Naturalist, 150, 1–23.

634

635 Kozłowski, J., Czarnołęski, M., Dańko, M., 2004. Can optimal resource allocation
636 models explain why ectotherms grow larger in cold? Integrative and Comparative 637
Biology, 44, 480–493.

638

639 Lapinski, W., Tschapka, M., 2014. Desiccation resistance reflects patterns of
640 microhabitat choice in a Central American assemblage of wandering spiders. The 641
Journal of Experimental Biology, 217, 2789–2795.

642

643 Lardies, M.A., Bozinovic, F., 2008. Genetic variation for plasticity in physiological and
644 life-history traits among populations of an invasive species, the terrestrial isopod 645
Porcellio laevis. Evolutionary Ecology Research, 10, 747–762.

646

647 Lawton, J.H., 1993. Range, population abundance and conservation. Trends in Ecology 648
and Evolution, 8, 409–413.

649

650 Le Lagadec, M.D., Chown, S.L., Scholtz, C.H., 1998. Dessication resistance and water
651 balance in southern African keratin beetles (Coleoptera, Trogidae): the influence of 652
body size and habitat. Comparative Biochemistry and Physiology B, 168, 112–122.

653

654 Magozzi, S., Calosi, P., 2015. Integrating metabolic performance, thermal tolerance,

655 and plasticity enables for more accurate predictions on species vulnerability to acute and
 656 chronic effects of global warming. *Global Change Biology*, 21, 181–194.
 657
 658 Massamba-N'Siala, G., Calosi, P., Bilton, D.T., Prevedelli, D., Simonini, R., 2012. Life
 history and thermal tolerance traits display different thermal plasticities and
 660 relationships with temperature in the marine polychaete *Ophryotrocha labronica* La
 661 Greca and Bacci (Dorvilleidae). *Journal of Experimental Marine Biology and Ecology*,
 662 438, 109–117.
 663
 664 Matthews, P.G., Seymour, R.S., 2010. Compressible gas gills of diving insects:
 665 measurements and models. *Journal of Insect Physiology*, 56, 470–479.
 666
 667 Mayr, E., 1963. *Animal species and evolution* (Vol. 797). Cambridge, Massachusetts:
 668 Belknap Press of Harvard University Press.
 669
 670 Millán, A., Abellán, P., Ribera, I., Sánchez, D., Velasco, J., 2006. The Hydradephaga of
 671 the Segura basin (SE Spain): twenty-five years studying water beetles (Coleoptera).
 672 *Memorie della Società Entomologica Italiana*, 85, 137–158.
 673
 674 Nelson, S.G., Armstrong, D.A., Knight, A.W., Li, H.W., 1977. The effects of
 675 temperature and salinity on the metabolic rate of juvenile *Macrobrachium rosenbergii*
 676 (Crustacea: Palaemonidae). *Comparative Biochemistry and Physiology*, 56, 533–537.
 677
 678 Nespolo, R.F., Lardies, M.A., Bozinovic, F., 2003. Intrapopulational variation in the
 679 standard metabolic rate of insects: repeatability, thermal dependence and sensitivity

680 (Q10) of oxygen consumption in a cricket. *The Journal of Experimental Biology*, 206,
 681 4309–4315.
 682
 683 Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change.
 684 *Annual Review of Ecology Evolution and Systematics*, 37, 637–669.
 685
 686 Poff, N.L., Brinson, M.M., Day, J.W., 2002. Aquatic ecosystems and global climate 687
 change. *Pew Center on Global Climate Change*, Arlington, VA, 44.
 688
 689 Popham, E.J., 1959. Respiration of Corixidae (Hemiptera-Heteroptera). *Nature*, 183,
 690 914.
 691
 692 Popham, E.J., 1960. On the respiration of aquatic Hemiptera Heteroptera with
 693 special reference to the Corixidae. In: *Proceedings of the Zoological Society* 694
 of London 135. pp. 209–242.
 695
 696 Pörtner, H.O., 2006. Climate-dependent evolution of Antarctic ectotherms: an
 697 integrative analysis. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53,
 698 1071–1104.
 699
 700 Pritchard, G., McKee, M.H., Pike, E.M., Scrimgeour, G.J., Zloty, J., 1993. Did the first 701
 insects live in water or in air? *Biological Journal of the Linnean Society*, 49, 31–44.
 702
 703 Prosser, C.L., 1991. *Environmental and metabolic animal physiology*. New York (NY):
 704 Willey-Liss Inc.

705

706 Sanders, B.M., Hope, C., Pascoe, V.M., Martin, L.S., 1991. Characterization of stress
707 protein response in two species of *Collisella* limpets with different temperature 708
tolerances. *Physiological and Biochemical Zoology*, 64, 1471–1489.

709

710 Savage, A.A., 1989. Adults of the British aquatic hemiptera heteroptera. A key with
711 ecological notes. Freshwater Biological Association, The Ferry House, Ambleside, 712
Cumbria LA22 0LP. United Kingdom.

713

714 Seebacher, F., White, C.R., Franklin, C.E., 2015. Physiological plasticity increases 715
resilience of ectothermic animals to climate change. *Nature Climate Change*, 5, 61–66.

716

717 Spicer, J., Gaston, K., 1999. *Physiological Diversity and its Ecological Implications*.
718 Blackwell Science Limited. Oxford. United Kingdom. 241 pp.

719

720 Stillman, J.H., 2003. Acclimation capacity underlies susceptibility to climate change.
721 *Science*, 301, 65–65.

722

723 Streicher, J.W., Cox, C.L., Birchard, G.F., 2012. Non-linear scaling of oxygen
724 consumption and heart rate in a very large cockroach species (*Gromphadorhina*
725 *portentosa*): correlated changes with body size and temperature. *The Journal of* 726
Experimental Biology, 215, 1137–1143.

727

728 Sweeney, B.W., 1984. Factors influencing life-history patterns of aquatic insects. pp.
729 56-11. In *The Ecology of Aquatic Insects* (V.H Resh and D.M. Rosemberg, eds).

730 Preaeeger Scientific, New York.

731

732 Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche,

733 M., Conradt, L., 2001. Ecological and evolutionary processes at expanding range 734
margins. *Nature*, 411, 577–581.

735

736 Todgham, A.E., Stillman, J.H., 2013. Physiological responses to shifts in multiple

737 environmental stressors: Relevance in a changing world. *Integrative and Comparative 738
Biology*, 53(4), 539–544. <http://doi.org/10.1093/icb/ict086>.

739

740 Tomanek, L., 2009. Variation in the heat shock response and its implication for

741 predicting the effect of global climate change on species' biogeographical distribution 742
ranges and metabolic costs. *The Journal of Experimental Biology*, 213, 971–979.

743

744 Travis, J.M.J., Dytham, C., 2004. A method for simulating patterns of habitat 745 availability
at static and dynamic range margins. *Oikos*, 104, 410–416.

746

747 Vannote, R.L., Sweeney, B.W., 1980. Geographic analysis of thermal equilibria: a

748 conceptual model for evaluating the effect of natural and modified thermal regimes on
749 aquatic insect communities. *American Naturalist*, 667–695.

750

751 Van't Land, J., Van Putten, P., Zwaan, B., Kamping, A., Van Delden, W., 1999.

752 Latitudinal variation in wild populations of *Drosophila melanogaster*: heritabilities and
753 reaction norms. *Journal of Evolutionary Biology*, 12, 222–232.

754

755 Velasco, J.A., Millán, A., Vidal-Abarca, M.R., Suárez, M.L. Guerrero, C.,
 Ortega, M.,
 756 2003. Macrophytic, epipellic and epilithic primary production in a semiarid 757
 Mediterranean stream. *Freshwater Biology*, 48, 1408–1420.
 758
 759 Verberk, W.C., Bilton, D.T., 2015. Oxygen-limited thermal tolerance is seen in a
 760 plastron-breathing insect and can be induced in a bimodal gas exchanger. *Journal of* 761
Experimental Biology, 218, 2083–2088.
 762
 763 Vucetich, J.A., Waite, T.A., 2003. Spatial patterns of demography and genetic processes
 764 across the species' range: null hypotheses for landscape conservation genetics.
 765 *Conservation Genetics Resources*, 4, 639–645.
 766
 767 Watson, S., Morley, S.A., Bates, A.E., Clark, M.S., Day, R.W., Lamare, M., Martin,
 768 S.M., Southgate, P.C., Tan, K.S., Tyler, P.A., Peck, L.S., 2013. Low global sensitivity
 769 of metabolic rate to temperature in calcified marine invertebrates. *Oecologia*, 174,
 45–
 770 54.
 771
 772 Whitman, D.W., Agrawal, A.A., 2009. What is phenotypic plasticity and why is it
 773 important? In: *Phenotypic Plasticity of Insects*, 10, 1–63. Whitman D.W. & 774
 Ananthakrishnan T.N. Eds.
 775
 776 Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Langham, G., 2008. Towards
 777 an integrated framework for assessing the vulnerability of species to climate change.
 778 *Plos Biology*, 6, 2621–2626.

SUPPORTING INFORMATION

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

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

Journal of Insect Physiology

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

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

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

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		

813 **S2.2.** Effects of temperature, salinity and their interaction on oviposition rate for the 814
marginal population of *S. selecta*.

815

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		

816

817

818 **S2.3.** Effects of temperature, salinity and their interaction on eggs volume for the core 819
population of *S. selecta*.

820

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		

821

822 **S2.4.** Effects of temperature, salinity and their interaction on eggs volume for the 823
marginal population of *S. selecta*.

824

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		

825

826

827

828 **S2.5.** Effects of temperature, salinity and their interaction on oxygen consumption rate 829
for the core population of *S. selecta*.

830

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		

831

832

833

834 **S2.6.** Effects of temperature, salinity and their interaction on oxygen consumption rate 835
for the marginal population of *S. selecta*.

836

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		

837

838

839 **Appendix S3.** Pearson product-moment correlation coefficients between metabolic

840 rates and oviposition rates for core and marginal populations of *S. selecta* at each 841
studied temperature.

842

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

843

844

845

FIGURES

Figure 1. European distribution of *Sigara selecta* and collection sites of marginal (A) and core (B) populations. A) Cuckmere River, Sussex, United Kingdom; B) Barranco 5 del Diablo, Rambla Salada, Murcia, Spain. *1.5-column fitting image.*

Figure 2. Average oviposition rate ($\pm$ SE) at four different temperature x salinity treatments. Significant differences determined by post hoc analysis employing Sidak correction are indicated as follows: Capital letters in legend indicate differences between populations; letters in histogram indicate differences between treatments; asterisks indicate differences between populations in temperature x salinity treatment. *1.5-column fitting image.*

Figure 3. Average egg volume ($\pm$ SE) at four different temperature x salinity treatments. Significant differences determined by post hoc analysis employing Sidak correction are indicated as follows: Capital letters in legend indicate differences between populations; letters in histogram indicate differences between treatments; asterisks indicate differences between populations in temperature x salinity treatment. *1.5-column fitting image.*

Figure 4. Average oxygen consumption rate ($\pm$ SE; $\text{nmol O}_2 \text{ h}^{-1} \text{ mg}^{-1} \text{ w.m. STP}$) at four different temperature x salinity treatments. Significant differences determined by post hoc analysis employing Sidak correction are indicated as follows; letters in histogram indicate differences between treatments. *1.5-column fitting image.*

FIGURES

Fig. 1

Fig. 2

Fig. 3

186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203
204
205
206
207

208
209
210
211

Fig. 4

212
213
214
215
216
217
218
219
220
221
222
223
224
225
226
227
228
229
230
231
232
233
234
235

TABLES

Table 1. Sampling site information (geographical coordinates, environmental variables and climatic variables obtained from weather stations) of marginal and core populations of *Sigara selecta* studied.

	Sample location	
	Core Barranco del Diablo, Rambla Salada, Murcia (Spain)	Marginal Cuckmere River, Sussex (United Kingdom)
Sampling date	20/05/2014	09/06/2014
Latitude	38° 07' N	50° 45' N
Longitude	1° 08' W	0° 08' E
Altitude (m)	140	1
Mean Conductivity (mS/cm)	57	39
Water temperature (°C)	24	19
Climatic information		
Mean annual air temperature (°C)	18.1	10.3
Summer average air temperature (°C)	26.3	17.1
Winter average air temperature (°C)	10.3	4.0
Maximum annual air temperature (°C)	33.1	21.8
Minimum annual air temperature (°C)	4.8	1.1
Thermal amplitude (°C)	28.3	20.7
Annual precipitation (mm)	293	742

Table 2. GLM showing the effect of population, treatment (temperature x salinity) and weight (as covariate-cov) on metabolic rate, oviposition rate and egg volume. GLM assuming Gaussian distribution and identity link function. SS: sum of square, df: degrees of freedom, *F*: F-ratio, *P*:

Trait	Source	SS	df	<i>F</i>	<i>P</i>
Oviposition rate	Full model	6.652	8	6.792	< 0.001
	Intercept	1.059	1	8.648	0.004
	Weight (cov)	1.788	1	14.602	< 0.001
	Population	0.889	1	7.258	0.008
	Treatment	2.469	3	6.723	< 0.001
	Population*Treatment	0.576	3	1.568	0.203
	Error	10.651	87		
Egg volume	Full model	0.015	7	21.804	< 0.001
	Intercept	0.547	1	5749.694	< 0.001
	Population	0.008	1	80.091	< 0.001
	Treatment	0.002	3	6.213	0.001
	Population*Treatment	0.005	3	17.966	< 0.001
	Error	0.021	72		
$\dot{M}O_2$	Full model	10916.663	8	3.479	0.002
	Intercept	5751.282	1	14.663	< 0.001
	Weight (cov)	1608.913	1	4.102	0.047
	Population	1068.375	1	2.724	0.104
	Treatment	6046.111	3	5.138	0.003
	Population*Treatment	245.221	3	0.208	0.890
	Error	24319.407	62		

Table 3. Plasticity of reproductive and metabolic traits of marginal and core populations of *S. selecta* to temperature at each studied salinity level. Oviposition rate and egg volume plasticity expressed as mean magnitude change between 15 and 25 °C. Temperature sensitivity of $\dot{M}O_2$ expressed as Q_{10} values. Q_{10} : temperature coefficient for the change in $\dot{M}O_2$ between two temperatures.

	Marginal population	Core population
	Salinity	

Trait plasticity	10	35	10	35
Δ Oviposition rate	0.42 ± 0.121	0.39 ± 0.105	0.13 ± 0.031	0.08 ± 0.027
Δ Egg volume	0.08 ± 0.002	0.06 ± 0.002	0.09 ± 0.002	0.10 ± 0.004
Q_{10}	1.16	1.53	1.20	1.43