

# A Mechanistic Model to Study the Thermal Ecology of a Southeastern Pacific Dominant Intertidal Mussel and Implications for Climate Change

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## ABSTRACT

Developing mechanistic models to predict an organism's body temperature facilitates the study of physiological stresses caused by extreme climatic conditions the species might have faced in the past or making predictions about changes to come in the near future. Because the models combine empirical observation of different climatic variables with essential morphological attributes of the species, it is possible to examine specific aspects of predicted climatic changes. Here, we develop a model for the competitively dominant intertidal mussel *Perumytilus purpuratus* that estimates body temperature on the basis of meteorological and tidal data with an average difference ( $\pm$ SE) of  $0.410^\circ \pm 0.0315^\circ\text{C}$  in comparison with a field-deployed temperature logger. Modeled body temperatures of *P. purpuratus* in central Chile regularly exceeded  $30^\circ\text{C}$  in summer months, and values as high as  $38^\circ\text{C}$  were found. These results suggest that the temperatures reached by mussels in the intertidal zone in central Chile are not sufficiently high to induce significant mortality on adults of this species; however, because body temperatures  $>40^\circ\text{C}$  can be lethal for this species, sublethal effects on physiological performance warrant further investigation. Body temperatures of mussels increased sigmoidally with increasing tidal height. Body temperatures of individuals from  $\sim 70\%$  of the tidal range leveled off and did not increase any further with increasing tidal height. Finally, body size played an important role in determining body temperature. A hypothetical 5-cm-long mussel (only 1 cm longer than mussels found in nature) did reach potentially lethal body temperatures,

suggesting that the biophysical environment may play a role in limiting the size of this small species.

## Introduction

For most marine organisms, seawater temperature provides a very good indicator of body temperature because the vast majority of these organisms are ectothermic poikilotherms and spend their whole lives in the water. However, for intertidal organisms, which spend a substantial amount of time exposed to air during low tides, seawater temperature does not adequately estimate body temperature during periods of emersion (Helmuth 1998; Stillman and Somero 2000; Muñoz et al. 2005). As with terrestrial organisms, the actual body temperature of intertidal organisms during periods of aerial exposure will be determined in large part by various meteorological conditions, habitat characteristics, and thermal properties of the organism (Porter and Gates 1969; Helmuth 1998).

Changes in body temperature, driven by changes in ambient temperature, have been shown to affect various attributes of intertidal invertebrates, including physiological and reproductive performance, survival, and local and biogeographical distributions. For example, ectothermic species, whose body temperatures tend to be correlated with ambient temperature, show positive linear relationships between metabolic rate and body temperature within the limits of thermal tolerance (Moon and Pritchard 1970; Bayne et al. 1976b; McMahon and Russell-Hunter 1977; Branch et al. 1988; Shick et al. 1988). The prey consumption rate of the keystone predator *Pisaster ochraceus* has been linked to the periodic changes in sea surface temperature (on the order of  $3^\circ\text{C}$ ) produced by upwelling events (Sanford 1999, 2002). The zonation of congeneric fiddler crabs of the genus *Petrolisthes* has been shown to be related to the thermotolerance of species and the maximum habitat temperatures that are found over a few meters in sites separated several thousands of kilometers (Stillman and Somero 2000). Similarly, a positive relationship has been observed between operative temperature and level of aggregation in the intertidal Littorinid *Echilitorina peruviana* (Muñoz et al. 2008). Furthermore, the break in the geographic distribution of two barnacle species from the East Coast of the United States was related to the thermal tolerances of these species that concur with changes in sea surface temperature (SST) at Cape Hatteras, North Carolina (Wetthey 1984, 2002).

Apart from a handful of exceptions, intertidal invertebrates

Table 1: List of terms used in the thermal energy budget and their definitions and units

Term	Definition	Unit
$A_c$	Surface area of convection	$m^2$
$A_{\text{evap}}$	Surface area of evaporation	$m^2$
$A_g$	Surface area in contact with the substratum	$m^2$
$A_{\text{IR, gnd}}$	Surface area exposed to infrared radiation from the ground	$m^2$
$A_{\text{IR, sky}}$	Surface area exposed to infrared radiation from the sky	$m^2$
$A_{\text{sol}}$	Surface area exposed to direct solar radiation	$m^2$
$a_{\text{sw}}$	Shortwave radiation absorption	$W m^{-2}$
$\Delta x$	Distance between the mussel and the ground	$m$
$\epsilon_g$	Emissivity of the ground	Unitless
$\epsilon_b$	Emissivity of the mussel	Unitless
$\epsilon_a$	Emissivity of the air	Unitless
$h_c$	Convection coefficient	$W m^{-2} K^{-1}$
$h_p$	Planck's constant	$J s$
$h_m$	Coefficient of evaporation	$m s^{-1}$
$k_g$	Thermal conductivity of heat in body	$W m^{-2} K^{-1}$
$l$	Latent heat of water	$J kg^{-1}$
$m_b$	Body mass of mussel	$kg$
$q_b$	Specific heat of mussel	$J kg^{-1} K^{-1}$
$\rho_{\text{H}_2\text{O}}$	Vapor density of water	$kg m^{-3}$
$\rho_{\text{air}}$	Vapor density of air	$kg m^{-3}$
$S$	Shortwave radiation intensity	$W m^{-2}$
$\sigma$	Steffan-Boltzman constant	$W m^{-2} K^{-4}$
$T_a$	Air temperature	$K$
$T_b$	Body temperature	$K$
$T_g$	Substratum temperature	$K$
$u_*$	Friction velocity	$m s^{-1}$

and algae are of marine origin and constantly face an oscillation between marine conditions during high tide and terrestrial conditions during low tide (Little and Kitching 1996). This tidal oscillation generates steep gradients in submersion time, temperature, pH, salinity, and oxygen availability over only a few meters that may last a few hours. Most notable are the changes in ambient temperature. During high tides, when marine conditions prevail, ambient temperature will be that of the sea submerging these organisms. On the other hand, during low tides, when terrestrial conditions prevail, ambient temperature may reach values that are  $\geq 15^\circ\text{C}$  higher than those that occur during marine conditions (Southward 1958), or it may drop below freezing during early morning winter low tides at higher latitudes.

Probably the most conspicuous feature of rocky shores worldwide is the organization of intertidal invertebrates and algae into distinct vertical bands, a pattern frequently called zonation (reviewed in Little and Kitching 1996). The lower limits to the distribution of intertidal organisms are usually attributed to biological factors such as competition and predation, while upper limits are attributed to desiccation and thermal stress (Connell 1972; Robles and Desharnais 2002). The idea that desiccation and thermal stress determine the upper zonation limits of intertidal organisms has been held as a paradigm (Kuhn 1962) for many years despite the fact that,

when considering the extensive coastlines and biological diversity on rocky intertidal shores around the world, relatively little data exist on the actual thermal regime encountered by these organisms (Helmuth 2002). Only recently has commercially available technology allowed the recording of in situ temperature over extended periods of time and multiple locations (Helmuth 2002). When matched to the thermal properties of the study organisms, these data loggers provide a measure of the actual thermal conditions experienced by organisms over a fixed period of time. One of the main limitations of this method is that thermal regimes are recorded only for the duration of the study or the capacity of the loggers. Unusual events occurring every few to tens of years may be responsible for some patterns we observe today (Gaines and Denny 1993; Denny and Gaines 2000).

An alternative method of evaluating the effects of environmental stresses involves a combination of direct measures of the thermal regimes and modeling of the main components affecting the organism's body temperature. Given measurements of solar radiation, air temperature, relative humidity, and wind speed, body temperatures can be estimated to within a few degrees using a thermal energy budget (TEB; Porter and Gates 1969; Porter et al. 1973) that can be validated against temperature data recorded in situ. This kind of model was recently adapted by Helmuth (1998) for intertidal mussels along

the Pacific coast of North America, with results that estimated body temperatures with a margin of error of  $\sim 1^\circ\text{C}$ . The advantage of this approach is that meteorological data covering longer timescales than in situ intertidal temperature measurements are frequently readily available. These data can be used to estimate body temperatures under different scenarios of changes in climatic conditions when in situ body temperature measurements are not available. For instance, the impact of historical anomalies, such as El Niño events, could be assessed, or the consequences of predicted climate changes could be explored.

The Intergovernmental Panel on Climate Change (IPCC) collected climatic data from reliable sources around the globe that show an increase in the mean surface temperature of  $\sim 1^\circ\text{C}$  over the last century, mostly within the last 50 yr. Forecasts suggest increases in the global mean surface temperature of  $1.5^\circ\text{--}6^\circ\text{C}$  during the next 50–100 yr (IPCC 2001). The Sustainable Biosphere Initiative of the Ecological Society of America (Lubchenco et al. 1991) highlighted widespread concern among scientists and recognized the importance of research on the ecological consequences of global warming. Among the consequences that have been recognized so far, ecologists have noted poleward shifts in the geographic ranges of terrestrial and marine species concurring with the rise in temperature (reviewed in Parmesan and Yohe 2003; Parmesan et al. 2004), as well as localized changes in the abundances and distributions of species (Southward et al. 1995). These scenarios have spawned interest among field ecologists to better understand the thermal regimes of species and to attempt to make predictions as to how further warming may affect species distributions in the near future.

The mytilid bivalve *Perumytilus purpuratus* is commonly found throughout the mid-intertidal zone along the South American coasts, from Guyaquil, Ecuador ( $3^\circ\text{S}$ ), south, all the way around Cape Horn ( $56^\circ\text{S}$ ), to the Atlantic coast of Argentina (Brattström and Johanssen 1983). Beds frequently occupy as much as 100% of the primary substrate in the mid-intertidal and sometimes low intertidal zones (Santelices et al. 1991; Alvarado and Castilla 1996; Guíñez and Castilla 1999; Broitman et al. 2001), providing a secondary habitat for a large number of other organisms (Navarrete and Castilla 1990; Tokeshi 1995). Like other mytilid species, *P. purpuratus* is a filter feeder, making it a key vehicle for pelagic nutrient capture and transfer to benthic intertidal communities (Wieters et al. 2003), as this organism is the primary prey item for a diverse guild of predators (Castilla et al. 1979; Castilla 1981; Castilla and Paine 1987; Soto 1996). It is worth pointing out that the maximum size of *P. purpuratus* is  $\sim 4$  cm in length (Alvarado and Castilla 1996).

Here, we develop a TEB model for *P. purpuratus* and validate it with in situ temperature measurements made in central Chile. Then we use the model to describe the interannual variation in the thermal regime of *P. purpuratus*, emphasizing the effects of the timing and duration of low tides, solar radiation, and ambient temperature (both of the air and of the sea surface) on body temperatures.

## Material and Methods

### TEB Model

To model the thermal regime of *Perumytilus purpuratus*, a TEB (Porter and Gates 1969; Porter et al. 1973) adapted for intertidal organisms (sensu Helmuth 1998) was developed. Details of the TEB and definitions and descriptions of the terms involved are presented in detail by Finke (2003).

Briefly, the model uses meteorological data (i.e., solar radiation, air temperature, relative humidity, and wind speed) to estimate the body temperature ( $T_b$ ) of *P. purpuratus*. In the steady-state form, the TEB is expressed as

$$m_b q_b \Delta T_b = Q_{\text{tot}} \pm G \pm C - E, \quad (1)$$

where  $m_b$  is the mass of the mussel,  $q_b$  is the specific heat of the mussel,  $\Delta T_b$  is the resulting change in body temperature,  $Q_{\text{tot}}$  is the total radiation absorbed and emitted by the organism,  $G$  is heat exchanged with the substratum by conduction,  $C$  is heat exchanged with the surrounding air via convection, and  $E$  is heat lost to the environment via evaporation.

Each of the terms in equation (1) was expanded following Helmuth (1998) and Finke (2003) to obtain the extended version of the steady-state TEB used to model  $T_b$  values of *P. purpuratus* in this study. The TEB used here has the following form:

$$\begin{aligned} \Delta T_b m_b q_b = & a_{\text{sw}} S A_{\text{sol}} + \sigma [A_{\text{IR, gnd}} (\varepsilon_g T_g^4 - \varepsilon_b T_b^4)] \\ & + A_{\text{IR, sky}} \sigma (\varepsilon_a T_a^4 - \varepsilon_b T_b^4) + \frac{k_g A_g (T_g - T_b)}{\Delta x} \\ & + h_c A_c (T_a - T_b) - l h_m A_{\text{evap}} (\rho_{\text{H}_2\text{O}} - \rho_{\text{air}}), \quad (2) \end{aligned}$$

with the variables as defined in Table 1. The variables can be summarized into three categories: meteorological variables,

Table 2: Morphological variables and values used in the thermal energy budget model

Parameter	Value	Unit	Source
$L$	Measured	m	
$W$	$-.000576 + .5660899 L$	m	$r^2 = .888$
$H$	$.0021797 + .4527716 L$	m	$r^2 = .851$
$A_p$	$.0000071 + .2187112 L^2$	$\text{m}^2$	$r^2 = .904$
$A_{\text{tot}}$	$(\pi/4)(LW + WH + LH)$	$\text{m}^2$	Dall 1979
$A_c$	$A_{\text{tot}}$	$\text{m}^2$	Helmuth 1998
$A_{\text{IR, gnd}}$	$.5 \times A_{\text{tot}}$	$\text{m}^2$	Helmuth 1998
$A_{\text{IR, sky}}$	$A_p$	$\text{m}^2$	Helmuth 1998
$A_{\text{sol}}$	$A_p$	$\text{m}^2$	Helmuth 1998
$\Delta x$	$.5 \times L$	m	Helmuth 1998
$m_b$	$.0001913 + 167.76155 L^3$	kg	$r^2 = .900$
$m_{\text{shell}}$	$.0001365 + 106.18248 L^3$	kg	$r^2 = .887$
$m_{\text{tissue}}$	$m_b - m_{\text{shell}}$	kg	

Note. Source column provides the reference for values taken from the literature or a regression values for values measured in this study.

Table 3: Transfer coefficients used in the calculation of the Thermal Energy Budget model, their values, and the source from which they were obtained

Constant	Value	Unit	Source
$a_{sw}$	.75	$W m^{-2}$	Campbell and Norman 1998
$c_p$	29.3	$J mol^{-1} K^{-1}$	Campbell and Norman 1998
$\varepsilon_g$	1.0	Unitless	Helmuth 1998
$\varepsilon_b$	.96	Unitless	Campbell and Norman 1998
$\varepsilon_a$	$.0054 T_{air} + .06851$	Unitless	Campbell and Norman 1998 <sup>a</sup>
$h_c$	$.135\sqrt{u/L_{char}}$	$W m^{-2} K^{-1}$	See "Material and Methods"
$h_m$	$h_c$	$m s^{-1}$	Helmuth 1998
$k_g$	.6	$W m^{-2} K^{-1}$	Denny 1993
$l$	2.48	$J kg^{-1}$	Campbell and Norman 1998
$q_b$	4,180	$J kg^{-1} K^{-1}$	Helmuth 1998
$\sigma$	$5.67 \times 10^{-8}$	$W m^{-2} K^{-4}$	Campbell and Norman 1998

<sup>a</sup> Formula provided is the linear fit values provided in Table A3 of Campbell and Norman 1998.

morphological variables (Table 2), and transfer coefficients and constants (Table 3).

Time series of air temperature, sea surface temperature, relative humidity, solar radiation, wind speed, and tidal height were used as input variables in a simulation model written in MatLab (ver. 6.1; MathWorks) to estimate the  $T_b$  values at given tidal heights on the shore using equation (2). The model compared the tidal height of a given time step with a position representing the *P. purpuratus* beds being modeled. If the tidal height at that time was greater than or equal to the position on the shore being modeled,  $T_b$  was assumed to be equal to sea surface temperature at that time. Otherwise,  $T_b$  was estimated using the TEB. The MatLab script can be obtained via e-mail from G.R.F.

#### Environmental Variables and Transfer Coefficients

Air temperature, photosynthetically active radiation (PAR), wind speed and direction, and relative humidity was measured in a Campbell Scientific meteorological station recording at 20-min intervals from April 1999 to June 2004 at the Estación Costera de Investigaciones Marinas (ECIM) in Las Cruces, Chile. Calculation of the TEB requires total solar radiation. PAR (the photon flux density in the spectral range of 40–700 nm and reported in units of  $\mu E s^{-1} m^{-2}$ ) was considered to be 50% of the total solar radiation (Campbell et al. 1985) converted from  $\mu E s^{-1} m^{-2}$  to  $W m^{-2}$  using the factor 1/4.6 of daylight conditions (McCree et al. 1985). The values used for shortwave radiation absorption ( $\alpha_{sw}$ ) and long-wave emissivity of the mussel's body ( $\varepsilon_b$ ), of the air (assumed to be clear sky;  $\varepsilon_a$ ), and of the ground ( $\varepsilon_g$ ) are provided in Table 2, along with their sources.

In the convection term, the coefficient  $h_c$  is a function of wind speed and how much of the mussel body projects into the wind. In the model,  $h_c$  was calculated as  $0.135(u_* / d)^{1/2}$ , where  $u_*$  is the shear velocity (Helmuth 1999) and  $d$  is the length of the mussel in flow (Campbell and Norman 1998). Because mussels in beds show various orientations to flow,  $d$  was estimated as the average of  $L$ ,  $W$ , and  $H$  for a given-sized

mussel. Calculation of the wind speed at the substratum entails knowing the boundary-layer conditions in the wind column. For a given height ( $z$ ), the corresponding wind speed ( $u_z$ ) can be estimated as

$$u_z = \frac{u_*}{k_c} \ln\left(\frac{z}{z_0}\right), \quad (3)$$

where  $k_c$  is von Kármán's constant ( $k = 0.41$ ) and  $z_0$  is an index of roughness along the surface (when  $z = z_0$ ,  $u = 0$ ) and was assumed to be 1.7 mm (Helmuth 1998). The ratio  $u_*/k_c$  is determined as the slope between velocity and the natural logarithm of height above the substratum.

Profiling the boundary layer requires the simultaneous use of several anemometers placed at different heights from the substratum into the free stream. Because of logistic constraints, an alternative method proposed by Porter et al. (1973) was used in this study to estimate the wind profile on the basis of the temperature profile. Wind speed at a given height was estimated using the temperature profile and the wind speed at a reference height via the relationship

$$\frac{u_z}{u_r} = \frac{T_z - T_s}{T_r - T_s}, \quad (4)$$

where the subscripts  $r$  and  $s$  refer to a reference height and the substratum, respectively. Thermocouple probes were mounted at 10 points along a 320-cm pole, starting at the base ( $T_s$ ) and then at heights of 1.5, 2.5, 5, 10, 20, 40, 80, 160, and 320 cm. Thermocouples were connected to a thermocouple card in a laptop computer to record temperature at 0.1 Hz for 5 min per trial. A total of four trials were performed at three different intertidal and supratidal rocky platforms around ECIM, all facing south-southwest. Wind speed was obtained from the meteorological station at a height of approximately 30 m above the platforms, and the 3.2-m thermocouple was used as the reference temperature. Wind profiles estimated through equa-

tion (4) were then used to determine the boundary layer height from equation (3) (Denny 1993).

Beds of *P. purpuratus* tend to be multilayered (Alvarado and Castilla 1996); therefore, the mussels on the top of a bed that are receiving direct solar radiation are not in direct contact with the rock substratum. Therefore, conduction was excluded from the TEB for this species because of the negligible contribution that it was expected to have on overall  $T_b$  (see also Helmuth 1998).

Relative humidity is the ratio of ambient vapor pressure to saturation vapor pressure at a given temperature (Campbell and Norman 1998). Therefore, the vapor pressure of the air,  $\rho_{\text{air}}$ , was calculated by multiplying the relative humidity registered by the meteorological station by the corresponding saturation vapor pressure at the air temperature registered by the station (from Table A3 in Campbell and Norman 1998, p. 280).  $\rho_{\text{H}_2\text{O}}$  is the vapor concentration of water at the surface of evaporation in a mussel's body and was calculated by assuming a relative humidity of 0.995 and converting to vapor pressure as above. This value was chosen by using the value of humidity for blood in Campbell and Norman (1998).

Tidal height was estimated for the same period as the meteorological data using the program Tides (v. 3.8; P. Lutus) and rescaled to be a percentage of the long-term (20-yr) tidal range (see Finke et al. 2007 for details). The remaining meteorological variables were taken from the ECIM meteorological station database, using  $T_{\text{air}}$  values in degrees C that were converted to degrees K and relative humidity values in percent. Seawater temperature during periods of high tide was taken from the ECIM database of SST from a subtidally mounted temperature data logger recording every 5 min.

#### Morphological Variables

A total of 327 *P. purpuratus* individuals were collected for morphological measurements including total wet mass, tissue dry mass, shell dry mass, maximum shell length ( $L$ ), shell width ( $W$ ), and shell height ( $H$ ). Mussels were randomly selected from within mussel beds and ranged from 0.96 to 3.77 cm in maximum shell length; the selection consisted mostly of adults ( $L \geq 1$  cm) and a handful of subadults. Water content in the mussel was calculated as the difference between the wet mass (mussels were removed from an aquarium and blotted with a dry paper towel) and dry mass (mussels were dried at 60°C for 24 h). Total surface area ( $A$ ) was calculated as  $A = (\pi/4)(LW + WH + LH)$  (Dall 1979). Planform area ( $A_{\text{pl}}$ ), the cross-sectional area of the mussel perpendicular to  $L$ , was calculated on the basis of the area of an ellipse ( $A_{\text{pl}} = (\pi HW)/4$ ). Linear regressions were then used to relate  $W$  and  $H$  to  $L$ , and second-order nonlinear regressions were used to relate  $A$  and  $A_{\text{pl}}$  to  $L$ .

#### Validation of Model Results

Actual body temperatures of a total of 95 live *P. purpuratus* individuals were measured in situ in Las Cruces, Chile, during

March (late summer) and July (winter) 2008. These measurements were made by prying the two valves open with a small screwdriver and swiftly inserting a thermocouple within the body cavity.  $T_b$  was measured within 10 s after insertion of the thermocouple to avoid changes in temperature that may be caused by evaporation or convection. Following measurement of  $T_b$ , a linear measurement of size (either maximum  $L$ ,  $W$ , or  $H$ ) was performed for the mussel, depending on accessibility of the mussel by vernier calipers. Using the morphological regressions described above, all measurements were converted to maximum shell length. A temperature logger (TidBit; Onset Computers, Pocasset, MA) was deployed to record temperature values every 30 s. The individual measurements of  $T_b$  were then compared with the closest value from a temperature time series recorded by the TidBit.

Between January 20, 2003, and May 24, 2003, a TidBit set to record temperature every 5 min was deployed near the midpoint of a mussel bed on a roughly horizontal intertidal bench ~500 m from ECIM. TEB model output was used to compare these values with temperatures registered in the field for the same time period, using mean-difference analyses and matched-pairs  $t$ -tests for the entire time series and only daily maxima. The  $T_b$  was modeled for a tidal height corresponding to that of the TidBit. For these comparisons, the model output was filtered to remove periods of high tides when the TidBit was measuring under water.

#### Descriptive Metrics of the Thermal Regime of *P. purpuratus*

Two metrics were calculated from the TEB output in order to make comparisons between years and tidal heights: cumulative degree hours and the monthly mean of the daily maximum temperature. Cumulative degree hours is the sum of the product of time and temperature for a given tidal height. Cumulative degree hours (or degree days) is frequently used in agriculture or developmental biology studies to compare climatic conditions necessary for growth or development. In this case, we used degree hours to compare different tidal heights. For every 10% of the relative tidal height from 0% to 100%, cumulative degree hours was calculated for each complete year of data (2000–2003).

Monthly means of daily maximum (MMDM) temperatures were calculated as a measure of chronic extreme temperatures experienced by intertidal mussels (Helmuth and Hofmann 2001). Daily maxima were calculated at 10% intervals of tidal height, using the highest value for each day, between 0000 and 2340 hours. Monthly means were calculated using the first to last day of each calendar month in a given year.

#### Lethal Temperatures

Mortality of *P. purpuratus* individuals in air was used as an indicator of thermal stress. Approximately 200 live individuals were placed in a wind tunnel with infrared lamps. The lamps were adjusted to maintain a temperature of 36°, 40°, or 43°C. Thirty-five randomly selected individuals were removed after

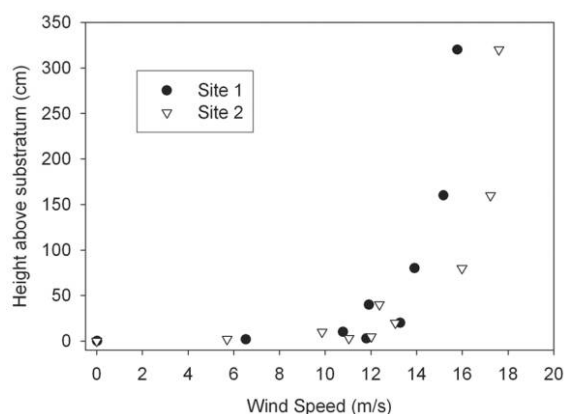


Figure 1. Wind profile and boundary layer of two sites in Las Cruces separated by  $\sim 200$  m.

30, 60, 90, and 120 min for the 40° and 43°C treatments, and the same amount was removed after 60, 120, 180 and 240 min for the 36°C treatment. These individuals were then placed in an aquarium with fresh running seawater and maintained for 24 h, after which time they were examined to determine whether they were alive.

## Results

### Boundary Layer Profile

An example of the wind profile, calculated from the temperature profile using equation (4), for two sites in Las Cruces that are separated by  $\sim 300$  m is shown in Figure 1. Regression values for  $\ln(h)$  vs.  $u$  were quite similar among the four recording sessions. Therefore, a pooled value of  $u_* = 0.552$  was used in the calculations of the wind profile.

### Morphological Variables

A summary of the morphological variables measured is presented in Table 2. In all cases, the independent variable used explained a high ( $r^2 > 0.8$ ) and significant fraction of the total variance in the dependent variable, making them good predictors.

### Validation of Model Results

Considering all individuals measured in the field, spanning a range of 18.1–33.2 mm in length, the TidBit tended to underestimate in situ  $T_b$  by an average of  $2.62^\circ \pm 0.18^\circ\text{C}$  ( $n = 95$ ). The linear relationship between the two measured temperatures was highly significant, with a slope slightly but significantly higher than 1.0 (TidBit value =  $-3.417 + 1.034 \times T_b$ ,  $r^2 = 0.964$ ,  $P < 0.0001$ ). There was a weak significant linear trend in the mean difference of the two measured temperatures when regressed against the average of  $T_b$  and TidBit value  $\text{Dif}_{(T_b - \text{TidBit})} = 3.77 - 0.0525 \times \text{mean}_{(T_b, \text{TidBit})}$ ,  $r^2 = 0.070$ ,  $P < 0.0093$ ), indicating that the difference between the two tended

to decrease with increasing temperature. Thus, the Tidbit value appears to be a conservative proxy for  $T_b$  of *Perumytilus purpuratus*, since the values of the former are consistently lower than those of the latter.

A regression between the subset of the TEB output (filtered to remove high-tide periods when SST was used as  $T_b$ ) against the TidBit data resulted in a tight and significant relation between the two ( $T_{\text{TidBit}} = 3.99 + 0.705T_{\text{TEB}}$ ,  $r^2 = 0.699$ ,  $P_{1,6233} < 0.0001$ ). On average, the  $T_b$  estimated by the TEB was  $0.410^\circ\text{C}$  higher than that measured in the field with the TidBit (SE = 0.0315,  $n = 6,235$ ), and  $>90\%$  of the modeled data was within  $5^\circ\text{C}$  of values measured by the TidBit. However during  $<1\%$  of the time, the difference exceeded  $\pm 10^\circ\text{C}$ . Extreme  $T_b$  differences (TEB – TidBit) during this 5-mo period were  $14.9^\circ\text{C}$  and  $-10.3^\circ\text{C}$  (Fig. 2). This variation is most likely caused by the fair degree of uncertainty when using tidal harmonics for predicting sea level at a specific location (see “Discussion”).

It has been suggested that maximum temperature can be as or more important than average temperature for organism survival (Helmuth and Hofmann 2001; Somero 2002). The daily maximum temperature registered by the TidBit was, on average,  $0.637^\circ \pm 0.323^\circ\text{C}$  lower than that modeled with the TEB (matched-pairs  $t$ -test,  $T = 0.05 \pm 1.97$ ,  $P_{1,124} = 0.0511$ ). The mean difference analysis showed a marginally significant trend with a very poor fit (TEB – TidBit =  $-2.01 + 0.125 \times \text{mean}$ ,  $P_{(1,123)} = 0.0437$ ,  $r^2 = 0.033$ ).

### Long-Term Thermal Regime Experienced by *P. purpuratus*

Modeled  $T_b$  for the entire period for which we have meteorological data at ECIM (April 10, 1999–May 6, 2004) for a mussel 3 cm in length at a tidal height corresponding to 50% of the total tidal range is presented in Figure 3.  $T_b$  values  $>30^\circ\text{C}$  were regularly found in the summer months of all years, and  $T_b$  values  $>35^\circ\text{C}$  were encountered in the summers of 1999–2000 and 2001–2002. The highest  $T_b$  values were estimated in the austral summer of 1999–2000. Maximum  $T_b$  values in this

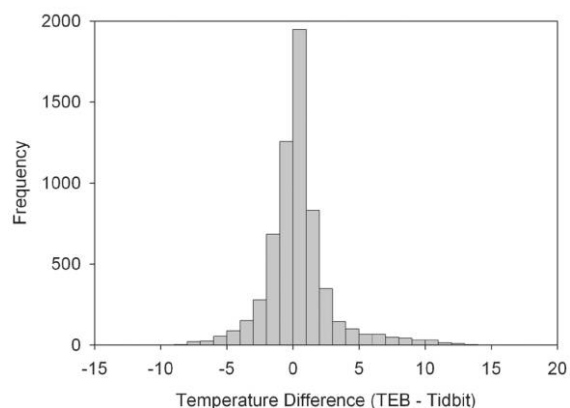


Figure 2. Histogram of the difference between thermal energy budget (TEB) output and in situ temperature data recorded with a TidBit temperature logger.

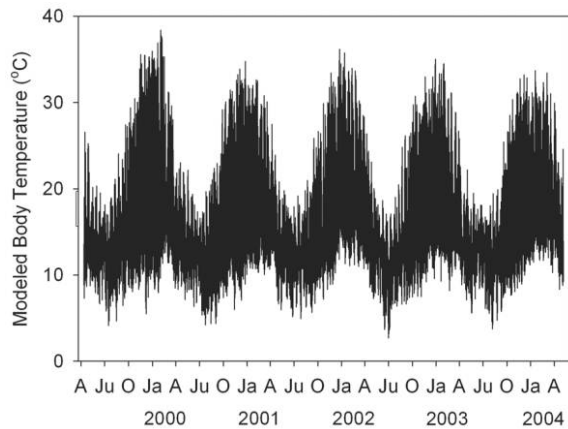


Figure 3. Long-term modeled body temperature of a 3-cm-long *Perumytilus purpuratus* located at a tidal height corresponding to 50% of the tidal range. The series range is from April 1999 to June 2004. A = April, Ju = July, O = Oct, Ja = January.

summer were  $>5^{\circ}\text{C}$  warmer than they were in the following summer (2000–2001) and were only  $2^{\circ}\text{C}$  higher than the maximum temperatures estimated for summer 2001–2002 (the second-warmest year).

As expected, mussel  $T_b$  values at higher tidal heights were higher than those at lower tidal levels, since exposure to terrestrial conditions is greater. However, the relationship between tidal height and cumulative body temperature was nonlinear (Fig. 4). The relationship between cumulative degree hours was rather level between tidal heights of 0% and 10% of the tidal range, it increased with tidal heights between 10% and 75% of the tidal range, and it leveled off at the highest tidal levels.

MMDM temperatures (Fig. 5) show that, during summer, daily maximum temperatures regularly exceed  $30^{\circ}\text{C}$  at tidal heights  $>50\%$  of the tidal range. The average for most of the summer was  $>30^{\circ}\text{C}$  in all years, especially in the summers of 1999–2000, 2000–2001, and 2001–2002, and also in the months of January and February 2003, December 2003, and February 2004.

Mussel size also played an important role in modeled mussel  $T_b$  values. Body temperatures modeled for body sizes ranging from 2 to 5 cm maximum shell length (the 5-cm size being a purely hypothetical case) showed that larger mussels reached higher  $T_b$  values. Only mussels  $>4$  cm in length reached  $T_b$  values  $>39^{\circ}\text{C}$  during the austral summer of 1999–2000 (Fig. 6). The hypothetical 5-cm mussel reached temperatures  $>39^{\circ}\text{C}$  for periods of time that were sufficiently long enough to induce mortality (see “Lethal Temperatures”).

#### Lethal Temperatures

Results of the mortality runs are presented in Figure 7. Only three mussels died after exposure to  $36^{\circ}\text{C}$  for 60 min, with no further mortality in the other three time treatments. At  $39^{\circ}\text{C}$ , a gradual increase in mortality was observed with exposures  $>60$  min, reaching almost 50% mortality after 120 min. At  $43^{\circ}\text{C}$ ,

$>50\%$  mortality was detected after only 30 min of exposure, and almost 100% mortality occurred after 90 min.

#### Discussion

The TEB developed here predicted values of  $T_b$  that were remarkably close to temperatures recorded with a temperature logger placed within a bed of live *Perumytilus purpuratus* in the mid-intertidal zone. Granted, although a difference was detected between the temperature logger and  $T_b$  measured in situ, the difference was small (on average,  $<2^{\circ}\text{C}$ ). Furthermore, because the TidBit registered values below the  $T_b$  values measured in this study, we suggest that testing of the TEB against the TidBit provides a conservative validation of the model. The average difference between modeled  $T_b$  values and  $T_b$  values mimicked by the TidBit was  $0.410^{\circ}\text{C}$ , whereas the average difference between  $T_b$  values measured in situ and  $T_b$  values mimicked by a TidBit was  $2.62^{\circ}\text{C}$ . The standard error of the differences between the TEB and the TidBit was  $<10\%$  of the mean, suggesting that these events were infrequent. Nonetheless, 80% of the modeled  $T_b$  values fell within  $\pm 2.5^{\circ}\text{C}$  of the values registered by the TidBit (Fig. 2). Occasionally, extreme differences were observed (up to  $14.9^{\circ}\text{C}$ ). Because daily maximum temperatures registered by the TidBit were very well correlated with the TEB (see “Results”), they were on average  $0.637^{\circ}\text{C}$  lower, and we suggest that the extreme differences result from the mismatch between predicted and observed tidal height at the site. Local weather conditions play a very important role on actual sea level, but they are not incorporated into harmonic tide predictions. For example, low barometric pressure and onshore winds tend to make the tide higher than predicted, and high barometric pressure and offshore winds tend to make the tide lower than predicted. Moreover, in a real situation on wave-exposed shores, waves and splash can largely determine the time an individual is exposed to air, especially when the tide is receding or coming in (Harley and Helmuth 2003). When waves are large, seawater wets the organisms even when the tide is low, thereby maintaining  $T_b$  values that are

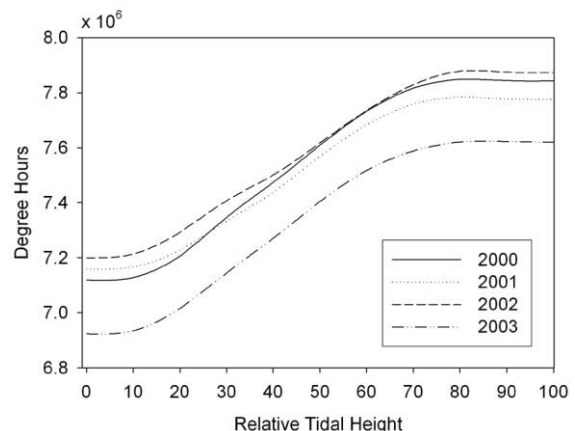


Figure 4. Cumulative degree hours based on thermal energy budget (TEB), modeled over a range of tidal heights.

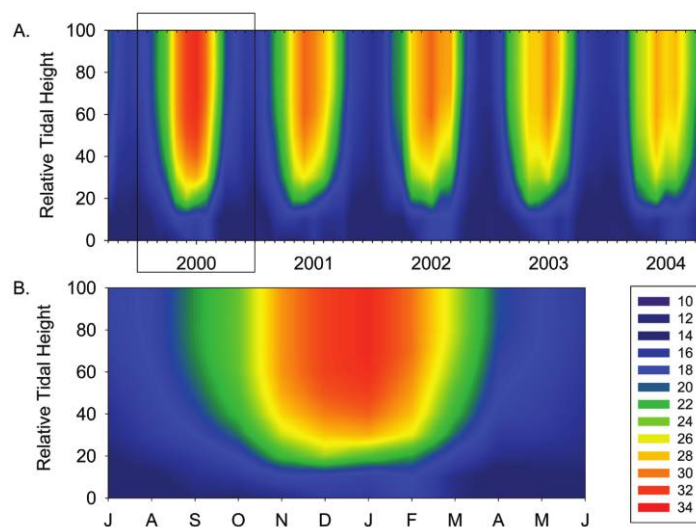


Figure 5. Monthly mean of daily maximum temperatures modeled using the thermal energy budget (TEB) for different tidal heights. A, Entire data set (April 1999–May 2004). B, Subset for July 1999–June 2000, as indicated by the rectangle in A.

closer to SST. Because short-term fluctuations in weather and wave climate cannot be predicted over the long term, these are not incorporated into tidal predictions, and observed values of sea level year round occasionally deviate from predicted values. Nonetheless, given the rarity of these extreme values and the significant relationship between the TEB and the in situ temperature recordings, we trust that the overall patterns exhibited by the TEB are representative of the actual thermal regime that *P. purpuratus* faces in the study site.

Modeled  $T_b$  values for *P. purpuratus* in central Chile regularly exceed 30°C in summer months, and values as high as 38°C can occur on occasion. Field-collected mussels were able to withstand  $T_b$  values of 36°C in air for up to 4 h with almost no mortality, and at 39°C, 50% mortality was observed after 120 min (Fig. 7). These results suggest that the temperatures reached by mussels in the intertidal zone in central Chile are not sufficiently high enough to induce significant mortality on adults of this species. However, if we consider extremely large 4-cm mussels or the hypothetical 5-cm mussel, body temperatures did reach values that exceeded 39°C in the austral summer of 2000 for periods of time that were sufficient to induce substantial mortality (Fig. 6). Furthermore, Bayne et al. (1976a) showed that the scope for growth of *Mytilus californianus* is greatest when body temperatures are between 17° and 22°C, and it drops off rapidly when temperatures exceed 26°C, suggesting that while the modeled  $T_b$  for *P. purpuratus* may not be lethal, these sublethal temperatures may affect the species' physiological performance. During periods of terrestrial conditions, physiological and biochemical mechanisms, such as ubiquitin and heat-shock proteins invoked to prevent protein unfolding and denaturation (Feder and Hofmann 1999), exist to help organisms deal with stressful conditions. The more these mechanisms are used, the more they need to be replaced or maintained during periods of submersion, resulting in poten-

tially significant effects on the animals' metabolic energy budgets (Somero 2002). Interestingly, *P. purpuratus* presents higher growth and survival rates at intermediate tidal heights rather than at lower tidal heights or subtidally (Cancino and Rojas 1986; S. A. Navarrete and R. M. Venegas, unpublished data). Further studies are needed to evaluate the effects of these chronic sublethal stresses on the survival, growth, and reproduction of this mussel.

Upper limits to the zonation of intertidal organisms are all too frequently attributed to the effects of increasing stress caused by increasing temperature and desiccation with height on the shore. Interestingly, the thermal regimes of the mid- to upper intertidal zones, as is modeled here for a site in central Chile, were remarkably similar. The MMDM temperature (Fig. 5) was roughly the same from ~60% of the tidal range up to the highest point (representing 100% exposure to air). Above 70% of the tidal range, there was no substantial increase in cumulative degree hours (Fig. 4). Although temperatures do not appear to reach levels that would cause significant mortality, other factors such as food availability and settlement or post-settlement survival could be more important in determining upper distributions. Along these lines, larvae and juvenile stages of marine invertebrates are generally considered to be more sensitive to fluctuations in abiotic conditions such as temperature (Gosselin and Qian 1997; Pechenik 1999). Because settlement of this species occurs roughly year-round, with marked peaks in summer (Navarrete et al. 2002; Narváez et al. 2006), further research on the thermal tolerances of the larvae and recent settlers of *P. purpuratus* is needed to evaluate whether the thermal regime is a factor affecting the upper limit of this species.

In the late winter to early spring of 1999 (between August and November), a large-scale mortality event of intertidal mussels and algae was observed at several sites in central Chile



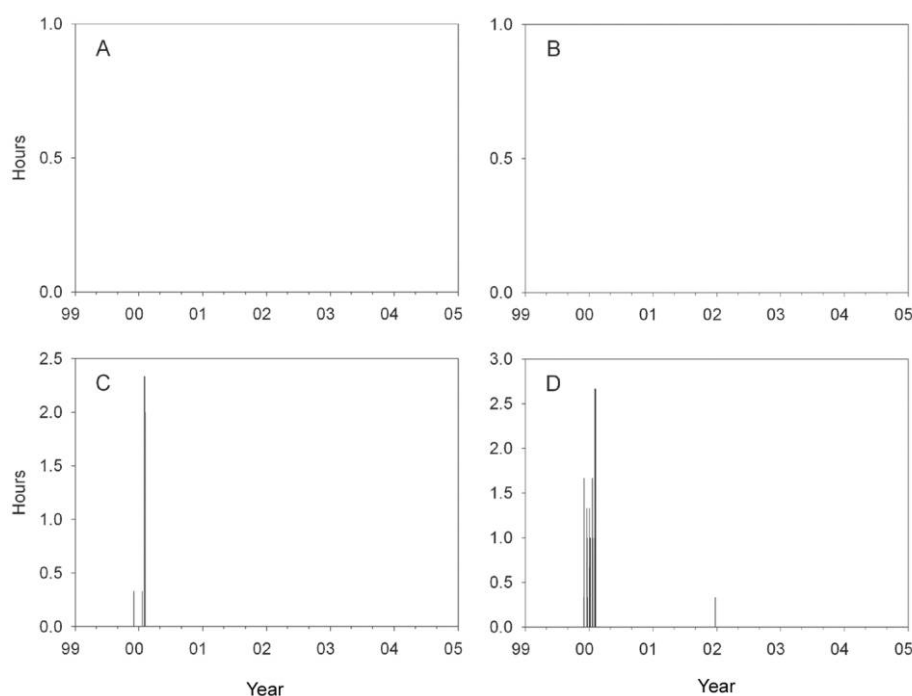


Figure 6. Duration (h) of events where modeled body temperatures of different-sized *Perumytilus purpuratus* individuals exceeded 39°C. Each panel represents an individual of a different maximum shell length: A, 2 cm; B, 3 cm; C, 4 cm; and D, 5 cm.

spanning  $>1^\circ$  in latitude. The event included losses of *P. purpuratus* and the bleaching and subsequent mortality of some intertidal algae such as *Gelidium* and *Mazzaella* species (S. A. Navarrete and E. A. Wieters, unpublished data). During that spring, air temperature and solar radiation were higher compared with the other years. Modeled mussel body temperatures were reaching MMDM between 22° and 24°C during September and were reaching daily maxima  $>30^\circ\text{C}$  in November (Fig. 5B). These infrequent events highlight the need to have predictive models to study the effects of desiccation on organisms and to assess long-term consequences and adaptations to these conditions.

Our model predicted an increase in  $T_b$  with increased body size of *P. purpuratus*. Indeed, a 5-cm-long mussel, ~1 cm longer than the largest mussel observed under natural conditions, produced temperatures that reached 42°C during January of 2000. These values are high enough to induce significant mortality in summer after 30 min (Fig. 7). While this result was robust in the model for different sets of parameters, it was difficult to estimate the effects of body size on body temperature in the field. Small mussels tend to be located deeper inside the bed matrix (Alvarado and Castilla 1996; Guíñez and Castilla 1999; Guíñez et al. 2005), and it is nearly impossible to register the  $T_b$  values of these individuals without disturbing them. Our result, therefore, opens an interesting question as to whether the ability of *P. purpuratus* is related to its small body size or, in other words, whether environmental conditions have limited the maximum size of this or other intertidal organisms along the coast of the South Pacific, where tidal regimes have exposed

organisms to potentially some of the most stressful aerial conditions in the world (Finke et al. 2007). Unfortunately, the absence of a phylogeny that includes this species does not allow us to eliminate the null hypothesis that small body size is a historical attribute and is potentially unrelated to current conditions experienced by this species.

Indeed, *P. purpuratus* is one of the smallest competitively dominant mussels in the world. The interaction between body

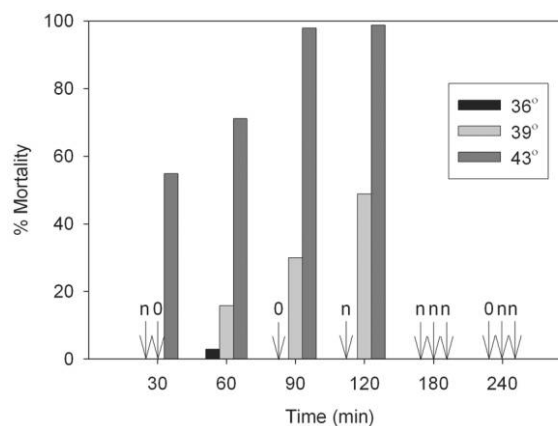


Figure 7. Mortality over time of mussels exposed to different temperatures. X-axis shows the amount of time mussels were exposed to given air temperatures before mortality was assessed. An *n* indicates that no mussels were evaluated for the treatment combination (temperature  $\times$  duration of exposure), and 0 indicates that no mussels died for a given treatment combination.

size and body temperature becomes especially intriguing when one considers that forecasts for global warming estimate increases in mean surface temperature of the globe by as much as 3°–6°C over the next 50–100 yr (IPCC 2001). If current body sizes are limited by present environmental conditions, then an increase in environmental temperature (mostly air temperature) in central Chile may produce a reduction in the body size of this species. Because thermal energy budget modeling incorporates an organism's physiological performance, it has the potential to be a very helpful tool for answering questions like this and others, for example, regarding the spatial distribution and geographical range changes in the face of global warming over finer temporal and spatial scales.

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