

MOSAIC PATTERNS OF THERMAL STRESS IN THE ROCKY INTERTIDAL ZONE: IMPLICATIONS FOR CLIMATE CHANGE

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Abstract. We explicitly quantified spatial and temporal patterns in the body temperature of an ecologically important species of intertidal invertebrate, the mussel *Mytilus californianus*, along the majority of its latitudinal range from Washington to southern California, USA. Using long-term (five years), high-frequency temperature records recorded at multiple sites, we tested the hypothesis that local “modifying factors” such as the timing of low tide in summer can lead to large-scale geographic mosaics of body temperature. Our results show that patterns of body temperature during aerial exposure at low tide vary in physiologically meaningful and often counterintuitive ways over large sections of this species’ geographic range. We evaluated the spatial correlations among sites to explore how body temperatures change along the latitudinal gradient, and these analyses show that “hot spots” and “cold spots” exist where temperatures are hotter or colder than expected based on latitude. We identified four major hot spots and four cold spots along the entire geographic gradient with at least one hot spot and one cold spot in each of the three regions examined (Washington–Oregon, Central California, and Southern California). Temporal autocorrelation analysis of year-to-year consistency and temporal predictability in the mussel body temperatures revealed that southern animals experience higher levels of predictability in thermal signals than northern animals. We also explored the role of wave splash at a subset of sites and found that, while average daily temperature extremes varied between sites with different levels of wave splash, yearly extreme temperatures were often similar, as were patterns of predictability. Our results suggest that regional patterns of tidal regime and local pattern of wave splash can overwhelm those of large-scale climate in driving patterns of body temperature, leading to complex thermal mosaics of temperature rather than simple latitudinal gradients. A narrow focus on population changes only at range margins may overlook climatically forced local extinctions and other population changes at sites well within a species range. Our results emphasize the importance of quantitatively examining biogeographic patterns in environmental variables at scales relevant to organisms, and in forecasting the impacts of changes in climate across species ranges.

Key words: biogeography; climate change; intertidal; mussel; *Mytilus californianus*; signal analysis; temperature; thermal stress; U.S. Pacific Coast.

INTRODUCTION

The effects of temperature on the survival and physiological performance of organisms, and the subsequent influence of physiological temperature tolerance on species distributions patterns, have been major foci of investigation for decades (Orton 1929, Hutchins 1947, Vernberg 1962, Somero 2005). Virtually all physiological

processes are affected to at least some degree by the temperature of an organism’s body. Recent technological innovations at molecular and biochemical levels have precipitated major advances in our understanding of how temperature drives organismal physiology and ecology (e.g., Somero 2002, Dahlhoff 2004, Hofmann 2005). Exploring the role of organism temperature in driving species distribution patterns has assumed a further sense of urgency given changes in global climate (Intergovernmental Panel on Climate Change 2001), the observable impacts of these changes on ecological patterns in nature (Root and Schneider 1995, Parmesan and Yohe 2003, Root et al. 2003, Parmesan and Galbraith 2004, Harley et al. 2006), and a pressing need to forecast the impacts of climate change on natural

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ecosystems (Clark et al. 2001, Halpin et al. 2004b, Gilman et al. 2006, Helmuth et al. 2006).

In many cases, however, our understanding of how the physical environment, and in particular aspects of climate, may limit the distribution of organisms is limited by our rather poor understanding of how physiologically relevant environmental factors vary in space and time (Hallett et al. 2004). In particular, we often know little of how "climate" is translated into patterns of body temperature, especially at spatial and temporal scales relevant to organisms (Helmuth 2002). Thus, while we have a general understanding of how large-scale climatic indices change over large geographic gradients (Stenseth et al. 2003), we often are at a loss as to how to explicitly test hypotheses relating to the influence of climate on levels of physiological performance (Chown et al. 2004, Hallett et al. 2004, Helmuth et al. 2005).

Mechanistically exploring the impacts of climate, and climate change, on the distribution of organisms in nature thus mandates a detailed knowledge of (1) how physiologically relevant environmental factors vary in space and time (Hallett et al. 2004, Holtmeier and Broll 2005); (2) how organisms interact with and perceive those environmental signals (Helmuth 2002, Helmuth et al. 2005, Gilman et al. 2006); and (3) what the physiological consequences of those varying signals are to the organism (Chown et al. 2004, Hofmann 2005, Somero 2005), including how organisms may adapt and physiologically acclimate to those signals (Clarke 2003, Stillman 2003). While significant progress has been made in all of these arenas, recent studies have emphasized that the physical environment can vary on scales that are not only highly complex but often counterintuitive (Underwood and Chapman 1996, Helmuth and Hofmann 2001, Helmuth and Denny 2003, Denny et al. 2004, Wright et al. 2004). The body temperatures of ectothermic organisms are often quite different from the temperature of the surrounding air or substratum (Porter and Gates 1969, Stevenson 1985, Huey et al. 1989). Subsequently, two organisms exposed to identical climatic conditions can experience markedly different body temperatures and thus very different levels of physiological stress, even when physiological responses to temperature are similar. Thus, patterns of organism temperature can vary over a wide range of temporal and spatial scales, even when broad-scale climatic patterns appear far simpler (Holtmeier and Broll 2005, Gilman et al. 2006). Moreover, physiological responses to fluctuating temperatures are often complex, and simple metrics such as average temperature may not be a sufficient indicator of physiological stress (Buckley et al. 2001, Halpin et al. 2004a). Knowing how and when to look for the effects of climate change, either through direct empirical observation or through modeling, therefore requires an explicit understanding of how potentially limiting factors such as body temperature vary over space and time, as well as knowledge of how physiological tolerance to those parameters varies along comparable scales (Halpin et

al. 2002, 2004a, Clarke 2003, Stillman 2003, Tomanek and Sanford 2003, Kearney and Porter 2004, Wright et al. 2004, Dethier et al. 2005, Stenseng et al. 2005).

The intertidal zone, the interface between marine and terrestrial environments, has long served as a model for examining the effects of climate on species distributions (Connell 1972) and may also prove an excellent model for the effects of climate change on species distributions (Hawkins et al. 2003, Harley et al. 2006, Helmuth et al. 2006). Here, we explicitly quantify spatial and temporal patterns in the body temperature of an ecologically important species of intertidal invertebrate, the mussel *Mytilus californianus*, along the majority of its latitudinal range from Washington to southern California, USA. We present long-term (5-yr) temperature records recorded at multiple sites along the west coast of the United States. We show that patterns of body temperature vary in potentially physiologically meaningful and often counterintuitive patterns over large sections of this species' geographic range. We use temporal autocorrelation to evaluate year-to-year consistency and temporal predictability in the mussel body temperatures along this large-scale gradient. Additionally, we evaluate the spatial correlations among sites to explore how body temperatures change along the latitudinal gradient, and explore the role of wave exposure at a subset of sites to explore the relative importance of wave splash in driving patterns of body temperature.

The roles of aerial and aquatic body temperatures in the intertidal zone

The upper zonation limits of many rocky intertidal organisms are thought to be set by some aspect of thermal or desiccation stress related to aerial exposure at low tide (Connell 1972), and organisms living in this habitat have been shown to exist at or near the edges of their thermal tolerance limits (Davenport and Davenport 2005). The intertidal zone is a model ecosystem for exploring the effects of climate, and climate change, on natural communities (Fields et al. 1993, Southward et al. 1995, Sagarin et al. 1999, Helmuth et al. 2006). The body temperature of intertidal invertebrates and algae at low tide is a crucial determinant of organism survival and performance (Somero 2002, 2005). Many studies have documented that the production of heat shock proteins (hsps) occurs after exposure to temperatures experienced during low tide (Sanders et al. 1991, Roberts et al. 1997, Hofmann 1999, Somero 2002, Tomanek 2002, Tomanek and Sanford 2003, Dahlhoff 2004, Halpin et al. 2004a, Li and Brawley 2004, Snyder and Ross 2004) and that the production of these proteins and their use in chaperoning activity exerts a metabolic cost (Heckathorn et al. 1996, Iwama et al. 1998). Other studies have shown physiologically significant impacts of aerial body temperature on the heart function of intertidal invertebrates (Stillman 2003, Stenseng et al. 2005).

Water temperature has also been shown to be an important limiting environmental factor, affecting rates

of feeding (Sanford 1999, 2002), larval mortality, and reproductive success (Hoegh-Guldberg and Pearse 1995). It may also influence the body temperature of intertidal organisms during low tide by setting the initial temperature following emersion, and by influencing rock temperature (Wethey 2002, Gilman et al. 2006). Moreover, it is an indicator of upwelling, another important driver of geographic distributions (Broitman et al. 2001, Leslie et al. 2005, Blanchette et al. 2006). While the relative importance of aerial and aquatic body temperatures to organismal survival remains unresolved, evidence suggests that both are likely important determinants of the physiological function and geographic distribution of intertidal species. As a result, the local and geographic responses of intertidal organisms are expected to display strong responses to changes in both terrestrial and aquatic climatic conditions (Lubchenco et al. 1993, Sanford 1999, Somero 2002, Harley 2003, Helmuth et al. 2006).

However, to date most studies have focused exclusively on the role of water temperature in driving temporal and spatial patterns of intertidal assemblages (e.g., Barry et al. 1995, Schiel et al. 2004). Moreover, physiological evidence suggests that not only the magnitude of extremes in temperature, but also the duration, frequency, and time history of these events may be important determinants of survival (Buckley et al. 2001, Crozier 2004, Halpin et al. 2004a, Wright et al. 2004). Explicitly quantifying spatial and temporal patterns in both aerial and aquatic body temperature is thus a necessary first step in generating hypotheses regarding the likely impacts of climatic variability on the geographic distributions of intertidal invertebrates.

Recent studies suggest that patterns of aerial body temperature may be more geographically complex than anticipated in coastal communities (Helmuth et al. 2002). Multiple factors interact to drive the body temperature of an intertidal alga or invertebrate during aerial exposure. The absolute tidal height of an organism on the shore, the amount of wave splash that it receives, and the local tidal cycle all interact to determine the timing and duration of exposure to terrestrial conditions at low tide. While exposed, substratum angle plays a major role in determining the amount of solar radiation received (Schoch and Dethier 1996, Helmuth and Hofmann 2001). Patterns of local climate such as fog can also have a significant modifying effect. Many of these factors (such as the effects of substratum aspect) can be very localized (Helmuth and Hofmann 2001). Other factors, such as regional differences in the timing of low tide (Denny and Paine 1998), may be sufficiently extensive to have biogeographic consequences for intertidal organisms (Helmuth et al. 2002). Yet other modifying influences, such as wave splash, may operate at intermediate scales (Schoch and Dethier 1996). As a result, while climatic conditions generally become increasingly colder moving poleward along coastlines, the occurrence of local "modifying factors" may theo-

retically override the impacts of climatic gradients, leading to mosaic patterns of temperature (Helmuth et al. 2006), as has been suggested for terrestrial ecosystems (Holtmeier and Broll 2005). This model suggests that the impacts of climate change will be most effectively detected by conducting investigations throughout species ranges rather than just at the margins of species ranges (Helmuth et al. 2002, Sagarin and Somero 2006). Specifically, this concept suggests that climate change may exhibit disproportionately large impacts at a series of "hot" and "cold" spots within species ranges (Helmuth et al. 2006), rather than causing simple latitudinal range shifts. Helmuth et al. (2002) for example, showed that because summer-time low tides occur in the middle of the day at northern latitudes, aerial body temperatures of mussels at sites in Oregon were as hot as some sites in Southern California, where summertime low tides seldom occur midday. As a result, Helmuth et al. (2002) predicted that mortality and physiological stress due to climate change would likely be detected not only at range margins, but also at hot spots within the species range. However, this study was conducted over only a one year time period, and at a limited number of sites.

Here, we explore this concept in detail using long-term, high-frequency measurements of temperatures relevant to the body temperatures of intertidal mussels (*Mytilus californianus*). We use this data set to test the hypothesis that aerial thermal regimes do not decrease monotonically with increasing latitude, and that "hot spots" and "cold spots" exist along the west coast of the United States. We furthermore explore the role of local patterns of wave splash in driving aerial thermal regimes, and patterns of temporal variability to investigate the concept that there exist geographic patterns in the predictability of thermal stress that may be detectable by intertidal organisms.

METHODS

Temperature instrumentation

Like terrestrial ectotherms (Porter and Gates 1969), the body temperatures of intertidal invertebrates during low tide are driven by multiple, interacting climatic factors such as solar radiation, wind speed, relative humidity and air and ground temperatures (Johnson 1975, Helmuth 2002). Furthermore, the shape, color, and mass of the organism also affect body temperature. Thus, two organisms exposed to identical climatic conditions can display very different temperatures (Porter and Gates 1969, Etter 1988, Helmuth 2002). As a result, during aerial exposure the body temperatures of intertidal organisms are often quite different from the temperature of the surrounding air, and can vary from one another by more than 15°C, even over scales of <20 cm (Bertness 1989, Helmuth 1998, Helmuth and Hofmann 2001).

As is the case for organisms, the shape, size and color of a data logger can influence the temperature that it records while in air (Heath 1964), and one type of logger

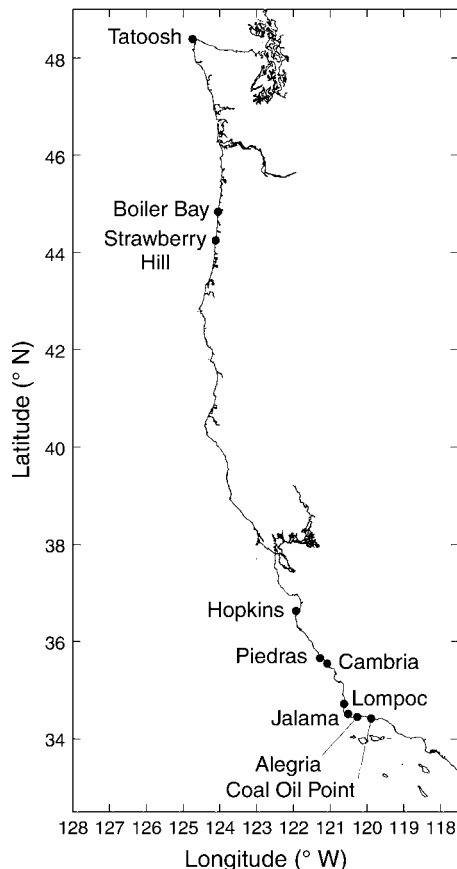


FIG. 1. Map of all deployment sites along the U.S. Pacific Coast.

is unlikely to serve as an effective proxy for all species at a site (Fitzhenry et al. 2004). We therefore matched the thermal characteristics of living mussels using a series of biomimetic sensors. Commercially available Tidbit loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) were either encased in black-tinted epoxy (Fitzhenry et al. 2004) or were placed in real mussel shells that were filled with silicone (Helmuth and Hofmann 2001). Fitzhenry et al. (2004) have previously shown that this species does not appear to cool via the evaporation of water even when forced to gape, and so does not behaviorally thermoregulate. Our loggers thus recorded the body temperatures of living mussels to within $\sim 2\text{--}2.5^\circ\text{C}$ during aerial exposure at low tide (Helmuth and Hofmann 2001, Fitzhenry et al. 2004).

Deployment sites

The primary goal of this study was to explore the role of the timing of low tide in driving latitudinal patterns in body temperature. We attempted to hold other local modifying factors such as wave splash, substratum aspect, and relative tidal height constant. Loggers were deployed at the seaward (wave-exposed) margins of 10 sites along the U.S. Pacific Coast (Fig. 1, Table 1): one

site in Washington (Tatoosh Island; see Plate 1); two sites in Oregon (Boiler Bay and Strawberry Hill); and seven sites in California (Hopkins, Piedras Blancas, Cambria, Lompoc, Jalama, Alegria, and Coal Oil Point [COP]). At three sites (Strawberry Hill, Boiler Bay, and Hopkins), loggers were additionally deployed at wave-protected (sheltered) areas adjacent to the wave-exposed sites to explore the role of wave splash. It should be noted, however, that the “wave protected” site at Boiler Bay, a bench landward of the wave-exposed bench, is less sheltered than the Hopkins or Strawberry Hill sites (Fitzhenry et al. 2004). All loggers were deployed on approximately horizontal substrata, which was verified using a Brunton inclinometer. Deployment durations varied from site to site, and were interrupted by instrument loss and damage. Our longest continuous deployment was at Hopkins (Monterey Bay, California), which was initiated in 1998 (Helmuth and Hofmann 2001) and is ongoing, while our shortest deployment was 431 days at Tatoosh Island. For some analyses, we grouped these sites into three regions: Washington–Oregon (WaOr; Tatoosh, Boiler Bay, and Strawberry Hill), Central California (CenCal; Hopkins, Piedras Blancas, and Cambria), and Southern California (SoCal; Lompoc, Jalama, Alegria, and COP). Data from a few additional sites were not included in the analysis because of data sparseness (short deployment or very recent deployment) but are included in the Appendix for comparison (Bamfield [Seppings Island], British Columbia; Cattle Point, Washington; Collin’s Cove, Washington; Bodega Bay, California; and Boat House, California).

Instrument deployment

Previous results indicated that variability between microsites at any given location was generally rather low, as long as instruments were deployed in regions with similar wave exposure, and on a uniform substratum angle (Helmuth et al. 2002, Harley and Helmuth 2003, Fitzhenry et al. 2004). Wave splash was quantified at each site using the method of Harley and Helmuth (2003) which compares the timing of “effective shore level” (the tidal height at which loggers are cooled by the returning tide) against the absolute tidal height (as measured using a laser level or theodolite; Table 2). The difference between the two values is estimated as the average wave run-up (AWR), i.e., the average distance that waves “run up” the shore above the still tide line after breaking. Loggers were affixed to the rock surface using Z-spar epoxy putty (Splash Zone compound A-788, Kop-Coat, Inc., Rockaway, New Jersey, USA) oriented in approximate growth position (Helmuth et al. 2002). The number of loggers retrieved varied due to instrument loss, ranging from three to six (Table 2). Each logger recorded average temperature at an interval of 10 or 15 min. Using the daily extremes of these high-frequency observations across all loggers deployed at a site, we calculated the average daily minima and

TABLE 1. Names and positions of all sites and locations discussed in the study, ordered from north to south.

Region	Location	Alongshore position (km)	Latitude (° N)	Longitude (° W)
WaOr	Tatoosh Island, WA	1660.1	48.39	124.74
WaOr	Boiler Bay, OR	1260.7	44.83	124.05
WaOr	Strawberry Hill, OR	1196	44.25	124.12
CenCal	Hopkins, CA	327.1	36.62	121.90
CenCal	Piedras Blancas, CA	208.11	35.66	121.28
CenCal	Cambria, CA	185.66	35.54	121.10
SoCal	Lompoc, CA	84.175	34.72	120.61
SoCal	Jalama, CA	57.722	34.50	120.50
SoCal	Alegria, CA	37.284	34.47	120.28
SoCal	Coal Oil Point (COP), CA	0	34.41	119.88

Notes: All coordinates were measured using the WGS84 system. State abbreviations: WA, Washington; OR, Oregon; CA, California.

maxima. Temperature observations during high tide (estimated by comparing temperature records against tide tables) were used to calculate average daily seawater temperature. We then used these daily statistics to calculate the average daily maxima and minima for the entire period of record for each site, a measure of “chronic” stress that incorporates both water and aerial temperature (Helmuth and Hofmann 2001), as daily extremes over the time period reflect extremes from both environments. We also calculated the highest and lowest temperatures recorded at each site for the period of February 2002–February 2003 in order to compare patterns of extreme or “acute” temperatures (Helmuth and Hofmann 2001), a reflection of aerial temperature extremes (Table 3). This time period represents the longest nearly continuous record available for most sites, with the exception of 2001, which was discussed in an earlier paper (Helmuth et al. 2002).

From the daily statistics, we calculated monthly summary statistics for each logger for every month with at least 25 days of data. Data for all sites, when available, are presented in the Appendix. For these long-term estimates, we applied a filter of 30 min as a smoothing function, calculating the highest and lowest temperature that occurred for a minimum of 30 min/d (the 97.9 and 2.1 percentile, respectively; Fitzhenry et al. 2004; Appendix).

Data analysis

Our hypothesis-testing framework was geared toward dissecting the main spatial and temporal patterns of variation of daily extremes in mussel body temperature. In order to examine spatial patterns, we relied on standard regression techniques to test for a latitudinal thermal gradient. Temporal patterns were examined with two different analyses to characterize the thermal regimes at every site with suitable temporal records. First, using temperature return times we examined the cumulative risk of experiencing a physiologically critical temperature. Second, we used temporal autocorrelation to examine the time-varying predictability in temper-

ature extremes. These spatial and temporal analyses are detailed in the next two subsections.

Spatial patterns

We tested for latitudinal gradients in daily maximum and minimum mussel body temperature using a regression model of the alongshore distance between sites and mussel body temperature statistics. This regression analysis tested the hypothesis that mussel body temperature extremes change with the large-scale (latitudinal) gradient in solar radiation and air temperature. We used the alongshore distance instead of latitude in order to appropriately represent the two Santa Barbara Channel sites (Alegria and COP), which are located along the same latitude (Table 1, Fig. 1), and preserve the spatial relationship across sites. The use of this criterion does not affect the general trend of decreasing temperature with latitude as the Santa Barbara Channel sites experience much warmer atmospheric and oceanographic conditions than the open coast sites (Lompoc and Jalama) located at approximately the same latitude (Cudaback et al. 2005). In order to examine the

TABLE 2. Descriptions of each wave-exposed site and of logger deployments.

Location	Average wave run-up (cm)	No. loggers	Tidal height (cm)	Tidal height (proportion of range)
Tatoosh Island	67.9	4–5	170	0.71
Boiler Bay	66.1	3–6	112	0.48
Strawberry Hill	47.4	3–5	157	0.68
Hopkins	94.3	4	175	1.09
Piedras Blancas	81.8	6	162	1.01
Cambria	NA	3	139	0.87
Lompoc	58.2	3–4	133	0.84
Jalama	50.0	4–6	114	0.72
Alegria	36.7	4	110	0.68
Coal Oil Point	31.0	3–4	81	0.50

Notes: Loggers were deployed near the middles of mussel beds at each site (reported as both height above mean lower low water [MLLW] and scaled as proportion of diurnal tidal range). Data are not shown for wave-protected subsites. Note that absolute tidal range increases with latitude and is ~50% higher at northern latitude sites than at southern sites.

TABLE 3. Long-term means of daily statistics and extremes for the period February 2002–February 2003 at all wave-exposed locations.

Location	Intertidal mussel temperature (°C)				
	Average	Daily average		Yearly maximum†	Month of maximum‡
		Minimum	Maximum		
Tatoosh Island	9.9604	8.0302	13.249	25.44 ± 4.36	May
Boiler Bay	11.465	8.6199	18.179	34.72 ± 2.22	July
Strawberry Hill	11.22	8.8817	16.621	27.08 ± 7.00	July
Hopkins	13.905	11.178	19.518	33.59 ± 2.38	April
Piedras Blancas	13.234	10.539	19.794	33.64 ± 3.59	April
Cambria	13.786	10.208	21.416	35.30 ± 0.86	April
Lompoc	13.871	11.134	19.861	31.15 ± 3.13	June
Jalama	14.995	11.645	22.452	35.46 ± 1.43	May
Alegria	15.691	11.92	23.434	39.50 ± 3.83	June
Coal Oil Point	15.713	12.688	20.636	34.32 ± 1.89	June

† Hottest temperature recorded for at least half an hour (mean ± sd for all loggers at each site).

‡ Month in which the extreme high temperature was recorded.

hypothesis that hot-spots and cold-spots may exist regardless of their latitudinal position we used a third-order polynomial regression of alongshore position with the long-term means of daily maximum and minimum temperature and plotted the bivariate relationship between residuals for each site using all data. The polynomial fit was used to remove the large-scale spatial structure in the data. Residuals from the large-scale model represent temperature variations due to local-scale processes (Legendre and Legendre 1998). We statistically tested the presence of cold and hot spots by fitting the polynomial regression across all sites during the only period when all sites had concurrent temperature measurements (13 January–18 July 2001, 183 days) and using a one-tailed *t* test to examine if the daily deviations from the large-scale model at every site were significantly smaller or greater than zero for average daily minima and maxima, respectively.

To compare the magnitude of variation within and among sites, we used variance components analysis to quantify the magnitude of variation in average daily maximum logger temperature among sites, replicate loggers within sites, and replicate days of observations within loggers. We independently tested for the influence of wave splash on mussel temperature, by regressing the residuals from the polynomial regression (i.e., deviations from the expectations based on latitude) against the average wave run-up (AWR) for each site. We similarly tested for the effects of logger intertidal height (both absolute and as a percentage of tidal range, Table 2) using linear regression analysis.

Temporal patterns

Because high-temperature stress is known to affect mussel distribution and physiology, we examined the distributions of daily maxima for all exposed sites for which we had a concurrent, continuous data set. We used a period from 12 January to 13 November 2001 at all exposed sites except Cambria and COP, where data were lacking. Previous data indicate that brief exposure

to temperatures above 30°C are sufficient to induce production of hsp's in *M. californianus* (Halpin et al. 2004a), so we used this temperature as a basis for comparing the potential for thermal stress among exposed sites. We calculated a survival distribution function ($1 - F(x)$, where $F(x)$ is the cumulative distribution function), from which we derived the probability of observing a daily maximum above 30°C.

We used the daily statistics to study the dynamical behavior of mussel body temperature by examining patterns of temporal autocorrelation using data from January 2000 through December 2004. We examined daily patterns of variation at short but physiologically relevant time scales with our maximal temporal scale being 28 days. The raw daily time series showed a strong seasonal cycle that can bias autocorrelation estimates through serial correlation (i.e., inflate autocorrelation at short time lags). Due to the limited number of years in the record and temporal gaps in several of the time series, it was not possible to remove the annual cycle using harmonic regression. Thus, we removed seasonality by first-order differencing such that the first difference, D , at time t and temperature T is $D = T(t) - T(t - 1)$. We then centered each time series by subtracting the mean and dividing by the standard deviation and calculated the unbiased temporal autocorrelation of mussel body temperature (Bendat and Piersol 1986, Denny et al. 2004). We computed conservative confidence intervals for autocorrelation by calculating them for the time series with fewer degrees of freedom at each lag in the comparisons by regions (see *Results*). Due to the limited length of the time series, autocorrelation estimates were calculated using all available pairs of data at each time lag.

Wave exposure

To examine the role of wave splash, we separately compared the three sites where a suitable record of different wave-splash regimes existed (Boiler Bay, Oregon; Strawberry Hill, Oregon; and Hopkins, Cal-

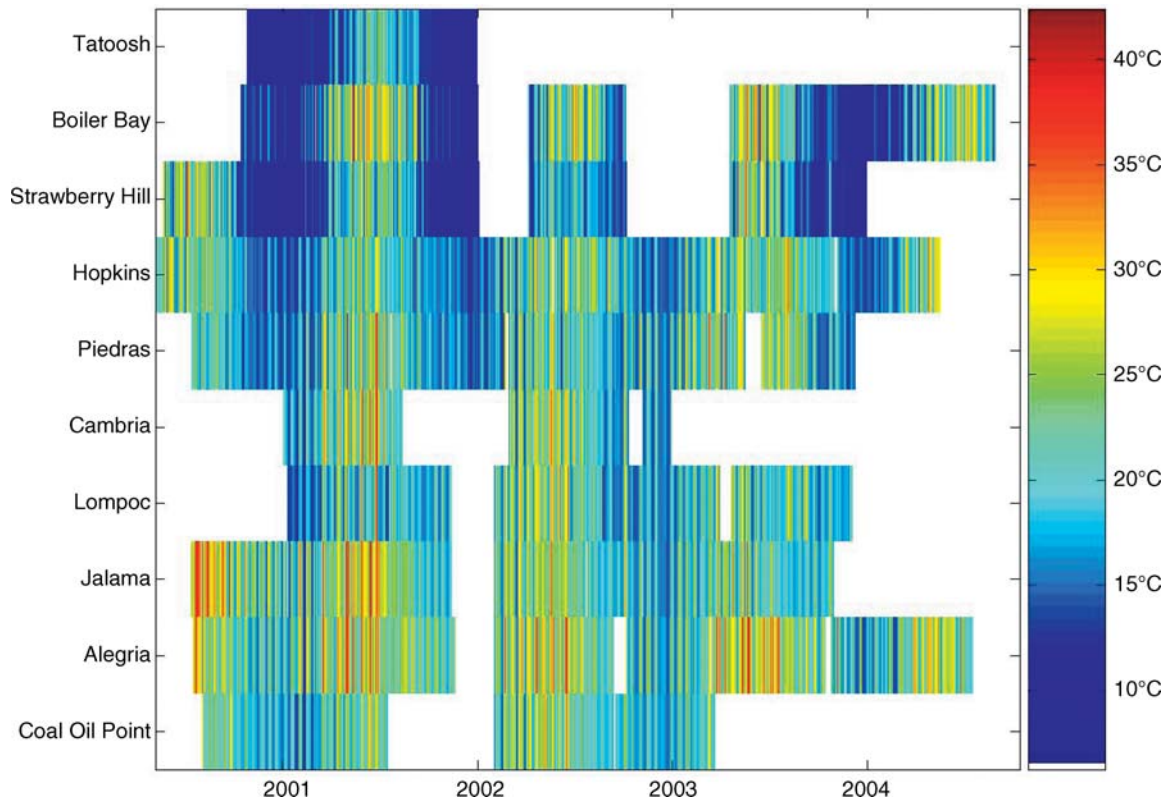


FIG. 2. Daily maximum mussel body temperature at all sites from 1 January 2000 to 31 December 2004. Sites are sorted latitudinally from north (top) to south (bottom). The color bar on the right side of the figure is the key to the temperatures shown in the figure, which range from 6° to 42°C.

ifornia). Specifically, we tested the hypothesis that mussels at wave-protected locations experience hotter and less variable temperature than their wave-exposed counterparts. In order to follow a hierarchical approach to examine temperature variability, we compared mussel body temperature extremes through correlation and examined their temporal dynamics through their autocorrelation functions at all three pairs of sites. This allowed us to examine temperature variations at the regional and local scales, over a range of temporal scales. Thus, we examined nested scales of variation, exploring the effect of wave splash on temperature over tens of meters and comparing differences in temperature due to latitude over hundreds of kilometers. All analyses were performed using Matlab 7.01 v.14 (Mathworks, Natick, Massachusetts, USA) or SAS (SAS Institute, Cary, North Carolina, USA).

RESULTS

Spatial patterns in extreme temperatures

In accordance with our previous results from 2001 (Helmuth et al. 2002), yearly extremes in maximum body temperature from 2002 revealed a highly variable thermal mosaic (Table 3, Fig. 2), with no clear latitudinal pattern. The probability of exposure to a temperature over 30°C, at which induction of the heat-

shock response is likely, also showed a complex spatial pattern, with sites having a relatively high probability interspersed with sites having a lower probability (Fig. 3). In contrast, the long-term averages of daily minimum and daily high tide body temperature did show a fairly strong latitudinal gradient (Table 3, Figs. 4 and 5).

Results of the ANOVA confirmed that between-site variability in logger temperature were greater than within-site variability. Separate analysis on daily maxima and minima both showed greater variance among sites than within sites (20% vs. 8% for maxima, 45% vs. 3% for minima). In both analyses, day-to-day variation within loggers represented the greatest variance component. The observation of greater variance among than within sites suggests that microsite differences were indeed quite low, and were unlikely to be driving site-level temperature differences. The regression of residuals vs. average wave run-up (a measure of wave splash) and logger height showed that there were no relationships between either maximum or minimum temperature for both of these metrics, again confirming that the patterns observed were not due to variability in logger placement.

The results of the polynomial regression of the daily minimum and maximum temperatures aid in elucidating the complex geographic pattern. Moreover, the analysis provides a means of objectively identifying sites as hot

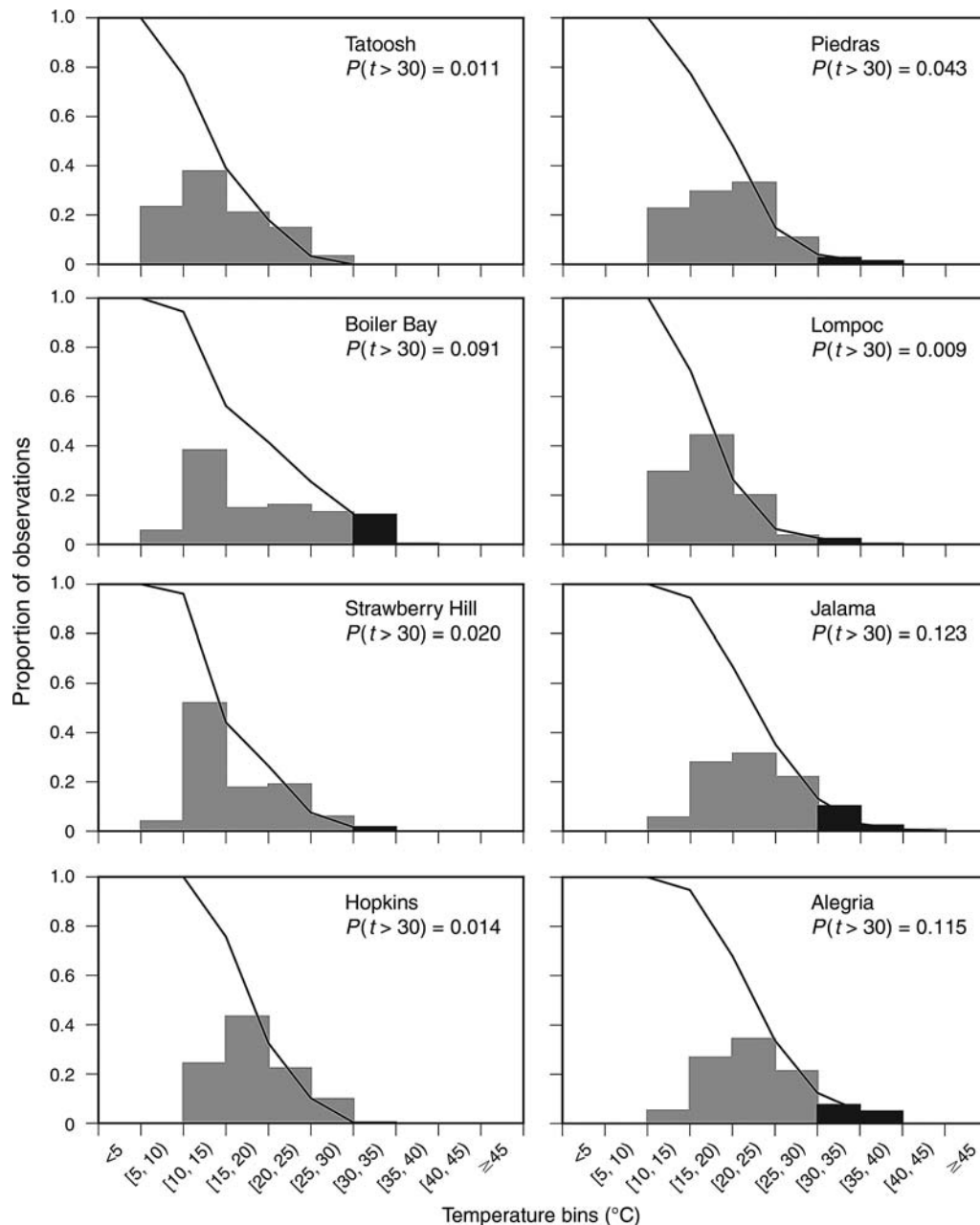


FIG. 3. Distributions and survival function for daily maximum body temperature at all wave-exposed sites (except Cambria and Coal Oil Point) ranging from northernmost to southernmost from top left panels to bottom right panels, for the period 12 January–13 November 2001. Temperatures are binned in 5° temperature bins, and histograms represent the proportional occurrences of temperatures in these bins in the time period. The $P(t > 30)$ in each case represents the probability that any given temperature will exceed 30°C.

and cold spots based on long term trends in daily minima and maxima. The polynomial regression demonstrates that while a simple spatial model can explain some variation in long-term measurements in daily maxima and minima (Fig. 6), important deviations from predicted temperatures remain, with sites having colder daily minima and hotter daily maxima than expected. The bivariate relationship between minimum and

maximum temperature residuals from the polynomial regression shows that departures from the latitudinal model are not sorted geographically (Fig. 7, Table 4). Here, we define a hot spot as a site with maximal daily temperatures that are warmer than expected based on the expectation of latitudinal gradient and a cold spot as a site with daily minimal temperatures that are colder than expected based on the latitudinal gradient. There



PLATE 1. Measurements of intertidal heights were conducted at most sites with a laser level, using a reference point obtained by observing still tidal height on multiple days. The site shown here is Strawberry Draw, Tatoosh Island, Washington, USA. Photo credit: B. Helmuth.

were at least four major hot spots among the locations examined: Boiler Bay (WaOr), Cambria (CenCal), and Alegria and Jalama (SoCal). The long-term average of the average daily maximum temperatures at these sites was around a full degree Celsius hotter than predicted by the geographic structure, with Alegria being 1.73°C hotter. Although departures from the latitudinal model were smaller in the case of average daily minima, the analysis identified four sites as cold-spots during the period of time examined: Boiler Bay (WaOr), Cambria (CenCal), and Alegria and Jalama (SoCal; Table 4). Strikingly, three sites appeared as both a hot and cold spot suggesting they experienced extreme thermal variability with respect to the rest of the sites used as the latitudinal sample. The one-tailed *t* test for the residuals of the daily latitudinal model supported the conclusions reached by examining only the residuals of the long-term means (Table 4).

Temporal patterns

In order to examine the dynamical behavior of extremes in mussel body temperature, we calculated the temporal autocorrelation at all exposed locations within each region. In the SoCal region, the dominant signal related to tidal forcing as evidenced by the positive autocorrelation estimates around 14- and 28-d lags (Fig. 8E and 8F). Similarly, negative autocorrelation is evident around opposite phases of the tidal cycle (i.e., 7- and 14-d lags). The tidal signal is more

pronounced in the autocorrelation of maximum body temperatures. Although the strength of the tidal signal is still evident in the autocorrelation of maximum and minimum daily mussel body temperature in the CenCal region (Fig. 8C and 8D), the tidal pattern is completely absent in the WaOr region (Fig. 8A and 8B). One of the most prominent features of the autocorrelation function is the large negative autocorrelation observed at short time lags. The pattern of temporal variability over short time lags is in striking contrast with the tidal signal, with the WaOr region showing the largest and more persistent negative autocorrelation estimates at short time lags (1–3 d) in the three regions. In the CenCal region, negative autocorrelation at short time lags was largely confined to 1-d lags and to the opposite phases of the tidal cycle. The SoCal region showed a moderate day-to-day variation in maximum body temperatures with marginally significant negative autocorrelation observed 1-d lags in maximum body temperatures, but with a persistent negative autocorrelation pattern over 1- to 10-d lags in minimum body temperatures.

Contrasts between exposed and protected locations

Daily maximum and minimum mussel body temperatures were always correlated between exposed and protected locations within sites (Fig. 9, Table 5). Tighter correlations were observed with measures of minimum temperatures at exposed and protected sites, and the linear trends tended to closely follow a 1:1 relationship

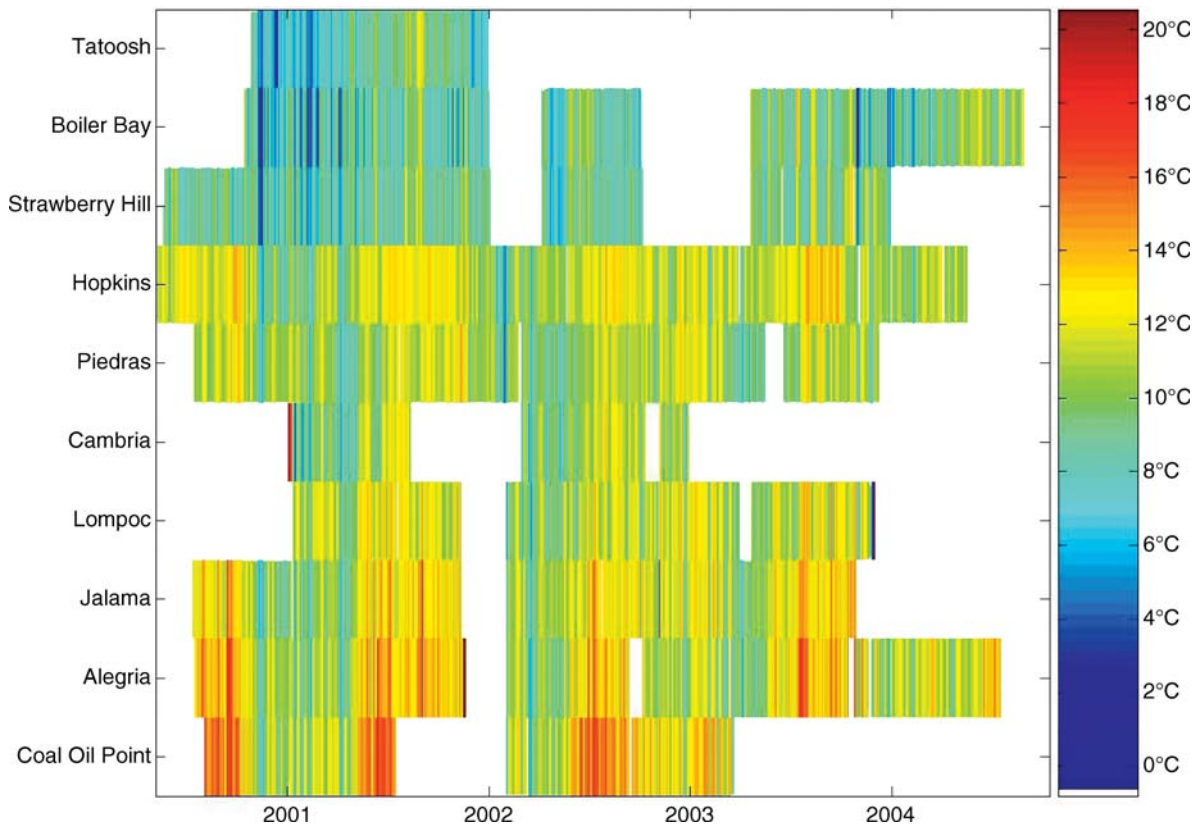


FIG. 4. Time series of daily minimum mussel body temperature at all sites from 1 January 2000 to 31 December 2004. Sites are sorted latitudinally from north (top) to south (bottom). Temperatures range from -1° to 21°C .

(Fig. 9A, C, and E; Table 5). In agreement with the correlation patterns, we did not find differences in minimum daily mussel body temperatures within any site (t test; Hopkins, $P = 1$; Strawberry Hill, $P = 1$; Boiler Bay, $P = 0.32643$, Table 5). Protected locations were hotter (on average) than their exposed counterparts when we compared maximum daily mussel body temperatures (t test; all locations, $P < 0.0001$, Table 5). It was apparent that at higher daily minimum temperatures, the temperatures at the exposed and protected locations converged (Fig. 9E) perhaps because the minima on those days reflect water temperature at high tide, when both protected and exposed locations are submerged. In contrast, at higher average daily maximum temperatures, exposed locations tended to stay cooler than protected locations, probably indicating the amelioration of high temperatures in exposed area by wave splash (Fig. 9F).

We found that patterns of autocorrelation in extreme temperatures at exposed and protected at any given site showed almost identical patterns. The autocorrelation function of minimum temperatures is strikingly similar at any given site regardless of wave exposure (Fig. 10A, C, and E). An interesting feature was the presence of a small-scale (1–2-d lags) negative autocorrelation indicating that minimum temperatures were extremely variable

from day to day. A similar picture was evident in the autocorrelation of maximum temperatures where exposed and protected locations behaved similarly across exposed and protected locations at all sites (Fig. 10B, D, and F). As we had detected before for all exposed locations, the tidal signal became stronger with decreasing latitude (Fig. 7) for both exposed and protected locations at all three sites. The magnitude of the negative autocorrelation at 1-d lag at the protected location in Strawberry Hill was the largest detected in the present study (Fig. 10D, $r = -0.36056$).

DISCUSSION

The significance of latitude

Geographic patterns of environmental variables play an important role in the ecology and evolution of broadly distributed species. Because abiotic factors such as solar radiation, day length, wave height, upwelling, the timing of low tide, and air and water temperature can all vary with latitude, physiological stress, and organismal performance are expected to change with latitude as well, but often in nonintuitive ways. Here, we show that the latitudinal patterns in the aerial body temperatures of *Mytilus californianus* are complex, and that patterns vary depending on whether one looks at water temperature, long-term averages of daily maxima and

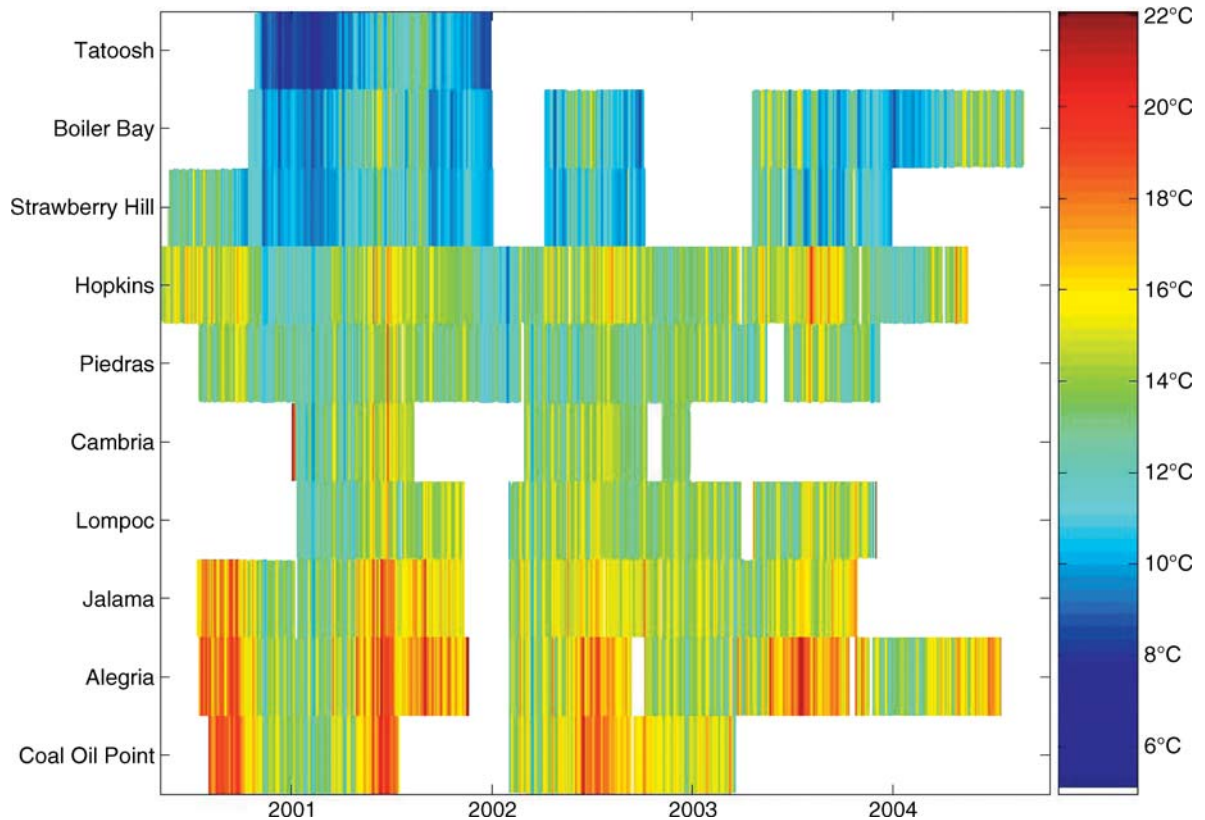


FIG. 5. Time series of daily mussel body temperature during high tide at all sites from 1 January 2000 to 31 December 2004. Sites are sorted latitudinally from north (top) to south (bottom). Temperatures range from 5° to 22°C.

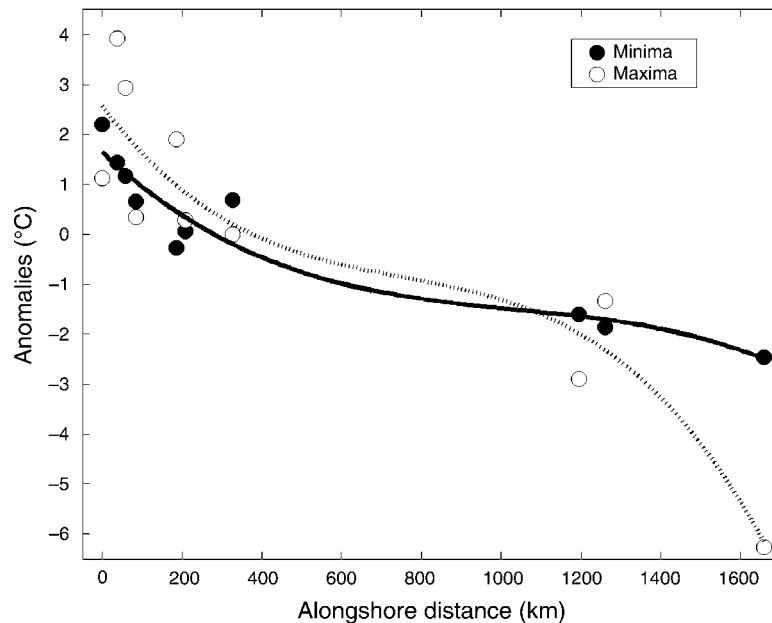


FIG. 6. Third-order polynomial regression of the alongshore position of all sites and their long-term means of maximum (open circles) and minimum (solid circles) mussel body temperatures. The solid line is the least-squares polynomial fit of alongshore position and maximum temperatures ($r^2 = 0.8604$, $F_{3,6} = 12.326$, $P < 0.001$) while the segmented line corresponds to the least-squares fit of the minimum temperatures ($r^2 = 0.90963$, $F_{3,6} = 20.132$, $P < 0.001$).

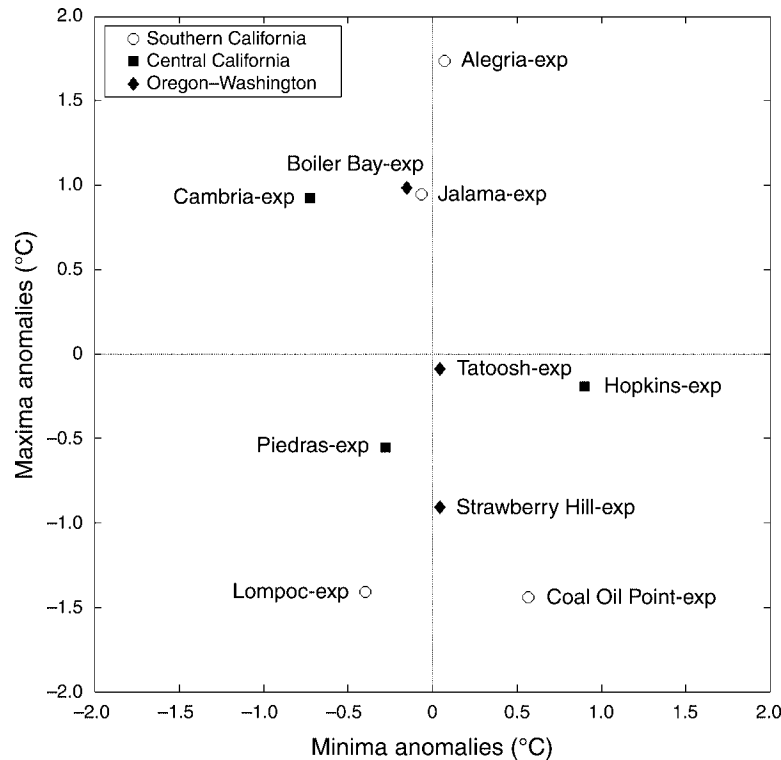


FIG. 7. Bivariate relationship between residuals from the polynomial regression of alongshore position and long-term daily maximum and minimum mussel body temperature for all exposed (exp) locations. Locations lying above the horizontal line show average daily maxima that are hotter than expected by their geographic position, while locations falling below the horizontal exhibit maxima that are less hot than expected. The vertical line depicts the same relationship for average daily minima, with sites lying on the left being colder and sites on the right being less cold than predicted by the latitudinal gradient. Sites are grouped by geographic region, with solid circles corresponding to the southern California locations, open squares to the central California locations, and solid diamonds to the Oregon–Washington locations.

minima (chronic stress), patterns of predictability, or at yearly extremes (acute stress). Specifically, latitudinal variation in average temperature increases with decreasing latitude. This is not surprising, since this metric is in part driven by water temperature, which shows a clear

TABLE 4. Results of one-tailed *t* test for differences between anomalies from the latitudinal model for maximal and minimal daily temperature values.

Location	Maximum daily temperatures		Minimum daily temperatures	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Coal Oil Point	-17.125	1	13.512	1
Alegria	14.424	<0.001	-1.0371	0.1505
Jalama	14.941	<0.001	-9.0401	<0.001
Lompoc	-19.267	1	1.5765	0.9416
Cambria	7.9847	<0.001	-13.472	<0.001
Piedras	2.0411	0.0213	-5.2718	<0.001
Hopkins	-5.6733	1	15.389	1
Strawberry Hill	-14.567	1	4.5958	1
Boiler Bay	14.983	<0.001	-8.2764	<0.001
Tatoosh	-14.697	1	16.666	1

Notes: The alternative hypothesis is that the anomaly is greater (for maximal temperatures) or smaller (for minimal temperatures) than 0. Boldface *P* values indicate rejection of the null hypothesis with $P < 0.01$ (all $df = 184$).

decrease with increasing latitude (Fig. 5). In contrast, while long-term averages of daily maxima and minima show a general trend with latitude over large scales (which likewise is not unexpected since daily maxima and minima during neap tidal cycles are reflective of body temperature during submersion), large deviations from this model occur in the daily maxima and minima at specific locations (hot and cold spots; Figs. 6 and 7) likely due to the impact of modifying factors such as the timing of low tides and local microclimates.

The complexity of the latitudinal pattern is even more apparent when examining values of yearly extremes (Table 3), which reflect only the influence of aerial body temperatures. For example, the maximum temperatures experienced at Boiler Bay (WaOr) in 2002 differ more from the neighboring site at Strawberry Hill, 60 km away, than they do from Hopkins (CenCal), even though the latter is >900 km south (Table 2) and loggers at the latter site were higher in the intertidal (Table 2). (It should be noted, however, that, in other years, Strawberry Hill and Boiler Bay displayed very similar high temperature extremes; Appendix.) Similarly, freeze events were recorded at Boiler Bay (November 2003), Hopkins (December 1998), and Lompoc (November

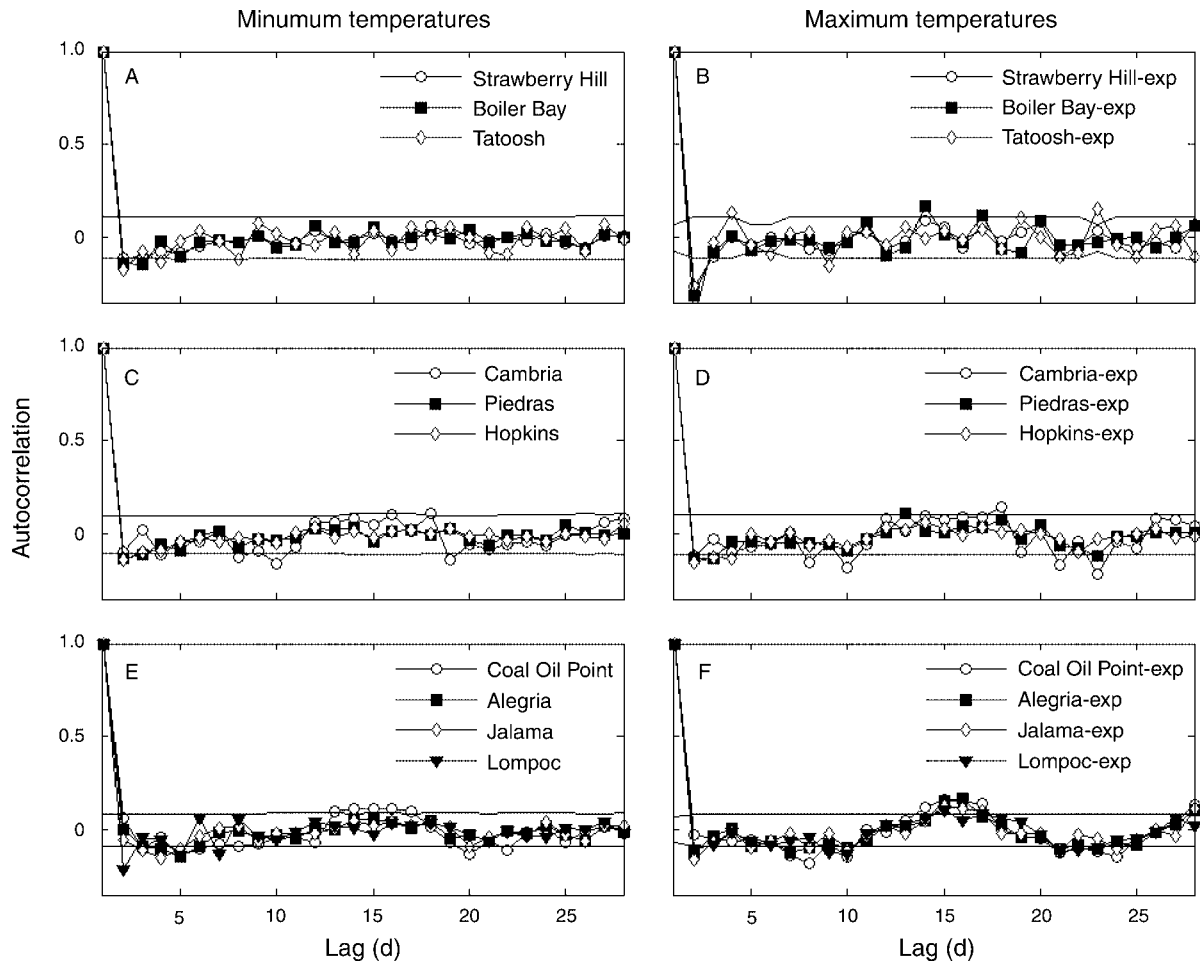


FIG. 8. Autocorrelation functions of daily minimum (A, C, and E) and maximum (B, D, and F) mussel body temperatures at all sites. Horizontal lines are Bonferroni-corrected ($\alpha = 0.05$) confidence intervals for significant autocorrelation. Notice the weakening of the tidal signal toward high-latitude sites, particularly for the autocorrelation of maximum daily temperatures and the presence of strong negative autocorrelation in both maximum and minimum temperatures at one- and two-day lags for all high-latitude sites. Autocorrelation trends show that the tidal signal is significantly negative at lags (distance in time) equivalent to half of a tidal cycle (~ 7 d) and is positive around a full tidal cycle (~ 14 d). This pattern is more evident in the maximal temperatures at lower latitudes (F); the harmonic characteristics of the signal are less evident at higher latitudes (panels D and B). To illustrate the decay in the tidal signal, sites are sorted latitudinally, from higher latitudes (top panels, WaOr region) toward lower latitudes (CenCal, mid panels, and SoCal, lower panels).

2003), but not at any of the other outer-coast sites (but see data for Puget Sound sites in Appendix).

As discussed by Helmuth et al. (2002), the daily pattern of immersion and emersion, as determined by tides and wave splash, interacts with the local terrestrial climatic regime to determine an intertidal organism's aerial thermal regime. Generally organisms with body temperatures driven largely by solar radiation experience maximum body temperatures in mid-day and early afternoon hours, especially during summer when levels of solar radiation are greatest. But, depending on the tides, intertidal organisms may be submerged and thus avoid exposure to solar radiation during this part of the day. Such is the case in southern California where low tides seldom occur midday in summer months (Helmuth et al. 2002). While many of the physical forcing factors

controlling body temperature exhibit strongly cyclical variation (e.g., solar radiation and wave heights on an annual cycle, tidal immersion on a 14-d cycle embedded in an 18.6-yr cycle [Denny and Paine 1998]), variability within these forcing mechanisms and the combination of their signals contribute to the thermal mosaic observed. The importance of the tidal cycle in driving geographic patterns of temperature is confirmed by our observation that peak temperatures at southern California sites typically occur in April and May, while those at northern sites occur in June and July (Table 3). Latitudinal variation in wave exposure may also contribute to observed patterns in temperature, especially at sites south of Point Conception where levels of wave splash are typically very low. In southern California, where low tides in summer seldom occur in

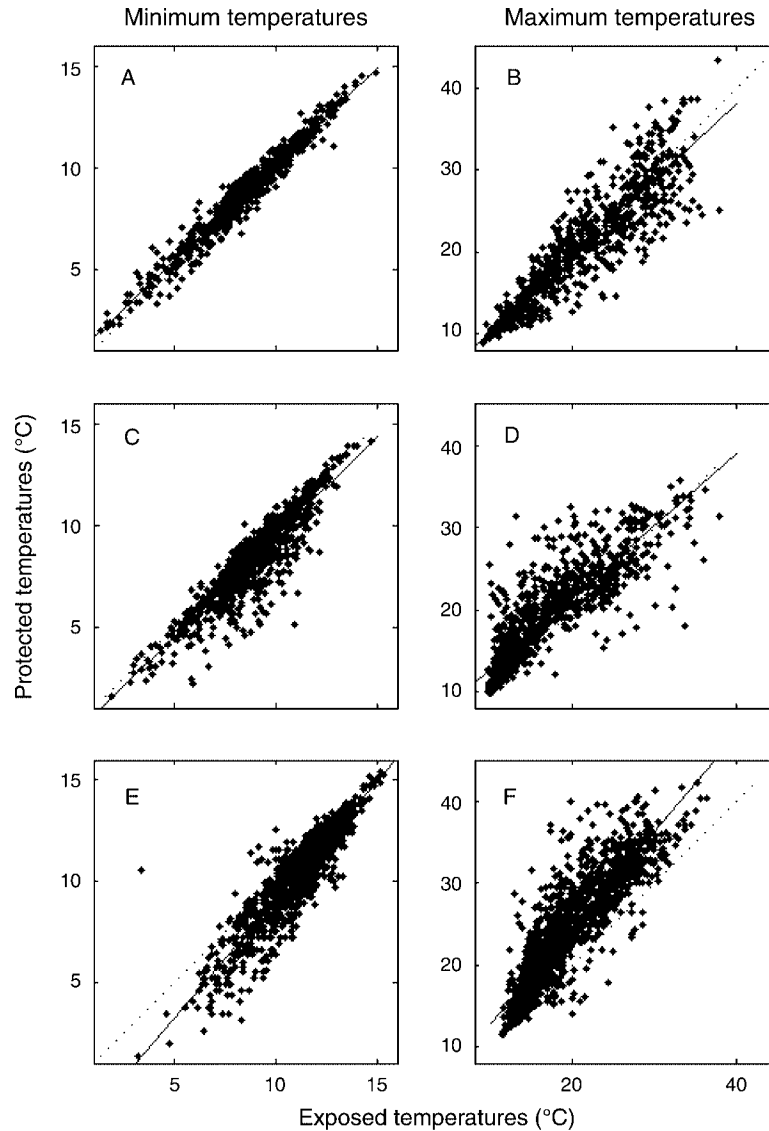


FIG. 9. Scatter plots between exposed and protected locations for minimum (A, C, and E) and maximum (B, D, and F) daily mussel body temperatures in the three sites with paired locations: Boiler Bay (A and B), Strawberry Hill (C and D), and Hopkins (E and F). All correlations are highly significant (see Table 2 for statistics). The solid line is the least-squares fit to the data, while the dotted line shows the 1:1 relationship.

TABLE 5. Statistics for the correlation between exposed and protected locations at all three sites where the comparison was possible for average daily minimum temperatures and average daily maximum temperatures.

Location	Average daily minimum temperatures				Average daily maximum temperatures			
	<i>r</i>	<i>t</i>	df	<i>P</i>	<i>r</i>	<i>t</i>	df	<i>P</i>
Hopkins	0.90901	10.958	3111	1	0.87063	-21.458	3111	< 0.001
Strawberry Hill	0.89441	6.1634	2060	1	0.86023	-7.1008	2060	< 0.001
Boiler Bay	0.97806	-0.4499	1128	0.32643	0.92838	-6.3482	1128	< 0.001

Notes: Values of *r* in boldface indicate significant correlations ($P < 0.001$); *t* is the *t* statistic after testing the alternative hypothesis that the mean of the protected location is greater than the mean of the exposed location with $\alpha = 0.05$; *P* is the probability that the null hypothesis is true; and rejections are shown in boldface type.

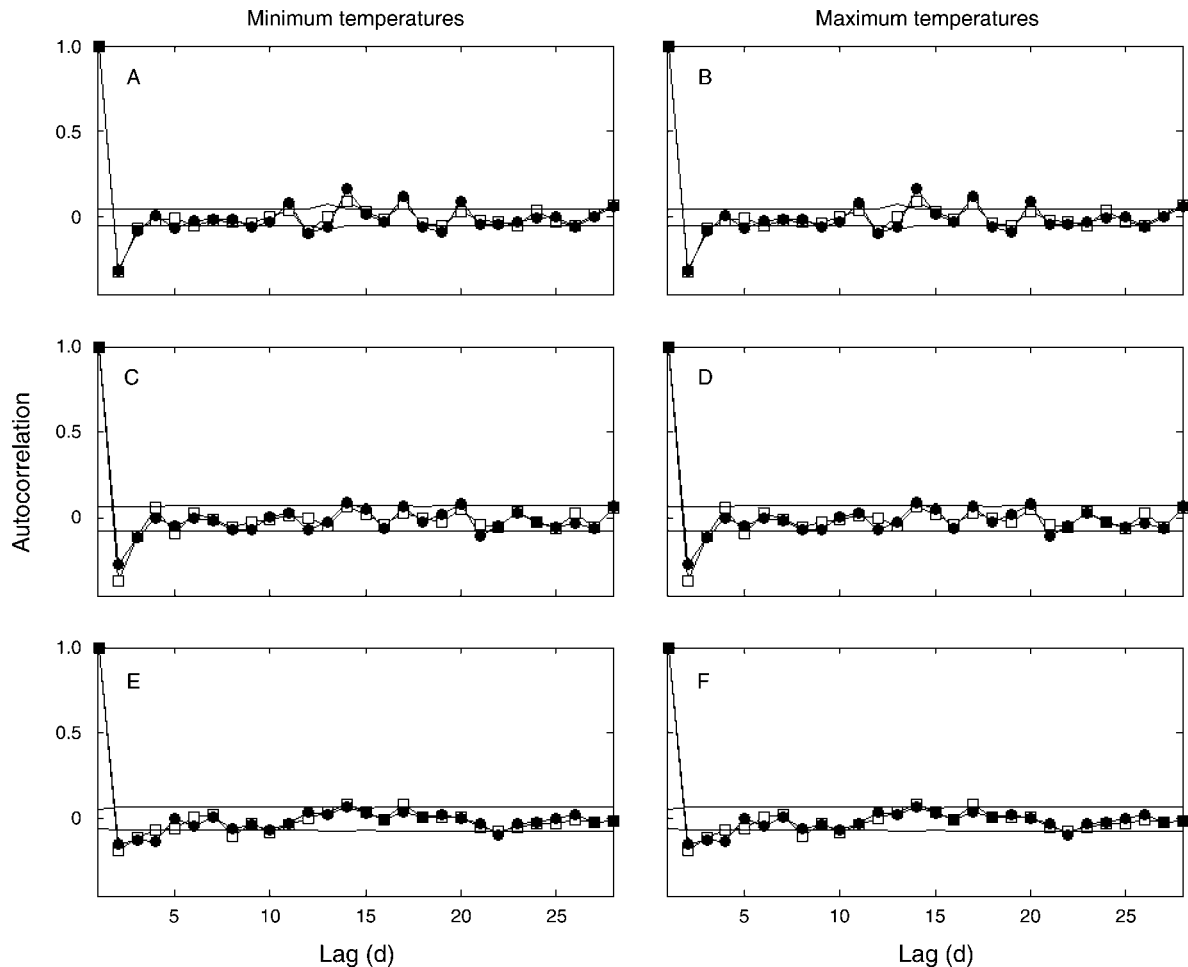


FIG. 10. Autocorrelation functions of daily minimum (A, C, and E) and maximum (B, D, and F) mussel body temperatures at exposed and protected locations at Boiler Bay (A and B), Strawberry Hill (C and D), and Hopkins (E and F). Horizontal lines are Bonferroni-corrected ($\alpha = 0.05$) confidence intervals for significant autocorrelation. Solid circles are protected locations, and open squares are exposed locations. Note the extreme similarity in the autocorrelation functions and the presence of large and significant negative autocorrelation over 1–2 d lags in the high-latitude sites (A–D).

the middle of the day, the risk of extreme body temperatures may typically be fairly low, especially in wave-exposed areas, even when terrestrial climatic conditions are hot (Helmuth et al. 2002). Thus yearly temperature extremes at Jalama (SoCal) were very similar to those at Boiler Bay (WaOr; Table 3).

At northern sites, thermal conditions at wave-exposed and wave-protected sites can be quite similar during periods of calm waves at extreme low tide (Fitzhenry et al. 2004; Appendix). For example, yearly maximum temperatures recorded at Strawberry Hill wave-exposed and wave-protected sites during the course of this study were very similar in magnitude, even though values of average daily maximum temperatures were higher in the wave-protected site (Fitzhenry et al. 2004; Appendix). Consequently, because animals may be less acclimated to elevated temperatures, they may be more at risk for

physiological stress in these wave-exposed areas than at wave-protected areas.

Physiological implications of spatial variation in thermal stress

We observed clear differences among regions in the frequency and magnitude of extreme events, as well as the thermal history of these events, which may have important physiological and biogeographic consequences. Interpreting the importance of these patterns requires a better understanding of the relative importance of submerged temperature, aerial body temperature, and thermal history on the physiology of *M. californianus*. Mussels living in southern California experience predictable cycles of thermal stress over a lunar tidal cycle. Because of this environmental predictability at relatively short time scales, mussels may be able to acclimate to stressful thermal conditions (Weber

1992, Dahlgard et al. 1998, Horowitz 2002). At higher latitudes, tidal rhythms in thermal stress are absent, and negative autocorrelations suggest that day-to-day thermal variability is highly unpredictable. In this context, organisms may be more vulnerable to damage from temperature maxima after periods of lower temperatures, and conversely, organisms at low-latitude sites may be less vulnerable, even when the absolute magnitude of the temperature maxima are the same. The interplay of the duration and magnitude of heat stress on an individual's subsequent acclimation to thermal stress is complex and poorly understood, although the process of "thermal hardening" is thought to be important (Krebs and Feder 1998). Clearly, more information on the time course of thermal acclimation will be of use in predicting organismal response to environmental variation. Interpreting the biological consequences of these complicated thermal will require that information about the physiological performance and tolerance of the organisms living along the North American west coast be collected on concomitant spatial scales (Hofmann 2005).

Implications for climate change

The mosaic of hot and cold spots across the distribution of *M. californianus* suggests a number of hypotheses regarding the geographic response of this species to future climate change. Latitudinal range shifts are commonly predicted consequences of climate change (e.g., Fields et al. 1993, Barry et al. 1995) and have been observed empirically in many systems (Parmesan et al. 1999, Walther et al. 2002). Local hot-spots may facilitate such poleward expansions by providing footholds for advancing populations, as has been hypothesized for some invasive populations (Ruiz et al. 1999). Alternatively, cold spots may function as thermal refugia as the ranges of colder water species contract to higher latitudes. If hot spots become sufficiently large, or occur adjacent to regions of unsuitable habitat, they could instead serve as barriers to dispersal, in effect creating disjunct populations (Helmuth et al. 2006). Because complex tidal regimes where latitudinal variability in the timing of low tide in summer and winter may be commonplace, the potential for hot spots and cold spots to be a worldwide phenomenon is very real. As a result, if thermal mosaics are a pervasive feature of many species' latitudinal ranges, a narrow focus on population changes only at the margins may overlook climatically forced local extinctions and other population changes at sites well within a species range. Our results therefore stress the importance of quantitatively examining patterns in environmental variables at scales relevant to organisms, and in forecasting the impacts of changes in climate across species range distributions.

Latitudinal trends in the temporal predictability of thermal stress also have implications for population responses to climate change. The temporal unpredictability (i.e., the low autocorrelation) of more northern

intertidal sites renders the organisms within them vulnerable to unsystematic deviations from the local mean. The true physiological impact of this prediction for a potential climate change scenario remains untested as far as we know. The level of temperature variability also influences the abilities of organisms to survive extreme temperature events (Kelty and Lee 2001) thus mussels at sites such as Cambria, which appeared as both a hot and a cold spot, may be better suited for rare climatic extremes than those from sites such as Tatoosh which exhibit more thermal stability.

Ultimately, however, the ecological and geographic responses of *M. californianus* to climatic change will depend not only on the direct physiological effects of temperature change on mussels, but also on ecological interactions with other species. For example, wherever the upper distributional limit of *M. californianus* shifts lower into the intertidal due to increases in aerial climatic stress, but that of its primary predators (*Pisaster ochraceous*) remains unaffected or shifts upward due to warming seawater temperatures (Sanford 1999), the prey will be "squeezed" out of the intertidal leading to local extinction (Harley 2003). In contrast, wherever the upper limits of both predator and prey are shifted downward by climatic stress, there will be no net effect of climate change on mussel beds. Moreover, all species are likely to be affected not only by shifts in aerial and aquatic climate, but by changes associated with sea level rise and wave height (Harley et al. 2006), both of which will determine emersion time.

Additional considerations

In sum, our results suggest that local patterns of wave splash and tidal regime can overwhelm larger-scale climatic gradients in driving patterns of body temperature (Helmuth et al. 2006), akin to what has been suggested for terrestrial ecosystems (Holtmeier and Broll 2005). Understanding the ecological relevance of these patterns, however, requires at least two other important areas of information not included in this study. First, the ability of organisms to evolve or physiologically acclimate to thermal stress must be considered (Clarke 2003, Chown et al. 2004) when determining when and where thermal extremes will cause mortality events. Second, if mortality events are to matter, then they must be of sufficient magnitude that larval supply is unable to repair or span the damage that occurs (Sotka et al. 2004). In other words, the spatial extent of the mortality must exceed the maximum dispersal of the larva to reinvade or traverse the hot spot or cold spot. Such an event may be particularly likely when a hot spot occurs adjacent to a region of unsuitable habitat.

Importantly, some of the patterns we describe here may be specific to the intertidal height at which they were measured. For example, organisms that live higher on the shore than *Mytilus californianus* may not experience predictable, two-week variation in thermal stress because daylight emersion occurs throughout the

fortnightly tidal cycle. Conversely, organisms that live very low in the intertidal will only be exposed by the low "spring tides" that coincide with new and full moons, and those at southern sites will almost never be exposed in the summer. Thus, tidal height can modulate the regional patterns observed in this study and our results may not apply to other species in this habitat. Thus the hot spots for mussels found in this study may not be hot spots for other groups living, for instance, in the high intertidal (Sotka et al. 2004). We strongly stress that the thermal environment in the intertidal zone must be considered from the perspective of the organism's interaction with the physical environment, as well as the physiological response of the organism to that environment.

Conclusions

In agreement with previous studies, we found a complicated pattern of organismal body temperatures along a large latitudinal gradient (Helmuth et al. 2002). The four major hot spots and cold spots identified here are spread along the entire geographic gradient with at least one hot spot and one cold spot in each of the three regions (WaOr, CenCal, and SoCal). Interestingly three sites, one in each region, appeared as both hot and cold spots, suggesting extreme thermal variability. These results suggest that extreme care must be exercised when choosing sites to serve as representatives of range edges and range centers, and are consistent with recent findings that several species do not display an "abundant center" distribution along the west coast of the United States (Sagarin and Gaines 2002a, b, Sagarin and Somero 2006). We also showed that considerably more information is present in the thermal signal when analyses of thermal data move beyond mean temperatures and water temperature. Investigations of the physiological or ecological effects of climate on organisms must carefully consider what metrics are most relevant (Gilman et al. 2006). Depending on the organism and the question, it will be essential to understand temporal patterns of thermal variability and predictability within sites, as well as differences in means and extremes among sites. With so many variables, ecologists must be careful to explicitly record environmental conditions relevant to organismal physiology and not rely on simple proxies, such as air or water temperature. Obviously, this complicates the work of the investigator, especially when choosing sites for comparison through space or time. However, without this degree of detail, ecologists and physiologists may miss crucial features of the physical environment that determine individual fitness, population and community dynamics, biogeographic patterns, and ecological responses to climate change.

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APPENDIX

Monthly summary statistics for temperatures at the study sites (*Ecological Archives* M076-017-A1).