

Importance of Behavior and Morphological Traits for Controlling Body Temperature in Littorinid Snails

Author(s): LUKE P. MILLER and MARK W. DENNY

Source: *Biological Bulletin*, Vol. 220, No. 3 (June 2011), pp. 209-223

Published by: The University of Chicago Press in association with the Marine Biological Laboratory

Stable URL: <https://www.jstor.org/stable/23046946>

Accessed: 16-02-2019 17:12 UTC

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/23046946?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

Marine Biological Laboratory, The University of Chicago Press are collaborating with JSTOR to digitize, preserve and extend access to *Biological Bulletin*

Importance of Behavior and Morphological Traits for Controlling Body Temperature in Littorinid Snails

LUKE P. MILLER^{1,*} AND MARK W. DENNY

Hopkins Marine Station, Stanford University, Pacific Grove, California 93950

Abstract. For organisms living in the intertidal zone, temperature is an important selective agent that can shape species distributions and drive phenotypic variation among populations. Littorinid snails, which occupy the upper limits of rocky shores and estuaries worldwide, often experience extreme high temperatures and prolonged aerial emersion during low tides, yet their robust physiology—coupled with morphological and behavioral traits—permits these gastropods to persist and exert strong grazing control over algal communities. We use a mechanistic heat-budget model to compare the effects of behavioral and morphological traits on the body temperatures of five species of littorinid snails under natural weather conditions. Model predictions and field experiments indicate that, for all five species, the relative contribution of shell color or sculpturing to temperature regulation is small, on the order of 0.2–2 °C, while behavioral choices such as removing the foot from the substratum or reorienting the shell can lower body temperatures by 2–4 °C on average. Temperatures in central California rarely exceeded the thermal tolerance limits of the local littorinid species during the study period, but at sites where snails are regularly exposed to extreme high temperatures, the functional significance of the tested traits may be important. The mechanistic approach used here provides the ability to gauge the importance of behavioral and morphological traits for controlling body temperature as species approach their physiological thresholds.

Introduction

Within the narrow band of habitat between the low and high tidemarks on seashores, the distribution of individual species and the structure of ecological communities are dictated by a variety of biotic and abiotic factors (Connell, 1961, 1972; Lewis, 1964; Paine, 1974; Dayton, 1975; Menge and Branch, 2001). Biological interactions such as predation, competition, and facilitation play out on a background of constantly shifting environmental conditions driven primarily by the action of tides and waves (Stephenson and Stephenson, 1972; Denny, 2006; Denny *et al.*, 2009). Changes in important environmental parameters such as light, temperature, and wave action can alter the suitability of the habitat for a given species at both small and large spatial scales (Wetthey, 2002; Denny *et al.*, 2004; Harley, 2008). The capacity of organisms to persist under these varied environmental conditions is mediated by the interaction of a suite of behavioral, morphological, and physiological traits.

Snails in the family Littorinidae are important herbivores in mid- and high-shore intertidal communities around the world (McQuaid, 1996a, b; Reid, 1996), and often exert control over macroalgal and microalgal communities (Castenholz, 1961; Hawkins and Hartnoll, 1983; Norton *et al.*, 1990; Hidalgo *et al.*, 2008). These snails can experience large swings in temperature over the course of a single tide cycle and must often contend with multi-day periods of aerial emersion when they live above the high tide line (Vermeij, 1972; Cleland and McMahon, 1986; McMahon, 1990; Judge *et al.*, 2009; Marshall *et al.*, 2010).

The importance of morphological and behavioral traits for managing body temperature has been demonstrated in many terrestrial ectotherms such as insects, reptiles, and gastropods (Schmidt-Nielsen *et al.*, 1971; Porter *et al.*, 1973; Stevenson, 1985; Huey, 1991; Kingsolver, 1996; Kearney *et al.*, 2009), and similar roles for morphological

Received 18 November 2010; accepted 21 April 2011.

¹ Current address: Marine Science Center, Northeastern University, 430 Nahant Rd, Nahant, MA 01908.

* To whom correspondence should be addressed. E-mail: contact@lukemiller.org

Abbreviations: HMS, Hopkins Marine Station.

and behavioral variation have been hypothesized for littorinid snails and other intertidal gastropods. Variation in shell color across geographic scales has been hypothesized to be a response to climatic conditions, with dark-colored morphs inhabiting cooler sites, while light-colored morphs dominate warmer areas (Markel, 1971; Vermeij, 1971b; Etter, 1988; McQuaid and Scherman, 1988; McQuaid, 1992, 1996a; Sergievsky, 1992; Phifer-Rixey *et al.*, 2008), as has been argued for terrestrial gastropods (Jones, 1973; Heath, 1975; Heller, 1981). Shell shapes can vary from globular to high-spired, which affects heating by absorption of shortwave radiation from the sun and determines the internal volume of fluid that can be stored in the shell to withstand desiccation (Vermeij, 1972, 1973; Chapman, 1995). In addition, the outer surface of the shell may be smooth, or it may be sculptured, with ribs, ridges, and nodules that increase the surface area of the shell (potentially increasing convective heat flux) without a concomitant increase in the projected area of the shell that captures heat energy from the sun (Vermeij, 1973; Britton, 1995). Although these morphological traits may impact body temperature, additional selective forces such as predation and wave action may drive the variation in shell morphology (Struhsaker, 1968; Johannesson, 1986; Seeley, 1986; Johannesson *et al.*, 1993; Trussell, 1997b, 2002).

Mobile intertidal grazers often seek refuge from hot conditions in crevices or under algal canopies. In contrast, littorinids—which often exploit food resources on open rock faces where thermal refuges are absent—may employ additional behavioral strategies to avoid stressful high temperatures. As with terrestrial gastropods that must withstand prolonged unfavorable weather conditions (Stearns, 1877; Machin, 1967; Schmidt-Nielsen *et al.*, 1972), littorinid snails commonly remove the foot from the substratum and anchor the shell using a dried mucous holdfast (Wilson, 1929; Newell, 1958; Vermeij, 1971b; Garrity, 1984). For a gastropod sitting on a surface warmed by the sun, the large surface area of the foot allows for substantial conductive heat exchange between the foot and substratum (Vermeij, 1971a; Denny and Harley, 2006). The ability to remove the foot from the surface reduces this conductive heat flux, keeping a snail several degrees cooler than the substratum (Schmidt-Nielsen *et al.*, 1972; Vermeij, 1973). Many littorinid snails can also reorient the shell, lifting the aperture away from the surface, leaving only the outer lip of the shell aperture attached to the substratum with dried mucus (Fig. 1A, B) (Denny, 1984). Thus, reorienting the shell alters conductive and convective heat flux and may change the projected area absorbing heat from the sun.

The relative importance of these morphological and behavioral characteristics for controlling body temperature can be estimated using a mechanistic heat-budget model (Porter and Gates, 1969; Gates, 1980; O'Connor and Spotila, 1992; Porter and Kearney, 2009), combining physical

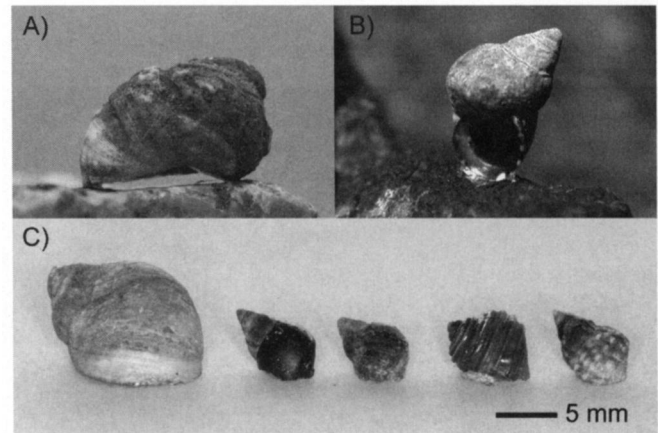


Figure 1. Littorinid snails can often be found (A) with the foot withdrawn into the shell and the shell glued to the substratum, or (B) with the shell elevated off the substratum and perched on the outer lip of the shell aperture. (C) Representative shells of the five species used in the heat-budget model. From left to right: *Littorina keenae*, *L. scutulata*, *L. plena*, *L. sitkana*, *Echinolittorina natalensis*.

parameters of the organism with environmental data to estimate body temperature through time. From a high-resolution decade-long data set on weather from Hopkins Marine Station, Pacific Grove, California (HMS), we create historical reconstructions of snail body temperatures to examine the effects of these morphological and behavioral changes, particularly during high-temperature aerial exposures. Specifically, we test four hypotheses: (1) light colored shells remain cooler than dark shells, (2) shells with surface ornamentation remain cooler than smooth shells, (3) removing the foot from the substratum lowers body temperature, and (4) reorienting the shell off the substratum lowers body temperature. For each trait, we compare its relative effectiveness for controlling body temperature during hot aerial exposures, and its effects on body temperature across the range of environmental temperatures experienced in the field.

Materials and Methods

To facilitate the manipulation of individual morphological and behavioral parameters, we developed heat-budget models for five species of littorinid snails (Fig. 1C). The snails included four of the five common rocky intertidal *Littorina* species from the temperate western North American coastline: *Littorina keenae* Rosewater, *L. scutulata* Gould (both collected at HMS), *L. plena* Gould (collected from Tatoosh Island, Washington), and *L. sitkana* Philippi (collected from San Juan Island, Washington). The fifth common species on these shores, *L. subrotundata* Carpenter (not used in this study), is morphologically similar to *L. sitkana*, so model results for *L. sitkana* should be similar for *L. subrotundata*. The final species used in this study,

Table 1

Measured shell parameters for the five littorinid species used in this study

Parameter	Units	<i>Littorina keenae</i>	<i>Littorina scutulata</i>	<i>Littorina plena</i>	<i>Littorina sitkana</i>	<i>Echinolittorina natalensis</i>
Shell length	mm	10.8	6.1	5.7	6.6	6.3
Area for conductive flux, foot extended	mm ²	58.5	10.3	10.9	15.5	11.4
Area for conductive flux, foot withdrawn	mm ²	2.20	1.02	0.84	1.02	0.71
Area for conductive flux, shell up	mm ²	0.34	0.14	0.10	0.29	0.25
Area for convective flux, shell down	mm ²	287.4	69.9	65.4	106.9	67.2
Area for convective flux, shell up	mm ²	347.8	81.1	77.0	123.1	85.6
Maximum projected area	mm ²	104.8	24.6	22.9	37.1	25.5
Minimum projected area	mm ²	65.8	14.3	13.0	22.4	16.5
Conduction distance (shell down)	mm	0.42	0.31	0.32	0.63	0.55
Conduction distance (shell up)	mm	2.57	1.41	1.25	1.44	1.32

Echinolittorina natalensis (formerly *Nodilittorina natalensis* Philippi, see Williams *et al.*, 2003), collected from Cape Vidal in the Natal region on the east coast of South Africa, provided an ornamented shell for comparison to the smooth-shelled *L. scutulata* and *L. plena*. Of the species used in this study, *L. sitkana* tends to live in low- to mid-intertidal zones (Boulding and Van Alstyne, 1993; Rochette and Dill, 2000), while the remaining species occupy the mid- and high-intertidal zone (Harger, 1972; Stirling, 1982; Behrens Yamada, 1989, 1992; Branch *et al.*, 2002).

Heat-budget model

The heat-budget model estimates an organism's body temperature by balancing the heat fluxes (W) into and out of the body (see Gates, 1980; Campbell and Norman, 1998).

$$W_{sw} \pm W_{conv} \pm W_{cond} \pm W_{evap} \pm W_{met} \pm W_{lw} = W_{stored} \quad (\text{Eq. 1})$$

The basic heat-budget model (Eq. 1) considers fluxes due to short-wave solar radiation, W_{sw} ; convective heat exchange with the air, W_{conv} ; conductive heat exchange with the substratum, W_{cond} ; heat lost or gained due to evaporation or condensation, W_{evap} ; metabolic heat production, W_{met} ; and long-wave radiative exchange between the organism and its surroundings, W_{lw} . The sum of these fluxes equals heat energy stored in the organism, W_{stored} . Our model was modified from a heat-budget model originally developed for the intertidal limpet *Lottia gigantea* (Denny and Harley, 2006), calculating the same heat flux components as the limpet model, but adding in a behavioral component by altering the area of conduction, surface area for convection, and projected area facing the sun depending on the modeled shell orientation and foot position (see below).

Because littorinid snails have a small mass and are un-insulated, we treat stored heat energy, W_{stored} , as negligible and set it equal to zero. Metabolic heat production and evaporative heat flux for small littorinids are approximately

0.07% and 1% as large as the heat flux due to short-wave radiation at midday, respectively (Newell, 1976; Kronberg, 1990; Miller, 2008). In accord with these estimates, we treat metabolic heat production and heat flux due to evaporation as negligible terms in the model, and therefore remove W_{met} and W_{evap} from the model. The simplified heat-budget model used for this study is

$$W_{sw} \pm W_{conv} \pm W_{cond} \pm W_{lw} = 0. \quad (\text{Eq. 2})$$

The methods used for the parameterization of the model are described in detail in Denny and Harley (2006) and Miller (2008). We made empirical measurements on a pair of snail shells from each species except *L. plena*, for which we had only a single shell. Projected area and substratum contact area were measured using size-referenced digital images analyzed in ImageJ, ver. 1.42q (Rasband, 1997–2011), and surface area was similarly estimated from digital images by using the method of Johnsen and Widder (1999). To estimate the heat transfer coefficient of each shell, we used silver casts of each shell to measure rates of convective heat exchange in a wind tunnel for shells both sitting down on the substratum and rotated up onto the lip of shell, allowing us to incorporate the effects of wind speed and shell orientation on the convective flux component of the model. Short-wave absorptivity (*i.e.*, color) was measured using shell fragments mounted in an integrating sphere attached to a Li-Cor 1800 spectroradiometer (LI-COR Biosciences, Lincoln, Nebraska). The thickness of any mucous attachment was treated as negligible and was not present in the model, so that heat flux was modeled as occurring directly between rock and shell surfaces. The rate-limiting step in conductive heat flux is assumed to be between the rock surface and the foot when the snail is crawling, and from the rock surface through the shell when the snail is withdrawn into the shell. Shell thickness values are given as “conductive distance” in Table 1, with the greater conduction distance through the lip of the shell reflected in the

greater distance given when the shell is elevated from the substratum. The snail body and any mantle water trapped in the shell are assumed to be at a single temperature due to blood circulation.

Model verification

Temperature predictions from the model were compared to temperature measurements of live snails and silver-epoxy-filled shells in the field and laboratory. Live *L. keenae* that were close in size to the modeled *L. keenae* shells were fitted with polyurethane-coated 0.08-mm-diameter thermocouple leads (Omega Engineering Inc., Stamford, Connecticut) inserted through a hole ground in the shell and covered with cyanoacrylate glue. The hole was positioned so that the thermocouple entered the main body whorl near ground level when the shell sat down on the substratum, and was designed to put the thermocouple tip in contact with the snail body when the animal was withdrawn into the shell. Measurements of body temperature of a live individual of *L. keenae* were carried out in a temperature-controlled wind tunnel (see Miller *et al.*, 2009) with the snail actively crawling or with the foot withdrawn into the shell. For field measurements, we filled the shells used for the size measurements (described above) with thermally conductive silver epoxy (two parts ground silver shavings, one part epoxy by volume; Devcon 2 Ton Clear Epoxy, ITW Devcon, Danvers, Massachusetts) and fitted a 0.08-mm thermocouple into a hole drilled in the epoxy filling. We deployed these shells on a high-shore granite rock at about 2.5 m above mean lower low water at HMS during two warm periods in April and June 2007. In addition, we fit thermocouples into two live specimens of *L. keenae* to be deployed in the field alongside the silver-epoxy-filled shells during the June experiment. Temperatures were monitored at 1-min intervals by a datalogger (23X, Campbell Scientific Inc., Logan, Utah) while air temperature (Viasala HMP45C, Campbell Scientific Inc.), wind speed (Wind Sentry, R. M. Young Co., Traverse City, Michigan), and solar irradiance (LI-200SB, LI-COR Biosciences, Lincoln, Nebraska) were concurrently monitored. The field site was not submerged during high tide and thus represented a worst-case scenario for snails on the shoreline.

Model comparisons

For long-term reconstructions of snail body temperatures in the field at HMS, we used a 10-year record of weather and sea-state data from HMS, spanning 1 August 1999 through 31 July 2009. This data set included air temperature, solar irradiance, wind speed, tide height, significant wave height, and water temperature, all measured or interpolated at 10-min intervals (Denny and Harley, 2006). After the shore height, wave exposure, and shell orientation are specified for a model snail, the heat-budget model calculates

a body temperature for each 10-min time step on the basis of the co-occurring environmental conditions. When the tide height exceeds the specified shore height, the snail body temperature is set equal to sea-surface temperature; and when the tide and waves recede below the modeled shore height, the snail heats or cools according to the sum of the heat fluxes to and from the surrounding environment. The heat-budget model was employed to analyze the effects of behavioral or morphological changes on predicted body temperatures for the snail species under a variety of weather conditions. Because the focus of the study was to examine the effects of these traits under a worst-case scenario, all species were modeled resting on a horizontal surface 2.0 m above mean lower low water, a height that is 0.4 m above the mean higher high water line at HMS and thus is submerged only during spring tides or when large waves are present. The predicted temperatures for pairs of snails of each species were generally within a fraction of a degree Celsius, and so we report results from only a single representative shell of each species. The model was implemented in MATLAB 7 (The Mathworks Inc., Natick, Massachusetts). Analyses were carried out in MATLAB and R 2.12.1 (R Development Core Team, 2010).

Two behavioral manipulations were carried out with the model. First, the effect of removing the foot from the substratum was simulated by changing the contact area of the snail with the rock while leaving other parameters constant. The modeled snail either kept the foot in contact with the rock constantly or withdrew it into the shell after 3 h of aerial emersion, mimicking the behavior of snails that close the operculum as the rock surface becomes dry. Second, the effect of reorienting the shell up onto the aperture lip was tested by using a further-reduced value of contact area and simultaneously altering values for the projected area facing the sun and the surface area of the shell, as the aperture of the shell is exposed to the air rather than being held against the substratum (see Table 1 for representative values for each shell).

Effects of shell color on body temperature were tested by altering the short-wave absorptivity of the shell (α , a dimensionless value) while leaving all other characteristics constant. Four shell colors were compared, nominally referred to as black ($\alpha = 0.85$), green ($\alpha = 0.82$), brown ($\alpha = 0.80$), and white ($\alpha = 0.67$). Shell color differences were also compared for snails over a range of substratum contact areas to illustrate the relative contributions of color and conduction to the overall heat budget of the snail. Black and white individuals of *L. keenae* were modeled with contact areas that scaled from full foot contact to having only the outer lip of the shell glued to the substratum. The effects of shell ornamentation were evaluated by comparing temperature predictions for *L. scutulata* and *E. natalensis*. These two high-spired species grow to similar overall sizes, but *E. natalensis* has rows of nodules on the shell surface, increas-

Table 2

Sites on the west coast of North America used to model maximum body temperature for *Littorina scutulata* from August 2007 to August 2009

Tide Station	NOAA Station ID	Latitude (°N)	Longitude (°W)	Maximum water level (m)*
Friday Harbor, WA	9449880	48.522	123.025	2.93
Neah Bay, WA	9443090	48.367	124.612	3.29
Toke Point, WA	9440910	46.707	124.042	3.65
Newport, OR	9435380	44.625	124.042	3.25
Charleston, OR	9432780	43.345	124.322	2.95
Crescent City, CA	9419750	41.745	124.182	2.67
Point Arena, CA	9416841	38.913	123.706	2.43
San Francisco, CA	9414290	37.806	122.465	2.26
Pacific Grove, CA	9413450	36.622	121.904	2.21
Los Angeles, CA	9410660	33.720	118.272	2.30
La Jolla, CA	SIO†	32.867	117.257	2.26

* Highest measured tide height during the survey period, referenced to mean lower low water.

† Data were obtained from the Scripps Institution of Oceanography archive.

ing the total surface area for convection while only slightly increasing the projected area for absorbing solar irradiance. Both snails were modeled with a brown shell to remove effects of color differences.

Effects of morphological and behavioral manipulations were compared by examining predicted body temperatures. Maximum body temperature or body temperature differences between model scenarios were calculated for the 10-year time series. Because the heat-budget model is deterministic, we report calculated temperatures and standard deviations rather than standard errors for the temperatures.

In addition to the 10-year hindcasts for HMS, we modeled body temperatures with different foot and shell positions for *L. scutulata* at 10 additional sites (Table 2) along the west coast of North America between August 2007 and August 2009 to gauge the effects of these behaviors at sites that might be more thermally stressful than HMS. Data for *L. scutulata* are reported because it is found throughout the west coast of the United States (Reid, 1996), although modeled estimates of body temperatures for the other species at each site are very similar. Tide height, water temperature, air temperature, and wind speed data were obtained from tide monitoring stations run by the U.S. National Oceanic and Atmospheric Administration's Center for Operational Oceanographic Products and Services, available through an online database (<http://tidesandcurrents.noaa.gov/>). When several hours or days of data were missing for a station, water temperatures were filled in from the nearest oceanographic buoy available in the NOAA database, and air temperature and wind speeds were obtained from the nearest weather station available in the MesoWest database maintained by the Department of Atmospheric Sciences at the University of Utah (University of Utah, 2002–2011). Data for La Jolla, California, were obtained from the Scripps Institution of Oceanography (SIO, 2011). Solar irradiance estimates for each site were obtained from

NOAA's National Environmental Satellite, Data, and Information Service, which produces a map of satellite-derived hourly down-welling shortwave radiation for North America, available through the Department of Atmospheric and Oceanic Science at the University of Maryland (University of Maryland, 2011). All data were linearly interpolated to a 10-min period. Predictions for 15 December 2008 to 8 January 2009 were discarded due to unavailable solar irradiance data. We predicted *L. scutulata* body temperatures for a black snail either with the foot extended at all times, the foot withdrawn into the shell resting on the rock, or the foot withdrawn and the shell rotated up onto the edge of the shell lip. Effects of wave surge were removed from the model due to uneven availability of data for the sites. We used the granite substratum characteristics from HMS for all sites. Because the vertical extent of the tide varies between sites, we modeled the snail at the high water mark for each site, which represents a likely worst-case scenario for thermal stress.

Live snail color comparisons

To complement the predictions of the heat-budget model, the effects of shell color on body temperature were evaluated with live specimens of *L. keenae* during a heat wave on 14–16 May 2008 at HMS, when the air temperature exceeded 27, 36 and 35 °C, respectively. Three pairs of similar-sized *L. keenae* were collected from the field. The shell of one snail from each pair was naturally black; the other, white. Shell length was within 0.2 mm and total mass within 0.05 g for each pair of snails. Maximum shell length was 13.25 mm; minimum shell length was 11.13 mm. A 0.08-mm-diameter thermocouple wire, coated with a thin layer of polyurethane glue, was inserted into a hole ground in the main body whorl of the shell. The hole in the shell was then covered in cyanoacrylate glue to minimize evaporative wa-

ter loss. Instrumented snails crawled normally in aquaria for the 24 h prior to deployment in the field. The snails were placed on a high-shore granite rock at midnight, 14 May 2008. The rock was wetted with seawater and the snails were allowed to crawl. As the rock dried, all snails withdrew the foot and glued the shell to the rock, but kept the shell aperture down against the rock surface. A datalogger recorded body temperatures once per minute for the subsequent 68 h.

Results

Model parameters

The measured shell parameters for the snails used in the study are given in Table 1. *Littorina keenae* was the largest snail used, with a maximum shell length of 10.8 mm from the spire tip to the outer edge of the aperture lip. *Littorina plena* was the smallest snail, at a maximum length of 5.7 mm. Parameters used for calculating heat exchange between the rock surface and the snail shell or between the sky and the snail shell are the same as those given in Denny and Harley (2006) and Miller (2008).

Model verification

For silver-epoxy-filled shells from all five species and for live *L. keenae* deployed in the field, the heat-budget model predicted temperatures that were typically within 1.5 °C of

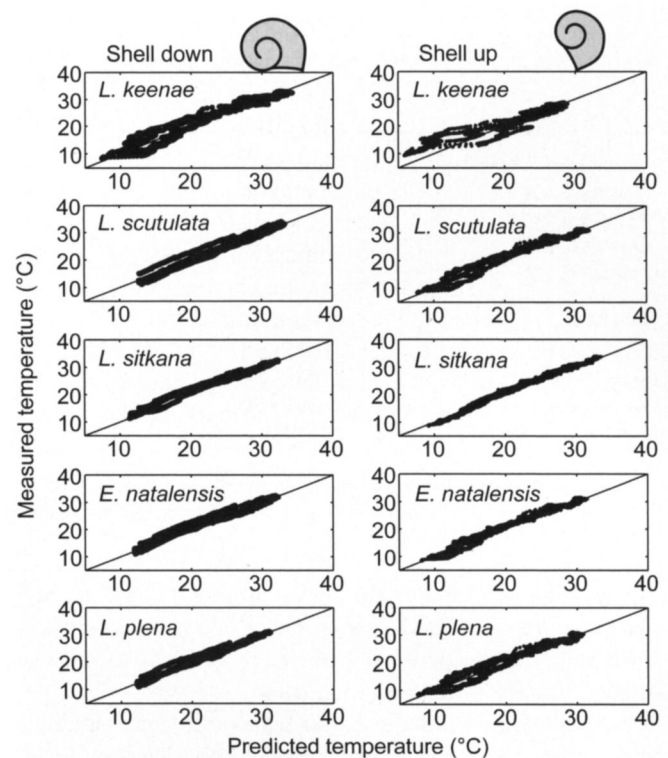


Figure 2. Measured versus predicted temperatures for silver-epoxy-filled shells set out in the field. The left column shows the relationship when the shells were positioned with the aperture down against the substratum. The right column shows data for the same shells reoriented up onto the edge of the shell lip. Data were collected during 23–29 April and 3–7 June, 2007, at HMS.

Table 3

Comparison of measured temperatures of epoxy-filled shells and live snails in the field with predicted model temperatures using weather data from the same time period

Species	Mean difference between all modeled and measured temperatures (°C ± SD)	Mean difference between modeled and measured temperatures for top 1% of temperatures (°C ± SD)
Shell mimic, shell down		
<i>Littorina keenae</i>	−1.13 (±1.51)	0.64 (±0.63)
<i>Littorina scutulata</i>	0.20 (±1.31)	0.05 (±0.46)
<i>Littorina sitkana</i>	−0.75 (±0.95)	−0.09 (±0.19)
<i>Littorina plena</i>	0.17 (±0.88)	−0.07 (±0.24)
<i>Echinolittorina natalensis</i>	−0.21 (±1.07)	0.00 (±0.41)
Shell mimic, shell up		
<i>Littorina keenae</i>	−1.47 (±2.40)	0.45 (±0.78)
<i>Littorina scutulata</i>	−1.03 (±1.14)	0.11 (±0.63)
<i>Littorina sitkana</i>	−0.10 (±0.79)	−0.21 (±0.28)
<i>Littorina plena</i>	−0.73 (±1.28)	0.16 (±0.81)
<i>Echinolittorina natalensis</i>	−0.55 (±0.89)	−0.17 (±0.62)
Live snails, shell down		
<i>Littorina keenae</i> 1	−0.56 (±1.50)	−0.06 (±0.86)
<i>Littorina keenae</i> 2	−1.00 (±1.50)	0.17 (±0.29)

the measured temperatures at each time point, and predictions for the hottest 1% of time points were within 0.64 °C of measured temperatures (Table 3, Fig. T2). The largest deviations between predicted and measured temperatures occurred during foggy conditions at night because our weather records do not record fog. The altered long-wave heat-flux during foggy periods should keep snails slightly warmer than predicted by our model. Temperature predictions for the live individuals of *L. keenae* measured in the temperature-controlled wind tunnel agreed closely with measured temperatures. The difference between measured and predicted temperatures was 0.18 ± 0.27 °C (mean ± SD) while the snail was actively crawling, and was 0.02 ± 0.40 °C when the foot was withdrawn and the shell rested on the substratum.

Effect of foot position

The effect of withdrawing the foot into the shell and leaving only portions of the shell in contact with the substratum was estimated by calculating the average temperature difference between the foot-out and foot-withdrawn positions during the hottest 1% of all 10-min time periods in

the 10-year data set ($n = 5260$). Snails modeled with the foot withdrawn were 2.3–3.2 °C cooler on average during these hot periods than snails that kept the foot attached to the substratum, with a maximum difference of 5.4 °C for the smallest species, *L. plena* (Fig. 3A). When the foot was left in contact with the surface, the maximum predicted temperature at HMS for all five species was between 40.4 and 40.7 °C. When the foot was withdrawn into the shell during low tide, the maximum temperature experienced by the five modeled species during the 10-year model run ranged from 38.4 to 39.0 °C. The smallest snail modeled, *L. plena*, stayed the coolest, and the largest species, *L. keenae*, reached the highest temperatures. The daily maximum body

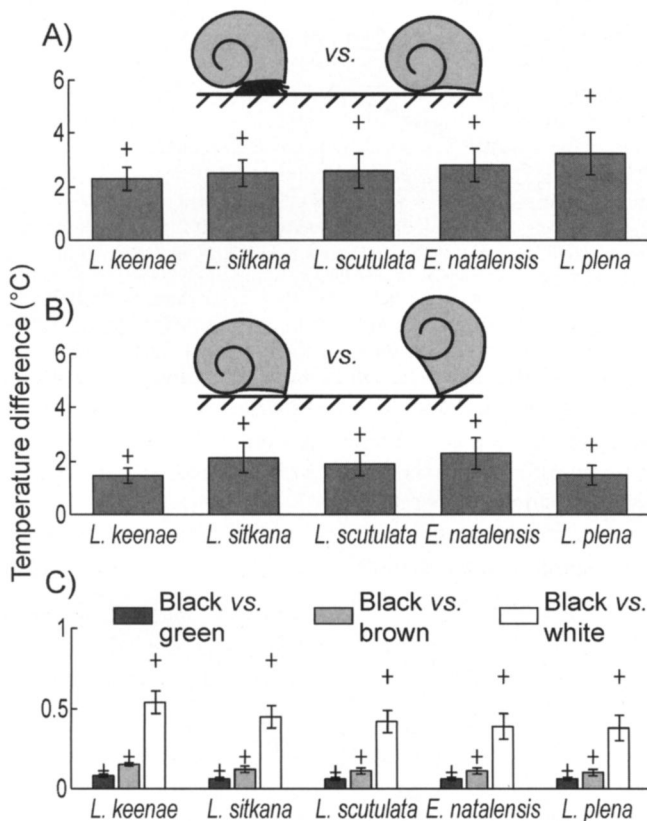


Figure 3. Mean temperature differences (± 1 SD) between modeled snails during the hottest 1% of all time periods in the 10-year weather data set ($n = 5620$). Maximum differences are denoted by the + symbol above each bar. (A) Comparison of snails modeled with the foot always on the rock, or withdrawn into the shell during hot periods. Snails with the foot in contact with the rock reach higher temperatures. (B) Comparison of snails modeled with the foot withdrawn into the shell, and the snail either resting aperture-down on the substratum or perched on the outer lip of the shell. Leaving the shell resting on the substratum results in higher body temperatures. (C) Temperature differences between a black shell and alternate shell color morphs. Each color morph was modeled with the foot withdrawn and shell perched on the outer lip of the shell. Black shells are always warmer than the alternate color morphs.

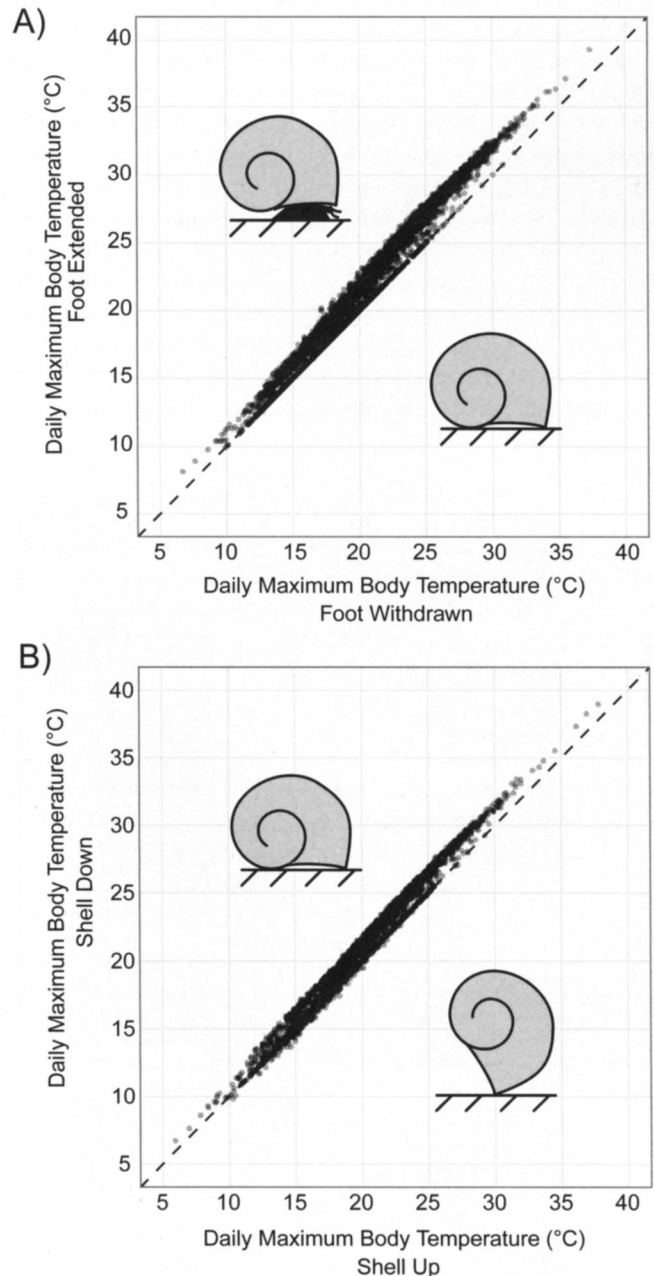


Figure 4. (A) Predicted daily maximum body temperatures for a black individual of *Littorina keenae* modeled with the foot out in contact with the substratum at all times or withdrawn into the shell during low tide. (B) Predicted daily maximum body temperatures for the same individual with the foot withdrawn and the shell sitting down on the substratum or with the shell tipped up on the edge of the aperture lip. Temperatures were predicted using environmental data for HMS from 1999 to 2009 ($n = 3652$ days). The snail was modeled on horizontal substratum at 2.0 m above mean lower low water. A line of unity is plotted in both panels.

temperature for each day in the 10-year time series ($n = 3652$) was generally higher for a snail with its foot in contact with the rock, as shown for *L. keenae* (Fig. 4A).

Effect of shell position

Standing the shell on edge yielded body temperatures that were on average 1.5 to 2.3 °C cooler during the hottest 1% of time points when compared to the same shell sitting down against the substratum with the foot withdrawn (Fig. 3B). For all species, the maximum temperature difference between the two shell orientations was between 2.2 and 3.5 °C. While snails in either orientation generally start from similar body temperatures in the pre-dawn hours, the difference in temperatures grows through the day and typically becomes largest during the hottest part of the day. Maximum temperatures reached by snails with the shell elevated off the substratum ranged from 36.9 °C (*L. plena*)

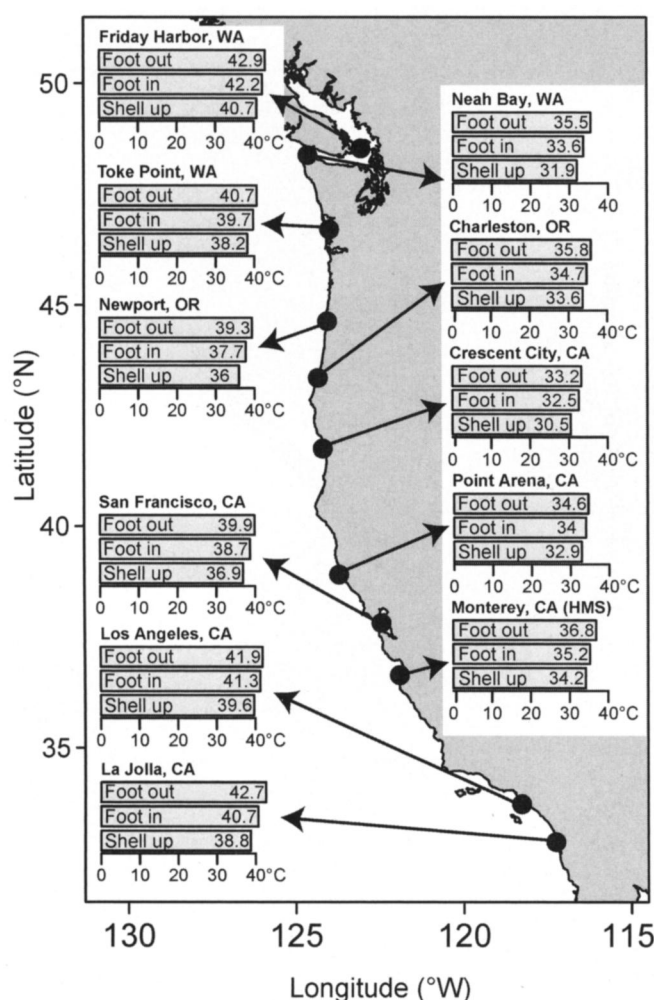


Figure 5. Maximum predicted body temperatures for a black individual of *Littorina scutulata* at 11 sites along the west coast of North America, using environmental data from 1 August 2007 through 1 August 2009. Temperatures are given for the same snail in three positions: with the foot out on the rock at all times, with the foot withdrawn into the shell at low tide, and with the shell tipped up on edge during low tide. All models were run with the snail sitting on a horizontal surface at the height of the maximum still tide level for each site.

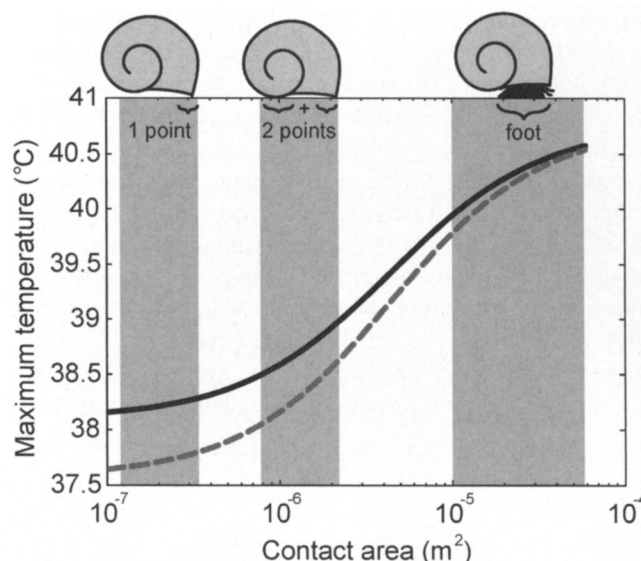


Figure 6. Maximum predicted body temperatures for a black snail shell (solid line) and white snail (dashed line) modeled with a range of contact areas on the substratum, using environmental data from HMS for 1999–2009. The shaded areas represent the typical range of contact areas for littorinid snails with only the lip of the shell glued to the substratum (1 point), resting on the lip and main whorl of the shell (2 points), or attached by the foot. As contact area increases, conductive heat flux reduces the effect of shell color differences on body temperature.

to 37.8 °C (*L. keenae*). Daily maximum body temperature for every day in the 10-year time series was higher for snails that left the shell on the substratum, except during occasional cooler periods when the elevated shells became warmer (Fig. 4B).

Latitudinal comparison

During 2007–2009, *L. scutulata* was predicted to reach the highest maximum temperatures near the edges of its latitudinal distribution (Fig. 5), both in the north at Friday Harbor, Washington (42.9 °C, 6 days > 40 °C) and Toke Point, Washington (40.7 °C, 2 days > 40 °C), and in the south in Los Angeles (41.9 °C, 2 days > 40 °C) and La Jolla, California (42.7 °C, 4 days > 40 °C). In all cases, a snail with the foot in contact with the rock reached the highest temperatures, whereas removing the foot from the rock reduced the predicted maximum temperature by 1.18 ± 0.53 °C (mean \pm SD), and elevating the shell reduced maximum temperature by an additional 1.56 ± 0.34 °C.

Effect of shell color

For black *versus* white comparisons, the model predicted average temperature differences of 0.38 to 0.54 °C during the hottest 1% of times in the data set, with maximal differences of 0.8 °C (Fig. 3C). Black shells were always

predicted to be warmer than white shells when exposed to the sun, while brown and green shells fell closer to black shells. The magnitude of the temperature difference between shell color morphs was influenced by conductive heat flux through the shell or foot, and greater conductive flux with the rock tended to homogenize body temperatures (Fig. 6). At colder environmental temperatures, a similar pattern in temperature differences between black and white shell color morphs was maintained. For daylight low tides when air temperatures were less than 15 °C, black morphs of *L. keenae* were 0.44 ± 0.2 °C (mean \pm 1 SD, for all seasons, $n = 80,476$ time points) warmer than white morphs when snails were modeled elevated off the substratum (Fig. 7A); for snails modeled with the foot always in contact with the substratum, the average predicted difference between black and white morphs was reduced to 0.03 ± 0.03 °C across all seasons (Fig. 7B).

Temperature differences measured between pairs of live black and white individuals of *L. keenae* were similar to those predicted by the model. Among the three pairs of snails, the average temperature difference between live black and white snails was less than 0.5 °C during daylight hours (Table 4). The maximal difference between black and white shells was 2.39 °C, though there were periods during the day when the white shell in each pair was hotter than the black shell.

Effect of shell sculpture

The influence of the shell sculpturing of *Echinolittorina natalensis* on body temperature during warm periods was minimal. The heat transfer coefficient was greater for the nodulose *E. natalensis* shell compared to the smooth-shelled *L. scutulata*, but the convective flux difference was greatest at high wind speeds (Fig. 8A), which rarely occur during the hottest days (see Denny and Harley, 2006, materials and methods, for the calculation of the heat transfer coefficient). On calm, hot days, the small difference in heat transfer coefficient resulted in an average predicted body temperature for *L. scutulata* of 0.2 ± 0.3 °C (mean \pm SD, $n = 5260$) warmer than a similarly sized and identically colored *E. natalensis* shell modeled in the same weather conditions (Fig. 8B).

Discussion

Littorinid snails often occupy the highest reaches of the intertidal zone, remaining exposed to terrestrial conditions for hours to days. As a result, these species may reach high body temperatures when weather and ocean conditions combine to create hot low tide periods. Although littorinids can move to refuges to avoid high temperatures and desiccation stress, this study has focused on littorinid snails living on open rock faces, where they may be the only species exerting grazing control over algal communities

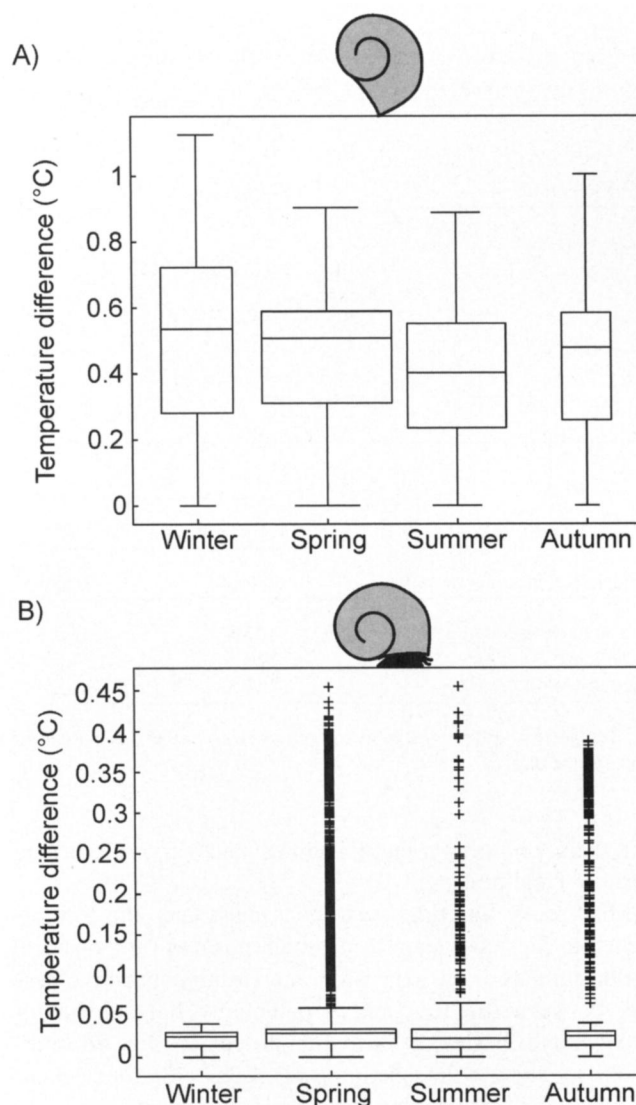


Figure 7. Temperature differences between black and white morphs of *Littorina keenae*, for all daytime low tide periods when air temperature was less than 15 °C. (A) Temperature differences for snails modeled with the foot withdrawn and the shell elevated up onto the outer lip of the aperture. Black shells were warmer than white shells. (B) Temperature differences for black versus white snails modeled with the foot always in contact with the substratum. Comparisons were made for each meteorological season using weather data from HMS for 1999–2009. The center line in each box represents the median temperature difference between the two color morphs at each time point, and the upper and lower bounds of each box denote the 1st and 3rd quartiles, respectively. Crosses above a boxplot represent outliers. Box width represents the relative sample size in each season (Spring = 29,918 samples in both panels). Sample size varies between seasons due to the timing of low tides, wave action, and day length.

(Norton *et al.*, 1990; McQuaid, 1996b). The behavioral and morphological traits of these species, combined with their physiological tolerance to heat and desiccation stress, per-

Table 4

Summary of temperatures of three pairs of similarly-sized live black-shelled and white-shelled *Littorina keenae* deployed on a high intertidal rock during a heat wave on 14–16 May 2008

Time interval	Measurement	Temperature difference (°C) between black and white shells*		
		Pair 1	Pair 2	Pair 3
0600–1800	Average \pm 1 SD, $n = 2160$	0.11 ± 0.69	0.43 ± 0.41	0.10 ± 0.71
	Maximum	2.29	2.39	2.15
	Minimum	–1.40	–0.78	–2.17
1100–1500	Average \pm 1 SD, $n = 720$	-0.08 ± 0.54	0.48 ± 0.33	0.31 ± 0.66
	Maximum	2.06	2.12	2.02
	Minimum	–1.08	–0.78	–1.61

Cumulative data, 14–16 May	Snail color					
	Pair 1		Pair 2		Pair 3	
	Black	White	Black	White	Black	White
Maximum temperature (°C)	43.8	42.5	43.4	42.7	43.7	42.9
Time above 30 °C (h)	18.7	18.5	19.2	19.1	19.4	19.1
Time above 40 °C (h)	1.5	1.25	2.05	1.47	2.38	2.0

* Temperature differences between each black and white pair are calculated for times from 1 h after sunrise to 1 h before sunset, and during the 4 hottest hours of the day.

mit them to occupy these habitats and survive extreme weather conditions.

Most rocky intertidal gastropods must keep the foot attached to the substratum to maintain position on the shore, but this comes at the expense of increasing conductive heat flux between the foot and a potentially hot substratum (Denny and Harley, 2006). The propensity for littorinid snails to anchor the shell to the rock with mucus and withdraw the foot into the shell provides a reduction in body temperature not available to most other intertidal gastropods (Vermeij, 1971a, 1973; McQuaid and Scherman, 1988) and results in body temperatures for the five species studied here that can be 3–5 °C lower than when the foot is left in contact with the rock. Withdrawing the foot into the shell has the added benefit of allowing the snail to seal the operculum, thereby reducing water loss (McMahon and Britton, 1985; Britton and McMahon, 1986). As a result, littorinid snails typically have very slow rates of evaporative water loss, permitting them to survive multi-day aerial exposures (Broekhuysen, 1940; Cleland and McMahon, 1986; Britton, 1995; Marshall *et al.*, 2010). The use of a mucous holdfast does, however, introduce a trade-off in terms of stability and attachment strength (Miller, 1974; Denny, 1984; Ohgaki, 1988), increasing the chance of dislodgement. Nevertheless, survival of dislodged snails is typically high, and they are commonly able to navigate back to their preferred high-shore habitats (Evans, 1961; Bock and Johnson, 1967; Miller *et al.*, 2007).

Reorienting the shell so that only the outer lip of the shell is in contact with the substratum further enhances littorinid snails' ability to minimize body temperature on warm days. Although we lack quantitative data on its frequency in the field, the shell-lifting behavior has been observed in all five species discussed here (L. Miller, pers. obs.), as well as in numerous other littorinid snail species (Garrity, 1984; Britton, 1995; Lang *et al.*, 1998; Wada and Ito, 2000). Lifting the shell from the substratum further reduces the surface area in contact with the substratum over the initial reduction achieved by pulling the foot into the shell (Table 1), but also changes other important components of heat flux. The re-oriented shell exposes a greater surface area to the surrounding air, increasing the rate of convective heat exchange, which cools a snail that is warmer than the air, as is often the case on hot days (Marshall *et al.*, 2010), while also lifting the shell higher into faster-flowing air in the boundary layer over the rock. Together, the reduction in conduction and increase in convection help minimize body temperature, as has been shown in many terrestrial organisms (Stevenson, 1985). Changing the shell's orientation could also change the projected area facing the sun, potentially minimizing absorption of shortwave radiation. Although some species of littorinid snails have been shown to orient parallel to the sun when resting against the substratum (Muñoz *et al.*, 2005), there is no evidence that the species studied here consistently orient the shell spire towards the midday sun (Miller, 2008).

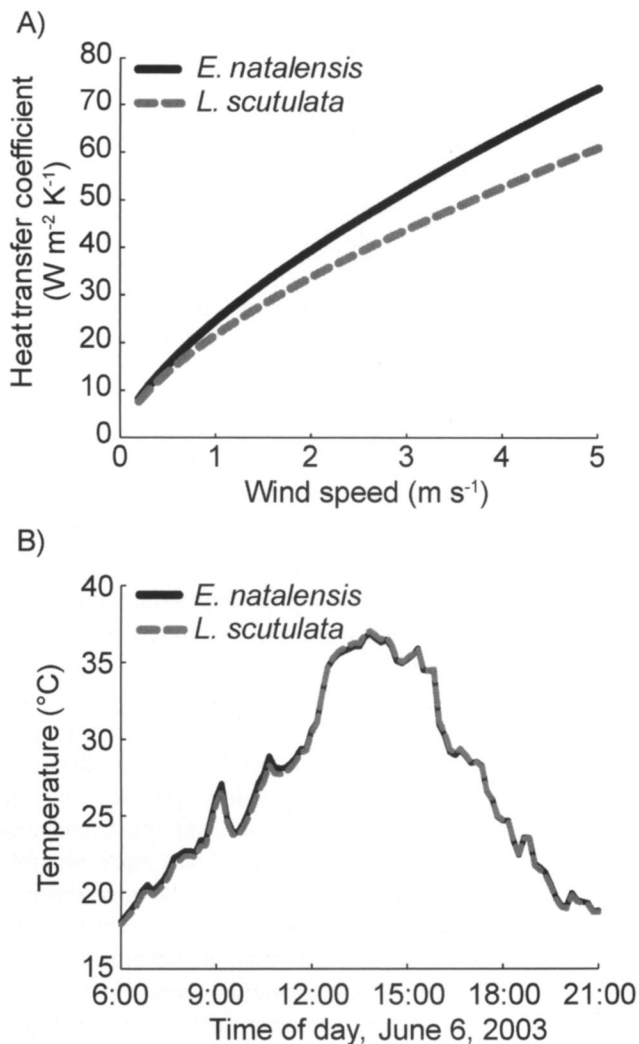


Figure 8. (A) Calculated heat transfer coefficients for similarly sized *Echinolittorina natalensis* (black line) and *Littorina scutulata* (gray line). Higher values increase the convective heat exchange with the surrounding air. Values are calculated for 25 °C air temperature and shells sitting with the aperture against the substratum. (B) Predicted body temperatures for a representative hot day, for brown snails of each species modeled with the foot withdrawn and shell resting on the substratum. The sculptured shell of *E. natalensis* was 0.2 °C cooler on average than the smooth shell of *L. scutulata* under identical weather conditions. The wind speed on this day was 1.2 ± 0.6 m s⁻¹ (mean \pm 1 SD).

The role of shell morphology in avoiding high body temperatures is relatively small. Within the range of shell colors tested, the reduction in body temperature created by having a white *versus* a dark shell is on average less than 0.5 °C, both for model snails of all five species and for live *L. keenae*. The complementary hypothesis—that dark shells should be advantageous in cool conditions by helping to warm these ectothermic animals—also receives minimal support (Jones, 1973; Phifer-Rixey *et al.*, 2008). The substantial influence of conductive heat flux between the snail foot and the rock substratum ensures that an actively graz-

ing littorinid snail does not deviate from the substratum temperature appreciably: differences in short-wave absorptivity between shell colors result in temperature differences of less than 0.5 °C in the model, while the range of reported differences between color morphs of other species of intertidal snails is on the order of 0–2 °C (Markel, 1971; Cook and Freeman, 1986; Reid, 1987; Phifer-Rixey *et al.*, 2008) and can be 3–5 °C in some larger snail species on certain substrata (Etter, 1988). The high thermal conductivity and heat capacity of seawater effectively homogenizes temperatures in the intertidal zone during high tide and when waves splash during rising and ebbing tides, removing any effect of shell color on body temperature during these periods. Thus, while thermal melanism may be important for warming the body in some terrestrial organisms (Kingsolver, 1996; Clusella-Trullas *et al.*, 2007), the importance to gastropods in intertidal systems is less clear. Differences in shell colors among intertidal snail populations could be driven by other factors such as visual predation by crabs and fishes (Reimchen, 1979; Hughes and Mather, 1986; Reid, 1987; Johannesson and Ekendahl, 2002; Manríquez *et al.*, 2009).

The functional significance of shell shape in intertidal snails has received substantial attention. Shell shape and size influence drag forces imposed by waves during high tide (Denny *et al.*, 1985; Boulding and Van Alstyne, 1993; Trussell, 1997a; Denny and Blanchette, 2000; Pardo and Johnson, 2005), determine the volume of fluid retained in the shell during emersion (Vermeij, 1973; Britton and McMahon, 1986), and protect against predators (Seeley, 1986; Trussell, 2000; Trussell and Nicklin, 2002; Johannesson, 2003). The importance of shell shape for mitigating stress due to exposure to extreme high temperatures in these small species is less clear. We have shown that when comparing *L. scutulata* and *E. natalensis*, the nodules on the outer surface of *E. natalensis* shells produce a negligible reduction in body temperature on hot days. These results mirror the minor contribution of shell sculpture to convective cooling found in intertidal limpet species (Harley *et al.*, 2009). Additionally, estimated temperatures for the globose, ribbed *L. sitkana* do not differ markedly from those of the other high-spined species examined here. Despite the relatively small effect of shell shape and shell sculpturing on body temperature in the temperate climate conditions used here, the trend within tropical intertidal gastropods, and particularly littorinids, is generally toward increased sculpturing and higher-spined shells at higher shore heights (Vermeij, 1973). The nodulose littorinids such as *E. natalensis* are primarily found in tropical or subtropical regions, so the importance of these characteristics to controlling body temperature may take on a greater importance at low latitudes where exposure to high temperature is more frequent.

Though the changes in body temperature created by the behavioral choices and color differences described here are

only a few degrees, they may be sufficient to help littorinid snail populations avoid substantial mortality due to thermal stress. The reported physiological thermal tolerances of *L. keenae* and *L. scutulata* ($> 42\text{--}44^\circ\text{C}$, Somero, 2002) exceed the body temperatures predicted for snails in the field at HMS, but snails at other sites along the coast may approach or exceed these temperature limits. The frequency and severity of thermal stress events are driven by the timing of the tides and the coincidence of calm, warm weather conditions with midday tides (Helmuth *et al.*, 2002, 2006; Denny *et al.*, 2009; Mislan *et al.*, 2009). Our model predicts that littorinids living throughout the species' latitudinal ranges could occasionally experience prolonged aerial emersion at midday during weather conditions hot enough to push body temperatures close to 42°C . Under these circumstances, the additive benefits of removing the foot from the rock, reorienting the shell, and having lighter shell colors could keep body temperatures several degrees below those lethal temperatures and help limit sublethal temperature stress. Work on the physiology of related littorinid snails has shown that as temperatures approach lethal limits, there is often an attendant decrease in aerobic respiration, increase in anaerobic metabolism, and eventual heart failure (McMahon and Russell-Hunter, 1977; Sokolova and Pörtner, 2003; Marshall *et al.*, 2010), along with the added energetic cost of repairing cellular-level damage through avenues such as the expression of heat shock proteins (Tomanek, 2010).

Although lighter shell colors help avoid temperature stress, the native snail populations in many of the warmer sites on the west coast of North America highlighted here contain a substantial fraction of dark-colored individuals (L. Miller, pers. obs.). All of the *Littorina* species discussed here, except *L. sitkana*, have a pelagic larval dispersal phase (Reid, 1996, 2002), so that mixture among populations may counteract any selection for lighter shell colors at hot sites. In subtropical and tropical habitats the role of shell color may be more important, as evidenced by experiments in South Africa demonstrating that black-painted littorine snails experienced acute thermally induced mortality on hot days (McQuaid, 1992). At sites with higher peak air and substratum temperatures, the small reduction in body temperature created by a light-colored shell may make the difference between survival and death on hot days, especially after the more effective behavioral options have been exhausted.

On the basis of the long-term weather records for our central California coast site, it appears unlikely that acute high temperature exposures regularly cause significant mortality in *Littorina* populations at HMS. However, when considered over the lifetime of an organism, the cumulative benefits of the small temperature reductions afforded by the behavioral and morphological traits examined here could be important for allowing littorinids to exploit high littoral

habitats. Sublethal temperatures will still incur metabolic costs that can be partially mitigated by having a lighter colored shell or minimizing conductive heat flux from a hot substratum. The attendant reduction in desiccation stress provided by these traits may also contribute to the success of littorinids in the high intertidal zone (Chow, 1989). While these behaviors or shell morphologies may have little effect on the occurrence of single-day thermal mortality events at HMS, on other shores, particularly tropical shores and sites where mid-day low tides frequently coincide with warm weather, these traits may be key in allowing littorinids to avoid thermally induced mortality.

Acknowledgments

We appreciate the help of Drs. C. D. G. Harley and K. Sink in providing access to snail shells used in this study. C. J. Sorte, C. Matassa, S. Kent, M. Jelenic, M. Doellman, and two anonymous reviewers provided useful suggestions for the manuscript. This work was supported by an NSF grant OCE 9985946 to M. W. Denny, and an award from the Dr. Earl H. Meyers and Ethel M. Myers Oceanographic and Marine Biology Trust to L. P. Miller. This is contribution number 394 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, funded primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation. This study was made possible in part due to the data made available by the governmental agencies, commercial firms, and educational institutions participating in MesoWest. Information downloaded from the web site <http://www.atmos.umd.edu/~srb/gcip/webgcip.htm> was generated under a joint effort between the National Oceanic and Atmospheric Administration (NOAA)/National Environmental Satellite Data and Information Service (NESDIS) and the University of Maryland. All animals were handled in accordance with university and government regulations.

Literature Cited

- Behrens Yamada, S. 1989. Are direct developers more locally adapted than planktonic developers? *Mar. Biol.* **103**: 403–411.
- Behrens Yamada, S. 1992. Niche relationships in northeastern Pacific littorines. Pp. 281–291 in *Proceedings of the Third International Symposium on Littorinid Biology*, J. Grahame, P. J. Mill, and D. G. Reid, eds. The Malacological Society of London.
- Bock, C. E., and R. E. Johnson. 1967. The role of behavior in determining the intertidal zonation of *Littorina planaxis* Philippi, 1847, and *Littorina scutulata* Gould, 1849. *Veliger* **10**: 42–54.
- Boulding, E. G., and K. L. Van Alstyne. 1993. Mechanisms of differential survival and growth of two species of *Littorina* on wave-exposed and on protected shores. *J. Exp. Mar. Biol. Ecol.* **169**: 139–166.
- Branch, G. M., C. L. Griffiths, M. L. Branch, and L. E. Beckley. 2002. *Two Oceans: A Guide to the Marine Life of Southern Africa*. David Philips Publishers, Cape Town.
- Britton, J. C. 1995. The relationship between position on shore and shell ornamentation in two size-dependent morphotypes of *Littorina*

- striata*, with an estimate of evaporative water loss in these morphotypes and in *Melarhaphe neritoides*. *Hydrobiologia* **309**: 129–142.
- Britton, J. C., and R. F. McMahon. 1986.** The relationship between vertical distribution evaporative water loss rate behavior and some morphometric parameters in four species of rocky intertidal gastropods from Hong Kong. Pp. 1153–1171 in *Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China*, Hong Kong, 1986, B. Morton, ed. Hong Kong University Press, Hong Kong.
- Broekhuysen, G. J. 1940.** A preliminary investigation of the importance of desiccation, temperature and salinity as factors controlling the vertical distribution of certain intertidal marine gastropods in False Bay, South Africa. *Trans. R. Soc. S. Afr.* **28**: 255–291.
- Campbell, G. S., and J. M. Norman. 1998.** *An Introduction to Environmental Biophysics*. Springer-Verlag, New York.
- Castenholz, R. W. 1961.** Effect of grazing on marine littoral diatom populations. *Ecology* **42**: 783–794.
- Chapman, M. G. 1995.** Spatial patterns of shell shape of three species of co-existing littorinid snails in New South Wales, Australia. *J. Molluscan Stud.* **61**: 141–162.
- Chow, V. 1989.** Intraspecific competition in a fluctuating population of *Littorina plena* Gould (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* **130**: 147–165.
- Cleland, J. D., and R. F. McMahon. 1986.** Upper thermal limit of nine intertidal gastropod species from a Hong Kong rocky shore in relation to vertical distribution and desiccation associated with evaporative cooling. Pp. 1141–1152 in *Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China*, Hong Kong, 1986, B. Morton, ed. Hong Kong University Press, Hong Kong.
- Clusella-Trullas, S., J. H. van Wyk, and J. R. Spotila. 2007.** Thermal melanism in ectotherms. *J. Therm. Biol.* **32**: 235–245.
- Connell, J. H. 1961.** Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* **31**: 61–104.
- Connell, J. H. 1972.** Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.* **3**: 169–192.
- Cook, L. M., and P. M. Freeman. 1986.** Heating properties of morphs of the mangrove snail *Littoraria pallescens*. *Biol. J. Linn. Soc.* **29**: 295–300.
- Dayton, P. K. 1975.** Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* **45**: 137–159.
- Denny, M. W. 1984.** Mechanical properties of pedal mucus and their consequences for gastropod structure and performance. *Am. Zool.* **24**: 23–36.
- Denny, M. W. 2006.** Ocean waves, nearshore ecology, and natural selection. *Aquat. Ecol.* **40**: 439–461.
- Denny, M. W., and C. A. Blanchette. 2000.** Hydrodynamics, shell shape, behavior and survivorship in the owl limpet *Lottia gigantea*. *J. Exp. Biol.* **203**: 2623–2639.
- Denny, M. W., and C. D. G. Harley. 2006.** Hot limpets: predicting body temperature in a conductance-mediated thermal system. *J. Exp. Biol.* **209**: 2409–2419.
- Denny, M. W., T. L. Daniel, and M. A. R. Koehl. 1985.** Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* **55**: 69–102.
- Denny, M. W., B. Helmuth, G. Leonard, C. D. G. Harley, L. J. H. Hunt, and E. K. Nelson. 2004.** Quantifying scale in ecology: lessons from a wave-swept shore. *Ecol. Monogr.* **74**: 513–532.
- Denny, M. W., L. J. H. Hunt, L. P. Miller, and C. D. G. Harley. 2009.** On the prediction of extreme ecological events. *Ecol. Monogr.* **79**: 397–421.
- Etter, R. J. 1988.** Physiological stress and color polymorphism in the intertidal snail *Nucella lapillus*. *Evolution* **42**: 660–680.
- Evans, F. 1961.** Responses to disturbance of the periwinkle *Littorina punctata* (Gmelin) on a shore in Ghana. *Proc. Zool. Soc. Lond.* **137**: 393–402.
- Garrity, S. D. 1984.** Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* **65**: 559–574.
- Gates, D. M. 1980.** *Biophysical Ecology*. Springer-Verlag, New York.
- Harger, J. R. E. 1972.** Competitive coexistence among intertidal invertebrates. *Am. Sci.* **60**: 600–607.
- Harley, C. D. G. 2008.** Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Mar. Ecol. Prog. Ser.* **371**: 37–46.
- Harley, C. D. G., M. W. Denny, K. J. Mach, and L. P. Miller. 2009.** Thermal stress and morphological adaptations in limpets. *Funct. Ecol.* **23**: 292–301.
- Hawkins, S. J., and R. G. Hartnoll. 1983.** Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.* **21**: 195–282.
- Heath, D. J. 1975.** Colour, sunlight, and internal temperatures in the land-snail *Cepaea nemoralis* (L.). *Oecologia* **19**: 29–38.
- Heller, J. 1981.** Visual versus climatic selection of shell banding in the landsnail *Theba pisana* in Israel. *J. Zool.* **194**: 85–101.
- Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002.** Climate change and latitudinal patterns of intertidal thermal stress. *Science* **298**: 1015–1017.
- Helmuth, B., B. R. Broitman, C. A. Blanchette, S. E. Gilman, P. M. Halpin, C. D. G. Harley, M. J. O'Donnell, G. E. Hofmann, B. A. Menge, and D. Strickland. 2006.** Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol. Monogr.* **76**: 461–479.
- Hidalgo, F. J., F. N. Firstater, E. Fanjul, M. C. Bazterrica, B. J. Lomovasky, J. Tarazona, and O. O. Iribarne. 2008.** Grazing effects of the periwinkle *Echinolittorina peruviana* at a central Peruvian high rocky intertidal. *Helgol. Mar. Res.* **62**: S73–S83.
- Huey, R. B. 1991.** Physiological consequences of habitat selection. *Am. Nat.* **137**: S91–S115.
- Hughes, J. M., and P. B. Mather. 1986.** Evidence for predation as a factor in determining shell color frequencies in a mangrove snail *Littorina* sp. (Prosobranchia: Littorinidae). *Evolution* **40**: 68–77.
- Johannesson, B. 1986.** Shell morphology of *Littorina saxatilis* Olivi: the relative importance of physical factors and predation. *J. Exp. Mar. Biol. Ecol.* **102**: 183–195.
- Johannesson, K. 2003.** Evolution in *Littorina*: ecology matters. *J. Sea Res.* **49**: 107–117.
- Johannesson, K., and A. Ekendahl. 2002.** Selective predation favouring cryptic individuals of marine snails (*Littorina*). *Biol. J. Linn. Soc.* **76**: 137–144.
- Johannesson, K., B. Johannesson, and E. Rolán-Alvarez. 1993.** Morphological differentiation and genetic cohesiveness over a microenvironmental gradient in the marine snail *Littorina saxatilis*. *Evolution* **47**: 1770–1787.
- Johnsen, S., and E. A. Widder. 1999.** The physical basis of transparency in biological tissue: ultrastructure and the minimization of light scattering. *J. Theor. Biol.* **199**: 181–198.
- Jones, J. S. 1973.** Ecological genetics and natural selection in mollusks. *Science* **182**: 546–552.
- Judge, M. L., R. Duell, L. Burriesci, and W. Moarsi. 2009.** Life in the supralittoral fringe: microhabitat choice, mobility and growth in the tropical periwinkle *Cenchritis* (= *Tectarius*) *muricatus* (Linnaeus, 1758). *J. Exp. Mar. Biol. Ecol.* **369**: 148–154.
- Kearney, M., R. Shine, and W. P. Porter. 2009.** The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc. Natl. Acad. Sci. USA* **106**: 3835–3840.
- Kingsolver, J. G. 1996.** Experimental manipulation of wing pigment pattern and survival in western white butterflies. *Am. Nat.* **147**: 296–306.
- Kronberg, I. 1990.** Heat production in *Littorina saxatilis* Olivi and

- Littorina neritoides* L. (Gastropoda: Prosobranchia) during an experimental exposure to air. *Helgol. Wiss. Meeresunters.* **44**: 125–134.
- Lang, R. C., J. C. Britton, and T. Metz. 1998. What to do when there is nothing to do: the ecology of Jamaican intertidal Littorinidae (Gastropoda: Prosobranchia) in repose. *Hydrobiologia* **378**: 161–185.
- Lewis, J. R. 1964. *Ecology of Rocky Shores*. English Universities Press, London.
- Machin, J. 1967. Structural adaptation for reducing water-loss in three species of terrestrial snail. *J. Zool.* **152**: 55–65.
- Manríquez, P. H., N. A. Lagos, M. E. Jara, and J. C. Castilla. 2009. Adaptive shell color plasticity during the early ontogeny of an intertidal keystone snail. *Proc. Natl. Acad. Sci. USA* **106**: 16298–16303.
- Markel, R. P. 1971. Temperature relations in two species of tropical west American littorines. *Ecology* **52**: 1126–1130.
- Marshall, D. J., C. D. McQuaid, and G. A. Williams. 2010. Non-climatic thermal adaptation: implications for species' responses to climate warming. *Biol. Lett.* **6**: 669–673.
- McMahon, R. F. 1990. Thermal tolerance, evaporative water loss, air-water oxygen consumption and zonation of intertidal prosobranchs: a new synthesis. *Hydrobiologia* **193**: 241–260.
- McMahon, R. F., and J. C. Britton. 1985. The relationship between vertical distribution, thermal tolerance, evaporative water loss rate, and behavior on emergence in six species of mangrove gastropods from Hong Kong. Pp. 563–582 in *The Malacofauna of Hong Kong and Southern China*. II, Vol. 1 and 2. *Second International Workshop: Hong Kong, Apr. 6–24, 1983*, B. Morton and D. Dudgeon, eds. Hong Kong University Press, Hong Kong.
- McMahon, R. F., and W. D. Russell-Hunter. 1977. Temperature relations of aerial and aquatic respiration in six littoral snails in relation to their vertical zonation. *Biol. Bull.* **152**: 182–198.
- McQuaid, C. D. 1992. Stress on the high shore: a review of age-dependent causes of mortality in *Nodilittorina knysnaensis* and *N. africana*. Pp. 85–89 in *Proceedings of the Third International Symposium on Littorinid Biology*, J. Grahame, P. J. Mill, and D. G. Reid, eds. The Malacological Society of London.
- McQuaid, C. D. 1996a. Biology of the gastropod family Littorinidae. I. Evolutionary aspects. *Oceanogr. Mar. Biol. Annu. Rev.* **34**: 233–262.
- McQuaid, C. D. 1996b. Biology of the gastropod family Littorinidae. II. Role in the ecology of intertidal and shallow marine ecosystems. *Oceanogr. Mar. Biol. Annu. Rev.* **34**: 263–302.
- McQuaid, C. D., and P. A. Scherman. 1988. Thermal stress in a high shore intertidal environment: morphological and behavioural adaptations of the gastropod *Littorina africana*. Pp. 213–224 in *Behavioral Adaptation to Intertidal Life*, G. Chelazzi and M. Vannini, eds. Plenum Press, New York.
- Menge, B. A., and G. M. Branch. 2001. Rocky intertidal communities. Pp. 221–251 in *Marine Community Ecology*, M. D. Bertness, S. D. Gaines, and M. E. Hay, eds. Sinauer Associates, Sunderland, MA.
- Miller, L. P. 2008. Life on the edge: morphological and behavioral adaptations for survival on wave-swept shores. Ph.D. thesis, Stanford University, Stanford, CA.
- Miller, L. P., M. J. O'Donnell, and K. J. Mach. 2007. Dislodged but not dead: survivorship of a high intertidal snail following wave dislodgement. *J. Mar. Biol. Assoc. UK* **87**: 735–739.
- Miller, L. P., C. D. G. Harley, and M. W. Denny. 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. *Funct. Ecol.* **23**: 756–767.
- Miller, S. L. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. *J. Exp. Mar. Biol. Ecol.* **14**: 99–156.
- Mislan, K. A. S., D. S. Wetthey, and B. Helmuth. 2009. When to worry about the weather: role of tidal cycle in determining patterns of risk in intertidal ecosystems. *Glob. Change Biol.* **15**: 3056–3065.
- Muñoz, J. L. P., G. R. Finke, P. A. Camus, and F. Bozinovic. 2005. Thermoregulatory behavior, heat gain, and thermal tolerance in the periwinkle *Echinolittorina peruviana* in central Chile. *Comp. Biochem. Physiol. A* **142**: 92–98.
- Newell, G. E. 1958. The behaviour of *Littorina littorea* (L.) under natural conditions and its relation to position on the shore. *J. Mar. Biol. Assoc. UK* **37**: 229–239.
- Newell, R. C. 1976. Adaptations to intertidal life. Pp. 1–82 in *Adaptation to Environment: Essays on the Physiology of Marine Animals*, R. C. Newell, ed. Butterworths, London.
- Norton, T. A., S. J. Hawkins, N. L. Manley, G. A. Williams, and D. C. Watson. 1990. Scraping a living: a review of littorinid grazing. *Hydrobiologia* **193**: 117–138.
- O'Connor, M. P., and J. R. Spotila. 1992. Consider a spherical lizard: animals, models, and approximations. *Am. Zool.* **32**: 179–193.
- Ohgaki, S.-i. 1988. Rain and the distribution of *Nodilittorina exigua* (Dunker) (Gastropoda: Littorinidae). *J. Exp. Mar. Biol. Ecol.* **122**: 213–223.
- Paine, R. T. 1974. Intertidal community structure—experimental studies on relationship between a dominant competitor and its principal predator. *Oecologia* **15**: 93–120.
- Pardo, L. M., and L. E. Johnson. 2005. Explaining variation in life-history traits: growth rate, size, and fecundity in a marine snail across an environmental gradient lacking predators. *Mar. Ecol. Prog. Ser.* **296**: 229–239.
- Phifer-Rixey, M., M. Heckman, G. C. Trussell, and P. S. Schmidt. 2008. Maintenance of clinal variation for shell colour phenotype in the flat periwinkle *Littorina obtusata*. *J. Evol. Biol.* **21**: 966–978.
- Porter, W. P., and D. M. Gates. 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**: 228–244.
- Porter, W. P., and M. Kearney. 2009. Size, shape, and the thermal niche of endotherms. *Proc. Natl. Acad. Sci. USA* **106**: 19666–19672.
- Porter, W. P., J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973. Behavioral implications of mechanistic ecology: thermal and behavioral modeling of desert ecotherms and their microenvironment. *Oecologia* **13**: 1–54.
- R Development Core Team. 2010. R: A language and environment for statistical computing. [Online]. R Foundation for Statistical Computing, Vienna, Austria. Available: <http://www.R-project.org/> [2011, May 2].
- Rasband, W. S. 1997–2011. ImageJ. [Online]. U. S. National Institutes of Health, Bethesda, MD. Available: <http://rsb.info.nih.gov/ij/> [2011, May 2].
- Reid, D. G. 1987. Natural selection for apostasy and crypsis acting on the shell color polymorphism of a mangrove snail, *Littoraria filosa* (Sowerby) (Gastropoda: Littorinidae). *Biol. J. Linn. Soc.* **30**: 1–24.
- Reid, D. G. 1996. *Systematics and Evolution of Littorina*. The Dorset Press, Dorchester, UK.
- Reid, D. G. 2002. Morphological review and phylogenetic analysis of *Nodilittorina* (Gastropoda: Littorinidae). *J. Molluscan Stud.* **68**: 259–281.
- Reimchen, T. E. 1979. Substratum heterogeneity, crypsis, and colour polymorphism in an intertidal snail (*Littorina mariae*). *Can. J. Zool.* **57**: 1070–1085.
- Rochette, R., and L. M. Dill. 2000. Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. *J. Exp. Mar. Biol. Ecol.* **253**: 165–191.
- Schmidt-Nielsen, K., C. R. Taylor, and A. Shkolnik. 1971. Desert snails: problems of heat, water and food. *J. Exp. Biol.* **55**: 385–398.
- Schmidt-Nielsen, K., C. R. Taylor, and A. Shkolnik. 1972. Desert snails: problems of survival. Pp. 1–13 in *Comparative Physiology of Desert Animals*, G. M. O. Maloiy, ed. Academic Press, London.
- Seeley, R. H. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. *Proc. Natl. Acad. Sci. USA* **83**: 6897–6901.
- Sergievsy, S. O. 1992. A review of ecophysiological studies of the

- colour polymorphism of *Littorina obtusata* (L.) and *L. saxatilis* (Oliv.) in the White Sea. Pp. 235–245 in *Proceedings of the Third International Symposium on Littorinid Biology*, J. Grahame, P. J. Mill, and D. G. Reid, eds. The Malacological Society of London.
- SIO (Scripps Institution of Oceanography). 2011.** Index of Weather Observations SIO Pier. [Online]. Scripps Institution of Oceanography Climate Research Division. Available: http://meteora.ucsd.edu/weather/observations/sio_pier/dat/ [2011, February 27].
- Sokolova, I. M., and H.-O. Pörtner. 2003.** Metabolic plasticity and critical temperatures for aerobic scope in a eurythermal marine invertebrate (*Littorina saxatilis*, Gastropoda: Littorinidae) from different latitudes. *J. Exp. Biol.* **206**: 195–207.
- Somero, G. N. 2002.** Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integr. Comp. Biol.* **42**: 780–789.
- Stearns, R. E. C. 1877.** On the vitality of certain land mollusks. *Am. Nat.* **11**: 100–102.
- Stephenson, T. A., and A. Stephenson. 1972.** *Life Between Tides on Rocky Shores*. W. H. Freeman, San Francisco.
- Stevenson, R. D. 1985.** The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* **126**: 362–386.
- Stirling, H. P. 1982.** The upper temperature tolerance of prosobranch gastropods of rocky shores at Hong Kong and Dar es Salaam, Tanzania. *J. Exp. Mar. Biol. Ecol.* **63**: 133–144.
- Struhsaker, J. W. 1968.** Selection mechanisms associated with intraspecific shell variation in *Littorina picta* (Prosobranchia: Mesogastropoda). *Evolution* **22**: 459–480.
- Tomanek, L. 2010.** Variation in the heat shock response and its implication for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. *J. Exp. Biol.* **213**: 971–979.
- Trussell, G. C. 1997a.** Phenotypic plasticity in the foot size of an intertidal snail. *Ecology* **78**: 1033–1048.
- Trussell, G. C. 1997b.** Phenotypic selection in an intertidal snail: effects of a catastrophic storm. *Mar. Ecol. Prog. Ser.* **151**: 73–79.
- Trussell, G. C. 2000.** Predator-induced plasticity and morphological trade-offs in latitudinally separated populations of *Littorina obtusata*. *Evol. Ecol. Res.* **2**: 803–822.
- Trussell, G. C. 2002.** Evidence of countergradient variation in the growth of an intertidal snail in response to water velocity. *Mar. Ecol. Prog. Ser.* **243**: 123–131.
- Trussell, G. C., and M. O. Nicklin. 2002.** Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology* **83**: 1635–1647.
- University of Maryland. 2011.** GEWEX Continental Scale International Project and GEWEX Americans Prediction Project Surface Radiation Budget Data. [Online]. Department of Atmospheric and Oceanic Science, University of Maryland. Available: <http://www.atmos.umd.edu/~srb/gcip/> [2011, March 2].
- University of Utah. 2002–2011.** MesoWest. [Online]. Department of Atmospheric Sciences, University of Utah. Available: <http://mesowest.utah.edu> [2011, February 24].
- Vermeij, G. J. 1971a.** Substratum relationships of some tropical Pacific intertidal gastropods. *Mar. Biol.* **10**: 345–320.
- Vermeij, G. J. 1971b.** Temperature relationships of some tropical Pacific intertidal gastropods. *Mar. Biol.* **10**: 308–314.
- Vermeij, G. J. 1972.** Intraspecific shore level size gradients in intertidal mollusks. *Ecology* **53**: 693–700.
- Vermeij, G. J. 1973.** Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Mar. Biol.* **20**: 319–346.
- Wada, S., and A. Ito. 2000.** Preliminary observation on “tip-lip” attachment in the periwinkle *Nodilittorina radiata*. *Bull. Mar. Sci. Fish. Kochi Univ.* **20**: 15–24.
- Wetthey, D. S. 2002.** Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Integr. Comp. Biol.* **42**: 872–880.
- Williams, S. T., D. G. Reid, and D. T. J. Littlewood. 2003.** A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the Southern Ocean. *Mol. Phylogenet. Evol.* **28**: 60–86.
- Wilson, D. P. 1929.** A habit of the common periwinkle (*Littorina littorea* Linn). *Nature* **124**: 443.