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Repeatable patterns of small-scale spatial variation in intertidal mussel beds and their implications for responses to climate change[☆]

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ABSTRACT

The interaction of ocean conditions and weather with small-scale physical features of a habitat can have profound effects on the experiences of individual organisms. On topographically complex shorelines, and particularly within dense aggregations of organisms such as mussel beds, a mosaic of environmental conditions can develop, and the resulting variation in conditions within the aggregation could drastically alter the performance of neighboring individuals. Using a suite of sensors mounted to individual *Mytilus californianus* mussels over two summer field deployments, we have characterized the temperature variation and valve gaping behavior differences found at two spatial scales: within a group separated by centimeters, and between groups of mussels located at the upper and lower extents of the natural mussel zone separated by meters. While temperature conditions near the lower edge of the mussel bed were generally more benign, temperature extremes were similar at both heights in the bed, and variation in body temperature among neighbors increased as the daily mean temperature increased. These patterns were similar across years despite a 3.8 °C difference in mean air and seawater temperatures between years. Gaping behavior was also highly variable among individuals, though that variability diminished at the high end of the mussel bed where the total time mussels spent submerged was much more constrained. These data indicate that an individual mussel's physiological status and past history can be drastically different than those of its nearby neighbors, complicating our ability to characterize representative conditions within a habitat. These observations also provide for the possibility that the impacts of future climate change will be highly specific to certain individuals based on their relative exposure or protection within the mosaic. To address such possibilities, future work must examine the correlation between genotypic and physiological traits that determine performance and individuals' unique experiences in their disparate micro-environments.

1. Introduction

The manner in which an organism experiences and responds to fluctuations in its local environment is driven by extrinsic factors that the organism may have no control over, and intrinsic factors that the organism can control to some extent. Characterizing the physiological status and stress tolerance of a species under current and future climate regimes requires insight into the range of inter-individual variation in how organisms experience their environment (Logan et al., 2012). At small spatial scales that are most relevant to individual organisms (particularly sessile organisms), the environment may be relatively stable, or highly variable, and the experiences of neighboring individuals just a few body lengths away might be radically different (Chapperon and Seuront, 2011; Chapperon et al., 2017; Denny et al., 2011; Lathlean et al., 2016; Miller and Dowd, 2017; Pincebourde et al., 2016). The potential for wide variation in how individuals experience their environment increases the chances that local populations might tolerate environmental extremes that extirpate certain individuals, leaving behind other members of the population that either tolerate the extreme conditions (Denny et al., 2011), or avoid the extreme conditions altogether through behavioral means (Miller and Denny, 2011) or by virtue of living in refuge microhabitats (Chapperon and Seuront, 2011; Garrity, 1984; Harper and Williams, 2001).

The intertidal zone, particularly rocky shores with high topographic complexity, is commonly characterized by large variation in environmental parameters driven by the oceanic and atmospheric conditions

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that alternate their effects on the habitat as the tide cycles high and low (Denny et al., 2009; Mislan et al., 2009). Relatively benign conditions may quickly transition to stressful situations as the confluence of tide height, wave splash, air temperature, water temperature, sun, and wind can create extremely hot, cold, desiccating, or high-flow stresses that exceed the physical or physiological limits of individual organisms (Denny et al., 2006; Helmuth et al., 2011). The extent and severity of these extreme conditions may be highly dependent on local physical and biological factors, so that neighboring individuals experience very different temperatures, desiccation stress, or water flow (Broitman et al., 2009; Helmuth, 2002).

Topographic complexity can create wide variation in microhabitat environmental conditions over the space of centimeters to meters. A particularly well-studied example is the effect of substratum orientation (slope and aspect) on solar exposure and resultant temperatures during low tide (Denny and Harley, 2006; Harley, 2008; Helmuth and Hofmann, 2001; Miller et al., 2009; Wethey, 1984). The orientation of the substratum, in concert with tide cycles, will influence the timing and severity of solar exposure that can lead to temperature extremes (Denny et al., 2006). East-facing surfaces can have more stressful temperature conditions during morning low tides, while west-facing surfaces are more likely to have stressful temperature conditions during afternoon low tides, and south-facing surfaces (or north-facing in the southern hemisphere) should endure the most extreme conditions during midday low tides (Harley, 2008; Hayford et al., 2015; Wethey, 1984). The orientation of the substratum may also influence exposure to wave splash, which can lower the 'effective' shore level by allowing splash or wave run-up to submerge a plot earlier than the still water level would predict (Gilman et al., 2006; Harley and Helmuth, 2003; Mislan et al., 2011). High topographic relief, particularly the presence of crevices that can funnel wave splash (O'Donnell and Denny, 2008) or shade an organism, can create thermal refuges in an otherwise thermally challenging location (Chapperon and Seuront, 2011; Chapperon et al., 2016).

In addition to the role of substratum complexity, biogenic structures can contribute to the patchwork of stressful or non-stressful conditions, and aggregations of sessile organisms, such as mussels and oysters, can create refugia within the three dimensional structure of the group (Chapperon et al., 2017; Helmuth, 2002; Lathlean et al., 2016; McAfee et al., 2018; Mislan and Wethey, 2015). Shading of neighbors or multilayer aggregations can promote the retention of moisture during low tide and moderate temperature swings, so that individual animals might experience relatively low-stress conditions while their nearby neighbors are exposed to extremes (Harley, 2008; Jurgens and Gaylord, 2017; Mislan and Wethey, 2015; Nicastro et al., 2012). Two-dimensional and three-dimensional structural complexity created by aggregations of organisms can also be a cause and consequence of wave-driven dislodgement that can create patchworks of gaps in aggregations (Cole and Denny, 2014; Denny, 1987; Guichard et al., 2003) that then create small-scale differences in water flow and solar exposure that could impact organismal behavior and performance (O'Donnell, 2008).

The cycling of the tides and ocean swell interact with shoreline topography and biogenic three-dimensional structures to control the opportunities for feeding, aerobic respiration, and waste removal, particularly for sessile bivalve filter feeders such as mussels and oysters (Mislan et al., 2011). At the scale of meters, particularly up and down the shore, the duration of submergence and aerial emersion can vary on the order of hours per day (Mislan et al., 2011), and these differences can affect gene expression patterns and physiological status differences over those scales (Place et al., 2012). Even at smaller spatial scales, the effect of wave run-up, splash, and neighbors or nearby topographic features could impact when individuals are submerged or emersed, and when they elect to open the valves to carry out the necessary tasks of feeding, aerobically respiring, and excreting wastes, or when they decide to close the valves, curtailing these processes, and waiting for more favorable conditions (Bayne et al., 1976).

Our primary goal in this study is to synthesize data from two summers of individual-scale observations to illustrate the range of variation in body temperature and gaping behavior that can be found within a mussel bed. We use the California mussel, *Mytilus californianus,* which is a dominant space holder in the mid-intertidal zone along much of the northeastern Pacific coast, and which can construct multi-layer beds that cover many square meters and provide structure for a multitude of other mobile and sessile species (Dayton, 1971; Lohse, 1993; Suchanek, 1979). These observations were carried out during summer with the goal of characterizing the amount of inter-individual variation in temperature stress during warm weather and periods of calm ocean swell. Although the hottest conditions for mussels occasionally occur outside of summer at this site (Helmuth et al., 2006), greater wave splash in other seasons might tend to homogenize individual temperature and valve gape patterns, so we targeted our observations to the calmer summer season. Using sensors to measure internal body temperature, valve gape, and orientation, we show that mussels living only centimeters apart at the same shore height can differ substantially in their individual experiences of environmental conditions, and that both the lower and upper ends of the mussel zone on the shore can experience these wide variations between individuals. We show consistency in the inconsistency of thermal stress and valve gaping behavior over small spatial scales across years, increasing confidence in the persistence of these patterns. We then discuss potential implications of these patterns for physiological variation within mussel aggregations and for efforts to forecast the biological outcomes of climate change. The existence of large differences in individual experiences of environmental variation may be key to estimating the resistance of this important foundation species to environmental stresses under future climate change.

2. Methods

2.1. Data acquisition system

During July and August of 2015 and 2016, we deployed MusselTracker datalogger systems in groups of adult *M. californianus* placed in the field at Hopkins Marine Station, in Pacific Grove, CA (HMS hereafter, 36.6217°N, 121.9043°W). The MusselTracker system has been previously described in Miller and Dowd (2017), and consists of custom designed microcontroller dataloggers that record data from a suite of sensors attached to live mussels. Each instrumented mussel had a 30 gauge K-type thermocouple wire inserted through a hole drilled at the midpoint of the ventral margin of the left valve, a combination 3-axis accelerometer and 3-axis magnetometer glued near the anterior end of the right shell valve, and a Hall effect magnetic sensor and neodymium magnet glued to opposite valves at the posterior end of the shell. From these sensors, we could obtain high frequency (1 Hz) measurements of internal body temperature, valve gape, and orientation (4 Hz).

The focal mussels were originally collected from two mussel beds at the same shore height at HMS, one relatively wave-exposed, and one relatively wave-protected (Denny et al., 2011; Dowd et al., 2013; Jimenez et al., 2015). Instrumented mussels (mean shell length = 66.5 mm, range = 60.8 to 72.0 mm in 2015; mean shell length = 65.1 mm, range = 60.6 to 69.1 mm in 2016) were placed on acrylic plates (45 × 30 cm), with watertight boxes attached to two ends of the plates to house the dataloggers and batteries. Additional 40–70 mm adult mussels collected from the shoreline at HMS were packed around the instrumented mussels to form a densely packed single-layer bed, creating densities ranging from 777 to 955 mussels m^{-2}. These densities were lower than nearby natural mussel beds composed primarily of mussels in the 40–70 mm size range, which have densities ranging from 1000 to 3325 mussels m^{-2} (L. Miller, pers. obs.). The mussels were held in flow-through seawater tables at HMS while sensors were being attached. While the mussels were held in the water table, they had the opportunity to attach to the acrylic plate and their neighbors using byssal threads. Prior to deployment in the field, the plates were covered with 5 mm plastic mesh to help hold the mussels in place for the first two days of the deployment.

2.2. Field deployment

In July 2015 and July 2016, we deployed experimental plates, each containing 12 instrumented mussels, to locations near the lower edge and upper edge of the *Mytilus* zone at HMS. The low-shore location (1.04 m above mean lower low water [MLLW]) was situated on a rock face tilted 45° from horizontal and facing southwest, while the high-shore location (1.72 m above MLLW) was on a horizontal rock surface. The two locations were separated by 4.5 m horizontal distance across the shore, with the low-shore location located closer to the ocean, and the high-shore site situated inshore. Data from the 2015 deployment have previously been described in Miller and Dowd (2017), along with a third plate deployed in a high-shore tide pool, which will not be considered here. The 2015 deployment ran from 15 July to 6 August (21 full days and two partial days), while the 2016 deployment spanned a similar period of the year, running from 3 July to 3 August (29 full days and two partial days). During the 2015 deployment, we lost three mussels at the high-shore location to predation by black oystercatchers, (*Haematopus bachmani*, detailed in Miller and Dowd, 2019), and one mussel to predation during 2016. One high-shore mussel may have died due to high temperature exposure during the 2016 deployment after reaching a maximum temperature of 37.2 °C, and one low-shore mussel appears to have been dislodged by wave action.

2.3. Environmental data

We obtained measured tide height values at 6 min intervals from the NOAA tide gauge located in the Monterey Harbor, approximately 2.3 km from the field site. A caretaker at HMS sampled water temperature each morning on a beach adjacent to the field site. A weather station at the field site collected air temperature. The Hopkins Marine Life Observatory manages a repository of water temperature and weather station data (http://mlo.stanford.edu). A wave rider buoy situated approximately 400 m north of the field site reported significant wave height twice per hour (Coastal Data Information Program buoy 158, Scripps Institute of Oceanography). Summary statistics for the environmental conditions are shown in Table 1.

2.4. Statistical analyses

We used R version 3.5.1 for all analyses (R Core Team, 2018). We refer to data from our previous 2015 deployment at the same locations on the low shore and high shore for comparison across years, and the summary statistics reported here were calculated using the same methods as the 2015 analysis (Miller and Dowd, 2017). Because a primary focus of this work was to elucidate variation among individuals in close proximity to each other, each mussel was treated as a biological replicate, but the fact that we only had a single experimental plate per shore location does limit the inferences that could be drawn about other mussel beds in other locations. Nonetheless, for adult populations of long-lived organisms such as mussels it is this highly local variation that influences individual and population success.

Table 1
Environmental conditions at Hopkins Marine Station during experimental deployments from July 15 to August 6 2015 and July 3 to August 2 2016.

Variable (units)	Overall maximum		Mean ± s.d. of daily maximum	
	2015	2016	2015	2016
Solar irradiance ($W\,m^{-2}$)	1107	1010	914 ± 116	853 ± 195
Air temperature (°C)	24.1	17.4	19.1 ± 2.0	15.3 ± 1.08
Sea surface temperature (°C)	21.0	15.1	17.1 ± 1.1	13.3 ± 0.9
Significant wave height (m)	1.45	1.51	0.61 ± 0.18	0.8 ± 0.12

Although we originally collected temperature and valve gape data at 1 s intervals, we elected to subset the large datasets and analyze temperature and gape data on 10 s intervals. For these relatively slow-changing quantities, this reduced dataset should not substantially alter the derived statistics.

2.5. Temperature analyses

For daily summary statistics related to body temperature, we analyzed all mussels on a plate that had no more than 1.5 h of missing data in a given day. Missing data were due mainly to battery failures or wire breakage of the delicate thermocouple leads. For each day, we extracted the maximum and minimum temperatures achieved by each mussel. The maximum heating rate and cooling rate on each day were estimated iteratively by fitting a linear regression fit to 45 min data windows throughout the day, shifting the window by 5 min each time. Among the available mussels on a plate on each day, we calculated the range of maximum and minimum temperatures achieved and the range of fastest heating and cooling rates, along with the mean and standard deviation of those ranges. To generate metrics of thermal history of mussels during the course of the deployment, we used the subset of mussels on each plate that had nearly complete temperature records, missing no more than 2 days out of 21 full days in 2015, or 7 days of data out of the 29 full days of the deployment. For these mussels, we calculated average daily maximum temperature and cumulative time spent at body temperatures above 25 °C, a temperature that generally marks the start of the stress response in intertidal ectotherms from this habitat (Buckley et al., 2001; Dong et al., 2008; Lockwood et al., 2010; Miller et al., 2009). For this same subset, we calculated the ranking of each mussel in terms of daily maximum temperature and used a Kruskal-Wallis test to determine if some individuals were consistently hotter than their neighbors on the same experimental plate. Using hourly temperature data derived from these mussels with interpolated temperature time series, we estimated autocorrelation functions for time lags up to two weeks.

We fit regression models to the average daily maximum temperature data for the subset of mussels with nearly complete temperature records on the two plates in 2016, using relative location on the plate as a predictor to look for evidence of a spatial gradient in temperature stress. On the horizontal high-shore plate, location was expressed as distance in cm from the northeast corner of the plate along the east-west and north-south axes. For the low-shore plate, which was situated on a rock tilted 45° above horizontal, location was expressed as a distance along the east-west axis, and along the upshore-downshore axis. We ran Mantel tests to examine potential correlations between the distance matrix of daily maximum temperatures and the distance matrix of mussel locations on each plate, both calculated using simple Euclidean distances and 9999 permutations using the R package *vegan* (Oksanen et al., 2019).

2.6. Valve gape analyses

Because of the potential for unique individual gaping behavior syndromes, we limited our comparison of inter-individual gaping behavior to mussels that had near-complete data records. During the 2015 deployment, 9 mussels at the low-shore site and 6 mussels at the high-shore site had nearly complete gape records, missing no more than 3 days out of the 21 full days of the deployment. For the 2016 deployment, both the high and low-shore plates had 5 mussels missing no more than 3 days out of the 29 full days of the deployment. The number of available mussels varied from day to day due to battery failure, sensor failure, or loss of the magnet. Based on plots of the empirical cumulative density functions for all mussels, we used a 20% gape opening as our threshold for delineating "closed" mussels from "gaped" mussels (Miller and Dowd, 2017). We calculated the maximum, minimum, mean, standard deviation and coefficient of variation of time mussels spent gaped wider than 20% on each day.

We examined the relationship between temperature variation and gape time variation by fitting models to data on the maximum temperatures achieved by individual mussels during a low tide period and their gape behavior during the subsequent 24 h using the 2016 data. We fit a linear model with the overall group maximum temperature during low tide as a predictor and range of gape time among mussels as the response, as well as a model with the range of maximum temperatures among the group of mussel during low tide as the predictor, and range of gape time as the response. Finally, we fit linear models of individual mussels' maximum temperatures during each low tide as a predictor against their individual time spent gaping wider than the 20% threshold during the subsequent 24 h, with a random effect for individual mussel identity to account for the repeated measures of mussels through the course of the deployment, using the R package *nlme* (Pinheiro et al., 2018). Models were fit for the high and low-shore locations separately.

3. Results

3.1. Body temperature

Temperature data from both the 2015 and 2016 summer field deployments showed similar maxima, minima, and ranges in most cases (Table 2). At the upper end of the mussel zone at HMS, we observed slightly higher average differences in individual daily maximum temperatures in 2016 (7.8 °C) compared to 2015 (7.0 °C), but average differences in daily maxima at the low-shore location were reduced in 2016 (2.9 °C vs. 4.5 °C in 2015). The greatest range of maximum temperatures achieved during a single day during each year was similar on the high-shore plate (14.2 and 14.0 °C, 2015 and 2016 respectively), although the low-shore location had a greater range of maximum temperatures within a single day in 2016 (15.8 °C) than 2015 (12.8 °C). On days with calmer wave conditions and warmer weather conditions, leading to higher maximum body temperatures, the difference in maximum temperatures achieved by the warmest and coolest individual mussels on a plate increased (Fig. 1, Fig. 2). The breadth of the range of maximum temperatures within a location actually varied more day to day at the low-shore site in both years (s.d. of the range of T_{max} = 3.63 to 4.29 °C) than the high site (s.d. = 2.6 °C), indicating that although the high location had a broader range of maximum temperatures each day, the low site was more variable day to day in how large that range might be. At the high-shore location in 2016, among the mussels with nearly complete temperature records, certain mussels had consistently higher daily maximum temperatures than their neighbors (Kruskal-Wallis rank sum test, $\chi_5^2 = 39.1$, $P < 0.001$), but there were not consistent differences among the mussels at the low-shore location. During the 2015 deployment, both the high and low-shore plates had a single mussel that was consistently ranked cooler than its neighbors (Kruskal-Wallis rank sum test, high shore: $\chi_5^2 = 18.9$, $P = 0.002$; low shore: $\chi_6^2 = 13.2$, $P = 0.039$), but the remaining mussels did not consistently rank warmer or cooler than the others.

Table 2

Inter-individual temperature variation and temperature change rate statistics for mussels deployed in the field during July and August 2015 or 2016. Sample sizes on each day ranged from 5 to 12 at the high-shore site (mean = 9 mussels per day), and 5 to 11 at the low-shore site (mean = 8 mussels per day).

Variable (units)	High shore		Low shore	
	2015	2016	2015	2016
Overall maximum temperature T_{max} (°C)	38.5	37.2	33.8	35.0
Mean range of T_{max} (°C)	7.0	7.8	4.5	2.9
s.d. of range of T_{max} (°C)	2.6	2.65	4.29	3.63
Max. range of T_{max} (°C)	14.2	14.0	12.8	15.8
Mean individual T_{max} (°C)	25.8	24.2	19.8	16.7
Overall minimum temperature (°C)	11.8	10.0	12.2	11.0
Mean range of T_{min} (°C)	0.94	0.58	1.3	0.62
s.d. of range of T_{min} (°C)	0.25	0.19	0.61	0.43
Max. range of T_{min} (°C)	1.5	1.0	2.75	1.8
Mean individual T_{min} (°C)	13.9	12.0	15.0	12.7
Overall maximum heating rate $Q_{max}{}^{+}$ (°C h^{-1})	20.2	15.6	12.4	14.2
Mean range of $Q_{max}{}^{+}$ (°C h^{-1})	5.4	5.4	1.8	2.7
s.d. of range of $Q_{max}{}^{+}$ (°C h^{-1})	4.15	3.28	2.58	3.63
Max. range of $Q_{max}{}^{+}$ (°C h^{-1})	14.7	13.0	10.8	12.5
Mean individual $Q_{max}{}^{+}$ (°C h^{-1})	6.8	6.1	1.3	2.1
Overall maximum cooling rate $Q_{max}{}^{-}$ (°C h^{-1})	−22.8	−22.4	−16.8	−35.5
Mean range of $Q_{max}{}^{-}$ (°C h^{-1})	6.2	7.9	2.4	4.1
s.d. of range of $Q_{max}{}^{-}$ (°C h^{-1})	3.10	3.75	3.99	6.61
Max. range of $Q_{max}{}^{-}$ (°C h^{-1})	13.5	17.2	16.0	30.7
Mean individual $Q_{max}{}^{-}$ (°C h^{-1})	−7.9	−8.3	−1.3	−2.9

Minimum temperatures showed a similarly small range of variation among individuals in both 2015 and 2016 (average range between 0.58 and 1.3 °C across both locations and years). Minimum temperatures were set either by ocean temperature or by nighttime low tide conditions. In both 2015 and 2016, the high-shore mussels experienced lower average minimum temperatures than the low-shore mussels (1 °C cooler on average in 2015, 0.7 °C cooler in 2016), primarily due to their more frequent nighttime aerial emersions during low tide.

Heating and cooling rates varied substantially in both 2015 and 2016 (Table 2, Fig. 3). The maximum heating rate measured at the high-shore location in 2016 was 15.6 °C h^{-1}, which was slower than the fastest heating rate observed in 2015 (20.2 °C h^{-1}). We found isolated examples of very high heating rates at the low-shore location, with a maximum rate of 14.2 °C h^{-1} that exceeded the fastest heating rate we measured there in 2015 (12.4 °C h^{-1}). These occasional high heating rates were accompanied in some instances by large differences in individual heating rates on the same day (maximum range of 13.0 °C h^{-1} on the high-shore plate, 12.5 °C h^{-1} on the low-shore plate in 2016), although the average range in heating rates across days tended to be much more restricted (5.4 °C h^{-1} on the high shore in both years, 1.8 to 2.7 °C h^{-1} on the low shore in 2015 and 2016 respectively). The fastest rates of cooling were faster in 2016 on the high and low-shore than in 2015. Fast cooling rates appear to be driven by warm mussels being suddenly splashed by the incoming tide, rather than cooling off while still emersed as the sun transits the sky, but both modes of cooling were present in our data set.

For mussels with nearly-complete temperature records, we found wide variation in the month-long thermal history of high temperature exposures among mussels at the high-shore location. The average daily maximum temperature among the six high-shore mussels with long term records in 2016 was 23.6 °C ± 2.43 °C (mean ± 1 s.d.), with a range of 21.2 °C to 27.7 °C. The accumulated hours where individual mussel body temperatures exceeded 25 °C ranged from 65.4 to just 0.6 h (mean ± 1 s.d.: 22.5 ± 25.7 h) among those high-shore mussels. The nine mussels with nearly-complete temperature records at the low-shore site in 2016 yielded more homogeneous average daily maximum body temperatures of 16.1 ± 0.56 °C (mean ± 1 s.d.). Only one of the nine mussels at the low-shore site with nearly-complete records exceeded 25 °C during the month, for a total of 47 min, although one other mussel on the plate with an incomplete temperature record exceeded 25 °C for 3.6 h over three days prior to the thermocouple failing. None of the other mussel temperature records from the low-shore location exceeded 25 °C during the 2016 deployment.

High-shore mussel body temperatures in 2015 and 2016 displayed positive autocorrelation peaks at time lags that corresponded to

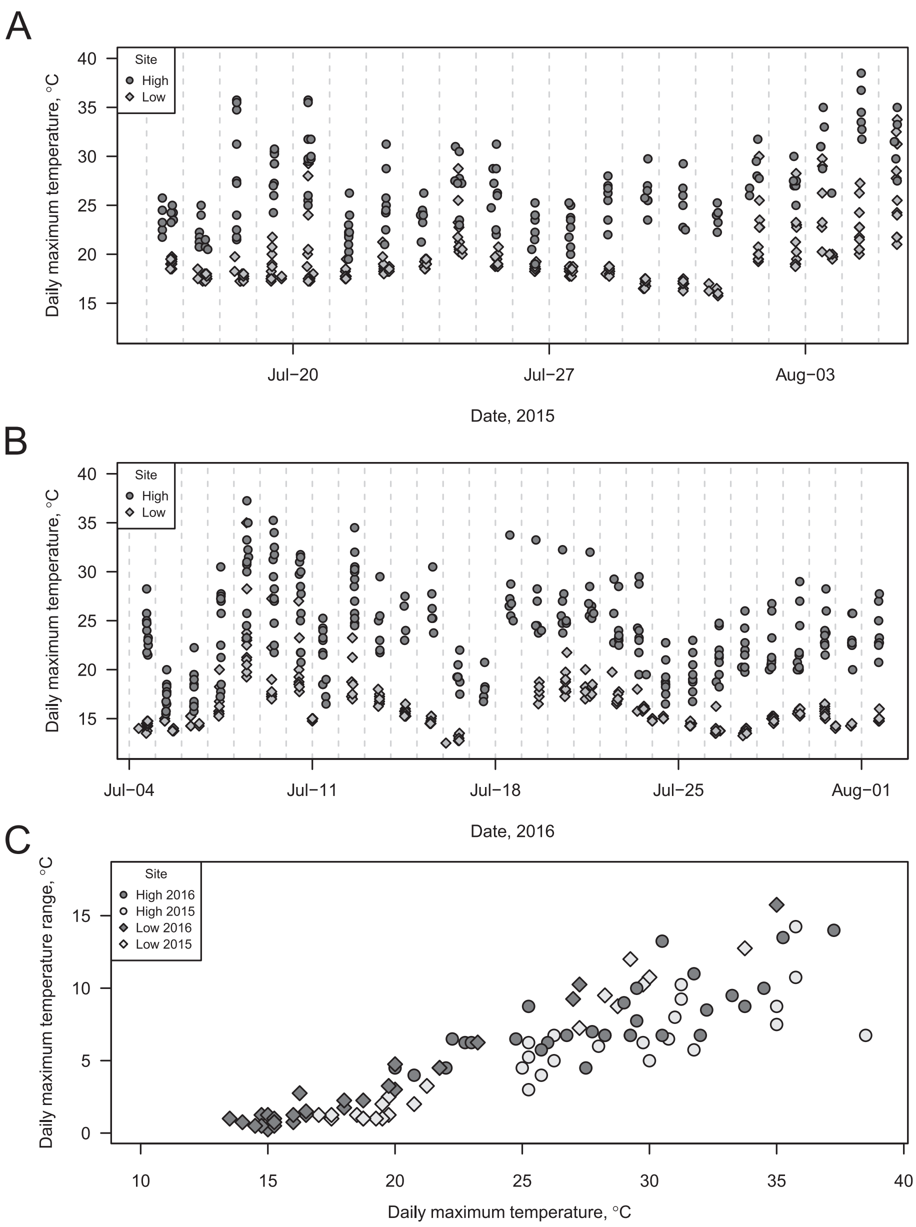

Fig. 1. Daily maximum temperatures for mussels at the high and low-shore locations during the (A) 2015 and (B) 2016 deployments. Points are arranged horizontally by the time of day the maximum temperature was achieved. No data were available for the low-shore location on July 17 & 18, 2016. C) Daily range between the hottest and coolest maximum mussel body temperatures on an experimental plate plotted against the maximum temperature of the hottest mussel on a given day during the 2015 and 2016 deployments. Each point represents data from one of the 21 or 29 full days of the deployment (2015 and 2016, respectively). High site $r = 0.68$ and Low site $r = 0.96$, $p < 0.001$ for both correlations. The data shown in each plot include all mussels from each day that were missing fewer than 1.5 h of data on that day. Sample size per day varied from n = 5–12 at the high-shore location and n = 5–11 at the low-shore location.

multiples of a 24 h cycle, so that for a given time of day, temperatures near the same time on subsequent days were positively correlated. Strong negative autocorrelation peaks occurred at time lags offset from the positive peaks by 12 h, indicating that body temperatures measured during the opposite phase of the tidal or diurnal cycle were negatively correlated. Low-shore mussels in both years had positive body temperature autocorrelations at time lags encompassing the first 48 h, and then became consistently negatively correlated for time lags between 3 and 9 days. Autocorrelation data from only one representative mussel per site are shown in Fig. 4, but each of the neighboring mussels with nearly-complete time series in each combination of shore location and year showed the same pattern as those displayed.

For the high-shore location in 2016, the regression model of temperature fit against relative location (distance from the northeast corner of the plate) showed no significant effect of east-west or north-south location on the plate (east-west: $F_{1,\ 3} = 5.49$, $P = 0.1$; north-south: $F_{1,\ 3} = 4.49$, $P = 0.3$). A Mantel test of the daily maximum temperature and distance between mussels on the plate revealed no relationship between distance and temperature dissimilarities among the six mussels with near-complete records (Mantel $r = 0.36$, pseudo-$P = 0.1$), although there was evidence of increasing temperature dissimilarity as distance increased when all available mussels on each day were included ($n = 5$–12 mussels per day, Mantel $r = 0.40$, pseudo-$P = 0.01$; Fig. 2A). On the low-shore experimental plate, which was oriented on a sloped rock so that one axis of the plate ran east-west, while the other axis ran upshore-downshore, the regression of average daily maximum temperature was associated with a significant effect of height on the plate ($F_{1,\ 8} = 10.3$, $P = 0.012$) and no effect of east-west location ($F_{1,\ 8} = 3.6$, $P = 0.1$), with mussels near the upper edge of the plate experiencing warmer temperatures more frequently than those nearer the bottom edge of the plate (Fig. 2B).

3.2. *Gaping behavior*

We observed large differences in the amount of time mussels spent with the valves gaped open at the low and high-shore sites in both years (Table 3, Fig. 5A), with mussels situated on the low-shore plate spending an average of 17.3 ± 2.1 h d^{-1} (mean ± 1 s.d.) with the valves opened in 2016, while high-shore mussels had a much more restricted average of 5.4 ± 0.95 h d^{-1} in 2016. The difference in time

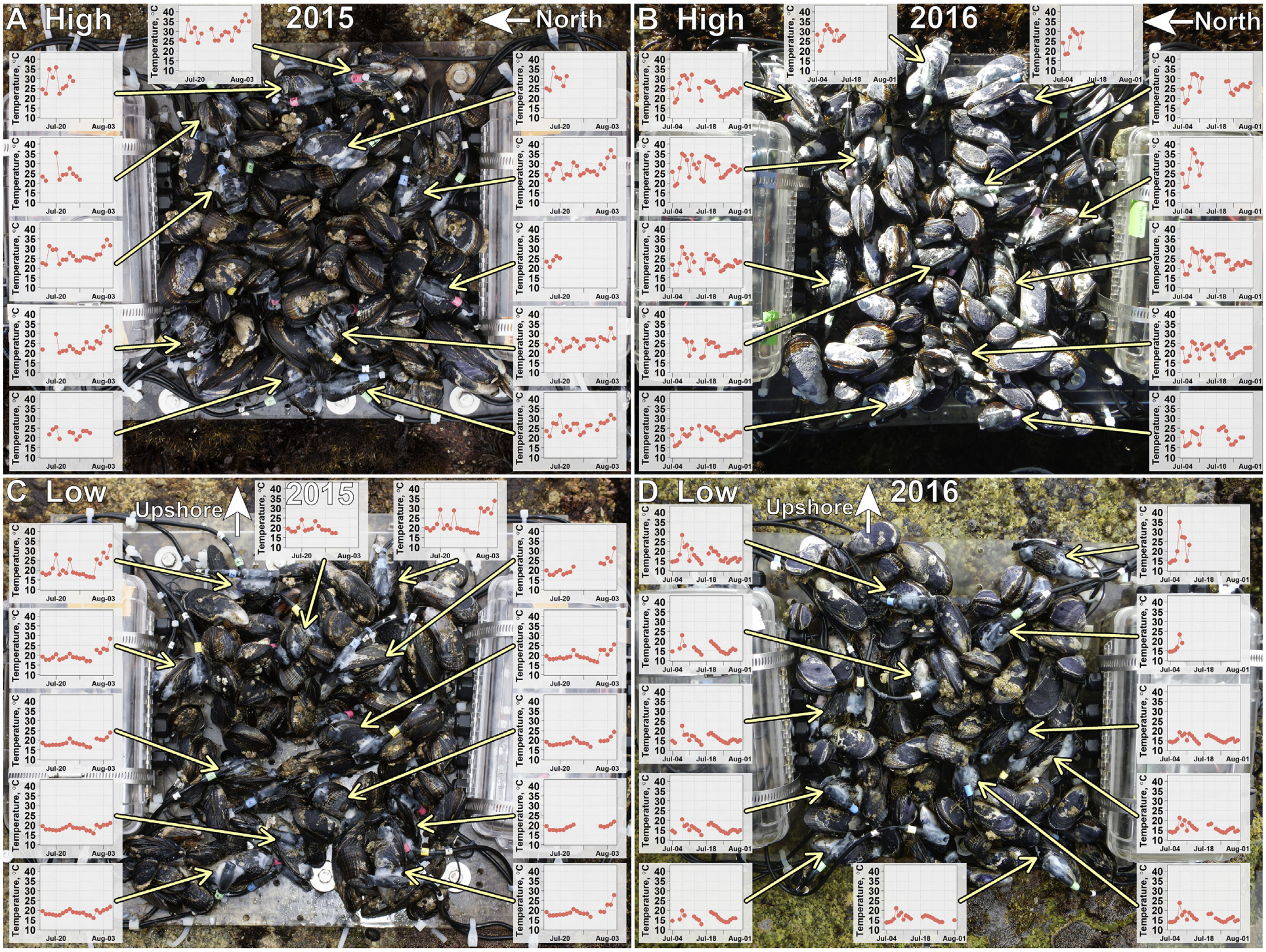

Fig. 2. Experimental plates deployed in 2015 and 2016 on the high shore (A, B) and low shore (C,D), with inset panels showing daily maximum temperatures for each day where an individual mussel had sufficient data. Arrows point from each graph to the respective mussel on the plate. The high-shore plate was horizontal, with the shoreward side of the plate at the top of the images and north indicated with an arrow. The low-shore plate was oriented 45° above horizontal, with the upshore direction labeled in the image. Due to malfunctioning temperature sensors, data for one additional mussel each on the high shore 2015 and low shore 2016 plots are not shown.

per day spent with the valves opened between the mussels that spent the most and least amount of time with valves gaped was 5.0 ± 2.87 h d^{-1} (mean ± 1 s.d.) on the low shore in 2016 (Fig. 5B). There was a smaller range of time per day spent gaped at the high-shore location (2.2 ± 1.4 h d^{-1} in 2016, mean ± 1 s.d.), likely due to the overall shorter time per day that these mussels spent submerged and the associated need to prevent desiccation during low tide by closing the shell valves tightly. The averages and ranges of time spent with the valves gaped open in 2016 are similar, though slightly higher than the values previously recorded in summer 2015 (Miller and Dowd, 2017). During the 2015 deployment, the average time gaped open was 14.4 ± 2.87 h d^{-1} (mean ± 1 s.d.) at the low-shore location and 4.4 ± 1.21 h d^{-1} at the high-shore site (Table 3). This difference was likely driven by the longer deployment in 2016 encompassing more days with spring tide conditions which would submerge both shore locations for longer during high tide, as well as higher swell conditions that kept the locations, particularly the high-shore location, wetted for longer before and after low tides.

When we analyzed the range in gape time against temperature data, we found no significant effects of either overall maximum temperature during a low tide (high shore: $F_{1,\ 49} = 1.49$, $P = 0.23$, low shore: $F_{1,\ 47} = 2.76$, $P = 0.10$), or range in maximum temperatures among mussels during a low tide (high shore: $F_{1,\ 49} = 0.33$, $P = 0.57$, low shore: $F_{1,\ 47} = 1.25$, $P = 0.27$). When we analyzed individual mussel gape time in the 24 h following each low tide against their maximum temperature achieved during the low tide, we found a significant negative relationship at both the high and low-shore sites. As maximum temperature during a low tide increased, time spent gaping in the following day declined (high shore: $\chi_1^2 = 13.1$, $P < 0.001$, estimate $= -4.2 \pm 1.4$ min C^{-1}, s.d. of random intercepts = 0.94; low shore: $\chi_1^2 = 68$, $P < 0.001$, estimate $= -44.9 \pm 5.4$ min C^{-1}, s.d. of random intercepts = 2.45).

4. Discussion

4.1. Persistent patterns of inter-individual differences across years

The structural complexity created by dense aggregations of mussels can greatly influence the body temperatures experienced by individual mussels, so that the short-term and long-term thermal histories of nearby neighbors might be quite different. Over the scale of centimeters within our high-shore mussel bed, we found individual mussels that differed in terms of daily maximum temperatures by an average of 7.0 to 7.8 °C across 21 and 29 d in two different summers, and daily

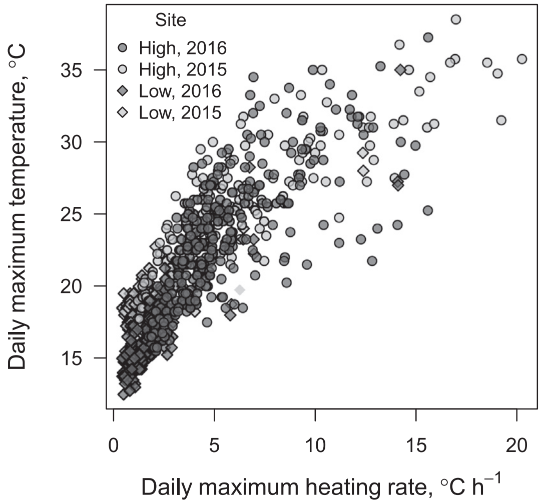

Fig. 3. Daily maximum temperature versus daily maximum heating rate over a 45 min period for each mussel for each day in 2015 and 2016. High site $r = 0.76$ and Low site $r = 0.75$, $p < 0.001$ for both correlations. The plot includes data from all mussels on each day that were missing fewer than 1.5 h of data on that day. Sample size per day varied from n = 5–12 at the high-shore location and n = 5–11 at the low-shore location.

Table 3
Inter-individual variation in length of time per day spent gaped wider than a threshold of 20% for mussels deployed at a high-shore and low-shore site during July – August 2015 and 2016. For each metric, the value was calculated among the available mussels with nearly-complete time series for each full day of the deployment, up to 21 days (2015) or 29 days (2016), and mean values were calculated across all days within each deployment. Sample sizes were $n = 6$ for the high shore 2015, n = 9 for the low shore 2015, and both locations had $n = 5$ in 2016.

Variable (units)	High shore		Low shore	
	2015	2016	2015	2016
Mean maximum time gaped > 20% (h day^{-1})	6.0	6.5	18.1	19.8
Mean time gaped > 20% (h day^{-1})	4.4	5.4	14.4	17.3
Mean s.d. of time gaped > 20% (h day^{-1})	1.21	0.95	2.87	2.09
Maximum range of time gaped > 20% (h day^{-1})	6.2	4.7	14.1	13.7
Mean range of time gaped > 20% (h day^{-1})	3.0	2.2	8.1	5.0
Mean s.d. of range of time gaped > 20% (h day^{-1})	1.6	1.38	3.1	2.87
CV of range of time gaped > 20%	0.54	0.63	0.38	0.57

maximum body temperature ranges of up to 14–14.2 °C within a single low-tide period. These small-scale differences are not just restricted to the upper edge of the mussel zone with its longer emersion times. Surprisingly, the most extreme difference in daily maximum temperatures on a single day (15.8 °C) occurred at our low-shore site when one mussel heated to 35.0 °C while a neighboring mussel located approximately 20 cm lower on the same plate only reached 19.2 °C during the same low tide exposure. Although the frequency of extreme temperature conditions may be lower on the low shore, the severity of thermal stress for some individuals may be similar to conditions higher on the shore, so that future climate change may cause impacts throughout the vertical range of *M. californianus* (Helmuth et al., 2011). The relative rankings of individual mussels in terms of their daily maximum body temperatures were only consistent for the warmest or coolest mussels in some locations in the two years; therefore, orientation and position in the bed alone make imperfect predictors of potential past and future

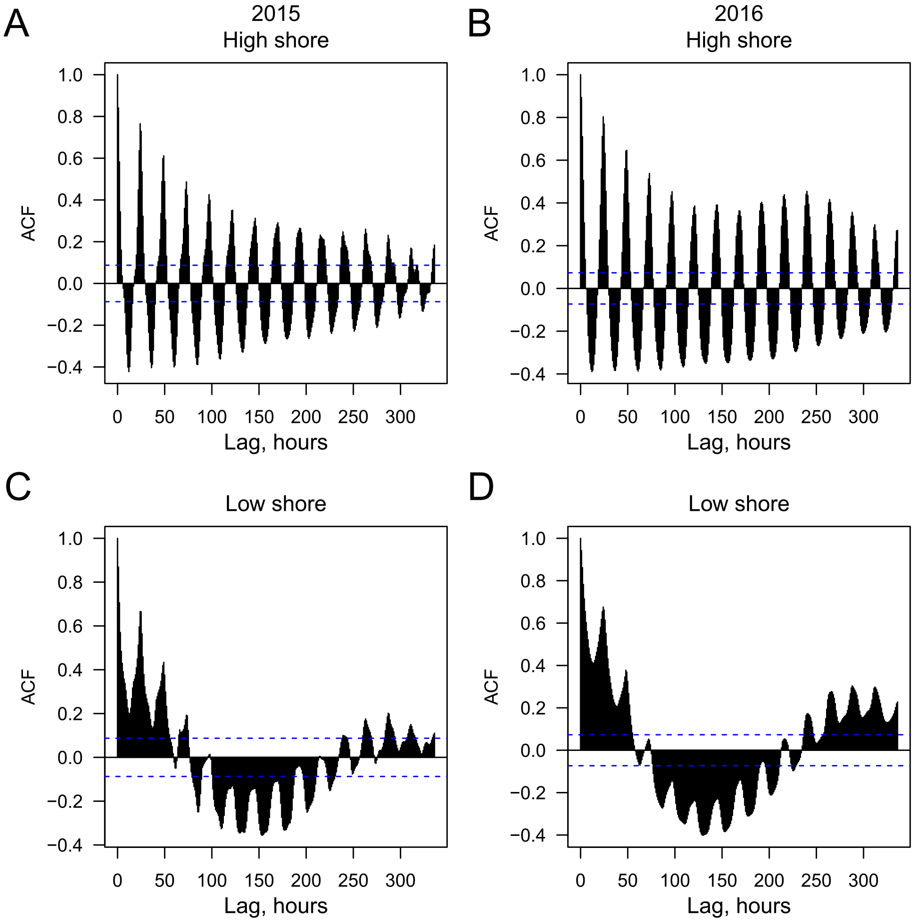

Fig. 4. Representative autocorrelation plots of hourly body temperatures of high-shore (A, B) and low-shore (C, D) mussels in 2015 (left column) and 2016 (right column). Dashed lines represent 95% confidence limits, where values within the limits are not distinguishable from autocorrelation produced by a random stationary time series. Data shown are for a single mussel in each location and year, but other neighboring mussels in the same location and year showed similar autocorrelation patterns.

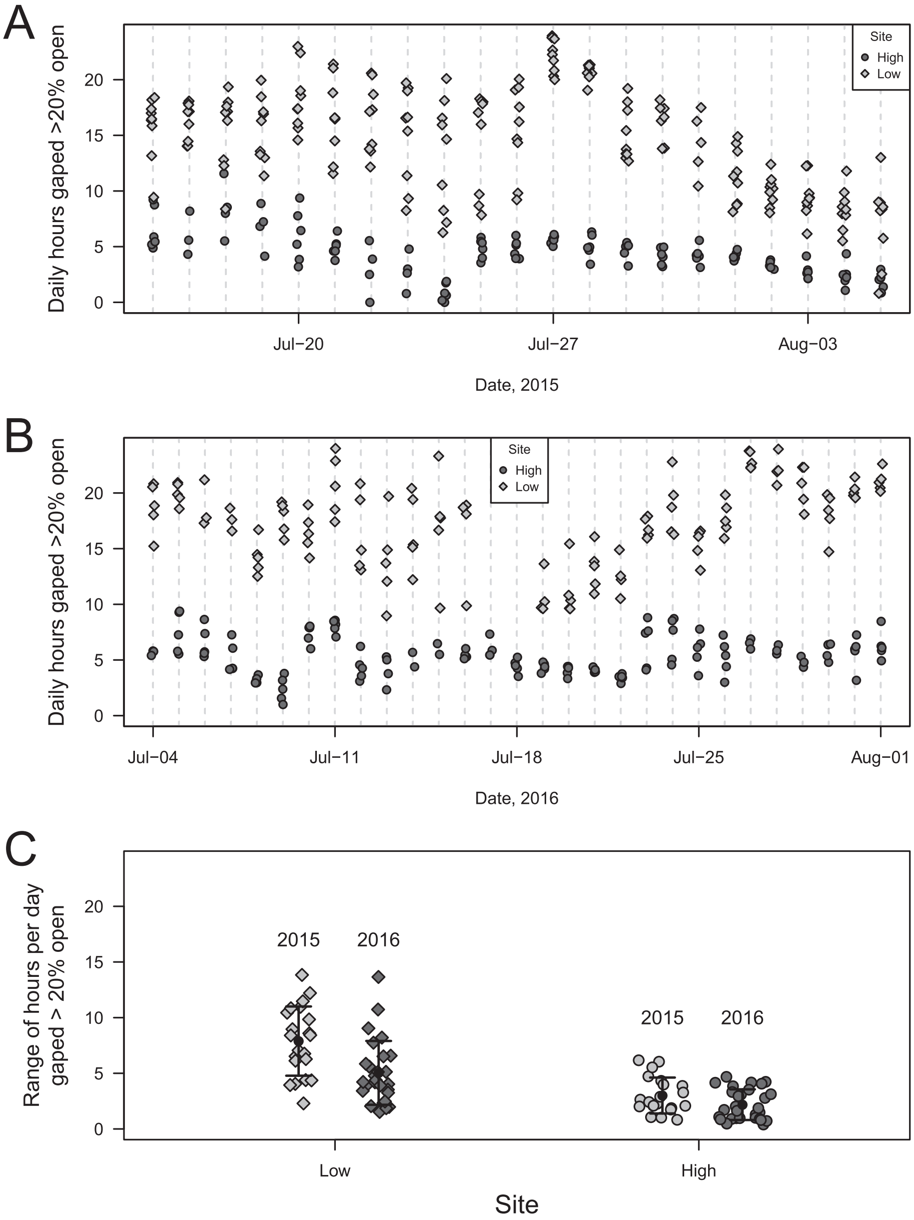

Fig. 5. Daily time spent with the valves gaped > 20% for each of the mussels at each shore location that had nearly-complete valve gape records in A) 2015 and B) 2016. Horizontal positions of points on each day are jittered slightly for clarity. C) Range of time between the longest-opened (> 20% gape opening) and shortest-opened mussels on each day at two shore locations in 2015 and 2016. Grey symbols represent values for each of 21 or 29 full days of the deployment (2015 and 2016, respectively), while black circles and error bars represent the overall mean and 1 standard deviation for each site.

thermal experiences (see also Miller and Dowd, 2017). At the high shore location, body temperatures at a given time were generally positively correlated with body temperature around the same time on subsequent days, and were negatively correlated with temperatures offset by approximately 12 h, presumably reflecting the strong influence of diurnal temperature fluctuations (Supplemental Fig. S1) and the influence of high and low phases of the tide. Mussels at the low shore site showed a pattern of autocorrelation of body temperatures that followed the autocorrelation of sea surface temperatures during both deployments (Supplemental Fig. S1), with positive correlations throughout a 0 to 48 h time lag, followed by negative correlations for time lags from approximately 72 h to 216 h.

The observed range of variation in body temperature over small scales illustrates the potential difficulty of obtaining a representative sample of mussels or other intertidal organisms from a location for the purposes of characterizing physiological performance (Logan et al., 2012) at broader spatial scales. Within a single shore, physical characteristics of groups of mussels, such as their shore height, exposure to wave splash, compass orientation etc. may have short-term and long-term consequences for the mussels living within those aggregations (Gracey et al., 2008; Harley, 2008; Helmuth and Hofmann, 2001; Jurgens and Gaylord, 2017; Place et al., 2012), necessitating carefully designed sampling schemes. For example, studies have shown evidence for differential stress tolerance for mussels originating from or growing in wave-exposed or wave-protected beds separated by only a few meters (Gleason et al., 2017; Helmuth and Hofmann, 2001; Jimenez et al., 2015) that could result from post-settlement selective processes linked to the particular microhabitat the mussels grew in or from developmental plasticity (Gleason et al., 2018). However, fine-scale physiological studies among individuals separated by a few to 10's of cm are likely to provide further insight (see below).

Although *M. californianus* is known to gape during aerial emersion in some laboratory conditions (Bayne et al., 1976; Dowd and Somero, 2013), mussels in our field experiments kept their valves closed until a rising high tide had begun to splash them following warm low tide exposures. Closed mussels transition to anaerobic respiration relatively rapidly (Bayne et al., 1976), and an oxygen debt accumulates during this time, presumably at a faster rate when body temperatures are warmer (notwithstanding potential downregulation of certain traits such as heart rate). Despite these potential costs, we see scant evidence for mussels increasing their time spent gaping the shell valves following prolonged warm aerial emersion in our field experiment. Analyzing individual mussels, we find that higher low-tide body temperatures were often followed by a shorter amount of time spent gaping the valves widely in the ensuing 24 h period, and as a group there was no relationship between mussels reaching higher temperatures and the variation in gaping behavior among members of the same bed. These patterns are complicated by other factors, such as the effects of wave splash and the timing of the tide cycle versus daily sun and wind conditions (Miller and Dowd, 2017), but in general it appears that *M. californianus* are limited when it comes to their ability to expand the time spent gaping to recover oxygen debt accumulated during low tide, because of an unwillingness to gape the valves before the incoming tide arrives.

This lack of a characteristic behavioral response following thermal stress is reflected in the astonishing amount of variation in time spent with the valves gaping within a single bed on a single day. The differences in mean time spent gaping between high and low-shore mussels were expected due to differences in time immersed in seawater, but the within-bed mean inter-individual ranges of time spent gaping were high in both years (e.g., 5.0 to 8.1 h day^{-1} at the low-shore site; Table 3). This high degree of variation in time spent gaping warrants further attention, in terms of clarifying the pattern (e.g., are there behavioral 'syndromes' of gapers and non-gapers?; Shick et al., 1988), identifying other potential drivers (e.g., does plankton density influence individual gaping patterns?; Riisgård et al., 2003; Riisgård et al., 2006), attributing physiological consequences (e.g., does reduced time spent gaping correlate with reduced growth rate?), and delineating the possible implications for ecological interactions (e.g., are gapers more susceptible to predation?; Miller and Dowd, 2019; Robson et al., 2010).

We have documented substantial small-spatial-scale variation in both temperature and gaping behavior among mussels, but it is important to note that these data represent only part of the summer season. We speculate that these differences might be lessened in other seasons, particularly when increased wave splash associated with larger winter waves might serve to keep body temperatures cooler and allow mussels to gape their valves for more of the day. However, the most extreme temperatures measured in mussel beds along the central coast of California often occur outside of the summer season, when midday extreme low tides occasionally coincide with calm ocean swell conditions and moderate or warm air temperatures (Helmuth et al., 2006). Thus, the large degree of variation among neighbors has the potential to arise in seasons other than summer.

4.2. Implications of these patterns for global change and future directions

These data indicate that the physiological status and history of individuals separated by only a few body lengths might be radically different. The inconsistency of experiences among individual mussels within our experimental mussel beds was similar across two summer periods, despite a 3.8 °C difference in both the local mean sea surface temperature and air temperature between the two experiments. Temperatures in summer 2015 were much warmer than summer 2016 due to the presence of the widespread "blob" of warm ocean water in the northeastern Pacific during 2015 (Gentemann et al., 2017). Serendipitously, our two years of field experiments thus cover a range of mean temperatures comparable to the magnitude of temperature change expected due to human activities over the coming century. The survival, growth, and reproductive output of mussels will be impacted by a number of exogenous physical and biotic factors, as well as behavioral choices of the mussels themselves, and our data indicate that individual mussels occupying the same mussel bed may differ greatly in their experience of these factors, both now and in the future.

There are several conclusions now well supported by these and other field data for *M. californianus*. First, nearby individuals experience their environment in substantially different ways. From an environmental forcing perspective, micro-scale variation in abiotic conditions generates substantial variation in body temperatures that manifests in two potentially important ways: considerable differences among individuals in time spent at body temperatures likely to impose cellular stress (here defined as temperatures > 25 °C, yielding a 3-fold difference in time in 2015 and a > 100-fold range at the high-shore location in 2016), along with variation in the magnitude of acute stress (i.e., the peak temperature experienced) on any single day. These observations are not unique to the intertidal zone (Pincebourde et al., 2016; Pincebourde and Woods, 2012), but few if any datasets offer comparable detail on the experiences of individual organisms within a complex environmental mosaic. From a biological perspective, adjacent individuals perform what are often assumed to be mundane tasks (gaping to respire, acquire food, and secrete wastes) with surprisingly different patterns. The remaining challenge is to examine the links between these relatively short-term measures of variation in experience (or behavior), variation in genotype, and, ultimately, variation in integrative, fitness-related metrics of physiological performance such as growth or reproductive output (Tanner and Dowd, this issue). For example, we have shown that individual mussels that experience warmer body temperatures tend to accumulate greater antioxidant defenses and quantities of putatively thermoprotective osmolytes (Gleason et al., 2017), but we have yet to link these instantaneous physiological observations to differential growth, survival, or reproductive output. Instead, most studies that incorporate micro-scale variation into their analyses focus on simple physiological metrics such as thermal safety margins and survival of isolated events (Denny et al., 2011; Dong et al., 2017). Integrating these approaches through time and across relevant spatial scales is difficult, particularly in light of the other conclusions presented below.

The second conclusion is that warmer average conditions result in increased levels of inter-individual variation in maximum body temperatures (Fig. 1B; Miller and Dowd, 2017). The observed heteroscedasticity in body temperature harbors potentially profound implications for biological responses to present-day extreme events and for global change as mean temperatures march increasingly higher. For example, current theory regarding the influence of micro-scale environmental variation on survival of single extreme events is founded on the (now disproven for mussels) assumption that variation in maximum temperature does not change as the mean temperature rises (Denny, 2018; Denny et al., 2011). Future work should incorporate a more realistic relationship between the mean and variance of body temperature, and we should extend the theory to repeated events. In the context of climate change, if this pattern of heteroscedasticity holds as temperatures continue to rise, we may expect the degree of inter-individual variation on the warmest days to continue to increase. Some individuals will find themselves in relative thermal refugia, while some will certainly perish during extreme episodic events (Denny et al., 2011), and the gap between the two ends of this spectrum will grow wider. Even during events that might not be considered "extreme," this widening disparity in thermal experience could have cumulative effects on individual performance and fitness, particularly if future environmental shifts expose underlying inter-individual variation that is masked in more benign conditions (see Tanner and Dowd, this issue).

The third conclusion, an extension of the previous two, is that micro-scale variation complicates simplistic forecasts of the biological consequences of environmental change (Chapperon et al., 2016; Mislan and Wethey, 2015). For example, if individual sites (e.g., a 1 m^2 mussel bed) harbor as much thermal variation as entire coastlines (Denny et al., 2011; Helmuth et al., 2006), expectations of uni-directional 'marches to the poles' start to appear questionable. For example, it is increasingly recognized that thermal refugia, perhaps acting in concert with behavior in some species, can mitigate at least some of the local impacts of warming (e.g., Dong et al., 2017; Sunday et al., 2014).

The fourth conclusion is that most present-day experimental designs are inadequate at capturing the complexity of current and likely future environmental scenarios. The desire to focus on simple, easily interpretable results is certainly understandable, but nature is complex and noisy. Considering temperature manipulations, shifts in mean temperature are straightforward to implement, but climate change will involve shifts in the variability around that mean as well (IPCC, 2013). Characterizing and implementing forms of that relevant variation in controlled circumstances can be challenging, but this approach can provide unique insight into the outcomes of biological processes (Pincebourde et al., 2012). These considerations apply to both longer-term acclimation-style experiments and single acute thermal stress trials. For instance, what is the appropriate temperature ramp rate for determining critical thermal maxima (or minima) or physiological responses to acute thermal stress (Harada and Burton, 2019; Peck et al., 2009; Rezende et al., 2011; Tomanek and Somero, 2000)? Our heating rate data for mussels in the field show that mean heating rates are less than half as fast as the maximum observed heating rates on the high shore, while the ranges of heating rates between neighboring mussels within a single day make values at either end of that scale (or even slower) plausible for some subset of mussels living near each other in a bed. Importantly, maximum heating rates are greatest for individuals that achieve the highest body temperatures, an important correlation to consider in the design of thermal tolerance studies. In acclimation studies where we wish to experimentally impose realistic inter-individual variation in body temperatures over time, our observations indicate that this variation should be considerable around daily maximum temperatures while being negligible for daily minimum temperatures, at least in the case of mussels.

The fifth conclusion is that attempts to distinguish forces such as balancing selection from others such as lottery recruitment or physiological plasticity in complex, mosaic environments will be confounded until we can better map individual experience to individual genotypes/phenotypes. For example, the barnacle *Semibalanus balanoides* maintains polymorphisms in certain metabolic genes that may be a result of balancing selection within local populations due to small-scale (vertical) environmental variation (Flight et al., 2010; Schmidt et al., 2000; Schmidt and Rand, 2001). The grain of environmental variation in a barnacle bed may be coarse enough to allow differing selective forces to act over small spatial scales on groups of barnacles in a manner sufficient to maintain the polymorphism within the population at a site. Our data suggest that the more complex matrix of a mussel bed may create a more fine-grained environmental variation relative to the size of a mussel. Attributing potential patterns in genotypes or phenotypes within a mussel bed or across mussel beds to the effects of selection by environmental stress may require detailed individual histories rather than attempting to infer those histories based on nearby dataloggers or local weather data. It is imperative that these sorts of longitudinal studies are pursued. For example, theory highlights the possibility of certain counter-intuitive outcomes, such as reduced survival rates within a population when individuals acclimatize strongly to their unique thermal experience (Denny, 2018). However, the results will be highly contingent on how functional variation "maps" in nature onto variation in experience.

The sixth conclusion is a cautionary reminder that a focus on temperature, or other major factors such as ocean acidification, can perhaps overlook other equally important, interacting factors. For example, variation in food and nutrient availability can have effects that rival those of temperature on physiological state (Dowd et al., 2013; Fitzgerald-deHoog et al., 2012; Gilman and Rognstad, 2018; Place et al., 2012). If we truly wish to forecast the effects of future ocean regimes on organismal function, attention must be given to interactions between the various factors that impinge on organisms, while acknowledging spatial and temporal patterns of variation in those interactions. The outcomes of such studies are likely to be surprising.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cbpa.2019.06.016.

Declaration of Competing Interest

None.

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References

Bayne, B.L., Bayne, C.J., Carefoot, T.C., Thompson, R.J., 1976. The physiological ecology of *Mytilus californianus* Conrad 2. Adaptations to low oxygen tension and air exposure. Oecologia 22, 229–250.

Broitman, B.R., Szathmary, P.L., Mislan, K.A.S., Blanchette, C.A., Helmuth, B., 2009. Predator-prey interactions under climate change: the importance of habitat vs body temperature. Oikos 118, 219–224.

Buckley, B.A., Owen, M.-E., Hofmann, G.E., 2001. Adjusting the thermostat: the threshold induction temperature for the heat-shock response in intertidal mussels (genus *Mytilus*) changes as a function of thermal history. J. Exp. Biol. 204, 3571–3579.

Chapperon, C., Seuront, L., 2011. Space-time variability in environmental thermal properties and snail thermoregulatory behavior. Funct. Ecol. 25, 1040–1050.

Chapperon, C., Volkenborn, N., Clavier, J., Séité, S., Seabra, R., Lima, F.P., 2016. Exposure to solar radiation drives organismal vulnerability to climate: evidence from an intertidal limpet. J. Therm. Biol. 57, 92–100.

Chapperon, C., Studerus, K., Clavier, J., 2017. Mitigating thermal effect of behaviour and microhabitat on the intertidal snail *Littorina saxatilis* (Olivi) over summer. J. Therm. Biol. 67, 40–48.

Cole, A., Denny, M., 2014. United we fail: group versus individual strength in the California Sea mussel, *Mytilus californianus*. Biol. Bull. 227, 61–67.

Dayton, P.K., 1971. Competition, disturbance, and community organization - provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41, 351–389.

Denny, M.W., 1987. Lift as a mechanism of patch initiation in mussel beds. J. Exp. Mar. Biol. Ecol. 113, 231–245.

Denny, M.W., 2018. Survival in spatially variable thermal environments: consequences of induced thermal defense. Integr. Zool. 13, 392–410.

Denny, M.W., Harley, C.D.G., 2006. Hot limpets: predicting body temperature in a conductance-mediated thermal system. J. Exp. Biol. 209, 2409–2419.

Denny, M.W., Miller, L.P., Harley, C.D.G., 2006. Thermal stress on intertidal limpets: long-term hindcasts and lethal limits. J. Exp. Biol. 209, 2420–2431.

Denny, M.W., Hunt, L.J.H., Miller, L.P., Harley, C.D.G., 2009. On the prediction of extreme ecological events. Ecol. Monogr. 79, 397–421.

Denny, M.W., Dowd, W.W., Bilir, L., Mach, K.J., 2011. Spreading the risk: small-scale body temperature variation among intertidal organisms and its implications for species persistence. J. Exp. Mar. Biol. Ecol. 400, 175–190.

Dong, Y., Miller, L.P., Sanders, J.G., Somero, G.N., 2008. Heat-shock protein 70 (Hsp70) expression in four limpets of the genus *Lottia*: interspecific variation in constitutive and inducible synthesis correlates with *in situ* exposure to heat stress. Biol. Bull. 215, 173–181.

Dong, Y.-w., Li, X.-x., Choi, F.M.P., Williams, G.A., Somero, G.N., Helmuth, B., 2017. Untangling the roles of microclimate, behaviour and physiological polymorphism in governing vulnerability of intertidal snails to heat stress. Proc. R. Soc. B Biol. Sci. 284, 1–10.

Dowd, W.W., Somero, G.N., 2013. Behavior and survival of *Mytilus* congeners following episodes of elevated body temperature in air and seawater. J. Exp. Biol. 216, 502–514.

Dowd, W.W., Felton, C.A., Heymann, H.M., Kost, L.E., Somero, G.N., 2013. Food availability, more than body temperature, drives correlated shifts in ATP-generating and antioxidant enzyme capacities in a population of intertidal mussels (*Mytilus californianus*). J. Exp. Mar. Biol. Ecol. 449, 171–185.

Fitzgerald-deHoog, L., Browning, J., Allen, B.J., 2012. Food and heat stress in the California mussel: evidence for an energetic trade-off between survival and growth. Biol. Bull. 223, 205–216.

Flight, P.A., Schoepfer, S.D., Rand, D.M., 2010. Physiological stress and the fitness effects of *Mpi* genotypes in the acorn barnacle *Semibalanus balanoides*. Mar. Ecol. Prog. Ser. 404, 139–149.

Garrity, S.D., 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology 65, 559–574.

Gentemann, C.L., Fewings, M.R., García-Reyes, M., 2017. Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. Geophys. Res. Lett. 44, 312–319.

Gilman, S.E., Rognstad, R.L., 2018. Influence of food supply and shore height on the survival and growth of the barnacle *Balanus glandula* (Darwin). J. Exp. Mar. Biol. Ecol. 498, 32–38.

Gilman, S.E., Harley, C.D.G., Strickland, D.C., Vanderstraeten, O., O'Donnell, M.J., Helmuth, B., 2006. Evaluation of effective shore level as a method of characterizing intertidal wave exposure regimes. Limnol. Oceanogr. Methods 4, 448–457.

Gleason, L.U., Miller, L.P., Winnikoff, J.R., Somero, G.N., Yancey, P.H., Bratz, D., Dowd, W.W., 2017. Thermal history and gape of individual *Mytilus californianus* correlate with oxidative damage and thermoprotective osmolytes. J. Exp. Biol. 220, 4292–4304.

Gleason, L.U., Strand, E.L., Hizon, B.J., Dowd, W.W., 2018. Plasticity of thermal tolerance and its relationship with growth rate in juvenile mussels (*Mytilus californianus*). Proc. R. Soc. B Biol. Sci. 285, 20172617.

Gracey, A.Y., Chaney, M.L., Boomhower, J.P., Tyburczy, W.R., Connor, K., Somero, G.N., 2008. Rhythms of gene expression in a fluctuating intertidal environment. Curr. Biol. 18, 1501–1507.

Guichard, F., Halpin, P.M., Allison, G.W., Lubchenco, J., Menge, B.A., 2003. Mussel disturbance dynamics: signatures of oceanographic forcing from local interactions. Am. Nat. 161, 889–904.

Harada, A.E., Burton, R.S., 2019. Ecologically relevant temperature ramping rates enhance the protective heat shock response in an intertidal ectotherm. Physiol. Biochem. Zool. 92, 152–162.

Harley, C.D.G., 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. Mar. Ecol. Prog. Ser. 371, 37–46.

Harley, C.D.G., Helmuth, B.S.T., 2003. Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. Limnol. Oceanogr. 48, 1498–1508.

Harper, K.D., Williams, G.A., 2001. Variation in abundance and distribution of the chiton *Acanthopleura japonica* and associated molluscs on a seasonal, tropical, rocky shore. J. Zool. (Lond.) 253, 293–300.

Hayford, H.A., Gilman, S.E., Carrington, E., 2015. Foraging behavior minimizes heat exposure in a complex thermal landscape. Mar. Ecol. Prog. Ser. 518, 165–175.

Helmuth, B., 2002. How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. Integr. Comp. Biol. 42, 837–845.

Helmuth, B.S.T., Hofmann, G.E., 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. Biol. Bull. 201, 374–384.

Helmuth, B., Broitman, B.R., Blanchette, C.A., Gilman, S.E., Halpin, P.M., Harley, C.D.G., O'Donnell, M.J., Hofmann, G.E., Menge, B.A., Strickland, D., 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. Ecol. Monogr. 76, 461–479.

Helmuth, B., Yamane, L., Lalwani, S., Matzelle, A., Tockstein, A., Gao, N., 2011. Hidden signals of climate change in intertidal ecosystems: what (not) to expect when you are expecting. J. Exp. Mar. Biol. Ecol. 400, 191–199.

IPCC, 2013. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J. ... Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jimenez, A.G., Jayawardene, S., Alves, S., Dallmer, J., Dowd, W.W., 2015. Micro-scale environmental variation amplifies physiological variation among individual mussels. Proc. R. Soc. Lond. B Biol. Sci. 282, 1–9.

Jurgens, L.J., Gaylord, B., 2017. Physical effects of habitat-forming species override latitudinal trends in temperature. Ecol. Lett. 1–7.

Lathlean, J.A., Seuront, L., McQuaid, C.D., Ng, T.P.T., Zardi, G.I., Nicastro, K.R., 2016. Cheating the locals: invasive mussels steal and benefit from the cooling effect of indigenous mussels. PLoS One 11, e0152556.

Lockwood, B.L., Sanders, J.G., Somero, G.N., 2010. Transcriptomic responses to heat stress in invasive and native blue mussels (genus *Mytilus*): molecular correlates of invasive success. J. Exp. Biol. 213, 3548–3558.

Logan, C.A., Kost, L.E., Somero, G.N., 2012. Latitudinal differences in *Mytilus californianus* thermal physiology. Mar. Ecol. Prog. Ser. 450, 93–105.

Lohse, D.P., 1993. The importance of secondary substratum in a rocky intertidal community. J. Exp. Mar. Biol. Ecol. 166, 1–17.

McAfee, D., Bishop, M.J., Yu, T.-N., Williams, G.A., 2018. Structural traits dictate abiotic stress amelioration by intertidal oysters. Funct. Ecol. 32, 2666–2677.

Miller, L.P., Denny, M.W., 2011. Importance of behavior and morphological traits for controlling body temperature in littorinid snails. Biol. Bull. 220, 209–223.

Miller, L.P., Dowd, W.W., 2017. Multimodal *in situ* datalogging quantifies inter-individual variation in thermal experience and persistent origin effects on gaping behavior among intertidal mussels (*Mytilus californianus*). J. Exp. Biol. 220, 4305–4319.

Miller, L.P., Dowd, W.W., 2019. Dynamic measurements of black oystercatcher (*Haematopus bachmani*) predation on mussels (*Mytilus californianus*). Invertebr. Biol. 138, 67–73.

Miller, L.P., Harley, C.D.G., Denny, M.W., 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. Funct. Ecol. 23, 756–767.

Mislan, K.A.S., Wethey, D.S., 2015. A biophysical basis for patchy mortality during heat waves. Ecology 96, 902–907.

Mislan, K.A.S., Wethey, D.S., Helmuth, B., 2009. When to worry about the weather: role of tidal cycle in determining patterns of risk in intertidal ecosystems. Glob. Chang. Biol. 15, 3056–3065.

Mislan, K.A.S., Blanchette, C.A., Broitman, B.R., Washburn, L., 2011. Spatial variability of emergence, splash, surge, and submergence in wave-exposed rocky-shore ecosystems. Limnol. Oceanogr. 56, 857–866.

Nicastro, K.R., Zardi, G.I., McQuaid, C.D., Pearson, G.A., Serrão, E.A., 2012. Love thy neighbour: group properties of gaping behaviour in mussel aggregations. PLoS One 7, e47382.

O'Donnell, M.J., 2008. Reduction of wave forces within bare patches in mussel beds. Mar. Ecol. Prog. Ser. 362, 157–167.

O'Donnell, M.J., Denny, M.W., 2008. Hydrodynamic forces and surface topography: centimeter-scale spatial variation in wave forces. Limnol. Oceanogr. 53, 579–588.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. Vegan: Community Ecology Package, R Package Version 2.5, 4 ed. .

Peck, L.S., Clark, M.S., Morley, S.A., Massey, A., Rossetti, H., 2009. Animal temperature limits and ecological relevance: effects of size, activity and rates of change. Funct. Ecol. 23, 248–256.

Pincebourde, S., Woods, H.A., 2012. Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms. Funct. Ecol. 26, 844–853.

Pincebourde, S., Sanford, E., Casas, J., Helmuth, B., 2012. Temporal coincidence of environmental stress events modulates predation rates. Ecol. Lett. 15, 680–688.

Pincebourde, S., Murdock, C.C., Vickers, M., Sears, M.W., 2016. Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. Integr. Comp. Biol. 56, 45–61.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2018. nlme: Linear and Nonlinear Mixed Effects Models. (3.1-137 ed).

Place, S.P., Menge, B.A., Hofmann, G.E., 2012. Transcriptome profiles link environmental variation and physiological response of *Mytilus californianus* between Pacific tides. Funct. Ecol. 26, 144–155.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rezende, E.L., Tejedo, M., Santos, M., 2011. Estimating the adaptive potential of critical thermal limits: methodological problems and evolutionary implications. Funct. Ecol. 25, 111–121.

Riisgård, H.U., Kittner, C., Seerup, D.F., 2003. Regulation of opening state and filtration rate in filter-feeding bivalves (*Cardium edule*, *Mytilus edulis*, *Mya arenaria*) in response to low algal concentration. J. Exp. Mar. Biol. Ecol. 284, 105–127.

Riisgård, H.U., Lassen, J., Kittner, C., 2006. Valve-gape response times in mussels (*Mytilus edulis*) - effects of laboratory preceding-feeding conditions and in situ tidally induced variation in phytoplankton biomass. J. Shellfish Res. 25, 901–911.

Robson, A.A., Garcia De Leaniz, C., Wilson, R.P., Halsey, L.G., 2010. Behavioural adaptations of mussels to varying levels of food availability and predation risk. J. Molluscan Stud. 76, 348–353.

Schmidt, P.S., Rand, D.M., 2001. Adaptive maintenance of genetic polymorphism in an intertidal barnacle: habitat- and life-state-specific survivorship of MPI genotypes. Evolution 55, 1336–1344.

Schmidt, P.S., Bertness, M.D., Rand, D.M., 2000. Environmental heterogeneity and balancing selection in the acorn barnacle *Semibalanus balanoides*. Proc. R. Soc. Lond. Ser. B Biol. Sci. 267, 379–384.

Shick, J.M., Widdows, J., Gnaiger, E., 1988. Calorimetric studies of behavior metabolism and energetics of sessile intertidal animals. Am. Zool. 28, 161–181.

Suchanek, T.H., 1979. The *Mytilus californianus* Community: Studies on the Composition, Structure, Organization, and Dynamics of a Mussel Bed. Department of Zoology. University of Washington, Seattle, pp. 285.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., Huey, R.B., 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc. Natl. Acad. Sci. 111, 5610–5615.

Tomanek, L., Somero, G.N., 2000. Time course and magnitude of synthesis of heat-shock proteins in congeneric marine snails (genus *Tegula*) from different tidal heights. Physiol. Biochem. Zool. 73, 249–256.

Wethey, D.S., 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: a field experiment. Biol. Bull. 167, 176–185.