

# Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores

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**ABSTRACT:** Temperature is among the main structuring agents on rocky intertidal shores. Although infrequent mortality events associated with high temperatures have been observed in several intertidal taxa, careful documentation of these events is rare, and small-scale variability in mortality patterns remains poorly understood. In Bodega Bay, California, USA, 2 mortality events occurred on exposed rocky shores during the spring of 2004 when low tides occurred around mid-day. Limpets *Lottia scabra* were killed during unseasonably warm weather in mid-March. In late April, record-high temperatures resulted in widespread mortality of the mussel *Mytilus californianus*. Levels of mortality for both species were closely associated with small-scale variability in temperature, which in turn was closely associated with substratum orientation. Invertebrates occupying surfaces facing the sun when stress was most intense were much more likely to die than those living on surfaces angled  $\geq 45^\circ$  away. Because the within-day timing of thermal stress varied seasonally, the highest mortalities were recorded on southwest-facing surfaces on the March afternoon low tide and on southeast-facing surfaces on the April morning low tide. Limpets and mussels showed little mortality during the events that were harmful to the other taxon, suggesting that these different taxa respond to different aspects of their thermal environment. If climate change results in more frequent and more severe episodes of thermal stress, future ecological change may also be heavily dependent on tidal dynamics and small-scale variation in substrate orientation.

**KEY WORDS:** Temperature · Thermal stress · Mass mortality · Substratum orientation · Rocky intertidal zone · *Lottia scabra* · *Mytilus californianus*

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## INTRODUCTION

Temperature is one of the most important environmental controls on organismal physiology, performance, and fitness (Hochachka & Somero 2002). The ecological importance of temperature is particularly apparent on rocky intertidal shores, which are among the most thermally variable and stressful habitats on earth. On rocky shores, temperature drives physiological acclimation and evolutionary adaptation (Schmidt & Rand 1999, Tomanek & Somero 1999, Somero 2002) and plays a key role in determining species distributions (Newell 1979) and community structure (Wetthey

1984, Leonard 2000, Harley 2003). Daily and seasonal thermal variation drive vertical migration patterns in the intertidal zone (Janssen 1960, Williams & Morritt 1995). Longer-term patterns associated with climate change also drive shifts in the distribution and abundance of intertidal organisms (Barry et al. 1995, Southward et al. 2005).

Despite intertidal ecologists' general acceptance of the overarching importance of temperature, documented mortality following natural periods of intertidal heat stress is surprisingly rare. In the tropics, heat kills have been observed in limpets (Williams et al. 2005), mussels (Liu & Morton 1994), and barnacles (Liu &

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Morton 1994, Chan et al. 2006). In the temperate zone, the few examples of temperature-driven mass mortality events also include limpets (Lewis 1954, Frank 1965, Sutherland 1970, Kohn 1993), mussels (Suchanek 1978, Tsuchiya 1983, Petes et al. 2007), and juvenile barnacles (Wethey 1984, E. Sotka pers. comm.). Although documented cases may be rare, infrequent disturbances such as thermally generated mass mortality events have a variety of ecologically important impacts including significant reductions in populations of ecological dominants (Turner & Dale 1998). Furthermore, because climate change is predicted to increase both mean temperatures and the frequency of extreme high temperature events (IPCC 2007), presently rare temperature-associated mass mortalities may become more common in the future. It is therefore of interest to understand the spatial and temporal patterns of such mortality events in an effort to predict how intertidal communities may be affected by thermal stress now and in the future.

The susceptibility of a population to a heat-related mortality event depends upon the spatial and temporal distribution of thermal stress, the relationship between environmental temperature and body temperature, and the relationship between body temperature and organismal performance. For example, thermal stress varies greatly from one microhabitat to the next, and organisms on north-facing surfaces in the Northern hemisphere remain cooler than their counterparts on horizontal or south-facing surfaces (Helmuth & Hofmann 2001, Harley 2003, Denny et al. 2006). The relationship between the abiotic environment and body temperature depends on organismal morphology and behavior (e.g. Bell 1995, Helmuth 1998, Denny & Harley 2006). The impact of high body temperature depends on an individual's or species' ability to upregulate physiological protective mechanisms (Stillman 2003) and upon an individual's or species' critical maximum temperature (Evans 1948, Southward 1958, Somero 2002). Furthermore, 'stress' as perceived by an organism may have as much to do with departures from the temperature to which the organism is acclimated as with the actual temperature reached (e.g. Stillman 2003). This complexity makes it difficult to predict the effects of any given thermal stress event. On rocky shores, our understanding of the ecological consequences of thermal stress is further limited by the paucity of concurrent measurements of organismal responses (e.g. mortality) and high-resolution, biologically relevant thermal time series.

In this study, I took advantage of 2 natural, temperature-related mortality events to explore the importance of temporal patterns and small-scale spatial variation in the thermal environment as well as interspecific differences in susceptibility. The first mortal-

ity event occurred in March 2004 and killed a number of limpets *Lottia scabra* but did not result in observed mortality in mussels *Mytilus californianus*. The second event, which killed large numbers of *M. californianus* but few if any *L. scabra*, occurred during a record-setting heat wave in April of the same year. Using *in situ* thermal data, temporal trends in species abundance, and post-mortality observations, I related the mortality observed in these 2 taxa to small-scale spatial variability in their thermal environment, and tie these patterns into seasonal thermal and tidal dynamics. I hypothesized that (1) invertebrate body temperature varied with substratum orientation, being highest on surfaces that faced the sun at low tide, (2) mortality depended on body temperature and therefore varied with substratum orientation, and (3) the specific spatial pattern of these relationships depended upon the timing of low tide.

## MATERIALS AND METHODS

**Study system.** This research was conducted on the wave-exposed rocky shores of the Bodega Marine Reserve in northern California, USA (38.36° N, 123.1° W). The intertidal area consists of gently sloping to nearly vertical granite benches. The organisms chosen for study, i.e. the limpet *Lottia scabra* and the mussel *Mytilus californianus*, are abundant and ecologically important species in the high- and mid-intertidal zones, respectively. In the high zone, *L. scabra* lives among barnacles (primarily *Chthamalus dalli* and *Balanus glandula*) and several species of macroalgae (most notably *Mastocarpus papillatus* and *Pelvetiopsis limitata*). Even though the northern limit of *L. scabra* is found in northern California (Gilman 2006), the species is still vulnerable to mass mortalities associated with hot, calm weather in this region (Sutherland 1970).

The mid-intertidal zone in northern California is dominated by the mussel *Mytilus californianus*. *M. californianus* is a competitive dominant and provides a habitat for dozens to hundreds of other species (Suchanek 1992, Smith et al. 2006a). Although there have been reports of temperature-induced mass mortalities in other species in the genus *Mytilus* (Suchanek 1978, Tsuchiya 1983), documentation of heat death in *M. californianus* is rare. Indeed, the evidence available from one cool site (Tatoosh Island, Washington) suggests that the upper limit of *M. californianus* may be more closely associated with emersion time than with temperature per se (Denny & Paine 1998, Harley & Helmuth 2003). The importance of temperature as a limiting factor for *M. californianus* at hotter sites is poorly understood.

**Environmental data collection.** Predicted tidal data for Bodega Bay were generated using XTide software ([www.flaterco.com/xtide/](http://www.flaterco.com/xtide/)). Long-term air temperature data were obtained from the Bodega Ocean Observing Node (BOON). Air temperature time series were recorded at the Bodega Marine Laboratory, which is situated within 1 km of all study sites. Significant wave heights were obtained from the National Oceanographic and Atmospheric Administration (NOAA) National Data Buoy Center (NDBC) for Buoy 46013 (38.23°N, 123.32°W). For simplicity, only daily maximum values for air temperature and wave height are reported here. Annual records of rock temperature in the intertidal zone were collected with iButton temperature loggers, which have been successfully used for this purpose elsewhere (Harley & Helmuth 2003). iButtons were wrapped in parafilm and epoxied (Sea Goin' Poxy Putty; Permalite Plastics) into shallow depressions chiseled into the rock. The iButton was thus covered by a 1–2 mm layer of epoxy, which was flush with the rock surface. To more accurately mimic the surface conditions (color and rugosity) of the surrounding rock, small-grained, color-matched beach sand was patted onto the epoxy surface as the epoxy was setting. These loggers were deployed immediately above and below the intertidal extent of the mussel bed ( $n = 1$  at each shore level) on an exposed, west-facing bench. Loggers recorded rock temperature at hourly intervals during the study period.

Because the temperature of the substratum is an excellent proxy for the body temperature of small limpets (Denny & Harley 2006), including *Lottia scabra* on Bodega Head (Wolcott 1973), long-term estimates of limpet temperatures were made by measuring rock temperature along the southern shore of Horseshoe Cove (see Morelissen & Harley 2007 for a map of the study sites). iButtons were deployed as described above in areas where the limpet *L. scabra* was abundant, and recorded rock temperature at 30 min intervals. Mussel temperatures were estimated by sealing iButton temperature loggers into 8 cm long mussel shells using silica caulk (Helmuth & Hofmann 2001). Empty mussel shells were pulled directly from the mussel beds into which they would be transplanted, which ensured that they were similar to live mussels in terms of size and color. In total, 5 of these loggers were deployed near the upper limit of the mussel bed in Horseshoe Cove. The mussel mimics were attached to the rock in growth position using Z-spar marine epoxy (A-788 Splash Zone Compound). All mussel mimics were deployed in continuous mussel beds and maintained contact with the neighboring mussels throughout their deployment. This method has been shown to produce reasonably accurate estimates of body temperature (within  $\sim 2^\circ\text{C}$ ) for individual mussels within a

bed, although the loggers may slightly underestimate mussel body temperatures at high temperatures (Fitzhenry et al. 2004).

**Quantifying mortality in the field.** Limpet densities were tracked in  $25 \times 25$  cm plots ( $n = 26$ ); each plot contained an iButton (see above). These plots were deliberately chosen to represent a wide array of substrate orientations. The intertidal height of the plots ranged from 1.33 to 2.63 m above Mean Lower Low Water (MLLW; mean  $\pm$  SD:  $2.00 \pm 0.32$  m above MLLW) as determined by multiple laser level measurements of shore height relative to the predicted still water level of the tide. Limpet abundance was quantified on 22 January 2004 and again on 8 April 2004 during pre-determined temperature logger replacements. Because the number of limpets per plot varied (initial mean  $\pm$  SD =  $10.9 \pm 5.2$ ), limpet mortality was expressed as proportional change in abundance on a per plot basis. Although the temporal gap between these dates is fairly large, measured differences in abundance should still accurately reflect mortality. *Lottia scabra* is a homing species with shells that fit precisely to the rock at an animal's home scar, and photographic evidence suggests that there is little immigration or emigration from plots.

No long-term plots had been established in the mussel beds prior to the mass mortality in late April 2004. However, dead mussels remained anchored to their living neighbors by byssal thread attachments well into July (author's pers. obs.), allowing mussel mortality to be estimated for a period of time after the individuals actually died. In this study, I made extensive measurements at Mussel Point (see Morelissen & Harley 2007 for map) on 9 May 2004, or 15 d after the putative date of the mortality event. I counted the number of live and dead *Mytilus californianus* visible in the surface layer in  $10 \times 10$  cm plots (there was very little mussel mortality in subsurface layers). The lack of evidence of mussels that had died and washed away, such as byssal threads and plaques on remaining mussels or on the rock, suggests that mortality estimates were reasonably accurate. Both live and dead mussels were in natural growth position (umbo down), and each shell was in contact with several neighboring shells. Mortality was quantified at each of 3 shore levels (25 plots each): near the upper edge of the mussel zone, in the middle of the mussel zone, and near the lower edge of the mussel zone. Each zone was separated from the next by approximately 1 vertical meter, and no samples were collected within 10 cm of the edge of the bed (including patches) to avoid edge effects.

For all limpet and mussel sampling plots, the orientation of the substrate (slope and azimuth) was measured along with patterns of mortality. Substratum slope was measured with an inclinometer, and azimuth was

determined with a compass (corrected to true north). These 2 measurements allowed me to calculate the angle of incidence of incoming solar radiation for any given date and time of day. The angle of incidence is defined as the angle between the path of incoming sunlight and a line emerging perpendicularly from the substratum; lower angles indicate that the sun is shining more directly on the surface in question. The position of the sun in the sky for particular dates and times at the latitude and longitude of the Bodega Marine Reserve were obtained from the NOAA online solar position calculator ([www.srrb.noaa.gov/highlights/sunrise/azel.html](http://www.srrb.noaa.gov/highlights/sunrise/azel.html)).

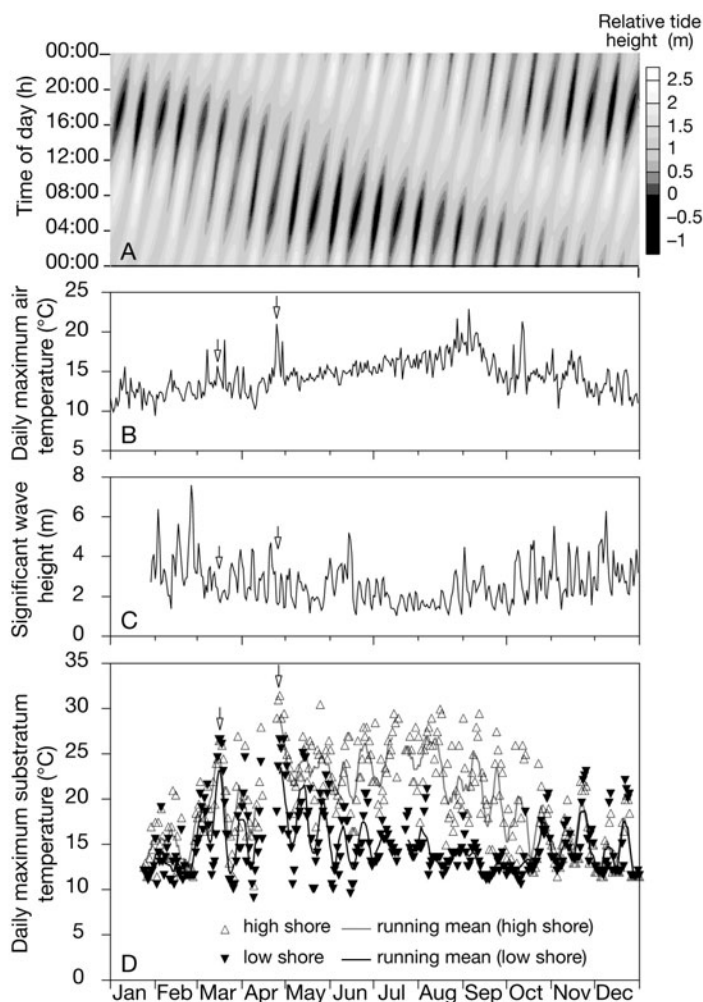


Fig. 1. Environmental conditions for Bodega Bay, California, in 2004. (A) Predicted tide heights (in m) are given relative to Mean Lower Low Water (MLLW). Note that the timing of low tides shifts from late afternoon in winter to mid-day in spring to early morning in summer. (B) Daily maximum air temperature recorded at the Bodega Marine Reserve. (C) Daily maximum significant wave height recorded offshore. (D) Daily maximum intertidal rock temperatures recorded at high and low shore heights. Solid lines in (D) represent 7 d running means of the daily thermal maxima. Arrows in (B)–(D) indicate the timing of the 2 mortality events

**Statistical analyses.** The effects of substratum orientation and shore height on (1) maximum substratum temperature and (2) proportional change in limpet abundance were determined with step-wise multiple regressions. If one of the independent variables was non-significant, a linear regression was run using the remaining (significant) variable. The residuals were normally distributed (Shapiro-Wilk  $W$ ,  $p > 0.1$ ) in all cases. Unlike limpets, no prior abundance data existed for mussels. Thus, proportion dead in each plot was used as a response variable, rather than proportional change in abundance. Furthermore, exact intertidal heights were not measured with respect to mussel mortality measurements. Rather, data were taken at each of 3 shore levels: high, mid, and low. Therefore, an analysis of covariance (ANCOVA) was used to analyze mussel mortality data across substrate orientation and shore height, as opposed to the multiple regression approach taken with limpets. When the effect of shore height was not significant in the ANCOVA model, a linear regression was run between substrate orientation and mortality. In order to achieve normally distributed residuals with respect to both the linear regression and the ANCOVA, angle of incidence was log-transformed and proportional mortality was arcsine(square-root) transformed. All statistical analyses were conducted in JMP 5.1 (SAS Institute).

## RESULTS

### Environmental time series

Tidal dynamics in Bodega Bay show a pronounced seasonal pattern in the timing of the high and low tides, as was apparent in 2004 (Fig. 1A). Low spring tides occurred in the late afternoon and early evening in January (winter). By March, the timing of low tides had shifted to the middle of the day. The precession to earlier times continued such that by July (summer), the lows occurred early in the morning, and organisms in the low intertidal were rarely exposed during the heat of the day. In late fall, the low tides were once again centered in the afternoon and evening. Note that the biweekly spring-neap cycle was readily apparent.

Air temperature in Bodega Bay followed a typical seasonal pattern (Fig. 1B), although summer maxima were somewhat muted by frequent fog. In 2004, the highest air temperatures occurred in late April, just prior to the summer fog season, and early fall, just following the summer fog season. There was also a seasonal pattern in wave exposure, although there was considerable day-to-day variability in wave heights (Fig. 1C). Calm days are possible during the spring, summer, and fall; in 2004, it was relatively calm for most of the summer.



Seasonal patterns in tidal dynamics, air temperature, and wave heights are accompanied by spatial and temporal patterns of potential thermal stress in the intertidal zone. Rock temperatures measured in the low intertidal zone exhibited a seasonal peak in the spring, when low tides occurred mid-day, and then remained cooler during the summer (Fig. 1D). In the high intertidal zone, where daytime tidal emersion is less sensitive to the timing of lower low tides, maximum daily rock temperatures remained high throughout the spring and summer (Fig. 1D). Rock temperatures in the 2 zones converged during the fall and winter, when the timing of lower low tides moves back into the daylight hours (see Fig. 1A). The importance of the spring-neap tidal cycle is apparent in the 7 d running means at both high and low shore levels, with relatively warm periods alternating with relatively cool periods on a 2 wk cycle throughout the year (Fig. 1D).

### Limpet mortality patterns

Rock temperatures in limpet monitoring plots were warm and wave heights were relatively low from 15 to 17 March 2004. Actual *Lottia scabra* mortality was only observed on 15 March, which was the hottest day of the warm spell. Many limpets were unable to remain attached to the substratum as evidenced by those that had fallen off of sloping surfaces. These individuals were shriveled, did not respond when poked in the foot or tentacles, and could not reattach to the substratum.

The low tide on 15 March occurred at 13:08 h. However, the hottest period of the day was between 13:45 and 14:40 h (data not shown), and modeling data suggest that limpet body temperatures can continue to rise even after solar noon (see Denny & Harley 2006). As a way of determining when solar heating was most likely to have the strongest effect on limpet body temperature, I correlated maximum substrate temperature of each plot with angle of solar incidence at 15 min intervals throughout the day. The best fit between maximum substrate temperature and angle of solar incidence occurred at 14:15 h (MS numerator = 900.9,  $F_{1,20} = 129$ ,  $p < 0.0001$ ,  $r^2_{\text{adj}} = 0.859$ ; Fig. 2A). When both substrate orientation and intertidal height were included in a multiple regression analysis, there was no relationship between the intertidal height of the plots and the maximum temperature reached (orientation effect  $F_{1,19} = 117$ ,  $p < 0.0001$ ; intertidal height effect  $F_{1,19} = 0.096$ ,  $p = 0.760$ ), despite the fact that plots spanned approximately 50 % of the tidal range.

In limpet monitoring plots, the total number of *Lottia scabra* per 625 cm<sup>2</sup> plot decreased from  $10.9 \pm 1.01$  to  $9.65 \pm 1.06$  (mean  $\pm$  SE,  $n = 26$ ), or 12.5 %. For comparison, the second largest population decline over a 3 to

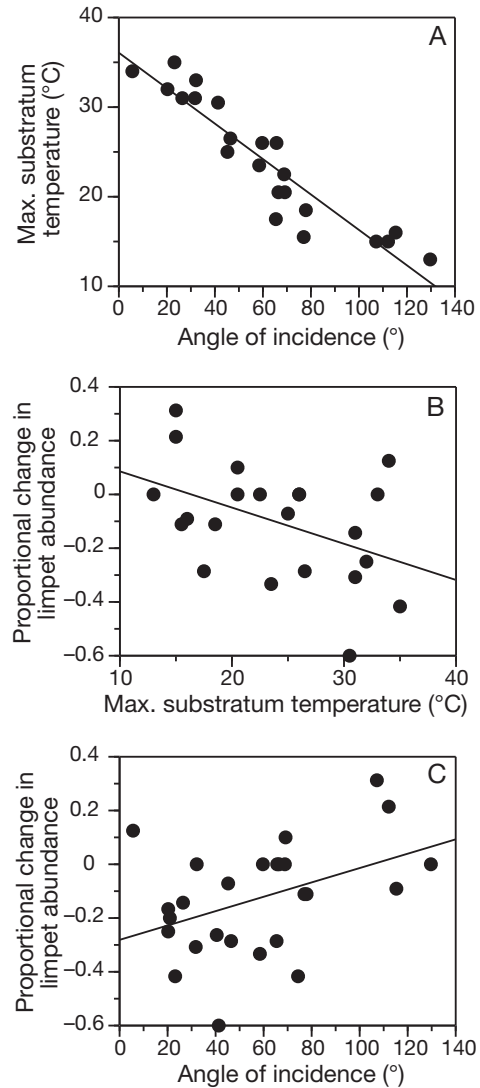


Fig. 2. *Lottia scabra*. Patterns of limpet mortality. (A) Relationship between substratum orientation and maximum temperature ( $n = 22$ ). Angle of solar incidence is the angle between incoming solar radiation (in this case, at 14:15 h) and a line perpendicular to the substrate. (B) Relationship between maximum substrate temperature and proportional change in limpet abundance in the study plots ( $n = 22$ ). (C) Relationship between substrate orientation (as in A) and proportional change in limpet abundance ( $n = 26$ ). Differences in sample size reflect temperature logger failure in 4 plots

4 mo span during the 18 mo monitoring period was only 3.2 % (data not shown). The 12.5 % average decline is somewhat misleading because it combines both low-stress and high-stress plots. In the 11 warmest plots (of the 22 with functioning temperature loggers), limpet abundance decreased from  $9.45 \pm 1.03$  to  $7.73 \pm 1.05$  or 18.2 %. In the 11 coolest plots, limpet abundance slightly increased from  $11.55 \pm 1.94$  to  $11.64 \pm 2.06$ . The proportional change in limpet abun-

dance was significantly negatively correlated with maximum substratum temperature; limpets tended to suffer larger declines in warmer plots ( $MS = 0.189$ ,  $F_{1,20} = 4.88$ ,  $p = 0.039$ ,  $r^2_{adj} = 0.156$ ; Fig. 2B). Similarly, the proportional change in limpet abundance was also correlated with the angle of solar incidence at 14:15 h ( $MS = 0.190$ ,  $F_{1,24} = 5.10$ ,  $p = 0.033$ ,  $r^2_{adj} = 0.141$ ; Fig. 2C). This suggests that limpets were most vulnerable on surfaces that faced southwest ( $220^\circ$ ) and were angled  $42^\circ$  above the horizon. Once again, there was no correlation between intertidal height and mortality patterns when intertidal height and substrate orientation were considered simultaneously (multiple regression: orientation effect  $F_{1,23} = 4.74$ ,  $p = 0.040$ ; intertidal height effect  $F_{1,23} = 0.006$ ,  $p = 0.942$ ).

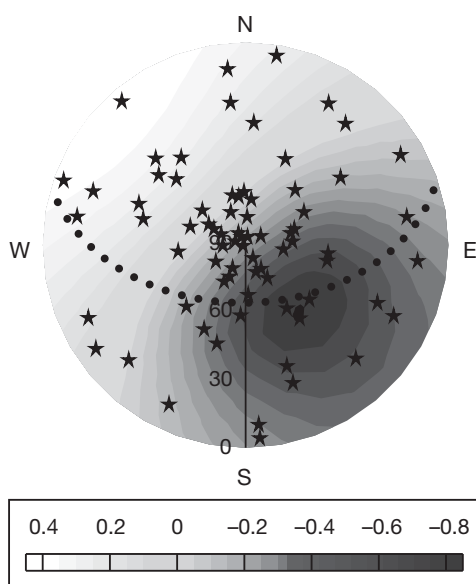


Fig. 3. *Mytilus californianus*. Contour plot of the correlation coefficient ( $r$ ) between angle of incidence and mussel mortality. Radial axis indicates degrees above the horizon, i.e. the center of the plot ( $90^\circ$ ) represents the correlation between mortality and angles of incidence measured from a point directly above the study area. The perimeter of the plot represents the horizon (compass directions are indicated). The track of the sun through the sky at 30 min intervals is shown by the black dots. Black stars indicate the orientations of the 75 sampled plots (e.g. a star near the center of the circle indicates a horizontal plot, and a star near the northern horizon indicates a vertical, north-facing plot). Regressions ( $n = 225$ ) were run to determine the relationship between proportional mortality in the 75 plots to the angle of incidence for a particular position in the sky; the 225 sky positions used in the 225 analyses were spaced approximately evenly (approximate separation =  $10^\circ$  of arc). Strong negative correlations between angle of incidence and mussel mortality (dark areas) indicate that mortality was highest in areas that most directly faced (e.g. had the lowest angle of incidence to) that portion of the sky. Mortality was most strongly correlated with substrate orientation relative to the position of the sun at ~11:30 h

### Mussel mortality patterns

Record-high air temperatures occurred along the coast of California on 25 and 26 April 2004. Over the following several days, dead and gaping mussels that were still anchored into the mussel bed by the byssal fibers of living mussels were observed. Averaged across all sampling plots (i.e. ignoring any orientation bias in mortality), the abundance (mean  $\pm$  SE,  $n = 75$ ) of living and dead mussels was  $18.2 \pm 0.87$  and  $2.36 \pm 0.48$  per  $100 \text{ cm}^2$ , respectively.

The low tide on 25 April occurred at 10:01 h. As with the limpet mortality event, air temperatures continued to rise as the tide came back in. Thermal data relevant to mussel body temperatures were limited (see below). Therefore, an attempt was made to relate mortality to changing patterns of solar angle of incidence over the course of the day for 75 plots distributed over 3 shore levels and a wide variety of substratum orientations (Fig. 3). Although these 75 samples were divided evenly among 3 shore levels located roughly 100 vertical cm apart, there were no differences associated with intertidal height ( $p > 0.25$ ); therefore, data were pooled. The high sample size allowed me to run regressions between mussel mortality and the angle of incidence to any given part of the sky, not just the solar track. The best regression fits are centered on the position occupied by the sun at ~11:30 h in the morning (Fig. 3, dark shaded area).

Using the angle of solar incidence at 11:30 h, mussel mortality was strongly related to substrate orientation (Fig. 4). Lower angles of incidence (e.g. surfaces nearly perpendicular to incoming solar radiation) had much higher levels of mortality than surfaces at higher angles of incidence (ANCOVA; log(angle of solar inci-

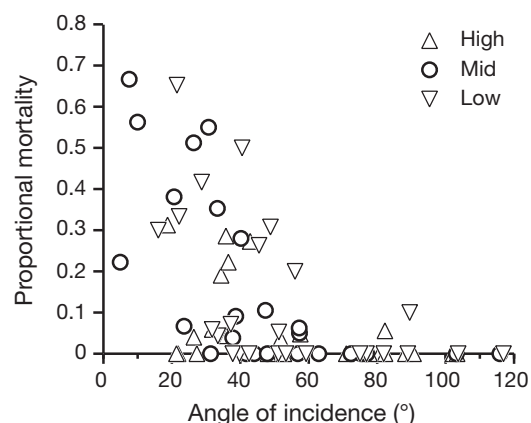


Fig. 4. *Mytilus californianus*. Relationship between shore level, substratum orientation, and mussel mortality on 25 April 2004. Angles of solar incidence were calculated for 11:30 h

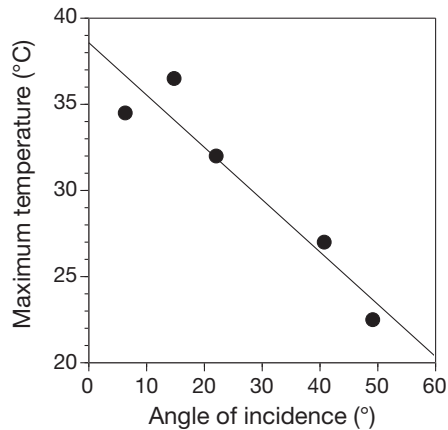


Fig. 5. Effect of substrate orientation on maximum temperature of mussel-mimic temperature loggers on 25 April 2004. Orientation is measured as the angle of incidence given the solar position at 11:30 h on that date

dence)  $F_{1,71} = 46.6$ ,  $p < 0.0001$ ). Mussels were most vulnerable on surfaces facing southeast ( $122^\circ$ ) and angled  $52^\circ$  above the horizon. Somewhat surprisingly, there was no relationship between mortality and intertidal height; mortality in the lower, middle, and upper portions of the mussel bed were similar (ANCOVA; intertidal height  $F_{2,71} = 1.21$ ,  $p = 0.303$ ). When intertidal height was ignored, the relationship between angle of incidence and mortality was negative (arcsine[square root(mortality)] =  $1.368 - 0.6867[\log(\text{angle of incidence})]$ ) and highly significant ( $MS = 2.47$ ,  $F_{1,73} = 48.9$ ,  $p < 0.0001$ ,  $r^2_{\text{adj}} = 0.393$ ).

The limited thermal data available support the contention that temperature was the causal mechanism underlying the strong relationship between substrate orientation and mussel mortality. The 5 mussel-mimic temperature loggers deployed at the time also showed a significantly negative relationship between angle of solar incidence at 11:30 h and maximum temperature ( $MS = 118.1$ ,  $F_{1,3} = 28.5$ ,  $p = 0.013$ ,  $r^2_{\text{adj}} = 0.873$ ; Fig. 5). The average temperature of these loggers was highest on 25 April, although 26 April was within  $1^\circ\text{C}$  for all 5 loggers.

## DISCUSSION

### Thermal mortality in mussels and limpets

Thermal stress events have been linked to mortality in mussels and limpets on a number of occasions (e.g. Sutherland 1970, Tsuchiya 1983, Kohn 1993, Petes et al. 2007). In the present study, mass mortalities of intertidal invertebrates were associated with 2 periods of unseasonably hot weather. In the case of mussels, the

temperatures of mussel mimics deployed within the mussel bed were very high and in one case exceeded  $36^\circ\text{C}$ . For comparison, the highest temperature at which *Mytilus californianus* is capable of protein synthesis is  $34^\circ\text{C}$  (Roberts et al. 1997). The very strong relationship between mussel mortality and substratum orientation (relative to the sun at low tide) also supports excessive heat as the cause of mortality. Changes in limpet density could be directly associated with substratum temperature, and this relationship was indeed negative (higher temperatures led to more pronounced decreases in abundance). It is possible that both direct and indirect effects of temperature played a role in changing limpet abundances. High shore limpets may become food limited during hot weather (Cubit 1984, but see Sutherland 1970). Thus, starvation or food-related emigration may have been the primary cause of changes in limpet densities, rather than temperature-related physiological stress. However, the direct observation of limpet mortality on 15 March coupled with home site fidelity in this species suggests that at least some of the change in population size was directly due to thermal stress. Unfortunately, the season-specific lethal thermal temperature for *Lottia scabra* is not known, preventing a direct comparison of measured temperatures and physiological maxima.

### Spatial and temporal variability of thermal stress

The relationship between the timing of low tides and intertidal thermal stress is well established (Helmuth et al. 2002, 2006). In northern California, the seasonal precession of the timing of low tides results in potentially stressful periods of emersion during the spring. Intertidal thermal mortality events documented in the vicinity of Bodega Bay generally occur during this period. For example, a prior mass mortality of *Lottia scabra* occurred on Bodega Head in May of 1967 (Sutherland 1970). Intertidal *Mytilus* spp. (*M. trossulus* and/or *M. galloprovincialis*) suffered extensive (~50%) mortality in nearby Tomales Bay in early May 2007 (R. Kordas pers. comm.).

Temperature also varies at a range of horizontal spatial scales in response to patch geometry, topographic orientation, local climate, and latitude (Helmuth 1998, Denny et al. 2004, Helmuth et al. 2006). Many mussel beds feature edges at a variety of scales (e.g. Snover & Commiato 1998), and mussels at edges or in gaps may reach higher body temperatures (Helmuth 1998). However, the beds examined here were continuous, and small-scale fractal geometry seems unlikely to have played a role in thermal stress. By contrast, local-scale variation in substratum orientation was pronounced on Bodega Head. The distribution of inter-

tidal organisms can be very sensitive to small-scale changes in substratum orientation (Castenholz 1963, Harley 2003), which is a strong determinant of ectotherm body temperatures on rocky shores (Helmuth & Hofmann 2001, Denny et al. 2006). The distribution of many organisms is restricted to cooler microhabitats, such as crevices, vertical walls, and surfaces that face away from the equator (i.e. north-facing surfaces in the northern hemisphere; Levings & Garrity 1984, Williams & Morritt 1995, Harley 2003). Such variation has important consequences for levels of sublethal stress experienced by intertidal organisms (Helmuth & Hofmann 2001). The results of the present study provide evidence that these patterns may also be due in part to rare lethal stress events.

Intertidal height is also an important axis of thermal stress. Potential thermal stress increases with intertidal height (Denny et al. 2006), and has long been associated with patterns of within- and among-species biological zonation on the shoreline (Newell 1979, Somero 2002). Indeed, intertidal height was an important determinant of *Lottia scabra* mortality on Bodega Head in the 1960s (Sutherland 1970), and of mussel mortality in New Zealand (Petes et al. 2007). Therefore, it was surprising that limpet and mussel mortality reported here were similar across shore levels. Limpet and mussel monitoring plots spanned 130 and ~200 vertical cm, respectively, or roughly half to three-quarters of the tidal range. For both species, animals living higher on the shore would be expected to reach higher temperatures and be exposed to potentially harmful temperatures for a longer period of time. The fact that mortality was not greater at higher shore levels may be related to a lack of statistical power, a lack of meaningful vertical variation in thermal stress, or to a countervailing gradient in the animals' thermal characteristics or thermal tolerance.

Although there was no vertical trend with either limpet plot substratum temperature or limpet population change, the power to detect a vertical trend in mortality was quite low for limpets (0.05 in the multiple regression with substrate orientation). Nevertheless, maximum rock temperatures in the high and low intertidal zones were identical (26.5°C, see Fig. 1) during the limpet mortality event. It seems probable that the duration of emersion across *Lottia*'s vertical zone was sufficient for body temperatures to reach an equilibrium with prevailing subaerial conditions at all shore levels; in other words, the gradual attainment of high temperatures on the low shore was not prevented by the return of the tide. Statistical power to detect shore height differences was also low for mussels (0.26 in the ANCOVA with substrate orientation), but the non-significant trend was opposite to what would be expected (i.e. mussels higher on the shore tended to

have the lowest levels of mortality). The lack of the expected vertical mortality trend on 25 April is not due to a lack of vertical thermal variation; high shore temperatures were 7.5°C warmer than low shore temperatures (Fig. 1). It is possible that mortality did not increase with shore level due to vertical variation in thermal tolerance; constitutive heat shock protein expression is higher at higher shore levels (Halpin et al. 2004). High shore mussels have also lost a greater proportion of their periostraca, which results in lower absorptivity and lower body temperatures relative to low shore mussels (C.D.G. Harley, J. Shinen unpubl. data). Either mechanism may have balanced out differences in duration of emersion across the intertidal gradient.

Finally, although the present study does not explicitly address the effects of thermal history in determining the importance of thermal stress, some suggestive patterns nevertheless emerge. For example, limpet mortality in 2004 occurred on 15 March when maximum rock temperature in the hottest monitoring plot only reached 35°C (mean across all plots: 24.0°C). There was no further significant mortality of *Lottia scabra* in 2004, despite the fact that rock temperatures in the *L. scabra* plots reached as high as 41°C on 25 April (mean across all plots: 32.5°C). The lack of limpet mortality in April probably reflects the seasonal upregulation of protective mechanisms such as constitutive heat shock proteins (see e.g. Roberts et al. 1997, Halpin et al. 2002, Sagarin & Somero 2006). Thus, a warm-spell in late winter/early spring may be more dangerous than a hot spell later in the spring or summer. Although *Mytilus californianus* also upregulates its heat shock response during the summer, the March stress event was evidently insufficient to result in any noticeable mortality. It is possible that seasonal variation in thermal tolerance is lower in *M. californianus* than it is in *L. scabra*.

### Implications for climate change

The types of mass mortalities reported here are not unprecedented. A much more significant mortality of *Lottia scabra* occurred in Bodega Bay on 15 to 16 May 1967 (Sutherland 1970). A mass mortality of *Mytilus californianus* was also observed in Bodega Bay in the late 1960s (J. Ackerman pers. comm.), although the exact timing and magnitude were not recorded. Although catastrophic thermal mortality events have occurred with some regularity in the past, their frequency may increase in the future.

Climate models predict that most coastal regions will warm by several degrees over the next century (IPCC 2007). As a result, intertidal organisms will experience



higher body temperatures. For example, the monthly average maximum body temperature of *Mytilus californianus* is predicted to increase by 1.0 to 4.1°C during the current century, depending on the geographic location and the warming scenario considered (Gilman et al. 2006). These potentially substantial increases in body temperature for mussels and other species will increase the frequency and magnitude of lethal thermal stress events, which in turn will increase rates of disturbance due to the removal of thermally sensitive organisms. Far-reaching changes are possible when the affected organisms are ecological dominants. Limpets including *Lottia scabra* play an important top-down role in intertidal communities (Cubit 1984, Morelissen & Harley 2007), and the selective removal of these (or other) herbivores may favor ephemeral algae that have rapid recovery rates and/or life-history escapes from deleterious high temperatures. Changes in mussel bed cover could affect hundreds of dependent species. The cover of *M. californianus* has decreased in southern (but not northern) California in recent decades, which may be related to climatic trends (Smith et al. 2006b). There have also been dramatic decreases in mussel bed species richness in California since the 1970s, another change which may be driven by shifts in regional climate (Smith et al. 2006a). It is likely that increasing frequencies of mass mussel mortalities would accelerate the rate of biodiversity loss.

## CONCLUSIONS

This study demonstrates that the intertidal impacts of warm climatic conditions will depend on the orientation of the substratum. In the cases documented here, season-specific patterns of topographic orientation play a much stronger role in determining body temperature and mortality than does the well-known gradient in intertidal height. Furthermore, the patterns of limpet and mussel mortality suggest that species are not affected equally by the same thermal stress events. Differences in organismal tolerance, and in the seasonal plasticity of this tolerance, may result in mortality for only a subset of potentially vulnerable species during any given stress event. Detailed information on the spatio-temporal distribution of both abiotic stress and organismal stress tolerance is required if we hope to accurately predict ecological change in a warming climate. Until we achieve such a synthesis, we risk underestimating the importance of increasing temperatures by assuming that 'average' topographic orientations and summer-time thermal tolerance limits adequately represent a wider range of spatial and temporal scales.

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