

Equatorial range limits of an intertidal ectotherm are more linked to water than air temperature

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Abstract

As climate change is expected to impose increasing thermal stress on intertidal organisms, understanding the mechanisms by which body temperatures translate into major biogeographic patterns is of paramount importance. We exposed individuals of the limpet *Patella vulgata* Linnaeus, 1758, to realistic experimental treatments aimed at disentangling the contribution of water and air temperature for the buildup of thermal stress. Treatments were designed based on temperature data collected at the microhabitat level, from 15 shores along the Atlantic European coast spanning nearly 20° of latitude. Cardiac activity data indicated that thermal stress levels in *P. vulgata* are directly linked to elevated water temperature, while high air temperature is only stressful if water temperature is also high. In addition, the analysis of the link between population densities and thermal regimes at the studied locations suggests that the occurrence of elevated water temperature may represent a threshold *P. vulgata* is unable to tolerate. By combining projected temperatures with the temperature threshold identified, we show that climate change will likely result in the westward expansion of the historical distribution gap in the Bay of Biscay (southwest France), and northward contraction of the southern range limit in south Portugal. These findings suggest that even a minor relaxing of the upwelling off northwest Iberia could lead to a dramatic increase in thermal stress, with major consequences for the structure and functioning of the intertidal communities along Iberian rocky shores.

Keywords: distribution gap, distribution limit, European Atlantic intertidal, heartbeat frequency, *Patella vulgata*, physiology, temperature, thermal stress

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Introduction

It is widely recognized that geographical distributions of species are, to a large extent, determined by environmental factors. Of those, temperature has received much attention, being described as a major element in the establishment of range limits and phenological timings (Southward, 1958; Wethey, 2002; Parmesan & Yohe, 2003; Lima *et al.*, 2007; Wethey *et al.*, 2011; Poloczanska *et al.*, 2013). Despite the recognition of its fundamental role, much is yet to be explored in order to fully understand how temperature governs the distributions of species. This is especially true for intertidal rocky shore ecosystems for three reasons. First, the intertidal thermal environment is inherently complex (Helmuth *et al.*, 2006a; Denny *et al.*, 2011; Seabra *et al.*, 2011; Lathlean *et al.*, 2014) and can hardly be described using averages (Helmuth *et al.*, 2006b, 2014; Vasseur *et al.*, 2014; Seabra *et al.*, 2015), in particular because of the continuous transition between

immersion and emersion resulting from tidal cycles. Secondly, animals inhabiting rocky shores are regularly exposed to environmental extremes not only of temperature, but also of desiccation and wave impact forces (Foster, 1971; Denny *et al.*, 1985; McMahon, 1990; Burrows *et al.*, 2008), thus complicating the unequivocal attribution of observed responses to temperature. Thirdly, recording intertidal environmental parameters across large geographical scales is notoriously difficult (Rutz & Hays, 2009; Gandra *et al.*, 2015; but see Seabra *et al.*, 2011, 2015), often leaving researchers with little option but to use remote sensed data. Such datasets, however, have spatial resolutions which are several orders of magnitude larger than the fine detail of rocky shores or the organisms therein, effectively obscuring the role microhabitat plays in determining their distribution patterns (Helmuth *et al.*, 2006b, 2010; Denny *et al.*, 2011; Potter *et al.*, 2013).

Detecting and predicting biological responses to climate change is one of the greatest challenges of today (Pereira *et al.*, 2010). It is now recognized that climate change is a spatially and temporally complex process

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(Easterling *et al.*, 2000; Lima & Wethey, 2012; IPCC, 2013; Vasseur *et al.*, 2014), affecting in a heterogeneous way the frequency and severity of extreme temperatures and precipitation events around the globe (Easterling *et al.*, 2000; Meehl *et al.*, 2009) and impacting the temperature of oceans and atmosphere differently (Belkin, 2009; Hansen *et al.*, 2010; Burrows *et al.*, 2011). As intertidal systems are the boundary between land and oceans, animals living there can be expected to be responding to combined effects of change in water and air temperatures (Southward, 1991; Harley *et al.*, 2006; Firth *et al.*, 2011, 2015). Furthermore, intertidal rocky shore communities in temperate zones are known to be highly structured by ecological interactions (Paine, 1974; Lubchenco & Menge, 1978; Menge & Lubchenco, 1981; Underwood, 1981), and much literature has been dedicated to describing the cascading implications of loss of certain key species (Paine, 1974; Underwood, 1980). This means complex and dramatic changes to community composition and function can occur as a consequence of climatic changes (Southward *et al.*, 1995; Sagarin *et al.*, 1999; Paine & Trimble, 2004; Girard *et al.*, 2012; Jurgens *et al.*, 2015).

This study focused on the intertidal limpet *Patella vulgata* Linnaeus, 1758, and aimed at identifying the thermal conditions likely limiting its geographical distribution. We used a recently described infrared heartbeat rate sensing system (Burnett *et al.*, 2013) to monitor in a noninvasive way the cardiac performance of animals exposed to a series of experimental conditions, which were specifically chosen to reflect immersion and emersion temperatures experienced at the middle and at the edges of the distribution range. Because in ectotherms cardiac rate is positively linked to metabolism (Frederich & Pörtner, 2000), elevated heartbeat frequencies are indicative of additional metabolic costs, which, if recurrent, reduce fitness and limit scope for growth (Somero, 2002, 2010; Woodin *et al.*, 2013) and may be used to disentangle the contribution of water and air temperature for the buildup of thermal stress. *Patella vulgata* is an ectotherm that can be abundantly found over the majority of the Atlantic European continental coast south of Norway, but reaches its southern distribution limit in southwest Iberia and is absent from the southeast Bay of Biscay (Fischer-Piette & Gaillard, 1959; Christiaens, 1973). Several other species of algae and invertebrates exhibit the same distribution pattern (Fischer-Piette, 1955; Crisp & Fischer-Piette, 1959). Hence, despite the necessary caution that must be taken when generalizing across species, studying the geography of thermal stress in *P. vulgata* may be informative for a wider range of organisms. In addition, *P. vulgata* is a keystone species whose grazing activities control, to a large extent, local biodiversity

and community structure throughout much of its range in Europe (Southward, 1964; Hawkins & Hartnoll, 1983; Jenkins & Hartnoll, 2001; Jenkins *et al.*, 2005; Coleman *et al.*, 2006). Thus, understanding the factors controlling its distribution can improve our ability to forecast responses of intertidal ecosystems to climate change.

Methods

Microhabitat temperature

Intertidal microhabitat temperatures were recorded at 15 exposed to moderately exposed shores along the Atlantic European coast, spanning nearly 20° of latitude, from southwest Scotland to south Portugal (Fig. 1a). Data were acquired using robolimpets – autonomous temperature sensing/logging devices mimicking the visual aspect and temperature trajectories of real limpets (Lima & Wethey, 2009). Loggers were deployed following Seabra *et al.* (2011) at six distinct combinations of height above the low water mark (low, mid and high shore) and exposure to sun (shaded and sun-exposed), thus covering most of the spectrum of microhabitats occupied by intertidal species, including *P. vulgata*. Data were collected continuously between the summers of 2010 and 2014, at a sampling interval of 60 minutes and a resolution of 0.5 °C. Separately for each shore, logged temperatures were averaged for each microhabitat whenever data from multiple sensors were available. Daily water temperature was extracted using the temperatures recorded by low- and mid-shore loggers at peak high tide (high-shore loggers were not used because they may have not been submerged during neap high tides). All data manipulation was performed using R 3.1.2 (R Development Core Team, 2014).

Distribution of Patella vulgata

Population densities of *P. vulgata* were measured during the summer of 2012 in all studied shores. At each field site, individuals were counted using a total of thirty 30 × 30 cm quadrats haphazardly placed at locations equivalent to the microhabitats where temperature loggers had been previously deployed (15 exposed to the sun and 15 in the shade). Because this species typically has an aggregated distribution, to reduce the likelihood of over-estimating densities the quadrats were deployed across any portion of habitat suitable for this species, regardless of the presence of any individual. Densities reported in this study correspond to average density across all quadrats, irrespective of their shore height and exposure to sun, thus reflecting the overall abundance of *P. vulgata* in each shore.

Exposure to thermal stress

During the population density survey, we confirmed the absence of *P. vulgata* from Biarritz and Evaristo (shores H and O, respectively, Fig. 1a). To determine the role of temperature

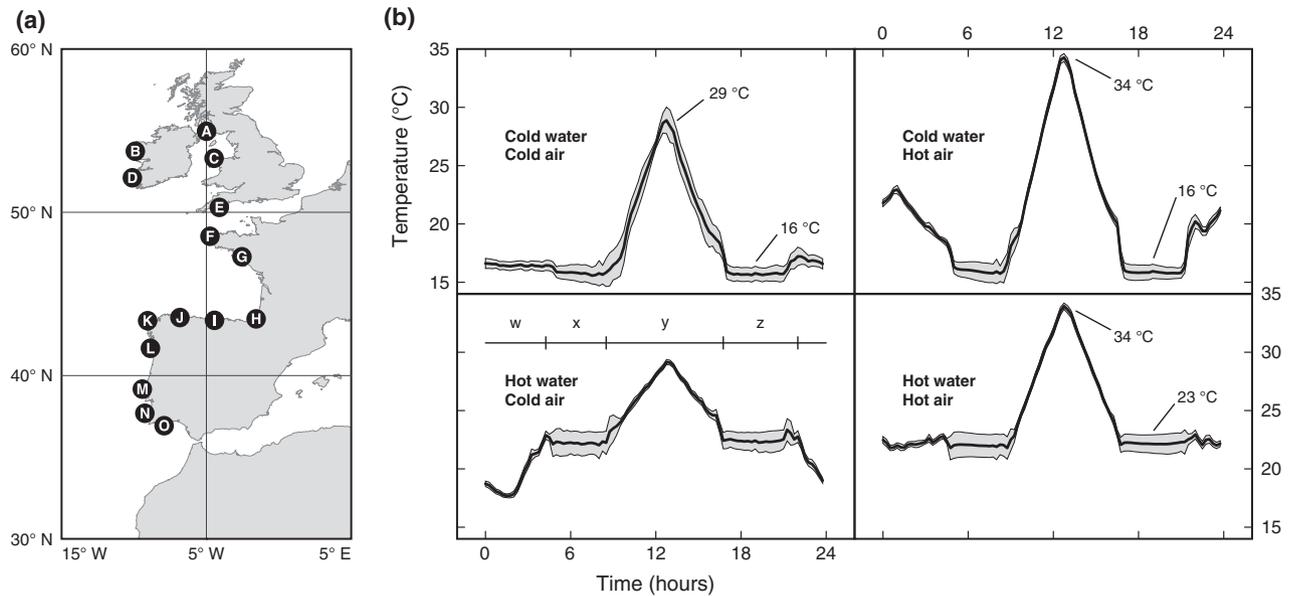


Fig. 1 (a) Map of the study area. Letters A–O indicate the locations of the 15 shores surveyed, which cover the majority of the southern portion of *Patella vulgata*'s distribution (A – South Cairn, UK; B – Emlagh, IE; C – Holyhead, UK; D – Annascaul, IE; E – Wembury, UK; F – Landunvez, FR; G – Batz-sur-Mer, FR; H – Biarritz, FR; I – Premezzo, ES; J – La Caridad, ES; K – Cabo Touriñan, ES; L – Moledo, PT; M – São Lourenço, PT; N – Alteirinhos, PT; O – Evaristo, PT). (b) Average daily temperature profile (black line) \pm SD (gray area) effectively experienced by limpets in each of the four stressful treatments. Treatments consisted of a nocturnal low tide and high tide, and diurnal low tide and high tide (w, x, y, z, respectively) repeated over the 30 days of experiment. The temperature combinations used were 'cold water, cold air', 'cold water, hot air', 'hot water, hot air' and 'hot water, cold air' (clockwise from top left), and the target temperatures were 29 °C and 16 °C for 'cold air', 'cold water', and 34 °C and 23 °C for 'hot air' and 'hot water', respectively. Map created in R (R Development Core Team, 2014) using the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) coastline data (Wessel & Smith, 1996).

in setting those limits, in August 2012 a total of 32 individuals of *P. vulgata* (maximum shell length between 30 and 35 mm) were collected from shaded mid-shore microhabitats at Moledo, northern Portugal (shore L, Fig. 1a). Limpets were collected and placed in four tanks in the laboratory (eight individuals in each). Animals were acclimated for 1 week (17 and 20 °C for water and air temperature, respectively) and then exposed to four thermally stressful treatments consisting of combinations of cold and hot air and cold and hot water, repeated over 30 days (Fig. 1b). Experiments were carried out in aquaria with tide and temperature control. Animals were kept at a density of 44.4 limpets m^{-2} in 30 \times 60 cm granite tiles. Tiles had been left for 1 month under running seawater with a 12 h/12 h photoperiod so that they would develop a layer of biofilm. Light was provided by two white LED strips per tank (wavelength between 450 and 650 nm), with a total output of 5600 lx. Limpets fed on the biofilm throughout the experiment. Previous preliminary experiments showed that the rate of biofilm growth was sufficient to sustain a similar density of limpets for more than one year, without mortality. Each day, tide and temperature conditions mimicked a typical semidiurnal tidal cycle – a nocturnal low tide, followed by high tide, and then a diurnal low tide and high tide (w, x, y, z, respectively, Fig. 1b). Fine control of body temperature during emersion was achieved using a microprocessor to regulate the output of two 150W infrared lamps. Two robolimpets deployed inside each tank provided temperature feedback to

the microprocessor. To keep the thermal conditions as realistic as possible, target temperatures for the diurnal and nocturnal low tides (air) and water, as well as the heating and cooling rates, were calculated using microhabitat temperatures recorded at the studied sites. As it has been suggested the equatorial range edge for this species is set by summer conditions (Bowman & Lewis, 1977), calculations for the target temperatures were made using data from August 2011 (the hottest month during the year preceding animal collection) from (i) two 'cold' shores which have cool summers and were found to harbor regionally high densities of *P. vulgata* (Landunvez and Moledo, shores F and L, respectively) and (ii) two 'hot' shores, which have hot summers and where *P. vulgata* was found to be absent from (Biarritz and Evaristo, shores H and O, respectively). We computed the 75th percentile of (i) daily maximum temperature during diurnal low tide, (ii) daily maximum temperature during nocturnal low tide and (iii) average daily water temperature to obtain 'day air', 'night air' and 'water' temperatures for both 'cold' and 'hot' shores. The target temperatures obtained were 29 °C, 16 °C and 16 °C for 'cold day air', 'cold night air' and 'cold water', and 34 °C, 22 °C and 23 °C for 'hot day air', 'hot night air' and 'hot water', respectively. Heating and cooling rates were determined individually for each treatment's combination of air and water temperatures by computing the average heating and cooling rates occurring in the field under similar conditions. To that end, we searched the microhabitat temperature

dataset for days with water and maximum air temperatures similar to each combination of target water and air temperatures (± 1 °C). Each day's temperature data were then processed to determine the timing of the transitions between immersion, emersion and subsequent re-immersion during the diurnal low tide period, as well as the time at which peak air temperature was reached (which does not necessarily coincide with peak low tide). Experimental heating and cooling rates were obtained by averaging all heating (water to maximum air temperature) and cooling (maximum air to water temperature) rates for each combination of target temperatures (e.g., for the 'cold water, hot air' combination we used all days in the microhabitat temperature dataset with water temperature between 15 and 17 °C and maximum air temperature between 33 and 35 °C). The resulting profiles can be found in Fig. 1b and will be hereafter referred as 'cold water, cold air', 'cold water, hot air', 'hot water, hot air' and 'hot water, cold air'. As a consequence of using this method for the establishment of realistic experimental thermal profiles, heating/cooling rates and emersion time varied between treatments, reflecting what indeed happens in the field when such temperatures occur.

Cardiac activity

Experimental design and execution. Throughout the experiment (acclimation and thermal stress), limpets' overall physiological response was evaluated from their cardiac activity. Cardiac data were obtained noninvasively using the method described by Burnett *et al.* (2013). Infrared sensors were glued to the shells during the first two days of acclimation and the cardiac activity of each animal was recorded during periods of one minute every 15 minutes. Every day, before the diurnal low tide, detached or malfunctioning sensors were replaced, and limpets which were not adherent to the substratum were declared 'ecologically dead' (Wolcott, 1973).

Data manipulation. A total of over 100 000 recordings of cardiac activity were obtained throughout the experiment. As discussed by Burnett *et al.* (2013), data obtained with this method can vary in quality, and hence, every recording was visually inspected to determine if a heartbeat signal was clearly detectable. All recordings with fragmented or undetectable heartbeats were discarded. Furthermore, fragmented data were also discarded. After filtering, we were able to retain data covering the entire temporal span of the experiment from a total of four, seven, five and five individuals for the 'cold water, cold air', 'cold water, hot air', 'hot water, hot air' and 'hot water, cold air' treatments, respectively. As the basal heartbeat frequency of limpets can vary greatly, we calculated normalized heartbeat frequencies using the average heartbeat frequency during the last day of acclimation and used this as the basal value. Therefore, cardiac activity was expressed as the ratio of each limpet's heartbeat frequency in relation to its own basal heartbeat frequency (if a limpet had an average basal heartbeat frequency of 0.8 Hz, a normalized heartbeat frequency of 2 would be equivalent to a frequency of 1.6 Hz, that is, a twofold increase in the heart rate).

Assessment of induced thermal stress. Levels of induced thermal stress were first analyzed by fitting linear regression models of cardiac activity as a function of temperature for each treatment and examining their slopes and adjusted means by analysis of covariance (ANCOVA). As the 'cold water, cold air' treatment was the least thermally stressful of the four treatments tested, we used its linear regression model as a descriptor of the basal relationship between cardiac activity and temperature. In other terms, the linear regression model for the 'cold water, cold air' treatment reveals the expected heartbeat frequency for any given temperature when *P. vulgata* is not thermally stressed. Therefore, stress levels in the remaining treatments were evaluated by comparing their linear regression models against the basal model. We tested the null hypothesis that slopes and adjusted means were statistically identical for all treatments – that is, that the thermal regimes imposed in each treatment did not affect the relationship between heartbeat frequency and temperature. During a preliminary analysis, we found that the temporal autocorrelation of the heartbeat frequency data approached zero for lags >6 hours. Therefore, to avoid temporal autocorrelation, we randomly selected subsamples of cardiac activity (one heartbeat frequency measurement per limpet, per 1 °C bin, per treatment, totaling 112 measurements) and used them to calculate 200 bootstrapped ANCOVAs. This procedure resulted in a highly conservative minimum time difference between measurements in all subsamples of ~19 hours. Homoscedasticity was tested with Levene's test and normality of residuals was assessed using the Shapiro–Wilk test. In both cases, a Bonferroni correction was used. ANCOVA models included heartbeat frequency as the dependent variable, temperature as the covariate and treatment as the independent variable. We compared the observed heartbeat frequencies in the stressful treatments with the heartbeat frequencies that would be expected if the basal relationship between cardiac activity and temperature was maintained in all treatments. To that end, a dataset of predicted cardiac activity was built for each treatment. Predicted cardiac activity was computed by applying the baseline linear regression model to the temperatures experienced by limpets in each treatment, throughout the entire length of the experiment. This predicted cardiac activity reveals what should be the cardiac response of limpets exposed to a stressful treatment if they were to exhibit the same cardiac activity vs. temperature relationship as the limpets in the 'cold water, cold air' treatment. Density curves of the residuals obtained from subtracting the predicted heartbeat frequencies from their observed counterparts reveal the collective shift of individual heartbeat frequency measurements – a positive shift means heart rates were faster than expected.

Past and future environmental conditions

Upon identifying the relationship between water and air temperatures in the buildup of thermal stress, we were interested in evaluating its importance for the distribution range of *P. vulgata*. To that end, we investigated past and future patterns of co-occurrence of high water and air temperatures along the studied sites. Average water temperature and

average daily maximum temperature for shaded microhabitats extracted from our biomimetic temperature dataset were used to obtain a highly detailed view of extreme heat events across the studied shores. The analysis of extreme heat events was extended using model output from the ENSEMBLES project (Hewitt & Griggs, 2004). This project used a combination of global circulation models (GCM) and regional circulation models (RCM) to generate predictions of daily sea surface temperature (SST) on a 25 km grid, for the period 1951–2099, under the A1B climate change scenario. We used model outputs from 9 GCM/RCM combinations available in the ENSEMBLES data archive (<http://ensemblesrt3.dmi.dk>, accessed 2015-08-01) (Appendix S1) to run 9 separate forecasts of years with at least 30 days with SST equal or exceeding 23 °C. This threshold corresponds to the ‘hot water’ treatments, which resulted in a marked increase of thermal stress levels in *P. vulgata*. Computations were performed individually for each model, and for each coastal pixel along the Atlantic European shores, from south Portugal to northwest France. The final output of the analysis depicts the number of models that agree that the threshold was, or will be crossed, per year.

Results

Cardiac activity

A total of ~41 000 valid heartbeat frequency readings were obtained over the 37 days of acclimation and thermal stress treatments. To generate 200 subsamples for

ANCOVA, a total of 267 subsamples were required, because although variances were homogenous for all the subsamples generated, residuals were not normally distributed in 25.1% of the cases. Overall, cardiac activity increased at a rate of 0.0417 normalized heartbeats for each 1 °C increase (regression slopes homogenous among treatments in 96% of 200 bootstraps, see also Fig. 2a). That positive link between temperature and cardiac activity encompassed the entire temperature range in all treatments [note the absence of a breaking point similar to the one described by Stillman & Somero (1996), Fig. 2a]. In addition, no mortality was observed during the experiment, confirming that animals never went beyond their thermal tolerance limit. This likely resulted from the relatively short time during which limpets were exposed to each treatments’ highest air temperature – approximately 15 minutes compared to hours in other studies (Dong & Williams, 2011; Fitzgerald-Dehoog *et al.*, 2012; Zhang *et al.*, 2014). Importantly, while slopes remained unchanged among treatments, adjusted means (elevations) of some regression lines differed (Fig. 2a,c). Heartbeat frequencies vs. temperature recorded in the ‘cold water, hot air’ treatment were collinear with the trajectories of the baseline treatment (‘cold water, cold air’), indicating that the few higher heartbeat rates recorded in the ‘cold water, hot air’ treatment resulted solely from the higher

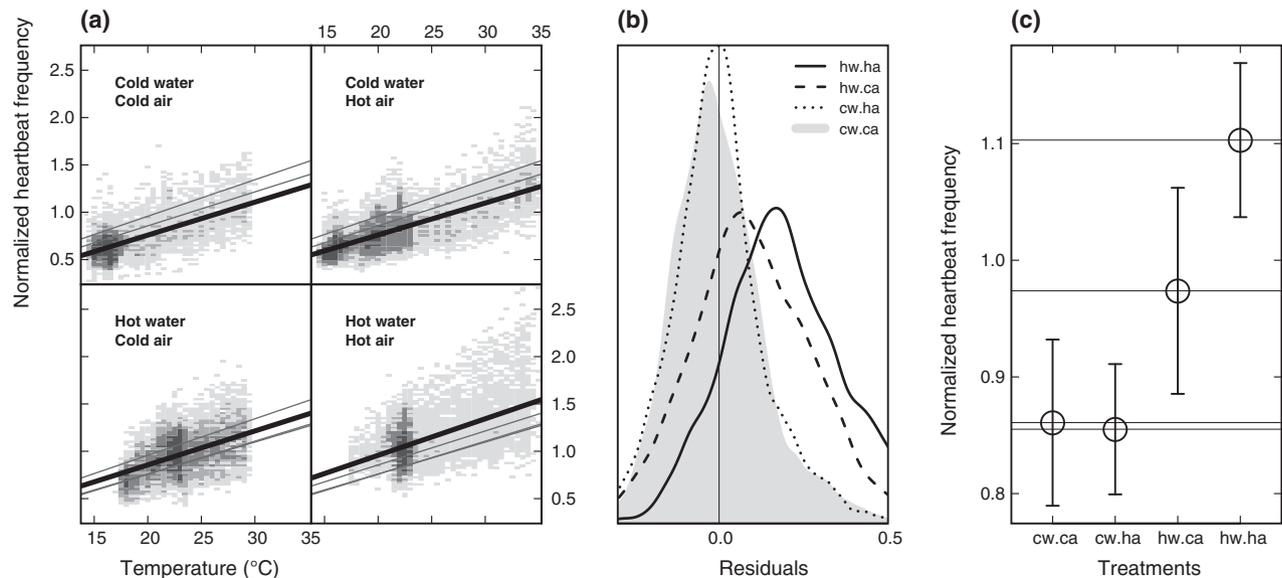


Fig. 2 Cardiac activity of *Patella vulgata*. (a) Scatterplots of normalized heartbeat frequencies as a function of temperature, for all four treatments. Darker pixels indicate values that occurred more often. Thick lines show the linear regression for each treatment, while thin lines show the linear regressions for all other treatments, for comparison. (b) Density curves of the differences between observed and predicted normalized heartbeat frequency. The shaded area represents the baseline treatment (‘cold water, cold air’). A positive shift means higher heartbeat frequencies than would be expected for a given temperature. (c) Adjusted means of the normalized heartbeat frequencies recorded in each of the four treatments \pm SD (calculated using 200 bootstrapped ANCOVAs). Data shown results from four, seven, five and five individuals for the ‘cold water, cold air’, ‘cold water, hot air’, ‘hot water, hot air’ and ‘hot water, cold air’ treatments, respectively.

temperatures experienced. This similarity was further evidenced by the virtually identical density curves of the residuals (Fig. 2b) and the adjusted means obtained with the ANCOVAs (Fig. 2c). On the other hand, on average, limpets in the 'hot water, cold air' treatment exhibited heartbeat frequencies 10% higher than 'cold water, cold air treatment', while limpets in the most extreme treatment ('hot water, hot air') had on average 21% faster heart rates than controls (Fig. 2b). Furthermore, density curves also showed that limpets in the 'hot water, cold air' and 'hot water, hot air' treatments only had heartbeat frequencies at or below the baseline 'cold water, cold air' frequencies during 29% and 10% of the time, respectively. This was also reflected in the increased adjusted means (Fig. 2c). In particular, the adjusted mean from the 'hot water, hot air' treatment was significantly higher than the adjusted means of any of the cold water treatments (Tukey's post hoc test significant in over 85% of 200 bootstraps).

Distribution of *Patella vulgata*

Population densities were highest in the British Isles – over 150 individuals per square meter – and steadily decreased southwards (gray bars, Fig. 3). Outside the British Isles, Landunvez and Moledo, shores F and L, respectively, exhibited the highest densities. Following extensive search, *P. vulgata* was confirmed absent from two shores, Biarritz and Evaristo (shores H and O, respectively). In São Lourenço (shore M), individuals were only found in shaded microhabitats.

Thermal limits

Microhabitat environmental conditions at the 15 locations surveyed, over the past five years, were summarized using the average daily maximum air temperature in shade and average daily water temperature (Fig. 3). The correlation between population densities and the sum of average air and water temperatures for each shore was remarkably high (correlation coefficient of -0.93 , $P < 0.05$). However, even though most locations in the Iberian Peninsula (shores I–O) exhibited high air temperature averages, the only two shores where *P. vulgata* was not found – Biarritz and Evaristo – were those with highest average water temperature (shores H and O, Fig. 3) and where water temperatures ≥ 23 °C occurred frequently (23 and 28 days per year, respectively, Fig. 4). This appears to suggest that the water temperature is the key factor controlling the distribution pattern of *P. vulgata*. Furthermore, by analyzing the pattern of co-occurrence of high water and air temperatures, we show that moderately high air temperatures occurred at shaded habitats of almost all

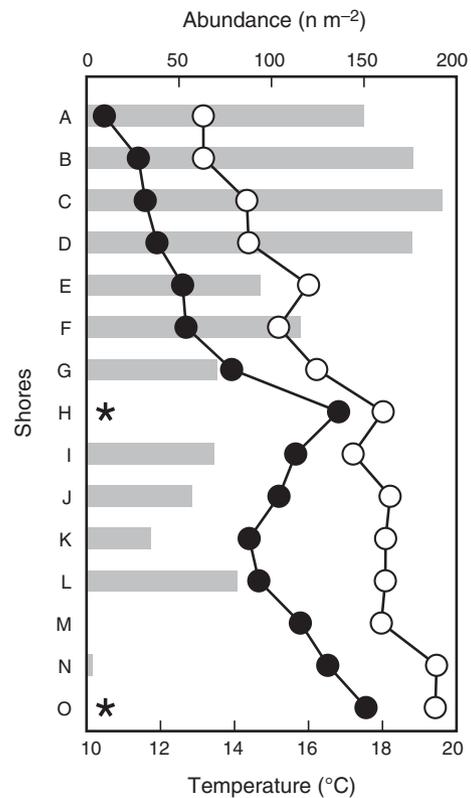


Fig. 3 Relationship between abundance of *Patella vulgata* and temperature recorded by robolimpets. Gray bars show average abundance in each shore across all microhabitats. Stars in shores H and O indicate absence of individuals. Closed circles show average water temperature and open circles show average air temperature in shaded microhabitats.

shores, but the degree of association between water and air temperature varied markedly. For example, the highest correlations between water and air temperatures were found in shores within the Bay of Biscay (shores G–I, correlation coefficients of 0.9, 0.95 and 0.9, respectively, $P < 0.05$), while the lowest occurred in shores along northwest Iberia (shores K and L, correlation coefficients of 0.43 and 0.5, respectively, $P < 0.05$). During summer, northwest Iberia typically experiences an oscillation between periods of upwelling intensification – high air temperature and low water temperature – and relaxation – low air temperature and high water temperature (Moncoiffe *et al.*, 2000; Relvas *et al.*, 2007). In northwest Iberia, the highest air temperatures never coincided with the highest water temperatures (Fig. 4).

On a wider timescale, analysis of ENSEMBLES model data revealed a major trend of deteriorating conditions in the coming years, from the perspective of *P. vulgata* (Fig. 5). Importantly, the general trend is clear despite known variability between model outputs (Brands *et al.*, 2011; Ramos *et al.*, 2011; Kharin *et al.*, 2013). The change is particularly remarkable along the southwest

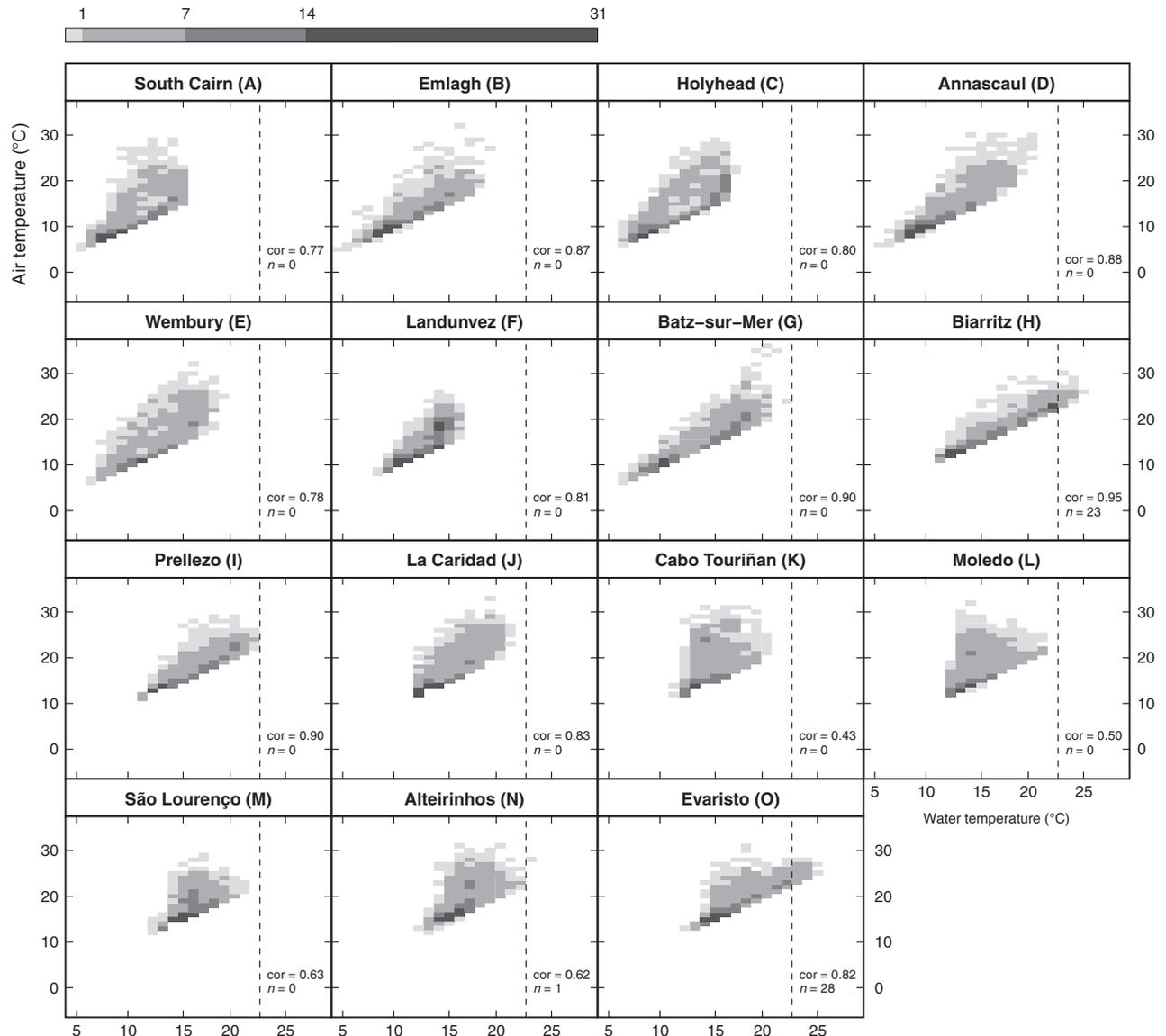


Fig. 4 Pattern of co-occurrence of water and air temperatures at all studied shores, based on temperatures recorded by the robolimpets. Dashed line marks the 23 °C SST threshold. Note that Moledo exhibits many days with high air temperatures and low water temperatures, a pattern typical from locations within regions with coastal upwelling. Biarritz and Evaristo are the only two shores where high water and air temperatures occurred during the study period. The correlation between water and air temperatures, and the number of days with water temperature at or above 23 °C are also depicted.

coast of Portugal (Fig. 5, between shores M and N), with most models agreeing that conditions will become unsurvivable by the end of the century. Conditions in the southeast Bay of Biscay (around shore H) are also forecasted to worsen, as indicated by the increasing number of models predicting that the 23 °C SST threshold will be crossed in the future. In other regions like northwest France and northwest Iberia (Fig. 5, northwards of shore G and between shores K and I), however, most models agree that the threshold will not be crossed, suggesting that these regions will remain habitable for *P. vulgata*.

Discussion

As heart rate and metabolism are positively linked in ectotherms (Frederich & Pörtner, 2000), elevated heart-beat frequencies are indicative of additional metabolic costs, which, if recurrent, reduce fitness and limit scope for growth (Somero, 2002, 2010; Woodin *et al.*, 2013). Thus, our results suggest that the intertidal ectotherm *P. vulgata* is especially susceptible to increases in water temperature and that elevated air temperature plays a secondary role, being relevant only when water temperature is also high. We speculate that this pattern

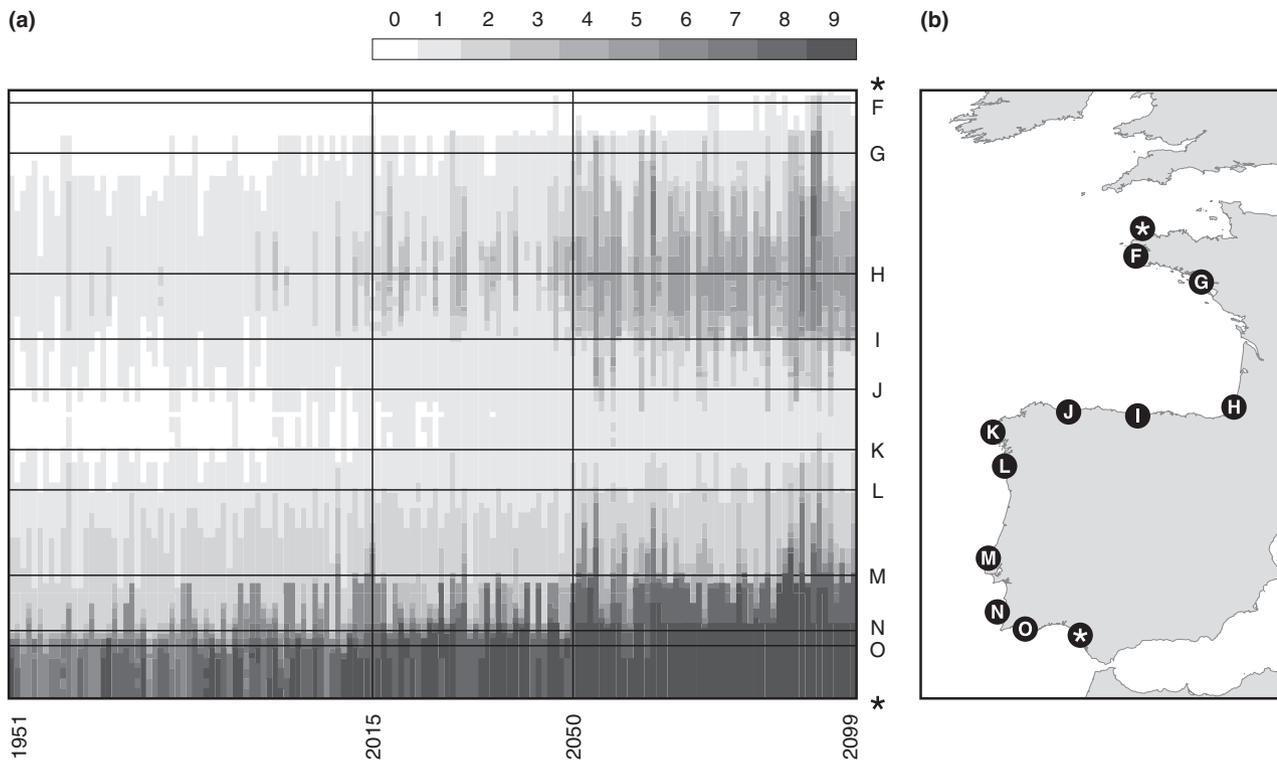


Fig. 5 (a) Long-term analysis of the occurrence of extreme water temperature for the period 1951–2009 along coastal areas from south Portugal to northwest France, a region encompassing the southern limit and a gap in the present distribution of *Patella vulgata*. Each pixel in the graph indicates number of ENSEMBLES models used that predicts 30 or more days with water temperature at or above 23 °C, per year, for each coastal pixel. Darker colors indicate higher agreement between models. A marked increase in the prevalence of such extreme events toward the end of the century can clearly be seen along most of the coast. Horizontal lines identify the locations of the shores surveyed (b) and asterisks mark the edges of the coastline analyzed. Map created in R (R Development Core Team, 2014) using Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) coastline data (Wessel & Smith, 1996).

may be linked to the rhythmic behavior exhibited by this species. Although *P. vulgata* displays a range of homing habits, it is most active during daytime high tides or during nocturnal low tides (Hartnoll & Wright, 1977; Hawkins & Hartnoll, 1982; Little *et al.*, 1991; Williams *et al.*, 1999). At lower latitudes, unless when air is extremely humid, these animals return to their home scar during the day, firmly clamping to the rock to reduce desiccation (Branch, 1981; Gray & Naylor, 1996). Thus, individuals stay immobilized during the part of the day when air temperature is higher. Therefore, it is plausible that the immersion period sets the basal metabolic level and controls the ability to recover from stressful periods, while the emersion period only influences the severity of the stress itself. Several studies on other marine invertebrates support this suggestion (Bayne *et al.*, 1976; Branch, 1981; Tomanek & Somero, 2000; Marshall *et al.*, 2010; Huang *et al.*, 2015; Mota *et al.*, 2015). Under this mechanism, if water is cold, proper recovery can be achieved even after a stressful event and metabolic levels remain largely unaltered. However, when water is hot, the basal metabolic level

is immediately elevated, and if air is also hot, recovery from its deleterious effect may become severely impaired, thus resulting in a further increase of the metabolic level.

The ecological significance of these findings is supported by our temperature dataset, which corroborates the hypothesis that SST is as a major driver of *P. vulgata*'s distribution (Fig. 3). In particular, regarding the identification of thermal regimes conducive to the exclusion of *P. vulgata*, there is convincing support for the existence of an upper threshold to water temperature above which even moderately high air temperatures result in unsustainable stress levels. Considering the results presented in this study, we suggest that this threshold is crossed when water temperature is equal or exceeds 23 °C. The existence of this threshold is in agreement with recent findings which revealed that *P. vulgata* is unable to acclimate to the conditions present at thermally stressful microhabitats (Chapperon *et al.*, 2016), and that the levels of thermal stress in *P. vulgata* are particularly high on shores close to its limit of distribution, even in shaded microhabitats (Lima *et al.*, 2016), as SST

on these shores regularly approach the 23 °C threshold (shores G, I and N, Appendix S1).

The present findings also highlight the central role played by regional oceanographic features in shaping the environmental mosaic. In particular, coastal upwelling, which is a dominant feature along northwest Iberia during summer (Lemos & Pires, 2004), can be seen severely disrupting the link between water and air temperature, ensuring that either water temperature is high, or air temperature is high, but never both (e.g., Moledo, shore L; Fig. 4). This means that in northwest Iberia limpets are either enduring very stressful low tides but subsequently recover during low tide, or their basal metabolic level is elevated but low tides are relatively forgiving. Conversely, in the southeast Bay of Biscay and south Portugal, limpets would have to withstand more than 20 days per year of highly stressful low tides from which recovery during high tide would not be possible, due to extremely high water temperature (Fig. 4).

When examining longer timespans, model data revealed a dramatic change in the thermal landscape along the Atlantic European coast over the period 1950–2100 (Fig. 5). Most models agree that conditions were largely favorable during the 1950s, and that the 23 °C SST threshold was consistently crossed only southwards of shore N. This pattern is inline with the distribution of *P. vulgata* reported at that time (Crisp & Fischer-Piette, 1959), especially regarding the southernmost range limit, which was described to be at Odeceixe, southwest Portugal, a shore <10 km south of shore N. In addition, uncertainty concerning the conditions in southeast Bay of Biscay (few models agreed conditions were severe during the 1950s; Fig. 5, around shore H) is also matched in the reports on the distribution of *P. vulgata* (Crisp & Fischer-Piette, 1959), which highlight its absence from wave-exposed locations around Biarritz (shore H), but presence in wave-sheltered areas of Saint-Jean-de-Luz (<15 km south of shore H). Toward the end of the 21st century, however, all models agree that conditions will severely deteriorate off southwest Portugal (i.e., almost all years after 2050 were predicted to have at least 30 days with SST at or above 23 °C; Fig. 4, between shores M and O), and most models agree that conditions will also worsen along the coast of the Bay of Biscay and off northwest Portugal (Fig. 5, between shores G and I, and L and M, respectively). By the end of the 21st century, only the northwest of France and northwest of Iberia are projected to still have thermal conditions that are permissive to *P. vulgata*. Thus, the degree at which this species will be able to maintain its equatorial limit in southern Portugal or withstand the warming in the Bay of Biscay will mostly depend on its ability to locally adapt to

elevated temperatures (Austin, 2002; Hoffmann & Sgrò, 2011).

The impending retreat of range limits identified here represents an important risk, well beyond the mere exclusion from a single stretch of coast. On the one hand, the westward widening of the gap in the Bay of Biscay would extend even further a natural gap present northward from Biarritz, where, with few exceptions, the coast is mostly sandy (i.e., not suitable for rocky shore organisms such as *P. vulgata*). This means connectivity between populations from northern Iberia and northwest France could become reduced, or even compromised. On the other hand, the northward shift of the southern limit would increasingly compress the Iberian populations into the northwest of the peninsula. Populations of *P. vulgata* in this region seem to be sustained by cool water temperatures during summer, brought about by regional coastal upwelling, which allow limpets to withstand the locally high air temperatures (shores J, K and L; Figs 3 and 4). As there are indications that the Iberian upwelling regime could be becoming more relaxed (Lemos & Pires, 2004; Lemos & Sansó, 2006; Pardo *et al.*, 2011), contrary to global intensification trends (Varela *et al.*, 2015; Wang *et al.*, 2015), or that it can be shifting northwards (Ryckaczewski *et al.*, 2015), there is a risk that rising SST could render the whole west Iberia too hot for many intertidal species. Conversely, if upwelling is maintained or intensified, some intertidal species may actually become even more buffered from increases in air temperatures.

Even though this study did not explicitly test the effects of variances in temperature, some insights may be drawn regarding their likely role in influencing ecological responses to edaphic factors. At a short temporal scale (i.e., daily), our results suggest that for some intertidal species increasing the daily temperature range is not necessarily detrimental – our most variable treatment – ‘cold water, hot air’ – didn’t result in elevated thermal stress levels. At larger temporal scales (i.e., seasonal or decadal) the outcome will be determined by the nature of the future climate variability. If an increase in the frequency of extreme events is observed mainly in air temperature, consequences will be small for species with responses similar to the one found in *P. vulgata*. If, on the other hand, such events also become more prevalent in water temperature, then the effects should be much more severe. In addition, the reported and predicted geographical heterogeneity of climate change, the different rates at which oceans and the atmosphere are warming (Lima & Wetthey, 2012), and the fact that this study focused on a single population from a location in the center of distribution of *P. vulgata*, further enhance the uncertainty of these scenarios, especially for populations at the distributional edges.

The present study emphasizes the role of thermal stress in shaping the distribution of organisms and provides tools for the establishment of highly detailed mechanistic models for the forecast of species' distributions via the characterization of a temperature threshold. It also illustrates how coupling information on the physiological limits of species with highly detailed microhabitat environmental data is crucial for the correct interpretation of complex biogeographic responses to climatic changes, as has been previously suggested (Wetthey *et al.*, 2011; Seabra *et al.*, 2015). These findings reinforce the notion that intertidal species are especially vulnerable to climate change, and that regional climatic and oceanographic features such as coastal upwelling may be of vital importance for the sustaining of current intertidal communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Global Circulation Model/Regional Circulation Model combinations used in ensemble predictions of future biogeographic change.