Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales

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Global climate change is expected to have broad ecological consequences for species and communities. Attempts to forecast these consequences usually assume that changes in air or water temperature will translate into equivalent changes in a species' organismal body temperature. This simple change is unlikely because an organism's body temperature is determined by a complex series of interactions between the organism and its environment. Using a biophysical model, validated with 5 years of field observations, we examined the relationship between environmental temperature change and body temperature of the intertidal mussel *Mytilus californianus* over 1,600 km of its geographic distribution. We found that at all locations examined simulated changes in air or water temperature always produced less than equivalent changes in the daily maximum mussel body temperature. Moreover, the magnitude of body temperature change was highly variable, both within and among locations. A simulated 1°C increase in air or water temperature raised the maximum monthly average of daily body temperature maxima by 0.07–0.92°C, depending on the geographic location, vertical position, and temperature variable. We combined these sensitivities with predicted climate change for 2100 and calculated increases in monthly average maximum body temperature of 0.97–4.12°C, depending on location and climate change scenario. Thus geographic variation in body temperature sensitivity can modulate species' experiences of climate change and must be considered when predicting the biological consequences of climate change.

ecological forecasting | geographic variation | global warming | *Mytilus* | biogeography

Temperature affects virtually all physiological processes (1) and many ecological interactions (2). Thus temperature changes associated with global climate change are expected to broadly alter species and communities (3–6). Accurately forecasting the direct physiological effects of temperature change on a species requires three pieces of information: (*i*) the current and future climatic conditions, (*ii*) the relationship between climate and the body temperature experienced by the species (hereafter body temperature sensitivity, BTS), and (*iii*) the thermal physiological tolerances of the species (hereafter organismal vulnerability). Additionally, because species are usually distributed over large geographic areas, geographic variation in all three components must also be considered. Although many studies have examined climatic change (e.g., refs. 7 and 8) and organismal vulnerability to body temperature changes (e.g., refs. 9–11), including geographic variation in both, much less is known about BTS to climate change in any species (12, 13). The flux of heat to and from an organism is driven by multiple, interacting climatic factors, including air temperature (T_a), surface temperature (T_s), solar radiation, cloud cover, and wind speed (14–16). Heat flux is also affected by an organism's size, color, shape, behavior, and material properties (14–16). Thus studies of individual species frequently find a unique relationship between climate and body temperature (13, 15–17). Moreover, because both organismal properties and environmental conditions vary geographically across a species' distribution, a simple change in one climate variable is unlikely to produce the same body temperature change among all populations of a species.

Here, we use a biophysical model to explore variation in the BTS of an ecologically dominant species of intertidal invertebrate, the mussel *Mytilus californianus*, across 1,600 km of its geographic range. We focus specifically on the effects of two variables, T_a and water temperature (T_w) and the mussel's daily body temperature maximum (DBTM). We examine whether geographic or local variation in environmental conditions influences the mussel BTS to these two variables. Previous studies have shown that DBTM are positively correlated with physiological indicators of thermal stress (10, 18–20) and may influence both the intertidal and biogeographic distributions of many intertidal species (9, 18, 19). We show that the relative importance of T_a and T_w to DBTM varies both geographically and with vertical position within locations. Consequently, a simple change in T_a or T_w will not have a consistent effect on body temperature across the species distribution.

Intertidal habitats (the regions between the high and low tide lines of the world's coastlines) have long served as models for investigating the effects of climate on species distributions (21) and monitoring the consequences of climate change for natural ecosystems (3, 4, 22). Intertidal organisms often experience temperatures near their thermal tolerance limits (18, 23), and they are thought to be among the first to exhibit responses to climate change (12, 25, 26). Because intertidal communities are exposed to both marine and terrestrial climates, both T_a and T_w influence body temperature extremes; however, the relative importance of these two variables to thermal heat stress is poorly understood. Studies of the effects of climate change on intertidal systems frequently emphasize changes in T_w (e.g., refs. 4 and 27); yet, both geographic and local distributions are also thought to be set by thermal stress during aerial exposure at low tide (19, 21, 22, 28). Thus correctly forecasting how intertidal species will respond to future temperature changes requires an improved understanding of the determinants of body temperature during aerial exposure.

Mussels are ubiquitous members of intertidal communities worldwide. In the northeastern Pacific, the mussel *M. californianus* is a major foundation species on wave-exposed coasts, occupying large swaths of intertidal benches and providing ecological opportunities for a suite of other organisms (29, 30). We modified two existing biophysical models (16, 28) to produce
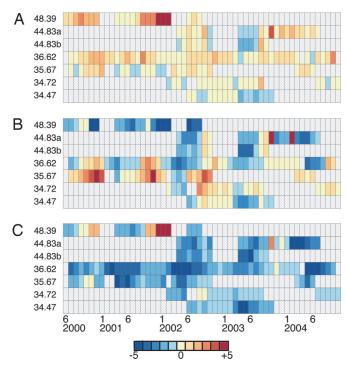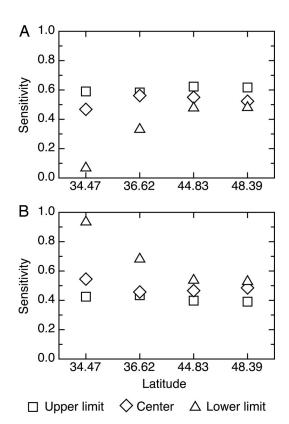

Fig. 1. Average fit (z score) of temperatures predicted by the model (A), T_a alone (B), and T_w alone (C), to field observations. Color indicates the difference between the predicted value and the average observed value, scaled by the standard deviation among replicate mussel data loggers. Each row contains results for a different location, denoted by latitude. The rows labeled 44.83a and 44.83b are neighboring locations that differ in wave exposure (see Table 4). Negative values indicate that the model predictions are cooler than observed values; positive values indicate predictions are warmer than observations. Months with too few data for comparison are indicated by gray hatching.

a model that predicts the body temperature of intertidal *M. californianus* at 10-min intervals by using environmental data recorded by ground- and satellite-based sensors. We used this model to examine how the sensitivity of body temperature to changes in T_a and T_w varies across *M. californianus*' geographic distribution. We addressed four specific questions: (*i*) Do T_a and T_w changes translate into an equal magnitude change in mussel body temperature? (*ii*) What is the relative importance of T_a and T_w to mussel body temperature? (*iii*) Does mussel BTS vary locally and/or geographically? (*iv*) How does a consideration of BTS alter predictions of the consequences of climate change for *M. californianus*?

Results and Discussion

Comparisons to multiple years of field observations at six separate locations revealed that our model accurately reproduced field measurements of *M. californianus* body temperatures recorded by data loggers. When pooled across all sites and months, the average difference between modeled and observed monthly averages of DBTM was <1°C. Moreover, of the 177 total site–months compared, 75% and 92% fell within one and two standard deviations, respectively, of observations made by replicate temperature loggers within a location (Fig. 1A). These findings compare favorably with the expectation of 69% and 94% of observations falling within one and two standard deviations of the mean of a normally distributed variable. In contrast, only 48% and 74% of monthly mean DBTM observations for air (Fig. 1B), and 28% and 54% of observations for water (Fig. 1C), were within one and two standard deviations, respectively, over the same times and locations.

Fig. 2. BTS to changes in T_a (A) and T_w (B) by location and vertical height. Standard errors are too small to visibly plot but are listed in Table 1.

Although the model provided a better overall fit to observed mussel temperatures, there were occasions in which the z scores for T_w or T_a were smaller than for the model (Fig. 1). In nearly all of these cases (>90%), the model still fell within one or two standard deviations of the replicate field observations, indicating that the model accurately predicted temperatures but that mussel temperatures during those months were similar to T_w or T_a. DBTM may approach T_w during times of the year when there is little or no daytime tidal emersion or in winter when body temperatures during daytime emersions are lower than T_w. In other months daytime emersions may frequently co-occur with clouds or fog, reducing the importance of solar radiation and driving DBTM toward T_a. Day-to-day variation in model fit may reflect minor differences between the modeled and observed patterns of emersion and/or between the meteorological observations used in the model and the conditions at the mussel bed. Overall, the model thus provided a far more reliable and accurate estimate of *M. californianus*' body temperature than did either T_a or T_w alone.

Mussel BTS to changes in T_a and T_w varied both among and within locations (Fig. 2), and several clear patterns emerged from our analysis. First, although both T_a and T_w influenced mussel DBTM at all locations examined, BTS to changes in T_a or T_w was always <1. Overall, BTS values ranged from 0.07 to 0.92 (Table 1), indicating that a change in T_a or T_w of anywhere from 14.71°C to 1.08°C is necessary to produce a 1°C change in mussel body temperature, depending on the location and temperature variable. Second, we observed significant geographic variability in BTS to both T_a and T_w (Fig. 2). Geographic variability was greatest at the lower vertical limits of the mussel bed, where BTS to T_a ranged from 0.07 to 0.48 and BTS to T_w ranged from 0.53 to 0.93 (Fig. 2, △). In contrast, at the upper limits BTS values were roughly similar across all locations examined (Fig. 2, □). Third, BTS to T_a generally declined, and

Table 1. Regression analysis of sensitivity

Location	df	β_o	β_a	β_w	β_{aw}
48.39°N					
Lower	21	0.037* (0.004)	0.480* (0.005)	0.528* (0.004)	−0.018* (0.003)
Center	21	0.039* (0.003)	0.523* (0.005)	0.485* (0.003)	−0.018* (0.002)
Upper	21	0.024* (0.003)	0.617* (0.004)	0.391* (0.003)	−0.012* (0.002)
44.83°N					
Lower	21	0.023* (0.002)	0.477* (0.004)	0.537* (0.002)	−0.012* (0.002)
Center	21	0.033† (0.006)	0.550* (0.008)	0.466* (0.006)	−0.020† (0.004)
Upper	21	0.017* (0.002)	0.623* (0.003)	0.398* (0.002)	−0.009* (0.001)
36.62°N					
Lower	21	0.028* (0.003)	0.331* (0.004)	0.681* (0.003)	−0.013* (0.002)
Center	21	0.012* (0.001)	0.562* (0.002)	0.457* (0.001)	−0.004† (0.001)
Upper	21	0.004‡ (0.001)	0.583* (0.001)	0.435* (0.001)	−0.003† (0.001)
34.72°N					
Lower	21	0.089* (0.009)	0.068* (0.013)	0.934* (0.009)	−0.042* (0.006)
Center	21	0.025* (0.003)	0.468* (0.004)	0.545* (0.003)	−0.013* (0.002)
Upper	21	0.017 (0.006)	0.590* (0.008)	0.425* (0.006)	−0.013‡ (0.004)

Regression equations are of the form: $\Delta T_b = \beta_0 + \beta_a \Delta T_a + \beta_w \Delta T_w + \beta_{aw} \Delta T_a \Delta T_w$, where ΔT_b refers to the change in T_b over the base model run, and ΔT_a and ΔT_w are the amounts of change in T_a and T_w inputs, respectively. Standard errors are listed in parentheses. *, $P < 0.0001$; †, $P < 0.001$; ‡, $P < 0.01$.

BTS to T_w increased, with decreasing vertical position within locations, but the magnitude of change was location-dependent. For example, at the highest latitude site (48.39°N) BTS to T_a for lower intertidal animals was reduced by 22% from that of upper intertidal animals, but in southern California (34.72°N) lower intertidal animals showed an 88% reduction in T_a sensitivity relative to upper intertidal animals.

The magnitude of the influence of T_w on body temperature at the upper limit of the mussel bed (0.39–0.44) is surprisingly large given that these animals reach DBTM during periods of aerial exposure. *M. californianus* mussel beds and the underlying rock substratum appear to have a substantial thermal "memory" of T_w caused by heat storage during low tide (28). This result suggests that T_w may play an unanticipated role in determining intertidal vertical zonation. Many intertidal ecosystems are characterized by strong vertical zonation patterns, with organisms showing pronounced upper and lower limits to distributions within shores. Upper limits of zonation in the intertidal zone are usually thought to be set by abiotic conditions associated with the terrestrial climate (21, 23, 28). Our results indicate that, for the upper vertical limits of mussel beds, T_w experienced during immersion has nearly as large an influence on body temperatures during emersion as T_a.

The spatial variation in BTS to T_a and T_w, observed at both local and geographic scales, occurs because the effect of any single climatic variable on body temperature is influenced by other aspects of an organism's environment (13, 15). There are seven such factors in our model that differed in value within or among locations: wind speed, solar radiation, wave regime, relative humidity, cloud cover, intertidal height, and tidal regime. Differences in one or more of these factors, and their interactions, must be driving the observed differences in BTS. In the case of variation in BTS among different portions of the mussel bed within a single site, these model runs differed only in vertical position and wave exposure regime, both of which influence the amount of time the modeled mussel bed was exposed to marine and terrestrial climates. Therefore, the within-site differences in BTS to T_a and T_w changes must be driven by these tidal exposure differences, which in turn determine the duration and timing of exposure to the other variables in the model. In particular, mussels at higher vertical positions on the shore experience terrestrial conditions more frequently and thus their body temperatures were more sensitive to changes in

T_a. Similarly, exploratory model runs of a purely terrestrial mussel bed, with no tidal submergence, revealed even greater BTS to air (0.95). Tidal regimes and intertidal heights also differed at the geographic scale, as did the five other climate factors, and some combination of these factors is likely contributing to geographic variation in BTS as well.

The association of geographic variation in BTS with environmental variation among sites points to the importance of multiple climatic variables in determining the body temperatures of intertidal organisms. This study focused on T_a and T_w as two of many environmental variables that could vary both among locations and under future climate change. We chose these variables because both are routinely used as proxies for body temperatures of intertidal organisms (26). Our results underscore the flaw of using such proxies: body temperature changes are not identical to T_a and T_w changes. A fully complete picture of *M. californianus* body temperature changes in response to climate change requires incorporating changes in multiple climatic variables. In addition to T_a and T_w, Helmuth (16) identified solar radiation and wind speed as important drivers of *M. californianus* body temperature during emersion. Other environmental conditions, such as sea level and wave heights, are also expected to change in coming decades (31). In many cases, the effects of these changes on species and communities are poorly understood (31). The modeling techniques used here present an opportunity to explore the consequences of a broad range of environmental changes on organismal body temperatures. Because all of these environmental factors are incorporated mechanistically into the body-temperature model, we can potentially test their relative importance under different scenarios of climate change.

Because air and water had a roughly additive effect on body temperature (Table 1), the net effect of future temperature changes on *M. californianus*' body temperature at a location depends on the magnitude of change in both T_a and T_w. To examine the consequences of spatial variation in BTS, we used BTS values along with predicted temperature changes at each site by 2100 under two climate change scenarios [Special Report on Emission Scenarios (SRES) B1 and A2, ref. 32] to predict mussel body temperature changes (Table 2). When all sites were compared under an average magnitude of climate change, geographic variation in BTS caused body temperature changes to vary among sites by up to 0.2°C for the B1 scenario and 1.2°C for

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Table 2. Predicted mussel body temperature response at the upper and lower limits of the mussel bed to future climate change for two climate change scenarios, SRES B1 and SRES A2

	Mean change		Response to mean		Local change		Response to local	
Latitude	T_a	T_w	Upper	Lower	T_a	T_w	Upper	Lower
SRES B1								
34.47	1.24	0.96	1.12	0.93	0.92	1.04	0.97	0.99
36.62	1.24	0.96	1.13	1.05	0.96	1.15	1.06	1.09
44.83	1.24	0.96	1.14	1.09	1.37	0.76	1.15	1.05
48.39	1.24	0.96	1.12	1.08	1.69	0.88	1.37	1.25
SRES A2								
34.47	4.22	2.74	3.50	2.36	2.89	3.31	2.99	2.89
36.62	4.22	2.74	3.62	3.11	2.96	3.62	3.27	3.31
44.83	4.22	2.74	3.61	3.34	5.51	1.82	4.07	3.49
48.39	4.22	2.74	3.54	3.26	5.51	2.21	4.12	3.59

The local change for each site was calculated for the nearest 1° grid from CM2.0 model output (32). Mean change is the average of the four local changes. Responses are calculated by applying the BTS values in Table 1 to predicted climate change.

Table 3. Definitions of additional model parameters

Term	Value	Source
k, thermal conductivity		
Mussels	0.3 W·m^{-1}·K^{-1}	16
Rock	2.1 W·m^{-1}·K^{-1}	36
Δy, layer thickness	0.01 m	
α, surface absorptivity	0.9	
ε_a, emissivity, atmosphere	$(0.74 + 0.0049 vp_a)$ $\cdot(1 - 0.17ccf^2)$	40, 41
q_{solar}, solar radiation		37
ε_s, emissivity, mussel surface	$\varepsilon_s = 0.75$	
σ, Stefan–Boltzmann constant	$5.67 \cdot 10^{-8}$ W·m^{-2}·K^{-4}	24
h_c, convective heat transfer	$\rho c_p u \cdot K^2/(\log(z/z_o))^2$	24
h_e, evaporative heat transfer	$u \cdot K^2/(Le^{1/3} \log(z/z_o))^2$	24
K, vonKarman's constant	0.4	24
ρ, density of air	1.1774 kg·m^{-3}	36
c_p, specific heat of air	1005.7 J·kg^{-1}·K^{-1}	36
u, wind speed		*
z, wind speed height	2 m	28
z_o, roughness height	0.008 m	
Sc, Schmidt number, water vapor	0.60	36
Pr, Prandtl number, air	0.708	36
ccf, cloud cover fraction		*
vp_a, water vapor pressure, air	$rh611.0e^{((L/Rv)(1/273-1/Ta))}$	24
vp_s, water vapor pressure, surface	$611.0e^{((L/Rv)(1/273-1/Ts))}$	24
rh, relative humidity		*
L, latent heat, evaporation	$2.456 \cdot 10^3$ J·g^{-1}	24
Rv, specific gas constant, water vapor	0.461 J·g^{-1}·K^{-1}	24

*National Center for Climatic Data.

the A2 scenario. When geographic variation in the magnitude of climate change was also considered, the difference rose to 0.4°C under the B1 scenario, but did not change under the A2 scenario (Table 2). In each of these four cases, the greatest disparity was shown by a different pair of sites. Thus accurate predictions of body temperature change require knowledge of geographic variation in both climate and BTS.

Two patterns emerged from these climate-change scenarios. First, in all four scenarios, larger changes in body temperature tended to occur at the upper vertical limits of the mussel bed than at the lower limits. Second, after incorporating geographic variation in climate change, greater body temperature changes were observed at higher latitudes. These results suggest that the consequences of climate change for *M. californianus* may be greatest at high latitudes and high intertidal locations across all latitudes. Because upper vertical limits are thought to be set by abiotic stress (21, 28), a decline in the vertical range of *M. californianus*, particularly at high-latitude sites, seems likely. However, an accurate assessment of the consequences of such temperature changes requires additional information. *M. californianus* inhabits a spatially complex thermal environment (22), and body temperature changes must be considered in the context of contemporary body temperature patterns (22). Moreover, many intertidal species show temporal and latitudinal variation in thermal tolerances (10, 33, 34), such that what constitutes a stressful temperature change may be highly site-specific. Thus correctly forecasting the biological consequences of climate change for *M. californianus* will require knowledge, from multiple populations across the species distribution, of (*i*) *M. californianus'* thermal environment and the magnitude of predicted climate change, (*ii*) *M. californianus*' BTS to climate, and (*iii*) this species' organismal vulnerability to changes in body temperature. Additionally, organismal vulnerability itself can be quite complex, including both physiological and evolutionary capacity for adaptation (9).

Our results demonstrate the importance of incorporating BTS into models of species' responses to climate change. In this study we explored the effects of changes in two environmental variables, T_a and T_w, on the change in body temperature of *M. californianus*. These are just a few of the many organismal and climatic factors that may vary across *M. californianus'* distribution (16, 22); thus our results may underestimate the total magnitude of variation in BTS. The observed variation in BTS of *M. californianus* is most likely to be driven by differences

within and among locations in temporal patterns of immersion and emersion. Yet we expect that geographic variation in BTS occurs in both marine and terrestrial species, because organismal body temperature is the product of a complex series of interactions between an organism and its environment, and both organismal properties and environmental conditions may vary greatly across a species distribution. Accurate forecasts of the biological consequences of climate change must account for such dynamics. Here, we have shown that models linking climate change to body temperature change, and ultimately to organismal vulnerability, are both feasible and essential for predicting the consequences of climate change on organisms in nature.

Methods

Biophysical Model. The body temperature simulations were based on a 1D model of heat transport through eight 1-cm thick layers representing the mussel bed and 42 1-cm thick layers representing the underlying rock. We used the temperature calculated for a layer 2 cm deep in the mussel bed as the mussel body temperature. During high-tide immersions, the outer layers of the mussel bed and the rock were fixed at T_w.

During low-tide emersions, the T_s of the top of the mussel bed was calculated by using an energy balance: conduction = convection + infrared radiation + shortwave radiation + evaporation. This energy balance is expressed as a finite difference equation and solved for T_s by using Newton's method (35):

$$-k(T_s - T_1)/\Delta y = h_c(T_a - T_s) + \alpha q_{solar} + \varepsilon_a \sigma T_a^4$$
$$- \varepsilon_s \sigma T_s^4 + h_e L(vp_a - vp_s). \quad [1]$$

Here, k is the thermal conductivity, T_1 is the temperature one layer deep in the mussel bed, and Δy is the layer thickness. The

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Table 4. The calculated tidal height and effect of wave action for each modeled location

Latitude	Longitude	Position	Height, cm	Wave slope, cm/m
48.39°N	124.74°W	Upper	216	−40.29
		Center	155	−29.83
		Lower	95	−15.59
44.83°N	124.05°W a	Upper	189	−28.05
	a	Center	140	−24.18
	a	Lower	102	−20.57
	b	Center	156	−36.93
36.62°N	121.90°W	Upper	174	−44.84
		Center	149	−37.69
		Lower	100	−37.69
35.67°N	121.29°W	Center	132.71	−34.95
34.72°N	120.61°W	Upper	116	−26.49
		Center	90	−28.24
		Lower	28	−15.63
34.47°N	120.28°W	Center	76.45	−25.09

At 44.83°N, a and b denote adjacent locations that differ in wave exposure parameters.

remaining model parameters are described in Table 3. After T_s was determined, transient heat conduction through the layers of the mussel bed and underlying rock was modeled by using an explicit forward in time, centered in space finite difference equation (36), and a 10-s time step.

For each location modeled, we used meteorological data from the nearest meteorological station reported by the National Climatic Data Center (data set DS-3505, http://hurricane.ncdc.noaa.gov/pls/plclimprod/poemain.accessrouter?datasetabbv=DS3505) for terrestrial variables (relative humidity, cloud cover fraction, T_a, wind) and by the National Data Buoy Center (www.ndbc.noaa.gov/index.shtml) for marine data (T_w, wave height), with two exceptions. Wind and T_a variables for the site at 48.39°N came from a National Data Buoy Center Station. Marine data for two locations, 34.72°N and 34.47°N, were furnished by the Coastal Data Information Program, Integrative Oceanography Division, operated by the Scripps Institution of Oceanography (http://cdip.ucsd.edu). Solar radiation was derived from geosynchronous satellite observations for the 0.5° grid square nearest each location (37). Tide predictions were made by using the XTIDE program (www.flaterco.com/xtide) for the nearest station to each site reported by the University of South Carolina tidal prediction web site (http://tbone.geol.sc.edu/tide).

The vertical height of each location and the effects of wave action on emersion time (Table 4) were estimated from the temperature time series collected by mussel data loggers at each location. Following ref. 38, we identified immersion events in the temperature time series as sharp drops in temperature and used the time of these events to identify the tide height and wave height at the time of immersion. We then developed a regression equation to predict the tide height of immersion from the wave height (38). This regression technique provides an estimate of the effect of wave action on the tide height at which the mussel transitions from emersed to immersed.

Model Validation. We compared predictions generated for six intertidal locations along the western United States coast with field observations collected by intertidal temperature data loggers designed to mimic the thermal characteristics of living mussels. These mimics provide accurate measurements of live *M. californianus* to within 2.5°C (22, 39). Three to six replicate loggers were deployed at multiple sites for up to 5 years. The instruments recorded average temperatures at intervals of 10–15

min, with an accuracy of 0.3 and resolution of 0.1°C. Comparisons between model and field observations were made only in months with a minimum of 7 days of both field observations and predictions. Any day missing >4 h of climate input data or temperature observations was excluded.

To calculate an overall estimate of model fit, we compared the average difference between the model and the mean of the loggers for DBTM. DBTM is the daily maximum temperature an organism is exposed to for a minimum of 30 min and represents the minimum length of exposure for *M. californianus* to experience negative physiological effects of warm temperatures (19). For each location we also calculated a z score for each month as the average difference between the daily model prediction of DBTM and the daily average of the DBTMs reported by the replicate loggers, divided by the average daily standard deviation of the replicate loggers for the month. This is the average daily difference between predicted and observed DBTM for the month, scaled by a measure of the variation among replicate field observations within a location.

Sensitivity Analysis. We selected four of the six locations for sensitivity analysis. All four had long-term records of climate data for all necessary model inputs and together span 1,600 km of *M. californianus*' geographic range. We used a 9-year range of climate data (1996–2004) for sensitivity analysis, because it was the extent of the satellite solar radiation database (37). We explored climate sensitivity at each location at three tidal heights representing the upper and lower vertical limits of the mussel and the approximate center.

To calculate the sensitivities we conducted 25 model runs for each location and tidal height. In each replicate model run we added or subtracted a fixed amount from each observation of T_a and/or T_w in the climate data set. We examined all possible combinations of changes to T_a and T_w of −2°C to +2°C by 1°C increments. For each run we pooled the output by month across years and calculated the average monthly DBTM for each month. We compared differences in the hottest month of each model run. Because initial plots of temperature change appeared highly linear, we used a regression model to compare the amount of body temperature change among model runs. The model contained terms for both temperature variables and their interaction (Table 1). The response variable was the net difference in the hottest monthly average DBTM of each model run from the base model run. Although the interaction term was significantly different from zero in all regression models ($P < 0.01$; Table 1), its effect was always at least one order of magnitude smaller than the main effects and is not discussed further. We report the regression coefficients as the BTS of mussels to changes in T_a and T_w (Table 1). BTS can also be considered the partial derivative of average DBTM with respect to T_a or T_w, evaluated under current climatic conditions.

Predicted Temperature Response. We used predicted T_a and T_w changes generated by the National Oceanic and Atmospheric Administration Geophysical Fluid Dynamics Laboratory's CM2.0 model (32) to explore the consequences of geographic variation in BTS on predicted body temperature change. We compared two Intergovernmental Panel on Climate Change scenarios, representing opposite extremes of change: B1 (atmospheric CO_2 concentration = 500 ppm by 2100) and A2 (CO_2 = 800 ppm by 2100). We used model output for the 1° grid box nearest each of the four sensitivity sites. To calculate the magnitude of T_a and T_s change expected by 2100, we averaged each variable by month over the periods 2000–2020 and 2080–2100 and calculated the difference in the hottest month of the climate data between the two periods. We computed the body temperature change for each location as the sum of the product of each temperature variable with the BTSs reported in Table 1.

To separate the effects of geographic variation in BTS from geographic variation in climate change, we also compared body temperature changes calculated for an average of T_a and T_w change at the four sites (Table 2).

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