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Thermal stress on intertidal limpets: long-term hindcasts and lethal limits

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Summary

When coupled with long-term meteorological records, a heat-budget model for the limpet, *Lottia gigantea*, provides a wealth of information regarding environmental and topographic controls of body temperature in this ecologically important species. (1) The maximum body temperature predicted for any site (37.5°C) is insufficient to kill all limpets, suggesting that acute thermal stress does not set an absolute upper limit to the elevation of *L. gigantea* on the shore. Therefore, the upper limit must be set by behavioral responses, sublethal effects or ecological interactions. (2) Temperatures sufficient to kill limpets are reached at only a small fraction of substratum orientations and elevations and on only three occasions in 5 years. These rare predicted lethal temperatures could easily be missed in field measurements, thereby influencing the interpretation of thermal stress. (3) Body

temperature is typically higher than air temperature, but maximum air temperature can nonetheless be used as an accurate predictor of maximum body temperature. Warmer air temperatures in the future may thus cause increased mortality in this intertidal species. Interpretation of the ecological effects of elevated body temperature depends strongly on laboratory measurements of thermal stress, highlighting the need for additional research on the temporal and spatial variability of thermal limits and sublethal stress. The lengthy time series of body temperatures calculated from the heat-budget model provides insight into how these physiological measurements should be conducted.

Key words: heat-budget model, intertidal zonation, thermal limits, limpet, *Lottia gigantea*, heat stress.

Introduction

Most intertidal algae and animals are of marine descent, but during aerial exposure at low tide, they are subjected to the thermal stress and desiccation characteristic of the terrestrial environment. These factors can affect the ability of intertidal organisms to survive and reproduce, and differential tolerance for the exigencies of terrestrial conditions plays a large role in maintaining the characteristic vertical zonation of species on wave-swept rocky shores (e.g. Stephenson and Stephenson, 1972; Wolcott, 1973; Newell, 1979). Furthermore, variation in terrestrial conditions underlies fluctuations in zonation patterns at a variety of spatial and temporal scales (e.g. Lawson, 1957; Wethey, 1983; Harley, 2003).

Research into interactions among the physical environment, physiology, and intertidal ecology has often focused on the role of thermal stress (e.g. Newell, 1979; Somero, 2002; Helmuth et al., 2005). In a typical study, the thermal limits of a species are measured in the laboratory and compared to temperature measurements made in the field. With few exceptions (e.g. Helmuth et al., 2002), these field temperature measurements are small scale (a small number of individuals at a few isolated sites), short term (hours to days), and episodic (measurements

taken on only a few occasions). As a result, our understanding of the full panoply of thermal stresses imposed on intertidal organisms is limited. For example, what sets the upper limit of species ranges on the shore? Short-term measurements have shown that, for many species, temperatures at the upper limit are not directly lethal (e.g. Wolcott, 1973; Davison and Pearson, 1996; Harley and Helmuth, 2003), suggesting that vertical limits for intertidal species are set by other factors, such as desiccation (Wolcott, 1973), competition (Choat, 1977), or the accumulated physiological stress resulting from repeated imposition of sublethal temperatures. However, the short-term measurements that support this conclusion might simply have missed the rare lethal events that actually set the upper limit. Thus, without measurements of temperature sufficiently long-term to capture rare lethal events, this conclusion remains tentative. We currently do not know for certain what sets the upper limit of intertidal species (Helmuth et al., 2005).

The problems involved in approaching a question such as this are, in part, ones of technology. Until quite recently, the only way to record the body temperature of an intertidal organism continuously was to insert a measuring device (a thermistor or thermocouple) into the plant or animal, and then

to cable that device to a recording instrument onshore. It is difficult to maintain this type of apparatus in the wave-swept environment, and measurements made using this technique are consequently of short duration.

The recent advent of small self-contained data loggers has revolutionized this process. For example, self-contained data loggers mounted in plastic models of the mussel *Mytilus californianus* Conrad were used to measure lengthy time series of body temperatures at multiple sites from California to Washington state (Helmuth et al., 2002), and data loggers were used to measure the temperature of the rock surface, an accurate surrogate for the temperature of acorn barnacles (Wethey, 2002; Harley and Lopez, 2003). These new techniques have their limitations, however. The current generation of data loggers (TidbiTs; Onset Computers, Bourne, MA, USA, and iButtons; Dallas Semiconductor, Dallas, TX, USA) are too large to fit into most intertidal algae and snails, and the temperatures of these organisms are likely to be different from that of the rock surface. Consequently, detailed, long-term thermal histories of these and other ecologically important intertidal species are still out of reach.

Direct field measurements of body temperature present other problems as well. Because data loggers record temperature in real time, their ability to provide long-term data is constrained: if one desires a 5-year record of temperature, one must wait 5 years to obtain it. Moreover, direct measurement of body temperature alone has limited utility. Unless simultaneous measurements are made of the many environmental parameters that can contribute to body temperature (solar irradiance, air temperature, wind speed, relative humidity, etc.), the causal circumstances that led to a particular measured temperature remain unknown.

These limitations can potentially be circumvented through the use of heat-budget models. A heat-budget model allows one to translate measured environmental data into body temperature. Thus, if an appropriate record of environmental parameters is available, a heat-budget model allows one to 'hindcast' body temperature for periods far in excess of those currently available from direct measurements. This is particularly advantageous when examining rare, catastrophic thermal events that can have drastic effects on community structure. And because heat-budget models provide a mechanistic prediction of body temperature, they are an ideal tool for exploring the causal relationship between individual environmental parameters and thermal stress.

In this study, we use the heat-budget model developed in the accompanying paper (Denny and Harley, 2006) to explore thermal stresses imposed on *Lottia gigantea* Sowerby, a limpet commonly found in the mid to upper intertidal zone of wave-swept rocky shores on the west coast of North America. *L. gigantea* is territorial, maintaining a 'garden' on the rock surface that it keeps clear of mussels, barnacles and other limpets. In this fashion, *L. gigantea* acts as a major competitor for space in the intertidal landscape (Stimson, 1970; Lindberg et al., 1998). In particular, it competes with the mussel *M. californianus*, and on the California coast, where settlement

rates of mussels are low, *L. gigantea* and *M. californianus* appear to be co-dominant. Furthermore, *L. gigantea* is an important food source for both shore birds and human subsistence harvesters (Lindberg et al., 1987; Pombo and Escofet, 1996; Lindberg et al., 1998; Kido and Murray, 2003). It is therefore of ecological interest to understand when and where *L. gigantea* may be killed by thermal stress, and what environmental factors control these lethal events.

Materials and methods

Heat budget model

The heat-budget model of Denny and Harley was used (Denny and Harley, 2006), with the following additions:

Substratum orientation

We assume the limpet is attached to an infinite planar substratum oriented with a particular compass direction and inclination (measured by θ , the azimuth angle, and ϕ , the altitude angle, respectively, see Fig. 1A). Note that our assumption of a planar substratum removes from consideration many of the potential complications of natural topography. For

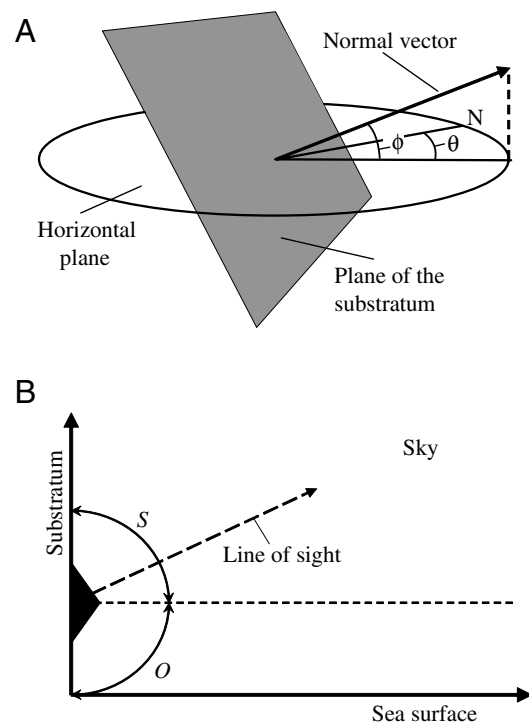


Fig. 1. (A) A schematic depiction of a planar substratum showing its altitude (θ) and azimuth (ϕ) angles. N, north. (B) For a limpet on a vertical planar substratum, lines of sight (depicted by the broken arrow) within arc S end at the sky, whereas lines of sight within arc O end at the ocean (which in this hypothetical case extends to infinity in a horizontal plane). Because arc S and arc O each account for half the 'visual field' of the limpet, each has a view factor of 0.5. The fraction of the view factor allocated to sky and ocean depends on the altitude angle of the substratum (see text, Eqn 1 and 2).

example, a limpet on an infinite, planar horizontal rock cannot be shaded by nearby vertical walls. The potential effects of this simplification are treated in the Discussion.

The inclination of the substratum can affect the long-wave radiative heat transfer between the limpet and its surroundings. When the substratum is horizontal (that is, when φ is $\pi/2$), all of the above-horizon sky is 'visible' to the lateral area of the limpet's shell and is available for radiative heat transfer. The view factor for the sky (V_s , the fraction of sky area available for radiative heat transfer) is therefore 1.0. By the same token, when the substratum is horizontal, none of the sea surface is visible to the shell, and the view factor for the ocean, V_o , is 0.

These values must be adjusted if the substratum is not horizontal. For example, when the substratum is vertical ($\varphi=0$, Fig. 1B), only half the sky is visible to the shell, and the remaining lines of sight are filled by the ocean. Thus, when the altitude angle of the substratum is 0, the view factors for both sky and ocean are 0.5. In general,

$$V_s = \frac{\varphi}{\pi} + 0.5 \quad 0 \leq \varphi \leq \frac{\pi}{2}, \quad (1)$$

$$V_o = 1 - V_s. \quad (2)$$

Long-wave radiative heat transfer between limpet and sky is calculated as described (Denny and Harley, 2006) using this modified view factor for the sky. Long-wave radiative heat transfer between the limpet and the ocean is calculated as for the sky, with the assumption that the emissivity of the sea is 0.96 (Campbell and Norman, 1998).

The angle, relative to the plane of the substratum, at which sunlight hits the shell is also affected by the orientation of the substratum (Gates, 1980):

$$\beta = \frac{\pi}{2} - \cos^{-1}[\cos(\varphi)\cos(\varphi_{\text{sol}})\cos(\theta_{\text{sol}}-\theta) + \sin(\varphi)\sin(\varphi_{\text{sol}})]. \quad (3)$$

Here θ_{sol} and φ_{sol} are the azimuth and altitude angles of the sun (respectively), both functions of the time of day.

Wave exposure

On wave-swept shores, limpets are wetted by waves even when the elevation of the animal on the shore is above the still-water level of the tide. With increasing wave heights, animals are wetted at higher levels on the shore for a given still-water level, and the duration of potential thermal stress at any given shore level is reduced (Harley and Helmuth, 2003). The effect of splash and wave run-up is incorporated into the model using measured data for significant wave height, the average height of the highest 1/3 of waves. Based on measurements made on the shore at Hopkins Marine Station (HMS) (O'Donnell, 2005), we assume that animals at exposed sites are wetted to a height 0.65 times the offshore significant wave height above still-water level. For example, if the still-water tidal level is +0.5 m [i.e. 0.5 m above mean lower low water (MLLW)], and the significant wave height is 1 m, we assume that the effective

height of the tide is $0.5+(0.65 \times 1)=+1.15$ m; that is, animals up to +1.15 m are wetted by the waves and thereby maintained at sea-surface temperature. For contrast, we also explore highly protected sites where animals are wetted only if their elevation is less than or equal to the still-water tidal elevation.

Experiments

Body temperatures were calculated for limpets at eight elevations on the shore (every 0.25 m from +0.50 to +2.25 m), encompassing the range at which this species is found at HMS. At each elevation, body temperatures were calculated for nine orientations of the substratum: horizontal ($\varphi=\pi/2$); vertical ($\varphi=0$) with azimuths of 0, $\pi/2$, π , and $3\pi/2$ (that is, north, east, south and west); and at a slope of $\pi/4$ with azimuths of 0, $\pi/2$, π and $3\pi/2$. Substrata with an altitude angle of $\pi/4$ are referred to as 'angled' substrata. Body temperatures at each elevation and orientation were calculated for both exposed and protected conditions. In total, we explored the temperature history of 144 'sites'.

In all cases, we assume that limpets are at the latitude of HMS in Pacific Grove, California (36.62°N, 121.88°W).

Environmental data

Parameters of the terrestrial environment were recorded by two weather stations at HMS. Solar irradiance to a horizontal surface (W m^{-2}) was measured using either a LI200X (Li-Cor, Inc., Lincoln, NE, USA) or a CM3 (Kipp and Zonen, Bohemia, NY, USA) pyranometer. Air temperature (at 2 m above the ground) was measured by a temperature sensor (HMP45C, Campbell Scientific, Logan, UT, USA) mounted in a radiation shield (UT12VA, Campbell Scientific). Wind speed (m s^{-1}) and direction at 3 m above the ground were measured by a model 5103 propeller anemometer (R. M. Young, Traverse City, MI, USA). All parameters were recorded every 10 min from August 1, 1999 through July 31, 2004 using model 23X data loggers (Campbell Scientific). At one of the stations, wind speed 25 cm above the ground was measured with an R. M. Young 3101-5 cup anemometer for 2 months in the winter of 2004. These near-ground measurements are used to translate the wind speeds measured 3 m above the ground to those likely to be present in the atmospheric boundary layer near the intertidal substratum. The near-substratum velocity was 62% of that at 3 m.

Ocean wave heights approximately 100 m off the HMS shore were measured using an SBE26 bottom-mounted wave gauge (SeaBird Electronics, Bellevue, WA, USA) at a depth of approximately 10 m. Data from the gauge allowed us to calculate significant wave height every 6 h. Hourly tidal elevations were obtained from the NOAA tide gauge at Monterey harbor, about 3 km from the HMS site. Sea-surface temperature was obtained from measurements made at HMS once per day (at 08:00 h). Significant wave height, tidal level, and sea-surface temperature change relatively slowly compared to terrestrial environmental parameters, and Fourier interpolation was used to estimate values for these marine parameters at 10-min intervals corresponding to those measured by the weather stations.

Thermal limits

We desired to mimic intertidal field conditions at HMS on a hot day. To that end, we constructed a chamber in which the temperature of the substratum, the temperature and relative humidity of the air, and the wind speed could be controlled separately. *L. gigantea* were collected from north-facing vertical walls in the intertidal zone at HMS in August, 2005. Sea-surface temperature typically sets the starting temperature for the day, and 14°C is a typical ocean temperature at HMS. Thus, limpets were placed on the substratum (an aluminum plate) with initial air and substratum temperatures of 14°C. The temperature of the substratum was then raised such that the limpet's body temperature (measured with a thermocouple) increased 8°C per hour until a given body temperature was reached. This rate of heating is among the highest predicted by our model. Body temperature was subsequently held constant until a total elapsed time of 3.5 h, a period that approximates the predicted average length of heating intervals in the field (3.7 h) for intervals with maximum temperatures in excess of 32°C. Relative humidity was maintained at 50–60% (typical of the intertidal zone at HMS) throughout the experiment. Air temperature tracked substratum temperature up to a maximum of 30°C and was then held at 30°C, and a wind speed of 0.25 m s⁻¹ (typical of a calm day) was used. At the end of 3.5 h, limpets were placed in 14°C seawater and their survival was assessed 24 h later. If at the end of 24 h a limpet was not adherent to the substratum, it was declared 'ecologically dead' (Wolcott, 1973). This

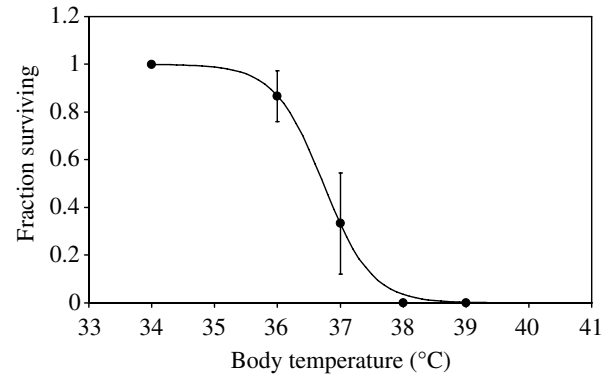


Fig. 2. Measured survivorship of *L. gigantea* as a function of temperature. The curve is drawn according to Eqn 4. Error bars are 95% confidence limits.

experiment was repeated for maximum body temperatures from 34 to 39°C, and the fraction of individuals dying at each maximum temperature was noted. Groups of 10 limpets were used in each experiment, and each experiment was replicated three times.

Results

Lethal limits

The response of *L. gigantea* to thermal stress is shown in Fig. 2. For the imposed thermal regime used in these

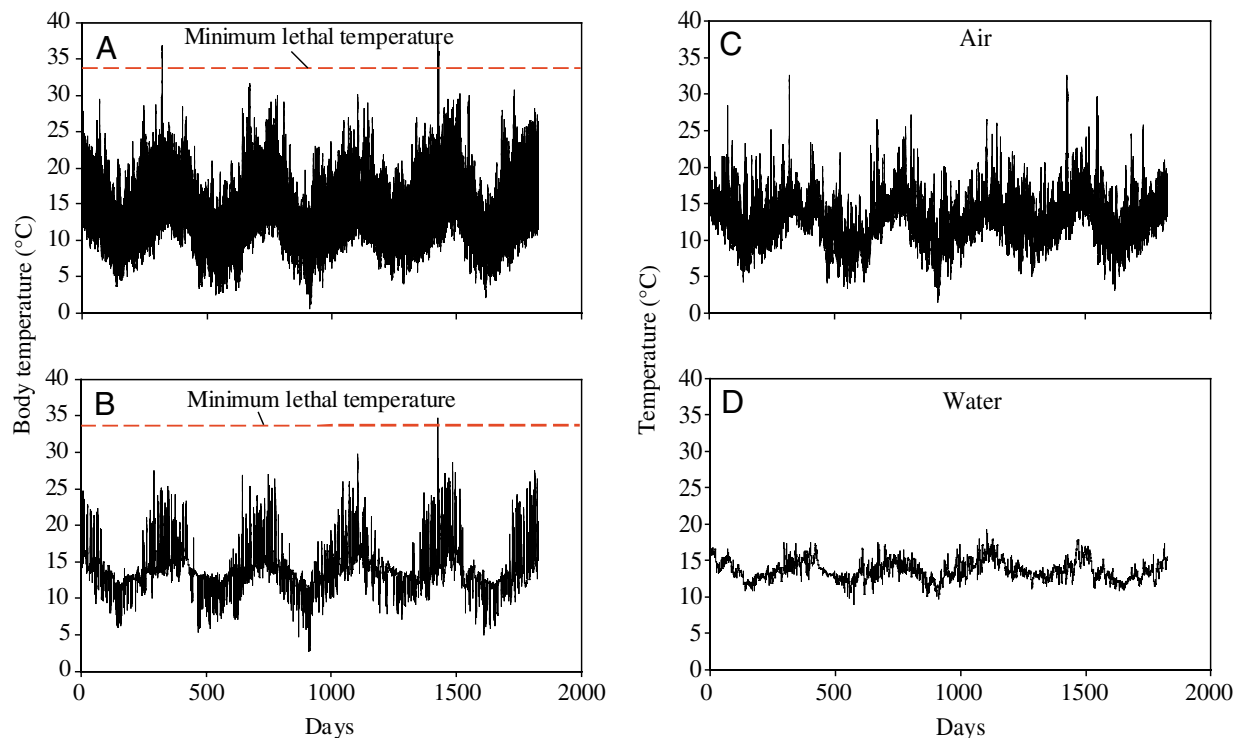


Fig. 3. Five years of predicted body temperatures (A,B) and measured air (C) and sea-surface (D) temperatures. (A) A horizontal surface 1.5 m above mean lower low water (MLLW), protected from waves. Note that the temperature spike near day 1400 is actually two spikes on sequential days. (B) A wave-exposed horizontal surface 0.5 m above MLLW.

experiments, the lower limit of lethality was 34°C, and 38.0°C killed all individuals tested.

The data for thermal tolerance can be approximated by a sigmoidal curve. The fraction, S , of individuals that survive a maximum temperature, T (°C), was

$$S \cong 1 - \frac{1}{1 + \exp\left(-\frac{T-36.73}{0.3863}\right)} \quad (4)$$

There was a slight deviation (<0.04) between the measured data and this curve for temperatures near 38°C. This curve suggests that 50% of *L. gigantea* die at 36.73°C.

Time series

A representative time series of predicted body temperatures is shown in Fig. 3A. Data are for a limpet 1.5 m above MLLW, a typical elevation for this species at HMS, and the substratum is horizontal and protected from waves. Seasonal variation is evident: as one might expect, temperatures are generally higher in summer and lower in winter. At this elevation and exposure, the pattern of body temperature more closely follows that of air temperature (Fig. 3C) than that of water temperature (Fig. 3D).

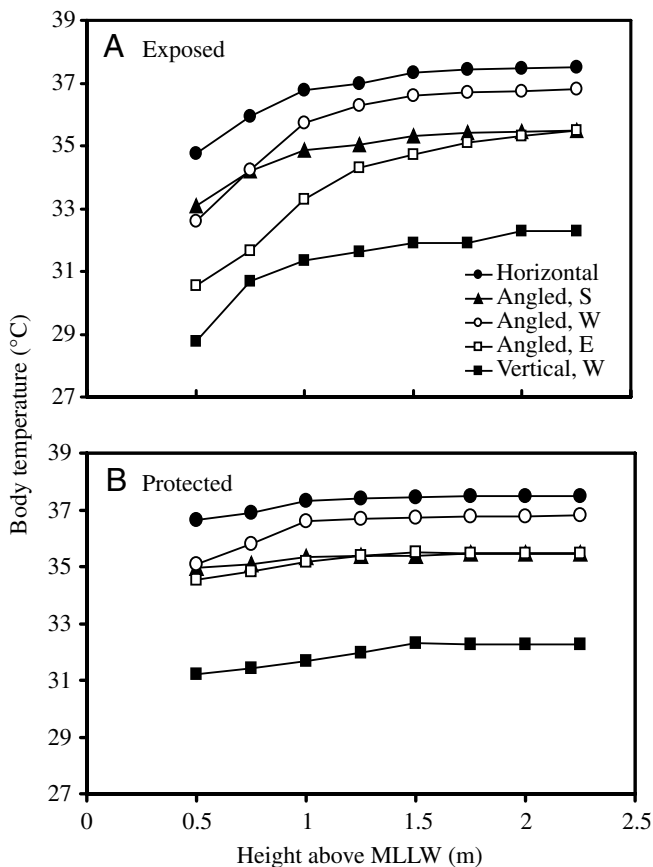


Fig. 4. Maximum body temperature as a function of shoreline elevation and substratum orientation on (A) wave-exposed and (B) wave-protected shores. MLLW, mean lower low water.

A time series typical of wave-exposed low shoreline elevations is shown in Fig. 3B for a limpet on a horizontal substratum at 0.5 m above MLLW. Body temperature tends to track sea-surface temperature (Fig. 3D), with brief excursions to temperatures slightly above air temperature.

There are only a few rare days during which body temperatures exceed 34°C, the lower limit of lethality: 3 days in 5 years at +1.5 m on a protected shore, 1 day at +0.5 m on a wave-exposed shore. Body temperatures on these rare days were substantially higher than in the bulk of the time series.

Maximum temperature

Maximum body temperatures during the 5-year simulation are shown in Fig. 4 as a function of shoreline elevation and substratum orientation. For clarity, of the vertical faces, only the warmest, west-facing is shown. Temperatures for north-facing angled substrata resemble those of vertical faces, and are similarly not shown. Four major points are evident.

First, regardless of azimuth, temperatures recorded on vertical faces are lower than those on horizontal or angled surfaces. In no case did the predicted body temperature on a vertical surface exceed 34°C, indicating that, during this 5-year period, no limpets on vertical surfaces would die from acute thermal stress.

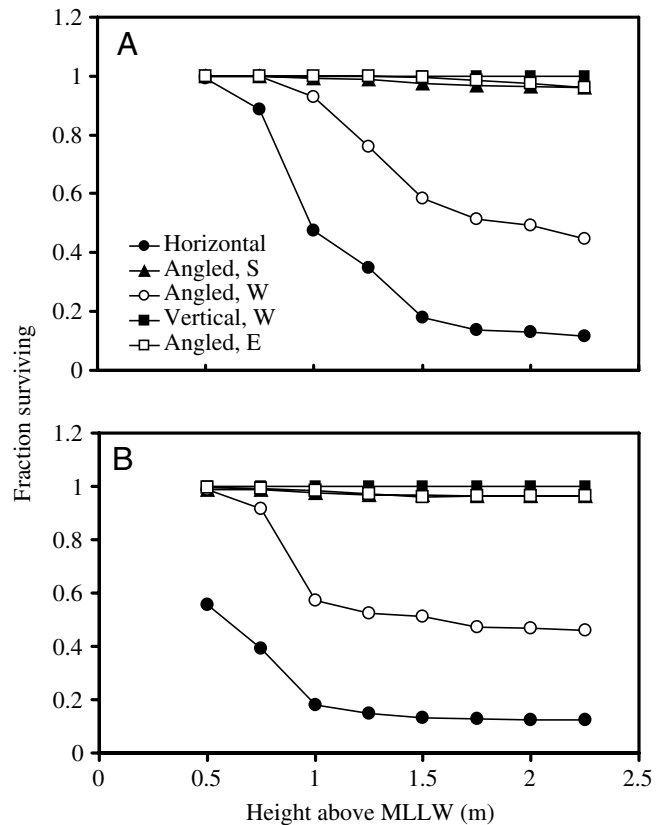


Fig. 5. The predicted fraction of limpets surviving the acute maximum temperatures shown in Fig. 4 for (A) wave-exposed and (B) wave-protected shores. Survivorship is low on horizontal and west-facing angled surfaces, but high elsewhere. MLLW, mean lower low water.

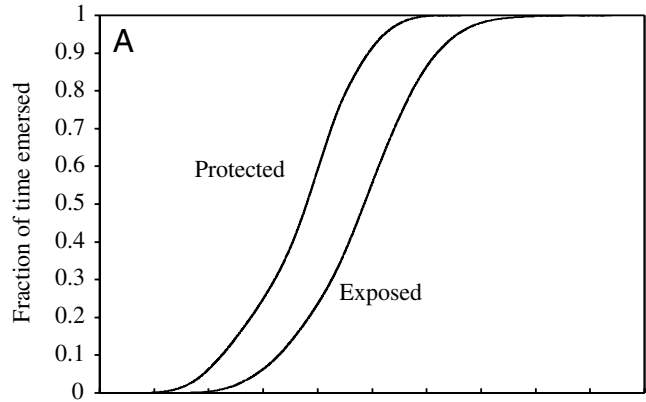
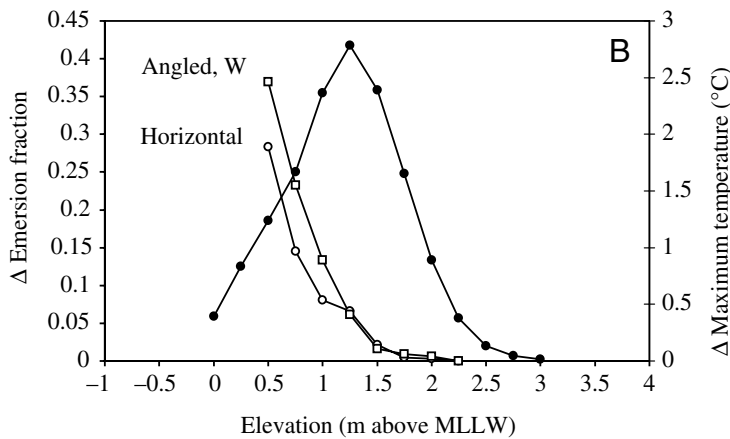


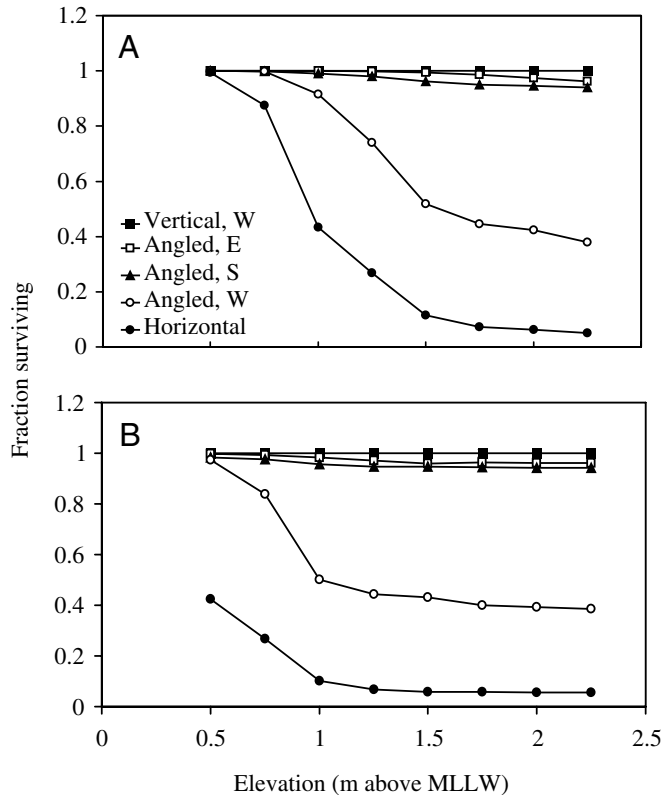
Fig. 6. Exposure to waves reduces the time spent out of water for shoreline elevations between 0 and +3 m. The difference in emersion fraction (closed circles) is greatest at +1.25 m, whereas the difference in maximum temperatures (open circles, horizontal surfaces; open squares, angled, west-facing surfaces) is greatest lower on the shore. MLLW, mean lower low water.



Second, the overall highest body temperature predicted is 37.5°C for limpets on horizontal surfaces 1.5–2.25 m above MLLW. Angled surfaces ($\phi=\pi/2$) facing west yield the next highest body temperature (36.8°C). The temperatures at these two orientations are substantially higher than those at other orientations.

Third, on wave-exposed shores (Fig. 4A), maximum temperature increases with increased shoreline elevation. However, this effect is greatest between +0.5 and +1.5 m, with little change higher on the shore. On wave-protected shores (Fig. 4B), there is much less variation in maximum temperature with elevation than on exposed shores (Fig. 4A).

Finally, at elevations below +1.0 m, temperatures are substantially lower on wave-exposed shores (Fig. 4A) than on protected shores (Fig. 4B). For example, on a horizontal substratum, the maximum temperature reached at a height of +0.5 m is 36.6°C on the protected shore, but only 34.8°C on the exposed shore. The corresponding temperatures for west-facing angled shores are 35.1°C and 32.6°C. The difference in maximum temperature between exposed and protected shores is negligible ($<0.06^\circ\text{C}$) for elevations above +1.5 m.



Survivorship

These data can be interpreted in terms of the fraction of individuals surviving a single imposition of the maximum temperature for each elevation and orientation (Fig. 5). Because limpets are not killed by maximum temperatures below 34°C, much of the variation in temperature with orientation and elevation does not translate into a variation in survival. Only on horizontal and west-facing angled substrata is there substantial mortality. On horizontal surfaces, the differences in survival between exposed and protected shores are greatest for surfaces at low elevations: at +0.5 m, 100% of animals are predicted to survive on exposed shores (Fig. 5A), but only 55% on protected shores (Fig. 5B). On west-facing angled surfaces, the greatest difference occurs at +1.0 m, where 96% of individuals survive on exposed shores, but only 55% on protected shores.

The effects of wave splash result from differences in the timing of emersion set by the combination of tide and waves. However, the link between emersion and temperature is not

Fig. 7. Five-year cumulative survivorship as a function of shoreline elevation and substratum orientation on (A) wave-exposed and (B) wave-protected shores. MLLW, mean lower low water.

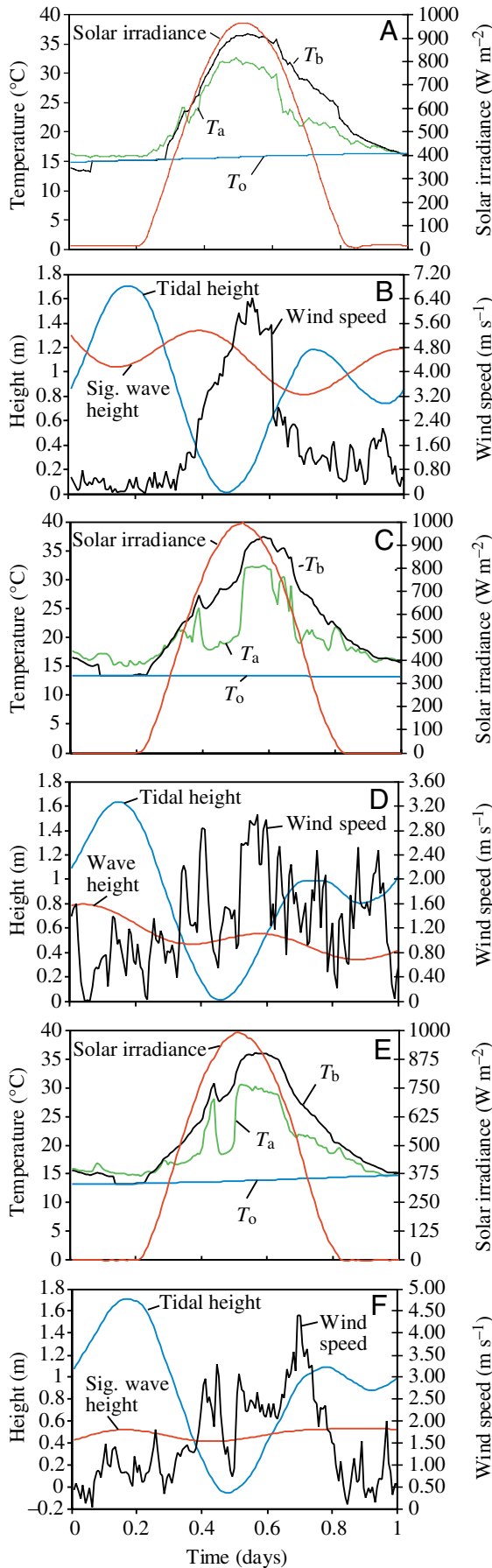


Fig. 8. Environmental characteristics of the three potentially lethal days (A+B, C+D, E+F) in the 5-year time series. T_b , body temperature; T_a , air temperature; T_o , ocean temperature.

straightforward. Fig. 6A shows the fraction of time that a given spot on the shore is emersed with and without waves: at any elevation between +0.5 and +2.25 m, the fraction of time limpets are emersed is lower in the presence of wave splash. Indeed, there are still substantial differences in emersion fraction between exposed and protected shores for elevations above +2.0 m, well above the elevation where maximum body temperatures converge (+1.5 m). This effect is highlighted in Fig. 6B, where the difference in the fraction of times spent emersed between exposed and protected shores is shown by the closed circles. This difference peaks at +1.25 m. In contrast, the difference in maximum body temperature between exposed and protected shores is largest at +0.5 m and decreases at elevations where the difference in emersion fraction is large. Thus, the difference in body temperatures between exposed and protected shores is not due solely to the difference in fraction of time emersed; the specific timing of emersion is also important. In this respect maximum body temperature may show a different pattern than feeding time (and hence growth rate) of suspension feeders, which should be more directly dependent simply on the fraction of time submersed.

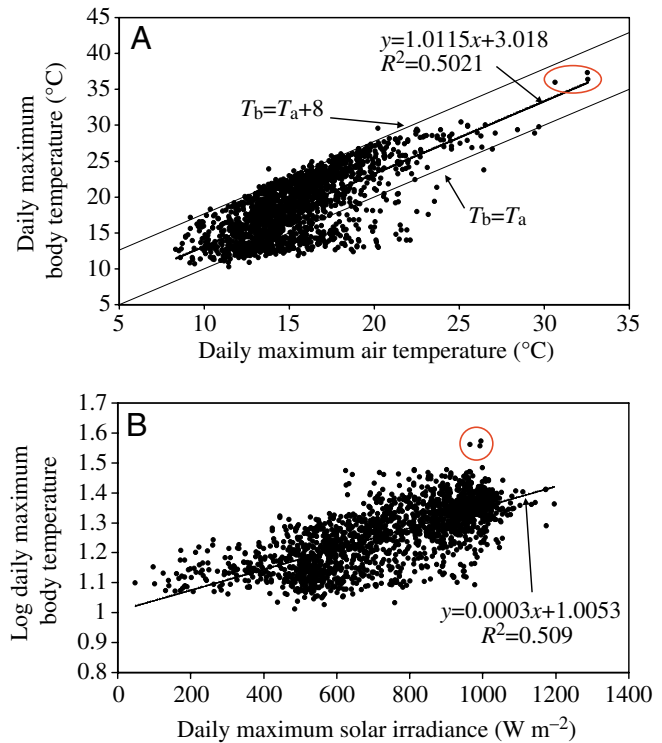


Fig. 9. (A) Daily maximal air temperature (T_a) accurately predicts daily maximal body temperatures (T_b), including the three potentially lethal body temperatures (circled). (B) Daily maximal solar irradiance also predicts maximal body temperature, but with less accuracy.

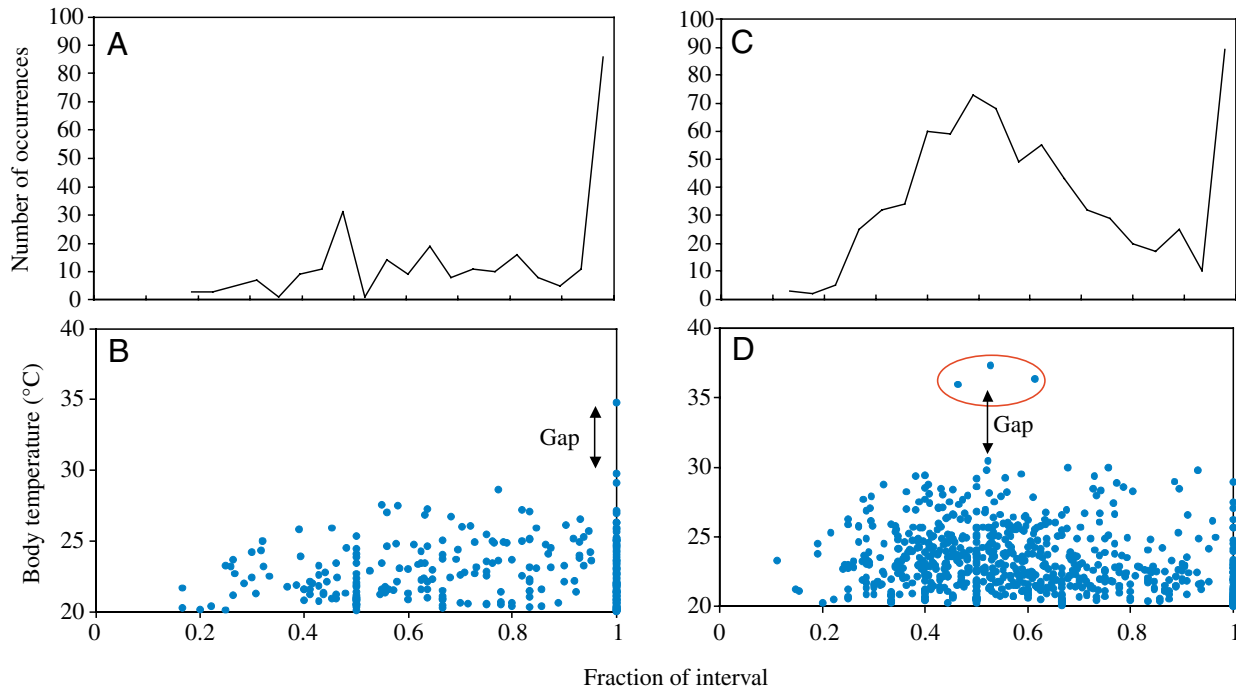


Fig. 10. Low in the intertidal zone (+0.5 m; A,B), maximal body temperature is typically reached at the end of a heating interval (Type A). Higher in the intertidal zone (+1.5 m; C,D), maximal body temperature may occur at the end of a heating interval, but occurs commonly near the middle of the interval (Type G). Potentially lethal temperatures are circled.

Cumulative thermal death

If we assume that (1) each daily imposition of potentially lethal temperatures is independent of other such events, and (2) limpets do not die from any cause other than thermal stress, we can estimate the total fraction of the limpet population

surviving our 5-year modeling period. For example, we know from our experiments that at a maximum temperature of 36°C, 87% of limpets survive one imposition of thermal stress (Eqn 4, Fig. 2). Thus, if there are 3 days during the 5 years when maximum temperature reaches 36°C and these events are independent, the fraction of individuals surviving at the end of 5 years is $0.87 \times 0.87 \times 0.87 = 0.66$.

The results are shown in Fig. 7. On wave-exposed shores (Fig. 7A), few limpets survive on horizontal surfaces, except at very low elevations. More than 35% of limpets survive on west-facing angled substrata, even at high elevations, and nearly all limpets (>93%) survive at all elevations for all other orientations. Cumulative survivorship is slightly lower on protected shores (Fig. 7B), especially at low elevations.

Characteristics of extreme days

Fig. 8 presents environmental data for the three days on which limpet body temperatures reached potentially lethal levels. As one would expect, each day was characterized by mid-day low tides and calm seas during emersion (significant wave height <1.4 m), and solar irradiance approached the yearly maximum of 1000 W m^{-2} . Wind speed varied both within and among days with no apparent pattern. Air temperature was exceptionally high (>30°C) on all three days.

At elevations and orientations where body temperatures may

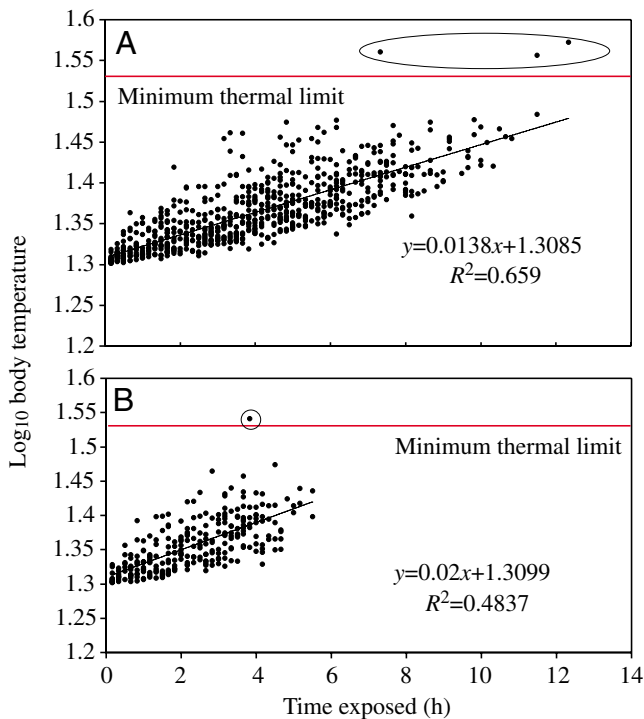


Fig. 11. Maximal body temperature increases with the length of time a limpet is exposed to temperatures above 20°C. (A) High in the intertidal zone (+1.5 m). (B) Low in the intertidal zone (+0.5 m).

potentially be lethal, daily maximum body temperature is significantly correlated with daily maximum air temperature. A representative example is shown in Fig. 9A for limpets on a horizontal surface 1.5 m above MLLW. This relationship accurately predicts the three potentially lethal body temperatures recorded during the modeling period (circled points). On average, the maximum body temperature is 3°C above the maximum air temperature. Virtually all maximum body temperatures lie within an envelope approximately 8°C above maximum air temperature.

Daily maximum body temperature is also correlated with daily maximum solar irradiance (Fig. 9B). In this case, however, the regression does not accurately predict the potentially lethal body temperatures recorded during the modeling period (circled points, well above the regression line), and there is no clear upper envelope to the data.

Periods of thermal stress

The heat-budget model allows us to characterize the time course of thermal exposure. From the predicted time series of body temperatures, it is possible to keep track of the time at which body temperature rises above a given threshold and the subsequent time when body temperature falls back below that threshold. The length of each of these intervals is then recorded. In addition, we record when in each interval the maximum temperature is reached and the magnitude of this maximum. The maximum sea-surface temperature during the 5 years of our hindcast was 19.7°C, so to define intervals of emersed thermal stress, we chose 20°C as our threshold. These data reveal several trends.

First, time courses of heating fall into two general categories. In the first (Type A, for 'abrupt'), body temperature rises more or less steadily through time until the limpet is immersed by the rising tide, whereupon body temperature abruptly returns to ocean temperature. In this pattern, maximum temperature is reached at the end of the above-threshold interval. In the second general pattern (Type G, for 'gradual'), body temperature rises to a peak and then falls gradually until the end of the interval. In this case, peak temperature occurs well before the end of the interval.

Representative distributions of maximum body temperatures and their relative location within intervals are shown in Fig. 10. For limpets at low elevations, maximum temperature is most often reached near or at the end of the above-threshold interval (Type A, Fig. 10A), as is the sole potentially lethal maximum body temperature recorded at this elevation (circled point, Fig. 10B). In contrast, at higher elevations (e.g. +1.5 m), the distribution of times of maximum temperature is distinctly bimodal (Fig. 10C): sometimes the maximum body temperature abruptly returns to ocean temperature (Type A), while at other times, body temperature rises and then falls gradually through the remainder of the interval (Type G). At this high elevation, the three potentially lethal maximum temperatures all occurred near the middle of the interval (circled points, Fig. 10D).

Note that for both low and high elevations, the rare,

potentially lethal body temperatures are separated by a substantial gap from other body temperatures. These events are not just incrementally higher than others, they are truly exceptional.

The information used to describe the pattern of heating and cooling also allows us to search for a relationship between the magnitude of heating and the length of the stressful interval. In general, the longer the time that body temperature is above 20°C, the higher the maximum temperature. This correlation is strong for limpets at high elevations (Fig. 11A, $r^2=0.659$), less so for limpets at low elevations (Fig. 11B, $r^2=0.484$). Note that the length of the interval for which limpets were exposed to temperatures above 20°C is quite variable among those exceptional days during which limpets might die from thermal stress (log maximum temperature >1.53). At the low elevation (+0.5 m, Fig. 11B), the single potentially lethal temperature (the circled point) was reached during an interval of less than 4 h above 20°C. At +1.5 m (Fig. 11A), one potentially lethal temperature was reached during an interval of about 7 h, and the others during intervals >11 h. In all cases, the potentially lethal temperatures would not be accurately predicted from the general relationship between interval length and maximum temperature (the circled points lie well above the regression line), again suggesting that prediction of body temperature based solely on time of emergence may not be practical.

Discussion

Vertical range limits

The range of lethal temperatures measured for *L. gigantea* (34–38°C) was similar to that of low intertidal snails *Tegula brunnea* (Phillippi) and *Tegula montereyi* Kiener at HMS (33–37°C), but was substantially lower than that for a mid-intertidal snail *Tegula funebris* (A. Adams) (40–43°C) and two species of high intertidal snails, *Littorina scutulata* Gould (42–49°C) and *Littorina keenae* Rosewater (44–50°C) (Somero, 2002).

Despite the relatively low thermal tolerance of *L. gigantea*, during the 5 years of our hindcasts, body temperatures predicted by our model were not sufficient to kill 100% of limpets at any elevation on the shore (based on our laboratory estimates of thermal tolerance), and on vertical surfaces, body temperature did not predict the death of any limpets at all. Thus, acute thermal mortality does not appear to set an absolute upper limit to the vertical range of this species at HMS. This conclusion is consistent with past work on limpets (Wolcott, 1973) and current thinking for both intertidal animals (for a discussion, see Harley and Helmuth, 2003) and intertidal algae (for a review, see Davison and Pearson, 1996), but it raises important questions.

For example, if lethal temperatures do not set the upper limit, what does? The lack of a lethal upper limit does not preclude a role for temperature. Instead, the limit may be set by cumulative physiological effects of acute sublethal temperatures, which can eventually lead to death or can have important implications for growth and reproduction (Somero,

2002) and for susceptibility to disease. For mobile organisms, for which local vertical zonation patterns may depend heavily on behavior, elevation-dependent sublethal stresses and intermittent partially lethal stresses (such as those documented here) may be important cues that animals use to avoid suboptimal habitats through behavior. Indeed, there is a negative correlation between a field-deployed proxy for body temperature and the upper limit of *L. gigantea* on vertical surfaces at HMS (C. D. G. Harley and L. Asbeck, unpublished). Note, however, that *L. gigantea* is territorial and effectively homing. These animals return to the same place on the rock at each low tide, and do not move during daytime emersion. Thus, for this species, while behavioral thermoregulation may play a part in determining the long-term upper limit, it likely plays little role in determining the upper limit on a tide-by-tide basis.

The importance of sublethal stress is an area of active research in a variety of intertidal species (for reviews, see Somero, 2002; Davison and Pearson, 1996; Helmuth et al., 2005), but one that is difficult to quantify and predict. In particular, sublethal responses to temperature stress likely vary with the thermal history of an organism, making it difficult (or impossible) to find a one-to-one association between a given temperature and a given reduction in growth or reproduction. The ability to hindcast, and thereby to quantify, thermal history, makes heat-budget models such as ours a potentially valuable tool for exploring this important aspect of ecophysiology.

Because the range of temperatures that separates survival from death for *L. gigantea* is narrow, predicted survivorship would change drastically if the thermal response of the limpet were shifted slightly up or down, and these changes could effect the interpretation of our results. For example, if the temperature required to kill 100% of limpets is shifted down 1°C (from 38°C to 37°C), our model predicts an absolute upper limit of +1.25 m for *L. gigantea* on wave-exposed horizontal surfaces (Fig. 4A). A downshift of 2°C would yield a similar absolute limit for west-facing angled substrata. The sensitivity of our conclusion to the lethal temperature raises important issues with regards to potential sources of error.

First, the accuracy and applicability of the estimate of an organism's thermal tolerance is critical. Accuracy can be improved by increasing the sample size of lethal limit experiments, but there are constraints on the accuracy one can hope to achieve. For example, thermal tolerance may depend on local genotypic or phenotypic adaptation (e.g. Rand et al., 2002), so lethal limits measured on one small population of limpets may not apply to another population only meters away. Furthermore, thermal tolerance of some intertidal species varies with acclimation temperature (Stillman and Somero, 2000) and with season (Foster, 1969), suggesting that the timing of thermal stress events relative to seasonal upregulation of thermal tolerance may affect our ability to predict range limits. Thermal tolerance may also depend on the dietary status of limpets (A. Underwood, personal communication).

The patterns of heating observed in our hindcasts can serve as a guide for how lethal limits can best be measured in the laboratory. As we have seen (Fig. 10) there are two general patterns of heating for *L. gigantea*. For a given rate of heating and a given maximal temperature, a limpet is subjected to high temperatures for a shorter time if the period of heating is brought to an abrupt end by the incoming tide (Type A) than if the limpet gradually cools as the sun goes down (Type G). Our data suggest that Type G heating is a more appropriate general test for conditions high in the intertidal zone (Fig. 10C,D), while Type A heating is a more appropriate general test for conditions low in the intertidal zone (Fig. 10A,B).

Although our data can provide generalizations regarding the time course of thermal stress, we note that these general patterns do not necessarily apply to any particular stressful event. For example, on two of the three most stressful days predicted by our model, body temperature rose rapidly to a plateau, and was then maintained for 3–4 h (see Fig. 8A,E). This is the pattern used in our test of thermal limits, but it does not precisely match either of the general categories described above. Again, further research is needed to determine if thermal limits vary when animals are exposed to different heating regimes. However, if limits do vary and can be categorized, our heat-budget hindcasts can be used to relate those laboratory findings to the potential existence of thermal range limits.

Discrepancies between model predictions and actual body temperatures in the field can also lead to inaccurate predictions of survivorship. Our model predicts maximum body temperature of live limpets within 0.29°C on average (Denny and Harley, 2006), so this source of error seems unlikely to affect our conclusions.

These potential complications inherent in predicting the role of body temperature in vertical range limits should be kept in perspective. Although a shift of 1°C in thermal tolerance, an increase of 10% in short-wave absorptivity [which would cause approximately a 1.3°C increase in 5-year maximum body temperature (Denny and Harley, 2006)], or an error of 1°C in predicted body temperature, could make the difference between presence or absence of an absolute upper limit on horizontal surfaces, a shift of nearly 6°C would be required to create an absolute upper limit for any vertical surface (Fig. 4A). Thus, our general conclusion is likely to be robust: for most substratum orientations, lethal thermal stress does not set an absolute upper limit in this species.

Aside from lethal and sublethal effects on limpets themselves, temperature may also define upper range limits indirectly *via* interactions with other species. In the case of *L. gigantea*, the upper limit of its distribution may depend on the availability of its microalgal food source: Denny et al. found an inverse relationship between maximum temperature and microalgal productivity at HMS (Denny et al., 2004). *L. gigantea* could also be limited by its response to desiccation, an effect not predicted by our heat-budget model. This seems unlikely, however. If desiccation set the upper limit, one would

assume that this limit would be higher for wave-exposed sites. But at HMS, the upper limit is independent of wave exposure once temperature has been taken into account (C. D. G. Harley and L. Asbeck, unpublished).

The utility of heat-budget models

In addition to informing us about the role of thermal stress in zonation, the extensive predictions of our heat-budget model provide insight into a variety of other environmental effects. For instance, the model reveals a potentially useful correlation between maximum body temperature and daily maximum air temperature. Helmuth rightly points out (Helmuth, 1998) that air temperature *per se* is not a useful proxy for the body temperature of intertidal animals. But at least in the case of *L. gigantea* at HMS, maximal air temperature can be a useful predictor of maximal body temperature. Our data suggest that maximum body temperature is seldom higher than approximately 8°C above air temperature and is typically 3°C above air temperature. Thus, unless maximum daily air temperature is within 3–8°C of the limpet's thermal limit, limpets should survive. For *L. gigantea* (with a minimum lethal limit of 34°C), air temperature must exceed 26–31°C to be potentially deadly, and air temperatures of this magnitude are rare on the central California coast. In the 5 years of weather data used in this study, air temperatures exceeded 26°C on only 13 days, and 31°C on only 2 days. Only a fraction of these potentially lethal air temperatures overlapped with low tides and calm seas, so the imposition of lethal body temperatures is rarer still.

The correlation between maximum body and air temperatures provides a potentially important link between intertidal physiological ecology and terrestrial climate change. If, as a part of global warming, the number of days with high air temperatures increases, the probability increases that limpets will be killed by thermal stress.

The results presented here demonstrate the utility of using heat-budget models (rather than field measurements) to provide long-term time series. In the 5 years examined here, only three thermal events occurred capable of killing more than 50% of limpets. Furthermore, this level of mortality occurred at only 18 of the 144 'sites' examined (12.5%). In other words, if one were to attempt to replicate our 'experiments' in the field, one would need to track a very large number of sites for an extended period of time to record the few events of interest. It would be daunting to physically install instruments and maintain such a field experiment, and it therefore seems likely that a practical field experiment would miss some or all of these rare, lethal events.

The heat-budget model can also be used to examine variation in parameters that cannot easily be controlled in the field. For example, thermal conductivity varies substantially among different rock types, and this parameter could be varied in the model to predict one effect of substratum composition on limpet survival. Similarly, the pattern of the tides could be changed in the environmental data set. For instance, summertime tides in central California occur early in the

morning, while farther north in Oregon and Washington, they occur closer to midday (Helmuth et al., 2002). The terrestrial data recorded at HMS could be coupled with tides predicted for Oregon or Washington to predict the effects of shifting the time of low tides. Effects of substratum orientation are also likely to vary with latitude. The possibilities are endless.

Caveats

Heat-budget model

There are several aspects of the current heat-budget model for *L. gigantea* that can be refined. First, as noted, the current model does not account for evaporative water loss. Experiments with live limpets (Denny and Harley, 2006) suggest that the rate of evaporative loss in this species is too slow to have appreciable effect on body temperature, but accounting for the loss will be necessary if the model is extended to predict the physiological effects of desiccation. Note that any effects of desiccation are taken into account in our measurements of thermal tolerance: limpets were free to desiccate in the experimental chamber.

The incorporation of wave action into the current heat-budget model is imprecise. As shown (Helmuth and Denny, 2003; Denny et al., 2004), wave-induced water velocities can vary drastically among intertidal sites separated by mere fractions of a meter. It is therefore likely that the predictions made here (which assume that wave splash on the shore is determined solely by offshore wave height) will be obscured on any real shore by the effects of local topography. No general solution to this problem is apparent. At present, the only accurate way to predict wave splash at a particular site on the shore is to measure splash directly at that site (e.g. O'Donnell, 2005). However, once these empirical measurements have been made, they can easily be incorporated into the heat-budget model to provide more accurate, site-specific predictions of body temperature.

Effects of topography

In making our calculations, we have assumed a simplified shoreline topography: limpets are assumed to live on infinite, planar substrata. Caution must be used in applying these predictions to real shores. For example, on any real shore, an area of horizontal substratum may, at times, be shaded by an adjacent area of vertical rock. The maximum temperature on this shaded area is likely to be lower than we predict, and limpet survivorship consequently higher. Conversely, nearby rock surfaces can also reflect solar energy, leading to higher body temperatures and lower survivorship. The heat-budget model can easily be adjusted to cope with these complications, but the adjustments must be made on a site-by-site basis.

Cumulative mortality

Our calculations of cumulative mortality may over- or underestimate actual rates of thermally induced death. For example, two of the extreme temperature events predicted by our model occurred on back-to-back days (26 and 27 June, 2003). One might suppose that limpets capable of surviving

35°C on one day would be capable of surviving it the next, so that the overall number killed by the 2-day event would simply equal the number killed on the first day. Alternatively, one might suppose that limpets that survived the first imposition of high temperature had little time to recover before the next imposition, and were therefore susceptible to dying at lower temperatures than they were previously capable of withstanding. Given this weakened state, the 2-day survival would be less than the square of the single day by itself. The magnitude of this problem increases with the number of sequential potentially lethal days. Yet again, further research on the physiology of lethal limits in this species will be necessary to resolve this question.

Concluding remarks

The heat-budget model for *L. gigantea* provides a wealth of information regarding the environmental and topographic control of body temperature in this ecologically important intertidal species. Interpreting this temperature information in a biological context relies on laboratory measurements of thermal limits, and the measurements presented here suggest that acute thermal stress does not set an absolute upper limit to the elevation of *L. gigantea*. This ecological interpretation depends strongly on the laboratory results, however, highlighting the need for additional research on the temporal and spatial variability of thermal limits and the cumulative effects of sublethal stress. Our heat-budget model can provide both insight into how these new tests should be conducted and a ready means of interpreting their results.

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