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Exposure to solar radiation drives organismal vulnerability to climate: Evidence from an intertidal limpet

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ARTICLE INFO

ABSTRACT

Understanding the physiological abilities of organisms to cope with heat stress is critical for predictions of species' distributions in response to climate change. We investigated physiological responses (respiration and heart beat rate) of the ectotherm limpet Patella vulgata to heat stress events during emersion and the role of seasonal and microclimatic acclimatization for individual thermal tolerance limits. Individuals were collected from 5 microhabitats characterized by different exposure to solar radiation in the high intertidal zone of a semi-exposed rocky shore in winter and summer of 2014. Upper thermal tolerance limits (heat coma temperatures – HCTs, and heart rate Arrhenius break temperatures - ABTs) were determined for individuals from each microhabitat in both seasons under laboratory conditions. While we found a clear seasonal acclimatization, i.e., higher HCTs and ABTs in summer than in winter, we did not find evidence for microhabitat-specific responses that would suggest microclimatic acclimatization. However, operative limpet temperatures derived from in-situ temperature measurements suggest that individuals from sun exposed microhabitats have a much narrower thermal safety margins than those from less exposed surfaces or within crevices. Microhabitat specific thermal safety margins caused by high thermal heterogeneity at small spatial scales and the lack of short term acclimatization will likely shape small scale distribution patterns of intertidal species in response to the predicted increase in the frequency and intensity of heat waves.

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1. Introduction

Climate-related changes in species' distributions have already been observed in benthic systems (Birchenough et al., 2015). Predicting future species distributions and biodiversity patterns in a changing climate has become a priority over the last decades (Borja, 2014) in order to anticipate the ecological and socio-economic impacts of climate related changes on local biodiversity (Sarà et al., 2014). Therefore, knowledge on the physiological abilities of ectotherms in response to changes in temperature is critical (Bozinovic et al., 2011). Organismal physiological performance and fitness affect population dynamics, species interaction and ecosystem functioning and are driven by the local environmental context (Doney et al., 2012). For instance, intertidal invertebrates face high spatial and temporal temperature heterogeneities caused by exposure to water and air over the tidal cycle, and microhabitat-specific exposure to solar radiation in different seasons (Chapperon and Seuront, 2011; Seabra et al., 2011). The microtopography of rocky substrates strongly influences the degree of exposure to solar radiation and shapes the variability in substrate temperature observed over the tidal cycle and in different seasons (Harley, 2008; Miller et al., 2009; Seabra et al., 2011).

Here we investigate whether microhabitat- and season-specific thermal histories of the limpet Patella vulgata affect its physiological ability to cope with sublethal thermal stress during emersion. Specifically, we examine the physiological responses of P. vulgata (respiration and cardiac activity) to heat stress in the laboratory and derived thermal safety margins for five microhabitats

Table 1
Definitions of thermal physiological descriptors used in the present study.

Thermal physiological descriptor	Definition
Heat Coma Temperature (*HCT*)	Temperature at which individuals became detached from support <u>and</u> did not show any response after pricking the foot and tentacles with a needle (Evans, 1948). Individuals showed a response to a test of irritability after 24 h. *HCT* was used as a proxy for the critical thermal limit (CT_{max}) of locomotor performance (Polgar et al., 2015)
Arrhenius Break Temperature (*ABT*)	Temperature above which heart beat rates decrease rapidly (Stillman and Somero, 1996), thus indicating cardiac function failure.
Thermal safety margin (*TSM*)	Difference between the upper thermal tolerance limit (defined as *HCT* in the present study) and the maximal estimated operative temperature (Sunday et al., 2014) recorded over a 14 days period in summer 2014 within each studied microhabitat.

characterized by contrasting exposure to solar radiation. We hypothesize that both microhabitat (short-term) and seasonal (long-term) thermal acclimatization in *P. vulgata* affect its thermal tolerance limits and physiological performance in response to heat stress. In particular, we expect individuals from microhabitats characterized by large daily temperature variations to show a greater ability to cope with thermal stress than individuals from microhabitats with more stable thermal conditions (Magozzi and Calosi, 2014). Similarly, we anticipate seasonal variations in the thermal sensitivities and thermal tolerance limits of limpets (i.e., we expect summer-adapted individuals to show a greater capacity to cope with heat stress than winter-adapted individuals, Davies, 1965).

2. Materials and methods

2.1. Sampling site

Individuals of *P. vulgata* were collected from a semi-exposed rocky shore (Dellec, Plouzané, France, 48°21′09″N, 4°34′01″W) in winter and summer 2014 during daytime ebbing low tide. At the study site, *P. vulgata* occurred at densities of 135 ± 18 individuals/m^2. Since one of the objectives was to examine the effect of the recent thermal history on physiological responses to heat stress during emersion, individuals were collected one day before laboratory measurements to avoid acclimation to laboratory conditions. Adult *P. vulgata* belonging to a similar size class (with average height and length of ca. 15 mm and 32 mm) were collected at the upper limit of their intertidal distribution where they experience the greatest temperature variations (Seabra et al., 2011). Limpets were collected from five microhabitats characterized by different levels of exposure to solar radiation and thus potential differences in thermal stress: crevices (C, very low exposure), vertical north exposed (NE, low exposure), vertical west exposed (WE, high exposure), flat rock (FR, higher exposure) and vertical south exposed surfaces (SE, highest exposure).

Intertidal ectotherms' body temperatures are not correlated to the air temperature as they are affected by multiple interactive abiotic factors such as exposure to solar radiation, wind chill and wave splash (Helmuth and Hofmann, 2001; Fitzhenry et al., 2004; Broitman et al., 2009). Body temperatures also depend on morphological properties like shell shape and color. To account for the influence of this suite of environmental and morphological factors on operative body temperatures, we deployed biomimetic loggers (robolimpets, Lima and Wethey, 2009) adjacent to substrate temperature loggers (iButton thermochron DS1921 G-F5, Homechip UK). Temperature loggers were significantly correlated to robolimpets across all microhabitats ($R^2 > 0.95$, $p < 0.05$; see Fig. 1 in Supplementary materials as an example) and had an average bias of 1.25 °C and a mean square error of 1.33 °C. Due to logistic reasons, robolimpets were not deployed in all

microhabitats and seasons. Instead, DS1922L iButton loggers were attached to the rocky substrate in each microhabitat using glazing tapes (Hodgson Sealants, UK) and temperature measurements were taken every 10 min over 14 days in both seasons. Note that summer recordings were conducted in September 2014 which was the month with the highest average daily maximum temperature for the period 2011–2014 as evidenced by data collected using biomimetic loggers at a shore less than 50 km away from our study site (see Fig. 2 in Supplementary materials). Operative limpets temperatures were thus estimated using the equations of the significant linear relationships obtained between robolimpets and ibuttons temperature in the different microhabitats (estimated operative limpet temperature hereafter).

2.2. Laboratory experiments

We assessed three descriptors of thermal tolerance during emersion: heat coma temperature, Arrhenius break temperature and thermal safety margin (*HCT*, *ABT* and *TSM*, respectively; see Table 1 for definitions).

Upon collection, individuals were brought to the laboratory within 30 min and placed into a tank with natural tidal cycle and 12 h photoperiod. Shells were scraped and carefully cleaned with ethanol to remove epibionts. To assess *HCT*, individuals were directly placed on the vertical walls of two cubic transparent plastic tanks (13 cm side). For combined respiration and heart beat rate measurements or heart beat rate measurements only, limpets were positioned on horizontal sandstone plates after gluing heart beat infrared sensors onto their shells. Animals were sprayed with seawater to allow replenishment of mantle water and attachment to their support (Williams et al., 2005). Seawater temperature was similar to that experienced by individuals at the collection site during immersion (10 °C in winter and 16 °C in summer). Room temperature was maintained to that of the seawater.

In all experiments, thermal stress during emersion was simulated by immersing containers (tanks or respirometry bottles without any water depending on experiments) within a thermostated water bath (Huber, Cryo-Polystat CC −20/200 °C 12 L, Avantec, France). Two similar thermal ramps were used in this study, both featuring a warming rate of 6 °C/h. However, for respiration and cardiac rate measurements, the water bath temperature was instantaneously raised 6 °C at the beginning of each hour, and kept constant until the next hour. On the other hand, on heat coma experiments and heart rate measurements, water bath temperature was raised using a smoother ramp of 1 °C every 10 min (i.e., each target temperature was held for ca. 10 min). Data loggers (DS1921G-F5 iButton thermochron, Homechip UK) were placed inside each tank (three per tank) and each bottle (one per bottle) to confirm that water bath temperature and the temperature inside each tank were similar. An absorbent tissue saturated with seawater was placed in each tank/bottle to maintain 100% humidity level.