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Microhabitat segregation and physiological differences in two species of intertidal porcellanid crabs (Genus *Petrolisthes*) on the southern coast of Chile

MARCELO E. LAGOS, JOSÉ L. MUÑOZ, DANIELA A. CONTRERAS and
CRISTIAN W. CÁCERES

Departamento de Ecología Costera, Facultad de Ciencias, Universidad Católica Sma. Concepción,
Alonso de Ribera 2850, Concepción Chile. E-mail: ccaceres@ucsc.cl

SUMMARY: Intertidal crustaceans have a high degree of physiological plasticity, which allows them to withstand periods of water emersion. In this study we examine the physiological constraints that determine the distribution and abundance of the intertidal porcellanid crabs *Petrolisthes laevigatus* and *Petrolisthes violaceus*. This study evaluates the distribution and abundance of the two species at different tidal heights, in relation to haemocyanin concentration and LDH activity, resistance to air desiccation, thermal tolerance, and resistance to hypoxic water. The results showed that *Petrolisthes laevigatus* was more abundant at the high tide level than *Petrolisthes violaceus*, which was more abundant at the low tide level. *Petrolisthes laevigatus* showed greater tolerance to high temperatures and lower tolerance to desiccation when exposed to air than *P. violaceus*, which was also more tolerant to hypoxia during prolonged exposure. No differences were found in haemocyanin concentration and LDH activity. These findings support the idea of an evolutionary gradient towards terrestrial adaptations. Of the two species, *Petrolisthes laevigatus* showed the most advanced physiological features for semi-terrestrial specialization.

Keywords: zonation, desiccation, hypoxia, physiological tolerance, *Petrolisthes*, Chile.

RESUMEN: DIFERENCIAS FISIOLÓGICAS Y SEGREGACIÓN DE MICROHÁBITAT EN DOS ESPECIES DE CRUSTÁCEOS PORCELÁNIDOS INTERMAREALES (GÉNERO *PETROLISTHES*) EN LA COSTA SUR DE CHILE. – Los crustáceos intermareales poseen un alto grado de plasticidad fisiológica, lo que les permite soportar periodos prolongados de emersión. En este estudio se examinaron algunas restricciones fisiológicas que determinan la distribución y abundancia de los porcelánidos intermareales *Petrolisthes laevigatus* y *Petrolisthes violaceus*. En este estudio se evaluó la distribución de estas dos especies a diferentes niveles del intermareal, relacionándolos con la concentración de hemocianina y actividad de la enzima LDH, resistencia a la desecación, tolerancia termal y la resistencia a agua hipóxica. Los resultados mostraron una mayor abundancia de *P. laevigatus* en la zona alta del intermareal y de *P. violaceus* en la zona baja. *P. laevigatus* mostró una mayor tolerancia a altas temperaturas y una menor tolerancia a la desecación durante la exposición aérea que *P. violaceus*, que además fue mas tolerante a prolongadas exposiciones a la de hipoxia. No se encontraron diferencias en la concentración de hemocianina y actividad de LDH entre las especies. Estos resultados apoyan la idea de un gradiente evolutivo hacia los sistemas terrestres. *P. laevigatus* mostró más adecuaciones fisiológicas para la especialización semi-terrestre.

Palabras clave: zonación, desecación, hipoxia, tolerancia fisiológica, *Petrolisthes*, Chile.

INTRODUCTION

Organisms inhabiting the intertidal zone are routinely exposed to environmental changes due to the tidal cycles and may sometimes spend 50% of their lives in semi-terrestrial conditions (Stillman and Somero,

1996). These conditions may include hours of air exposure, increased temperatures, and ambient hypoxia (Allen and Burnet, 2008).

Traditionally, the classic distribution patterns of intertidal organisms in discrete vertical zones have been explained as the interplay between abiotic factors (e.g.

temperature, aerial exposure) (Connell, 1961; Somero, 2002) and biotic interactions (e.g. competition, predation). In general, abiotic factors are considered to be more important in the upper intertidal zone, whereas biotic factors are more relevant in the lower intertidal zone (Hofmann and Somero, 1995; Stillman and Somero, 1996; Somero, 2002; Stillman, 2002). In spite of these generalizations, there is only limited information on the physiological specializations that have allowed species with similar evolutionary histories to inhabit different positions in the intertidal zone.

Several lineages of benthic marine animals have made the evolutionary transition from aquatic to terrestrial habitats. When a change in habitat takes place, either on an evolutionary timescale for a particular lineage or on the current ecological timescale for an individual, the transition between two distinct physical environments, such as water and air, may have great molecular and physiological costs (Greenaway, 2003). We hypothesize that the position in the intertidal zone is representative of a species' position in the evolutionary transition from marine to land realms. Thus, the more advanced characteristics associated with terrestrial life, such as water conservation and temperature tolerance, should be present in species of the upper intertidal zone, and the more plesiomorphic characteristics associated with a mainly aquatic life should be observed in species characterizing the lower intertidal zone.

Porcelanid crabs are conspicuous organisms inhabiting the intertidal zone, with several species distributed along the Pacific coast of North and South America (Carvacho, 1980; Stillman and Reeb, 2001). For this group, life in the intertidal zone demands physiological and biochemical adaptations related to desiccation, temperature, and salinity tolerance, and the capability to withstand environmental variations (Jensen and Armstrong, 1991; Stillman and Somero, 1996; Yaikin *et al.*, 2002). In terms of oxygen availability, changes in water temperature could affect the efficiency of capturing oxygen, and consequently provoke an increase in anaerobic metabolism, resulting in lactate accumulation (Stillman, 2000; Yaikin *et al.*, 2002). To respond to these disturbances, organisms must change their physiology to modify their oxygen consumption, take oxygen from the environment and transport it efficiently to their tissues. One of these changes is the modification of the oxygen-haemocyanin binding affinities through an allosteric interaction with ions like lactate (Decker and Foll, 2000).

Intertidal porcelain crabs show wide differences in their tolerances to high temperatures. Research on *Petrolisthes cinctipes*, *P. eriomerus* and other species from the Porcellanidae family has shown that the upper tolerance limit of these species is very close to the temperature of their environment (Jensen and Armstrong, 1991; Somero, 2002; Stillman, 2003). In this sense, any modification in this variable due to macro-scale phenomena like global warming, could cause problems for the survival of these organisms (Helmuth *et al.*, 2002).

Two common inhabitants of the Chilean shore are the Porcelain crabs *Petrolisthes laevigatus* and *Petrolisthes violaceus* (Viviani, 1969). These species exhibit different zonation patterns and degrees of exposure to terrestrial conditions. *Petrolisthes laevigatus* inhabits the upper intertidal zone, hiding underneath large rocks (Viviani, 1969). In contrast, *P. violaceus* inhabits the lower intertidal zone, immediately below *P. laevigatus*, down to the subtidal zone, where it is found underneath stones and on coarse sand (Viviani, 1969). Both species are likely to experience marked shifts in ambient temperature owing to variations in microhabitat isolation and tidal submersion/emersion patterns.

To test if differences in physiological responses are associated with their position in the intertidal zone, we evaluated differences in abundance of *Petrolisthes laevigatus* and *P. violaceus* at different intertidal heights in relation to their resistance to desiccation and the effects of high temperatures, the concentration of oxygen in the water, and also haemolymph physiology (LDH activity, haemocyanin concentration).

MATERIALS AND METHODS

This study was carried out in the rocky intertidal zone of Lenga, San Vicente Bay, Concepción, Chile (36°45'S 73°10'W), during low tides in austral summer (January) 2004 (Fig. 1).

We sampled crab abundance under large rocks in the rocky intertidal zone. The density was measured during the daytime low tides along three five-meter-long transects perpendicular to the shoreline, extending from the water's edge to the upper intertidal zone, with 10 m between each transect. Along each transect, we measured crab density under rocks using 0.09 m² quadrants at five intertidal heights: 0.2, 0.6, 1.2, 1.6 and 2.0 m above mean low water (MLW).

For the experimental studies, similar sized animals, ranging between 12.9 and 19.5 mm cephalothorax length (CL), were collected at the study site and transported in refrigerated containers to the Physiology Laboratory of the Universidad Católica de la Santísima Concepción. In the laboratory, the animals were kept in individual aquaria and acclimated without food at 14°C for three days (Chen and Chia, 1997; Lucu and Devescovi, 1999; Castillo-Blasco *et al.*, 2009), in filtered and aerated seawater. Following acclimatization, each animal was assigned to an experimental treatment.

To assess the effect of aerial exposure on the respiratory abilities of *P. laevigatus* and *P. violaceus*, we measured the haemolymph concentrations of haemocyanin and the activity of the lactate dehydrogenase enzyme (LDH). For this, 40 organisms of each species were placed in individual plastic containers (500 mL) at 14°C and assigned to four treatments: (N=10 individuals per treatment) three different times of aerial exposure (0, 3 and 6 h) and a final treatment

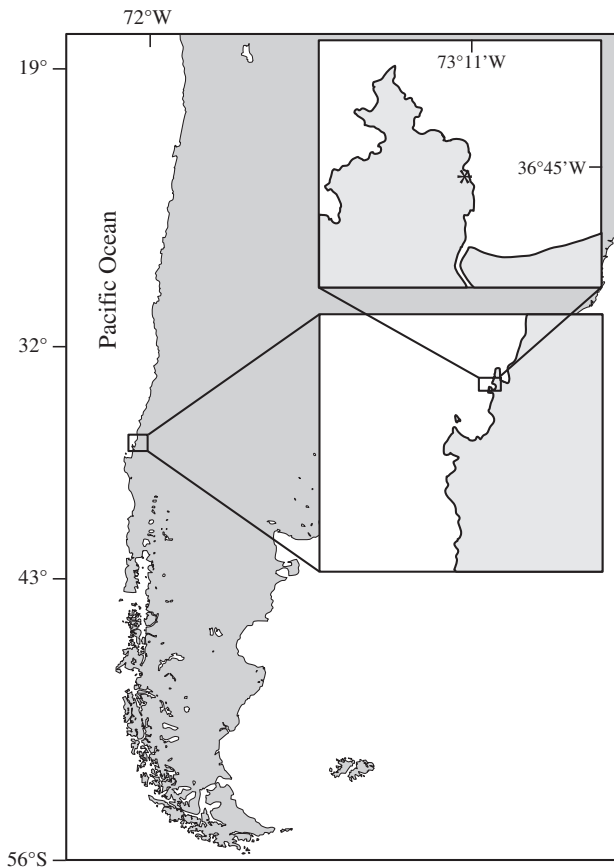


FIG. 1. – Map of the study site (asterisk) in Caleta Lengua (36°45'S 73°10'W), San Vicente Bay, Chile.

of reimmersion in aerated sea water for 1 h. Each individual was measured only once. Haemolymph was extracted from each specimen by puncturing the chelae with 1 mL syringes. The haemocyanin concentration was measured as described in Astete-Espinoza and Cáceres (2000); LDH concentrations were measured using the kinetic UV method (Gay *et al.*, 1968).

To evaluate differences in the capacity for water conservation, we measured the water loss of the two species in aerial conditions. For this, 24 individuals of each species were weighed and placed in individual plastic containers at 15°C with a paper towel moistened with sea water, and exposed to emersion conditions for 1, 2, 4 and 6 h (N=6 individuals per treatment) with a relative air humidity of 30-40%. Individuals were weighed at the end of each experimental time. Afterwards, in order to estimate total water content, all individuals were dried in an oven for 48 h at 60°C until a constant weight was achieved.

The different water thermal tolerances of *P. violaceus* and *P. laevigatus* were evaluated by placing three replicates with 40 individuals of each species in 5 L containers with seawater in a thermoregulated bath ($\pm 1^\circ\text{C}$) at four experimental temperatures (15, 25, 30, 35°C). To assess their capacity to tolerate water hypoxia, we used ten individuals of each species per treatment, which were exposed individually to three

TABLE 1. – Mean abundance (\pm SD) of *Petrolisthes laevigatus* and *P. violaceus* at different levels of intertidal zone at Caleta Lengua (36°45'S 73°10'W).

Intertidal height (m)	Abundance (ind. m ⁻²)	
	<i>P. laevigatus</i>	<i>P. violaceus</i>
0.2	25.9 \pm 3.7	706.7 \pm 134.7
0.6	318.2 \pm 124.3	636.4 \pm 157.5
1.2	610.5 \pm 83.3	214.6 \pm 48.5
1.6	1206.2 \pm 403.8	321.9 \pm 52.4
2	799.2 \pm 221.1	3.7 \pm 3.7

TABLE 2. – Average values of haemocyanin concentration and LDH activity at different times of aerial exposure and reimmersion (average \pm SD).

Time (h)	0	3	6	reimmersion
LDH Activity (UI mL ⁻¹)				
<i>P. laevigatus</i>	2.70 \pm 0.72	2.75 \pm 0.81	3.05 \pm 0.35	2.85 \pm 0.66
<i>P. violaceus</i>	2.93 \pm 0.29	3.05 \pm 0.29	2.93 \pm 0.37	3.19 \pm 0.13
Haemocyanin concentration ($\mu\text{mol mL}^{-1}$)				
<i>P. laevigatus</i>	4.52 \pm 1.24	4.53 \pm 1.46	5.12 \pm 0.63	4.86 \pm 1.19
<i>P. violaceus</i>	4.93 \pm 0.59	5.13 \pm 0.52	5.40 \pm 0.23	4.52 \pm 1.24

different water-oxygen concentrations: 1.0 mg O₂ L⁻¹ (low), 2.5 mg O₂ L⁻¹ (medium), and 5.5 mg O₂ L⁻¹ (high) in 500 mL chambers. At the end of each experiment the criteria for survival was the presence of antennal movements (Haye and Ojeda, 1998).

Statistical analysis

For each species, the relationship between intertidal height and species abundance was evaluated using Pearson correlation coefficients (Zar, 1996). The variations in haemocyanin concentration, LDH activity, temperature and hypoxia tolerance were analyzed by fixed, two-way or three-way ANOVA models, using species, time, temperature or oxygen concentration as fixed factors. Data were normal and homoscedastic following logarithmic transformation. When significant differences were detected, a posteriori comparisons were made with Tukey's test (Zar, 1996).

RESULTS

Both species showed different patterns of density along the intertidal zone. *Petrolisthes violaceus* was most abundant (706.7 \pm 134.7 ind m⁻²) at 0.2 m over MLW and least abundant at 2 m over MLW (3.7 \pm 3.7 ind m⁻²) ($r = -0.83$, $p < 0.01$). In contrast, *P. laevigatus* was most abundant in the upper intertidal zone at 1.6 and 2.0 m over MLW (1206.2 \pm 403.81 and 799.2 \pm 221.16 ind m⁻²) and its density decreased with the tidal level (25.9 \pm 3.7 ind m⁻² at 0.2 m over MLW) (Table 1) ($r = 0.69$, $p < 0.01$).

In experiments of aerial exposure followed by reimmersion, the haemocyanin concentration and LDH activity did not show differences among species, time

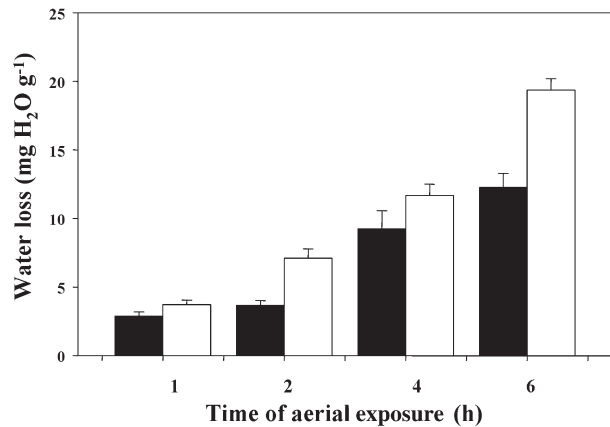


FIG. 2. – Mean water loss of *Petrolisthes violaceus* (white bars) and *P. laevigatus* (black bars) over different times of aerial exposure ($\bar{x} \pm SE$).

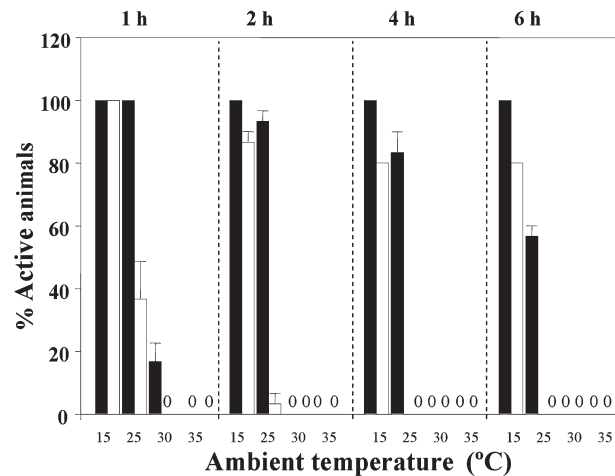


FIG. 3. – Observed activity of *Petrolisthes violaceus* (white bars) and *P. laevigatus* (black bars) over time at different temperatures ($\bar{x} \pm SE$).

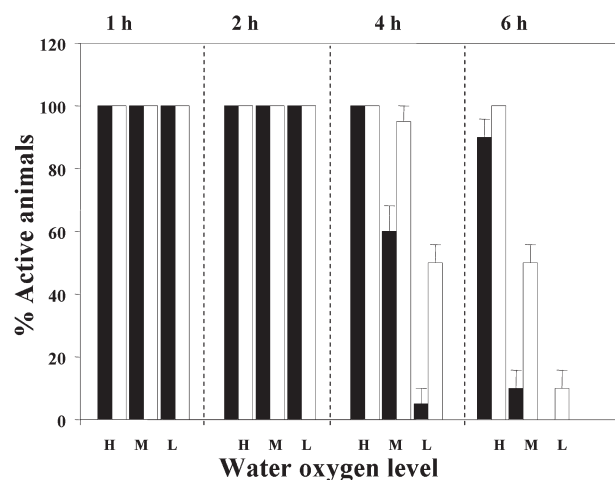


FIG. 4. – Observed activity of *Petrolisthes violaceus* (white bars) and *P. laevigatus* (black bars) over time at different water oxygen concentrations ($\bar{x} \pm SE$). L, low oxygen concentration (1.0 mg O₂ L⁻¹); M, medium oxygen concentration (2.5 mg O₂ L⁻¹); and H, high oxygen concentration (5.5 mg O₂ L⁻¹).

or an interaction between the two factors (Table 2), and had mean values of $4.52 \pm 1.24 \mu\text{mol mL}^{-1}$ for haemocyanin concentration and $2.70 \pm 0.72 \text{ UI mL}^{-1}$ for LDH activity.

The initial body water content was similar in the two species, averaging $59.97 \pm 0.67\%$. In the desiccation experiments, the two species had different capacities for tolerating aerial exposure, and *P. violaceus* showed the greater water loss (Fig. 2). The emersion time was a significant factor for water loss. The statistical analysis showed an interaction between species and time (Table 3c), in which *P. violaceus* at 6 h of emersion was the group with the highest water loss (Fig. 2).

The results of the thermal tolerance experiments revealed differences between species, temperature and time, and *P. laevigatus* was less susceptible than *P. violaceus* to temperature. No activity (as defined above) was observed over 30°C in *P. violaceus* or over 35°C in *P. laevigatus* (Tukey *a posteriori* $p < 0.05$). The three-way variance analysis showed a strong effect of factors (species, time, temperature), an interaction between time and temperature, and between all three factors (Fig. 3, Table 3d). In the water hypoxia experiments, the three factors showed statistically significant effects. *Petrolisthes violaceus* showed a greater ca-

TABLE 3. – Statistical analyses for each variable under study. P, probability value $P < 0.05$.

	DF	MS	F	p
a) Haemocyanin concentration				
Species	1	0.372	1.423	0.241
Time	3	0.087	0.334	0.800
Species*time	3	0.114	0.438	0.726
Error	32	0.262		
b) LDH				
Species	1	0.553	0.570	0.455
Time	3	0.685	0.706	0.555
Species*time	3	0.413	0.425	0.735
Error	32	0.970		
c) Water loss				
Species	1	143.707	38.371	<0.001
Time	3	375.089	100.151	<0.001
Species*time	3	21.28	56.819	0.002
Error	40	3.745		
d) Thermal tolerance				
Species	1	2.976	280.363	<0.001
Time	3	0.301	28.344	<0.001
Temp.	3	10.279	968.282	<0.001
1*2	3	0.017	1.643	0.188
1*3	3	1.342	126.435	<0.001
2*3	9	0.092	8.690	<0.001
1*2*3	9	0.043	4.031	<0.001
Error	64	0.011		
e) Water oxygen concentration				
Species	1	0.627	50.270	<0.001
Time	3	3.618	290.100	<0.001
Oxygen	2	3.007	241.110	<0.001
1*2	3	0.237	18.980	<0.001
1*3	2	0.157	12.550	<0.001
2*3	6	1.082	86.760	<0.001
1*2*3	6	0.076	6.080	<0.001
Error	70	0.013		

capacity to maintain its activity in hypoxic waters than *P. laevigatus*, with significantly higher activity in all oxygen concentrations (Tukey *a posteriori* $p < 0.001$). At medium and low oxygen concentrations, and for an exposure time greater than 4 h, *P. laevigatus* did not show observable movements (Tukey *a posteriori*) (Fig. 4, Table 3e).

DISCUSSION

In agreement with previous reports, our results showed an evident spatial segregation in abundance between *P. laevigatus* and *P. violaceus*. On average, *P. laevigatus* was the most abundant species in the upper intertidal zone. In contrast, the maximum density of *P. violaceus* was found in the lower intertidal zone. These opposing distribution patterns can be attributed mainly to differences in the physiological capacity of each species to cope with desiccation, anoxia, and temperature in both aquatic and aerial environments. This predominance of physiological limits over biotic interactions (*sensu* Connell, 1961) in determining the distribution of congeneric species inhabiting the same area has been reported in other field studies with porcellanids, although only the limitation in the colonization of the upper intertidal by the low intertidal species was attributed to physiological constraints (Jensen and Armstrong, 1991).

The lack of differences in the haemolymphatic haemocyanin concentration and LDH activity in emersion and subsequent immersion could indicate the physiological capability of the two species to tolerate transient air exposure without falling into metabolic decompensation. This could be due to air respiration through membranous gas windows on the walking legs (Stillman and Somero, 1996; Stillman 2000). Vargas *et al.* (2010) reported that aerial exposure in *P. laevigatus* and *P. violaceus* is altered by their physiological homeostasis, producing haemolymphic acidification, by which *P. violaceus* is the most affected. Considering this, although the haemocyanin concentration was not negatively affected, there is probably an alteration in the oxygen-haemocyanin binding affinities, which are moderated through an allosteric interaction with inorganic ions and other effectors such as protons; this modification can help to maintain an adequate oxygen supply to the tissue (Powell and Watts 2006).

Water loss for *P. laevigatus* was significantly lower than for *P. violaceus*. This difference between species inhabiting low and high intertidal zones has been described for other crab species (Jones and Greenwood, 1982) and attributed to local differences in air humidity along intertidal levels caused by the effect of waves and tidal rhythms. In this work, we did not measure the effect of wind on evaporative water loss, although the general trend should be similar to that found in the laboratory experiments. The differences in water loss are congruent with the increased capacity for the intertidal species, *P. laevigatus*, to tolerate aerial exposure.

We believe that resistance to desiccation is an important factor that determines fitness in environments with low water availability or air with low water saturation. These differences could be associated with difference in exoskeleton permeability or a more efficient chemical mechanism of water conservation in *P. laevigatus*. In addition, these species have different behavioural characteristics, and *Petrolisthes laevigatus* is less active and less aggressive than *P. violaceus* (M. Lagos, pers. obs.). Several other studies (Vannini and Ferretti, 1997; Greenaway, 2003) have interpreted these differences in activity as a mechanism for minimizing water loss, which could complement the physiological rates of water loss. In our results, *P. laevigatus*, the species that inhabits the upper intertidal zone, showed a greater capacity for coping with thermal stress than *P. violaceus*. In the 25°C aerial exposure experiments, the latter species was inactive after a short time (2 h), whereas *P. laevigatus* withstood 6 h under these conditions. Neither species survived over 1 h under conditions over 30°C. Stillman and Somero (2001) reported 50% mortality of the same species at 30°C over an aerial exposure period of 8 h. These authors used specimens from a site near Valparaíso (33°01'S, 71°38'O), about 500 km north of our study site, where the mean maximum temperature in summer is about 30°C, whereas the maximum summer temperature in Concepción is around 25°C. In all cases, these species live in conditions near their tolerance limits, and consequently are very susceptible to major climate changes such as global warming (Helmuth *et al.*, 2002; Stillman, 2003).

The current increases in global mean temperature produced by global warming could lead to a higher frequency and severity of heat waves. These phenomena may be a strong selective agent in intertidal animals, because their upper limits of distribution are linked with their ability to survive in extreme thermal events (Harley, 2008; Stillman and Tagmount, 2009). How the fitness and distribution of these organisms will change under the current scenario of climate change will depend on their ability to acclimatize and adapt to the increases in the extreme hot weather events that are likely to occur (Somero 2002; Stillman, 2003; Stillman and Tagmount, 2009).

Our experiments showed different capacities for living in aquatic environments. The crab from the low intertidal zone, *P. violaceus*, was better able to cope with water hypoxia than *P. laevigatus*; this capacity is a key factor for an organism that lives mainly in marine water due to its position in the lower intertidal zone. We speculate that in aquatic conditions, *P. violaceus* probably has an oxyconformer strategy, adapting to the oxygen demand without compromising its survival in an oxygen fluctuating environment. In addition, changes in pH associated with aerial exposure (Lagos and Cáceres, 2008) could be related to change in the haemocyanin carrying capacity (Bohr effect) during hypoxic periods (Truchot, 1980). No inactivity was

observed in either species during the first two hours of exposure to water hypoxia. In the following hours, the percentage of individuals without observable activity was higher in *P. laevigatus*. This indicates the capacity of *P. violaceus* to spend longer periods of time in water hypoxia (Yaikin *et al.*, 2002).

Finally, it is necessary to carry out further studies of the ways in which the whole-organism physiology can provide insights into the underlying mechanisms and consequences of environmental change in a macrophysiological context. This means investigating the variation in physiological traits over large geographical and temporal scales and understanding the ecological implications of this variation.

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