

6-1-2011

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

Luke Miller

Stanford University, luke.miller@sjsu.edu

Mark Denny

Stanford University

Follow this and additional works at: https://scholarworks.sjsu.edu/biol_pub



Part of the [Biology Commons](#)

Recommended Citation

Luke Miller and Mark Denny. "Importance of Behavior and Morphological Traits for Controlling Body Temperature in Littorinid Snails" *The Biological Bulletin* (2011): 209-223. <https://doi.org/10.1086/BBLv220n3p209>

This Article is brought to you for free and open access by the Biological Sciences at SJSU ScholarWorks. It has been accepted for inclusion in Faculty Publications, Biological Sciences by an authorized administrator of SJSU ScholarWorks. For more information, please contact scholarworks@sjsu.edu.

1 Running head: Littorinid temperature relations

2

3 The importance of behavior and morphological traits for controlling body temperature in
4 littorinid snails

5

6

7 Luke P. Miller^{1,*} and Mark W. Denny

8 Hopkins Marine Station, Stanford University

9 Pacific Grove, CA 93950

10

11 ¹Current address: Marine Science Center, Northeastern University, 430 Nahant Rd, Nahant, MA,
12 USA 01908

13 * email: contact@lukemiller.org

14

15 **Keywords:** thermal stress, shell color, shell shape, *Littorina*, *Echinolittorina natalensis*, heat-
16 budget model, intertidal zone, conduction, convection

17

18 **Summary**

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

36 **Introduction**

37 Within the narrow band of habitat between the low and high tidemarks on
38 seashores, the distributions of individual species and the structure of ecological communities are
39 dictated by a variety of biotic and abiotic factors (Connell, 1961; Lewis, 1964; Connell, 1972;
40 Paine, 1974; Dayton, 1975; Menge and Branch, 2001). Biological interactions such as
41 predation, competition, and facilitation play out on a background of constantly-shifting
42 environmental conditions driven primarily by the action of tides and waves (Stephenson and
43 Stephenson, 1972; Denny, 2006; Denny *et al.*, 2009). Changes in important environmental
44 parameters such as light, temperature, and wave action can alter the suitability of the habitat for a
45 given species at both small and large spatial scales (Wetthey, 2002; Denny *et al.*, 2004; Harley,
46 2008). The capacity of organisms to persist under these varied environmental conditions is
47 mediated by the interaction of a suite of behavioral, morphological, and physiological traits.

48 Snails in the family Littorinidae are important herbivores in mid- and high-shore
49 intertidal communities around the world (McQuaid, 1996a, b; Reid, 1996), and often exert
50 control over macroalgal and microalgal communities (Castenholz, 1961; Hawkins and Hartnoll,
51 1983; Norton *et al.*, 1990; Hidalgo *et al.*, 2008). These snails can experience large swings in
52 temperature over the course of a single tide cycle and must often contend with multi-day aerial
53 emersion periods when they live above the high tide line (Vermeij, 1972; Cleland and
54 McMahon, 1986; McMahon, 1990; Judge *et al.*, 2009; Marshall *et al.*, 2010).

55 The importance of morphological and behavioral traits for managing body temperature
56 has been demonstrated in many terrestrial ectotherms such as insects, reptiles, and gastropods
57 (Schmidt-Nielsen *et al.*, 1971; Porter *et al.*, 1973; Stevenson, 1985; Huey, 1991; Kingsolver,
58 1996; Kearney *et al.*, 2009), and similar roles for morphological and behavioral variation have

59 been hypothesized for littorinid snails and other intertidal gastropods. Variation in shell color
60 across geographic scales has been hypothesized to be a response to climatic conditions, with
61 dark-colored morphs inhabiting cooler sites, while light-colored morphs dominate warmer areas
62 (Markel, 1971; Vermeij, 1971b; Etter, 1988; McQuaid and Scherman, 1988; McQuaid, 1992;
63 Sergievsky, 1992; McQuaid, 1996a; Phifer-Rixey *et al.*, 2008), as has been argued for terrestrial
64 gastropods (Jones, 1973; Heath, 1975; Heller, 1981). Shell shapes can vary from globular to
65 high-spined, which affects heating by absorption of shortwave radiation from the sun and
66 determines the internal volume of fluid that can be stored in the shell to withstand desiccation
67 (Vermeij, 1972, 1973; Chapman, 1995). In addition, the outer surface of the shell may be
68 smooth, or it may be sculptured, with ribs, ridges, and nodules that increase the surface area of
69 the shell (potentially increasing convective heat flux) without a concomitant increase in the
70 projected area of the shell that captures heat energy from the sun (Vermeij, 1973; Britton, 1995).
71 While these morphological traits may impact body temperature, there are additional selective
72 forces such as predation and wave action that may drive the variation in shell morphology
73 (Struhsaker, 1968; Johannesson, 1986; Seeley, 1986; Johannesson *et al.*, 1993; Trussell,
74 1997b, 2002).

75 Mobile intertidal grazers often seek refuge from hot conditions in crevices or under algal
76 canopies. In contrast, littorinids—which often exploit food resources on open rock faces where
77 thermal refuges are absent—may employ additional behavioral strategies to avoid stressful high
78 temperatures. As with terrestrial gastropods that must withstand prolonged unfavorable weather
79 conditions (Stearns, 1877; Machin, 1967; Schmidt-Nielsen *et al.*, 1972), littorinid snails
80 commonly remove the foot from the substratum and anchor the shell using a dried mucus
81 holdfast (Wilson, 1929; Newell, 1958; Vermeij, 1971b; Garrity, 1984). For a gastropod sitting

82 on a surface warmed by the sun, the large surface area of the foot allows for substantial
83 conductive heat exchange between the foot and substratum (Vermeij, 1971a; Denny and Harley,
84 2006). The ability to remove the foot from the substratum reduces this conductive heat flux,
85 keeping a snail several degrees cooler than the substratum (Schmidt-Nielsen *et al.*, 1972;
86 Vermeij, 1973). Many littorinid snails can also re-orient the shell, lifting the aperture away from
87 the substratum, leaving only the outer lip of the shell aperture attached to the substratum with
88 dried mucus (Fig. 1A, B) (Denny, 1984). Thusly, reorienting the shell alters conductive and
89 convective heat flux, and may change the projected area absorbing heat from the sun.

90 The relative importance of these morphological and behavioral characteristics for
91 controlling body temperature can be estimated using a mechanistic heat-budget model (Porter
92 and Gates, 1969; Gates, 1980; O'Connor and Spotila, 1992; Porter and Kearney, 2009),
93 combining physical parameters of the organism with environmental data to estimate body
94 temperature through time. From a high-resolution decade-long weather data set from Hopkins
95 Marine Station, Pacific Grove, California (HMS), we create historical reconstructions of snail
96 body temperatures to examine the effects of these morphological and behavioral changes,
97 particularly during high-temperature aerial exposures. Specifically, we test four hypotheses: 1)
98 light colored shells remain cooler than dark shells, 2) shells with surface ornamentation remain
99 cooler than smooth shells, 3) removing the foot from the substratum lowers body temperature,
100 and 4) reorienting the shell up off the substratum lowers body temperature. We compare the
101 relative effectiveness of each trait for controlling body temperature during hot aerial exposures,
102 and their effects on body temperature across the range of environmental temperatures
103 experienced in the field.

104 **Materials and Methods**

105 To facilitate the manipulation of individual morphological and behavioral parameters, we
106 developed heat-budget models for five species of littorinid snails (Figure 1C). The snails
107 included four of the five common rocky intertidal *Littorina* species from the temperate western
108 North American coastline: *Littorina keenae* Rosewater, *L. scutulata* Gould (both collected at
109 HMS), *L. plena* Gould (collected from Tatoosh Island, Washington, USA), and *L. sitkana*
110 Philippi (collected from San Juan Island, Washington, USA). The fifth common species on these
111 shores, *L. subrotundata* Carpenter (not used in this study), is morphologically similar to *L.*
112 *sitkana*, so model results for *L. sitkana* should be similar for *L. subrotundata*. The final species
113 used in this study, *Echinolittorina natalensis* (formerly *Nodilittorina natalensis* Philippi, see
114 Williams *et al.*, 2003), collected from Cape Vidal in the Natal region on the east coast of South
115 Africa, provided an ornamented shell for comparison to the smooth-shelled *L. scutulata* and *L.*
116 *plena*. Of the species used in this study, *L. sitkana* tends to live in low- to mid-intertidal zones
117 (Boulding and Van Alstyne, 1993; Rochette and Dill, 2000), while the remaining species occupy
118 the mid- and high-intertidal zone (Harger, 1972; Stirling, 1982; Behrens Yamada, 1989, 1992;
119 Branch *et al.*, 2002).

120 *Heat-budget model*

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

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

123

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

134 Because littorinid snails have a small mass and are uninsulated, we treat stored heat
135 energy, W_{stored} , as negligible and set it equal to zero. Metabolic heat production and evaporative
136 heat flux for small littorinids are approximately 0.07% and 1% as large as the heat flux due to
137 short-wave radiation at midday, respectively (Newell, 1976; Kronberg, 1990; Miller, 2008).
138 Based on these estimates, we treat metabolic heat production and heat flux due to evaporation as
139 negligible terms in the model, and therefore remove W_{met} and W_{evap} from the model. The
140 simplified heat-budget model used for this study is

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

141
142 The methods used for the parameterization of the model are described in detail in Denny
143 and Harley (2006) and Miller (2008). We made empirical measurements on a pair of snail shells
144 from each species, except for *L. plena*, for which we only had a single shell. Projected area and
145 substratum contact area were measured using size-referenced digital images analyzed in Image-J

146 (Rasband, 1997-2010), and surface area was similarly estimated from digital images using the
147 method of Johnsen and Widder (1999). To estimate the heat transfer coefficient of each shell, we
148 used silver casts of each shell to measure rates of convective heat exchange in a wind tunnel for
149 shells both sitting down on the substratum or rotated up onto the lip of shell, allowing us to
150 incorporate the effects of wind speed and shell orientation on the convective flux component of
151 the model. Short-wave absorptivity (i.e. color) was measured using shell fragments mounted in
152 an integrating sphere attached to a Li-Cor 1800 spectroradiometer (LI-COR Biosciences,
153 Lincoln, Nebraska, USA). The thickness of any mucus attachment was treated as negligible and
154 was not present in the model, so that heat flux was modeled as occurring directly between rock
155 and shell surfaces. The rate-limiting step in conductive heat flux is assumed to be between the
156 rock surface and the foot when the snail is crawling, while conduction from the rock surface
157 through the shell is assumed rate-limiting when the snail is withdrawn into the shell. Shell
158 thickness values are given as "conductive distance" in Table 1, with the greater conduction
159 distance through the lip of the shell reflected in the greater distance given when the shell is
160 elevated from the substratum. The snail body and any mantle water trapped in the shell are
161 assumed to be at a single temperature due to blood circulation.

162

163 *Model verification*

164 Temperature predictions from the model were ground-truthed against temperature
165 measurements of live snails and silver-epoxy-filled shells in the field and laboratory. Live *L.*
166 *keenae* were close in size to the modeled *L. keenae* shells were fitted with polyurethane-coated
167 0.08 mm diameter thermocouple leads (Omega Engineering Inc., Stamford, Connecticut, USA)
168 inserted through a hole ground in the shell and covered with cyanoacrylate glue. The hole was

169 positioned so that the thermocouple entered the main body whorl near ground level when the
170 shell sat down on the substratum, and was designed to put the thermocouple tip in contact with
171 the snail body when the snail was withdrawn into the shell. Measurements of body temperature
172 of a live *L. keenae* were carried out in a temperature-controlled wind tunnel (see Miller *et al.*,
173 2009) with the snail actively crawling or with the foot withdrawn into the shell. For field
174 measurements, we took each of the shells used for the size measurements described above, filled
175 the shells with thermally-conductive silver epoxy (two parts ground silver shavings, one part
176 epoxy by volume; Devcon 2 Ton Clear Epoxy, ITW Devcon, Danvers, Massachusetts, USA),
177 and fitted a 0.08 mm thermocouple into a hole drilled in the epoxy filling. We deployed these
178 shells on a high-shore granite rock at approximately 2.5 m above mean lower low water at HMS
179 during two warm periods in April and June 2007. In addition, we fit thermocouples into two live
180 *L. keenae* to be deployed in the field alongside the silver-epoxy-filled shells during the June
181 experiment. Temperatures were monitored at 1-minute intervals by a datalogger (23X, Campbell
182 Scientific Inc., Logan, Utah, USA) while concurrently monitoring air temperature (Viasala
183 HMP45C, Campbell Scientific Inc.), wind speed (Wind Sentry, R. M. Young Co., Traverse City,
184 Michigan, USA), and solar irradiance (LI-200SB, LI-COR Biosciences, Lincoln Nebraska,
185 USA). The field site was not submerged during high tide and thus represented a "worst-case
186 scenario" for snails on the shoreline.

187 *Model comparisons*

188 For long-term reconstructions of snail body temperatures in the field at HMS, we used a
189 10 year record of weather and sea-state data from HMS, spanning August 1, 1999 through July
190 31, 2009. This data set included air temperature, solar irradiance, wind speed, tide height,
191 significant wave height, and water temperature, all measured or interpolated at 10 min intervals

192 (Denny and Harley, 2006). After specifying the shore height, wave exposure, and shell
193 orientation for a model snail, the heat-budget model calculates a body temperature for each 10
194 min time step based on the co-occurring environmental conditions. When the tide height exceeds
195 the specified shore height, the snail body temperature is set equal to sea surface temperature, and
196 when the tide and waves recede below the modeled shore height, the snail heats or cools
197 according to the sum of the heat fluxes to and from the surrounding environment. The heat-
198 budget model was employed to analyze the effects of behavioral or morphological changes on
199 predicted body temperatures for the snail species under a variety of weather conditions. Because
200 the focus of the study was to examine the effects of these traits under a "worst-case" scenario, all
201 species were modeled resting on a horizontal surface 2.0 m above mean lower low water, a
202 height which is 0.4 m above the mean higher high water line at HMS and thus is only submerged
203 during spring tides or when large waves are present. The predicted temperatures for pairs of
204 snails of each species were generally within a fraction of a degree Celsius, and so we only report
205 results from a single representative shell of each species. The model was implemented in
206 MATLAB 7 (The Mathworks Inc., Natick, Massachusetts, USA). Analyses were carried out in
207 MATLAB and R 2.12.1 (2010).

208 Two behavioral manipulations were carried out with the model. First, the effect of
209 removing the foot from the substratum was simulated by changing the contact area of the snail
210 with the rock while leaving other parameters constant. The modeled snail either kept the foot in
211 contact with the rock constantly, or withdrew the foot into the shell after three hours of aerial
212 emersion, mimicking the behavior of snails that close the operculum as the rock surface becomes
213 dry. Second, the effect of reorienting the shell up onto the aperture lip was tested by using a
214 further-reduced value of contact area and simultaneously altering values for the projected area

215 facing the sun and the surface area of the shell, as the aperture of the shell is exposed to the air
216 rather than being held against the substratum (see Table 1 for representative values for each
217 shell).

218 Effects of shell color on body temperature were tested by altering the short-wave
219 absorptivity of the shell (α , a dimensionless value) while leaving all other characteristics
220 constant. Four shell colors were compared, nominally referred to as "black" ($\alpha = 0.85$), "green"
221 ($\alpha = 0.82$), "brown" ($\alpha = 0.80$), and "white" ($\alpha = 0.67$). Shell color differences were also
222 compared for snails over a range of substratum contact areas to illustrate the relative
223 contributions of color and conduction to the overall heat budget of the snail. Black and white *L.*
224 *keena*e were modeled with contact areas that scaled from full foot contact to having only the
225 outer lip of the shell glued to the substratum. Shell ornamentation comparisons were carried out
226 by comparing temperature predictions for *L. scutulata* and *E. natalensis*. These two high-spined
227 species grow to similar overall sizes, but *E. natalensis* has rows of nodules on the shell surface,
228 increasing the total surface area for convection while only slightly increasing the projected area
229 for absorbing solar irradiance. Both snails were modeled with a brown shell to remove effects of
230 color differences.

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

236 In addition to the ten year hindcasts for HMS, we modeled body temperatures with
237 different foot and shell positions for *L. scutulata* at ten additional sites (Table 2) along the west
238 coast of North America between August 2007 and August 2009 to gauge the effects of these
239 behaviors at sites that might be more thermally stressful than HMS. Data for *L. scutulata* are
240 reported because it is found throughout the west coast of the US (Reid, 1996), although modeled
241 estimates of body temperatures for the other species at each site are very similar. Tide height,
242 water temperature, air temperature and wind speed data were obtained from tide monitoring
243 stations run by the U.S. National Oceanic and Atmospheric Administration's Center for
244 Operational Oceanographic Products and Services, available through an online database
245 (<http://tidesandcurrents.noaa.gov/>). When several hours or days of data were missing for a
246 station, water temperatures were filled in from the nearest oceanographic buoy available in the
247 NOAA database, while air temperature and wind speeds were obtained from the nearest weather
248 station available in the MesoWest database maintained by the Department of Atmospheric
249 Sciences at the University of Utah (<http://mesowest.utah.edu/>). Data for La Jolla, CA, were
250 obtained from the Scripps Institute of Oceanography
251 (<http://meteora.ucsd.edu/weather/observations/sio-pier/dat/>). Solar irradiance estimates for each
252 site were obtained from NOAA's National Environmental Satellite, Data, and Information
253 Service, which produces a map of satellite-derived hourly down-welling shortwave radiation for
254 North America, available through the Department of Atmospheric and Oceanic Science at the
255 University of Maryland (<http://www.atmos.umd.edu/~srb/gcip/>). All data were linearly
256 interpolated to a 10-minute period. Predictions for 15 December 2008 to 8 January 2009 were
257 discarded due to unavailable solar irradiance data. We predicted *L. scutulata* body temperatures
258 for a black snail either with the foot extended at all times, the foot withdrawn into the shell

259 resting on the rock, or the foot withdrawn and the shell rotated up onto the edge of the shell lip.
260 Effects of wave surge were removed from the model due to uneven availability of data for the
261 sites. We used the granite substratum characteristics from HMS for all sites. Because the vertical
262 extent of the tide varies between sites, we modeled the snail at the high water mark for each site,
263 which represents a likely worst-case scenario for thermal stress.

264 *Live snail color comparisons*

265 To complement the heat-budget model predictions, a comparison of shell color effects on
266 body temperature was carried out with live *L. keenae* during a heat wave on May 14-16, 2008 at
267 HMS, when the air temperature exceeded 27, 36 and 35 °C respectively. Three pairs of similar-
268 sized *L. keenae* were collected from the field. The shell of one snail from each pair was naturally
269 black, the other, white. Shell length was within 0.2 mm and total mass was within 0.05 g for each
270 pair of snails. Maximum shell length was 13.25 mm, minimum shell length was 11.13 mm. A
271 0.08 mm diameter thermocouple wire, coated with a thin layer of polyurethane glue, was inserted
272 into a hole ground in the main body whorl of the shell. The hole in the shell was then covered in
273 cyanoacrylate glue to minimize evaporative water loss. Instrumented snails crawled normally in
274 aquaria for the 24 hrs prior to deployment in the field. The snails were placed on a high-shore
275 granite rock at midnight, May 14, 2008. The rock was wetted with seawater and the snails were
276 allowed to crawl. As the rock dried, all snails withdrew the foot and glued the shell to the rock,
277 but kept the shell aperture down against the rock surface. A datalogger recorded body
278 temperatures once per minute for the subsequent 68 hr.

279 **Results**

280 *Model parameters*

281 The measured shell parameters for the snails used in the study are given in

282

283 **References**

- 284 **Behrens Yamada, S. 1989.** Are direct developers more locally adapted than planktonic
285 developers? *Mar. Biol.* **103**: 403-411.
- 286 **Behrens Yamada, S. 1992.** Niche relationships in northeastern Pacific littorines. Pp. 281-291 in
287 *Proceedings of the Third International Symposium on Littorinid Biology*, J. Grahame, P.
288 J. Mill and D. G. Reid, eds. The Malacological Society of London.
- 289 **Bock, C. E., and R. E. Johnson. 1967.** The role of behavior in determining the intertidal
290 zonation of *Littorina planaxis* Phillipi, 1847, and *Littorina scutulata* Gould, 1849.
291 *Veliger* **10**: 42-54.
- 292 **Boulding, E. G., and K. L. Van Alstyne. 1993.** Mechanisms of differential survival and growth
293 of two species of *Littorina* on wave-exposed and on protected shores. *J. Exp. Mar. Biol.*
294 *Ecol.* **169**: 139-166.
- 295 **Branch, G. M., C. L. Griffiths, M. L. Branch, and L. E. Beckley. 2002.** *Two Oceans: A Guide*
296 *to the Marine Life of Southern Africa*. David Philips Publishers, Cape Town.
- 297 **Britton, J. C. 1995.** The relationship between position on shore and shell ornamentation in two
298 size-dependent morphotypes of *Littorina striata*, with an estimate of evaporative water
299 loss in these morphotypes and in *Melarhaphe neritoides*. *Hydrobiologia* **309**: 129-142.
- 300 **Britton, J. C., and R. F. McMahon. 1986.** The relationship between vertical distribution
301 evaporative water loss rate behavior and some morphometric parameters in four species
302 of rocky intertidal gastropods from Hong Kong. Pp. 1153-1171 in *Proceedings of the*
303 *Second International Marine Biological Workshop: The Marine Flora and Fauna of*
304 *Hong Kong and Southern China, Hong Kong, 1986*, B. Morton, ed. Hong Kong
305 University Press, Hong Kong.

306 **Broekhuysen, G. J. 1940.** A preliminary investigation of the importance of desiccation,
307 temperature and salinity as factors controlling the vertical distribution of certain intertidal
308 marine gastropods in False Bay, South Africa. *Trans. R. Soc. S. Afr.* **28:** 255-291.

309 **Campbell, G. S., and J. M. Norman. 1998.** *An Introduction to Environmental Biophysics.*
310 Springer-Verlag, New York.

311 **Castenholz, R. W. 1961.** Effect of grazing on marine littoral diatom populations. *Ecology* **42:**
312 783-794.

313 **Chapman, M. G. 1995.** Spatial patterns of shell shape of three species of co-existing Littorinid
314 snails in New South Wales, Australia. *J. Molluscan Stud.* **61:** 141-162.

315 **Chow, V. 1989.** Intraspecific competition in a fluctuating population of *Littorina plena* Gould
316 (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* **130:** 147-165.

317 **Cleland, J. D., and R. F. McMahon. 1986.** Upper thermal limit of nine intertidal gastropod
318 species from a Hong Kong rocky shore in relation to vertical distribution and desiccation
319 associated with evaporative cooling. Pp. 1141-1152 in *Proceedings of the Second*
320 *International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong*
321 *and Southern China, Hong Kong, 1986* B. Morton, ed. Hong Kong University Press,
322 Hong Kong.

323 **Clusella-Trullas, S., J. H. van Wyk, and J. R. Spotila. 2007.** Thermal melanism in ectotherms.
324 *J. Therm. Biol.* **32:** 235-245.

325 **Connell, J. H. 1961.** Effects of competition, predation by *Thais lapillus*, and other factors on
326 natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* **31:** 61-104.

327 **Connell, J. H. 1972.** Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol.*
328 *Syst.* **3:** 169-192.

329 **Cook, L. M., and P. M. Freeman. 1986.** Heating properties of morphs of the mangrove snail
330 *Littoraria pallescens*. *Biol. J. Linn. Soc.* **29**: 295-300.

331 **Dayton, P. K. 1975.** Experimental evaluation of ecological dominance in a rocky intertidal algal
332 community. *Ecol. Monogr.* **45**: 137-159.

333 **Denny, M. W. 1984.** Mechanical properties of pedal mucus and their consequences for
334 gastropod structure and performance. *Am. Zool.* **24**: 23-36.

335 **Denny, M. W. 2006.** Ocean waves, nearshore ecology, and natural selection. *Aquat. Ecol.* **40**:
336 439-461.

337 **Denny, M. W., and C. A. Blanchette. 2000.** Hydrodynamics, shell shape, behavior and
338 survivorship in the owl limpet *Lottia gigantea*. *J. Exp. Biol.* **203**: 2623-2639.

339 **Denny, M. W., T. L. Daniel, and M. A. R. Koehl. 1985.** Mechanical limits to size in wave-
340 swept organisms. *Ecol. Monogr.* **55**: 69-102.

341 **Denny, M. W., and C. D. G. Harley. 2006.** Hot limpets: predicting body temperature in a
342 conductance-mediated thermal system. *J. Exp. Biol.* **209**: 2409-2419.

343 **Denny, M. W., B. Helmuth, G. Leonard, C. D. G. Harley, L. J. H. Hunt, and E. K. Nelson.**
344 **2004.** Quantifying scale in ecology: lessons from a wave-swept shore. *Ecol. Monogr.* **74**:
345 513-532.

346 **Denny, M. W., L. J. H. Hunt, L. P. Miller, and C. D. G. Harley. 2009.** On the prediction of
347 extreme ecological events. *Ecol. Monogr.* **79**: 397-421.

348 **Etter, R. J. 1988.** Physiological stress and color polymorphism in the intertidal snail *Nucella*
349 *lapillus*. *Evolution* **42**: 660-680.

350 **Evans, F. 1961.** Responses to disturbance of the periwinkle *Littorina punctata* (Gmelin) on a
351 shore in Ghana. *Proceedings of the Zoological Society of London* **137**: 393-402.

352 **Garrity, S. D. 1984.** Some adaptations of gastropods to physical stress on a tropical rocky shore.
353 *Ecology* **65**: 559-574.

354 **Gates, D. M. 1980.** *Biophysical Ecology*. Springer-Verlag, New York, USA.

355 **Harger, J. R. E. 1972.** Competitive coexistence among intertidal invertebrates. *Am. Sci.* **60**:
356 600-607.

357 **Harley, C. D. G. 2008.** Tidal dynamics, topographic orientation, and temperature-mediated mass
358 mortalities on rocky shores. *Mar. Ecol. Prog. Ser.* **371**: 37-46.

359 **Harley, C. D. G., M. W. Denny, K. J. Mach, and L. P. Miller. 2009.** Thermal stress and
360 morphological adaptations in limpets. *Funct. Ecol.* **23**: 292-301.

361 **Hawkins, S. J., and R. G. Hartnoll. 1983.** Grazing of intertidal algae by marine invertebrates.
362 *Oceanography and Marine Biology: an Annual Review* **21**: 195-282.

363 **Heath, D. J. 1975.** Colour, sunlight, and internal temperatures in the land-snail *Cepaea*
364 *nemoralis* (L.). *Oecologia* **19**: 29-38.

365 **Heller, J. 1981.** Visual versus climatic selection of shell banding in the landsnail *Theba pisana*
366 in Israel. *Journal of Zoology* **194**: 85-101.

367 **Helmuth, B., B. R. Broitman, C. A. Blanchette, S. E. Gilman, P. M. Halpin, C. D. G.**
368 **Harley, M. J. O'Donnell, G. E. Hofmann, B. A. Menge, and D. Strickland. 2006.**
369 Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate
370 change. *Ecol. Monogr.* **76**: 461-479.

371 **Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A.**
372 **Blanchette. 2002.** Climate change and latitudinal patterns of intertidal thermal stress.
373 *Science* **298**: 1015-1017.

374 **Hidalgo, F. J., F. N. Firstater, E. Fanjul, M. C. Bazterrica, B. J. Lomovasky, J. Tarazona,**
375 **and O. O. Iribarne. 2008.** Grazing effects of the periwinkle *Echinolittorina peruviana* at
376 a central Peruvian high rocky intertidal. *Helgol. Mar. Res.* **62:** S73-S83.

377 **Huey, R. B. 1991.** Physiological consequences of habitat selection. *The American Naturalist*
378 **137:** S91-S115.

379 **Hughes, J. M., and P. B. Mather. 1986.** Evidence for predation as a factor in determining shell
380 color frequencies in a mangrove snail *Littorina* sp. (Prosobranchia: Littorinidae).
381 *Evolution* **40:** 68-77.

382 **Johannesson, B. 1986.** Shell morphology of *Littorina saxatilis* Olivi: the relative importance of
383 physical factors and predation. *J. Exp. Mar. Biol. Ecol.* **102:** 183-195.

384 **Johannesson, K. 2003.** Evolution in *Littorina*: ecology matters. *J. Sea Res.* **49:** 107-117.

385 **Johannesson, K., and A. Ekendahl. 2002.** Selective predation favouring cryptic individuals of
386 marine snails (*Littorina*). *Biol. J. Linn. Soc.* **76:** 137-144.

387 **Johannesson, K., B. Johannesson, and E. Rolán-Alvarez. 1993.** Morphological differentiation
388 and genetic cohesiveness over a microenvironmental gradient in the marine snail
389 *Littorina saxatilis*. *Evolution* **47:** 1770-1787.

390 **Johnsen, S., and E. A. Widder. 1999.** The physical basis of transparency in biological tissue:
391 ultrastructure and the minimization of light scattering. *J. Theor. Biol.* **199:** 181-198.

392 **Jones, J. S. 1973.** Ecological genetics and natural selection in mollusks. *Science* **182:** 546-552.

393 **Judge, M. L., R. Duell, L. Burriesci, and W. Moarsi. 2009.** Life in the supralittoral fringe:
394 microhabitat choice, mobility and growth in the tropical periwinkle *Cenchritis*
395 (= *Tectarius*) *muricatus* (Linneaus, 1758). *J. Exp. Mar. Biol. Ecol.* **369:** 148-154.

396 **Kearney, M., R. Shine, and W. P. Porter. 2009.** The potential for behavioral thermoregulation
397 to buffer "cold-blooded" animals against climate warming. *Proc. Natl. Acad. Sci. U.S.A.*
398 **106:** 3835-3840.

399 **Kingsolver, J. G. 1996.** Experimental manipulation of wing pigment pattern and survival in
400 western white butterflies. *The American Naturalist* **147:** 296-306.

401 **Kronberg, I. 1990.** Heat production in *Littorina saxatilis* Olivi and *Littorina neritoides* L.
402 (Gastropoda: Prosobranchia) during an experimental exposure to air. *Helgol. Wiss.*
403 *Meeresunters.* **44:** 125-134.

404 **Lang, R. C., J. C. Britton, and T. Metz. 1998.** What to do when there is nothing to do: The
405 ecology of Jamaican intertidal Littorinidae (Gastropoda: Prosobranchia) in repose.
406 *Hydrobiologia* **378:** 161-185.

407 **Lewis, J. R. 1964.** *Ecology of Rocky Shores*. English Universities Press, London.

408 **Machin, J. 1967.** Structural adaptation for reducing water-loss in three species of terrestrial
409 snail. *Journal of Zoology* **152:** 55-65.

410 **Manríquez, P. H., N. A. Lagos, M. E. Jara, and J. C. Castilla. 2009.** Adaptive shell color
411 plasticity during the early ontogeny of an intertidal keystone snail. *Proc. Natl. Acad. Sci.*
412 *U.S.A.* **106:** 16298-16303.

413 **Markel, R. P. 1971.** Temperature relations in two species of tropical west American littorines.
414 *Ecology* **52:** 1126-1130.

415 **Marshall, D. J., C. D. McQuaid, and G. A. Williams. 2010.** Non-climatic thermal adaptation:
416 implications for species' responses to climate warming. *Biology Letters* **6:** 669-673.

417 **McMahon, R. F. 1990.** Thermal tolerance evaporative water loss air-water oxygen consumption
418 and zonation of intertidal prosobranchs: a new synthesis. *Hydrobiologia* **193:** 241-260.

419 **McMahon, R. F., and J. C. Britton. 1985.** The relationship between vertical distribution,
420 thermal tolerance, evaporative water loss rate, and behavior on emergence in six species
421 of mangrove gastropods from Hong Kong. Pp. 563-582 in *The Malacofauna of Hong*
422 *Kong and Southern China. II, Vol. 1 and 2. Second International Workshop: Hong Kong,*
423 *Hong Kong, Apr. 6-24, 1983.*, B. Morton and D. Dudgeon, eds. Hong Kong University
424 Press, Hong Kong.

425 **McMahon, R. F., and W. D. Russell-Hunter. 1977.** Temperature relations of aerial and aquatic
426 respiration in six littoral snails in relation to their vertical zonation. *Biol. Bull.* **152**: 182-
427 198.

428 **McQuaid, C. D. 1992.** Stress on the high shore: a review of age-dependent causes of mortality
429 in *Nodilittorina knysnaensis* and *N. africana*. Pp. 85-89 in *Proceedings of the Third*
430 *International Symposium on Littorinid Biology*, J. Grahame, P. J. Mill and D. G. Reid,
431 eds. The Malacological Society of London, London.

432 **McQuaid, C. D. 1996a.** Biology of the gastropod family Littorinidae. I. Evolutionary aspects.
433 *Oceanography and Marine Biology: an Annual Review* **34**: 233-262.

434 **McQuaid, C. D. 1996b.** Biology of the gastropod family Littorinidae. II. Role in the ecology of
435 intertidal and shallow marine ecosystems. *Oceanography and Marine Biology: an Annual*
436 *Review* **34**: 263-302.

437 **McQuaid, C. D., and P. A. Scherman. 1988.** Thermal stress in a high shore intertidal
438 environment: morphological and behavioural adaptations of the gastropod *Littorina*
439 *africana*. Pp. 213-224 in *Behavioral Adaptation to Intertidal Life*, G. Chelazzi and M.
440 Vannini, eds. Plenum Press, New York.

441 **Menge, B. A., and G. M. Branch. 2001.** Rocky Intertidal Communities. Pp. 221-251 in *Marine*
442 *Community Ecology*, M. D. Bertness, S. D. Gaines and M. E. Hay, eds. Sinauer
443 Associates, Inc., Sunderland, Massachusetts.

444 **Miller, L. P. 2008.** Life on the edge: morphological and behavioral adaptations for survival on
445 wave-swept shores, PhD Thesis, Biology, Stanford University.

446 **Miller, L. P., C. D. G. Harley, and M. W. Denny. 2009.** The role of temperature and
447 desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia*
448 *gigantea*. *Funct. Ecol.* **23**: 756-767.

449 **Miller, L. P., M. J. O'Donnell, and K. J. Mach. 2007.** Dislodged but not dead: survivorship of
450 a high intertidal snail following wave dislodgement. *J. Mar. Biol. Assoc. U. K.* **87**: 735-
451 739.

452 **Miller, S. L. 1974.** Adaptive design of locomotion and foot form in prosobranch gastropods. *J.*
453 *Exp. Mar. Biol. Ecol.* **14**: 99-156.

454 **Mislan, K. A. S., D. S. Wethey, and B. Helmuth. 2009.** When to worry about the weather: role
455 of tidal cycle in determining patterns of risk in intertidal ecosystems. *Global Change*
456 *Biology* **15**: 3056-3065.

457 **Muñoz, J. L. P., G. R. Finke, P. A. Camus, and F. Bozinovic. 2005.** Thermoregulatory
458 behavior, heat gain, and thermal tolerance in the periwinkle *Echinolittorina peruviana* in
459 central Chile. *Comparative Biochemistry and Physiology, Part A* **142**: 92-98.

460 **Newell, G. E. 1958.** The behaviour of *Littorina littorea* (L.) under natural conditions and its
461 relation to position on the shore. *J. Mar. Biol. Assoc. U. K.* **37**: 229-239.

462 **Newell, R. C. 1976.** Adaptations to intertidal life. Pp. 1-82 in *Adaptation to Environment: Essays*
463 *on the Physiology of Marine Animals*, R. C. Newell, ed. Butterworths, London, UK.

464 **Norton, T. A., S. J. Hawkins, N. L. Manley, G. A. Williams, and D. C. Watson. 1990.**
465 Scraping a living: a review of littorinid grazing. *Hydrobiologia* **193**: 117-138.

466 **O'Connor, M. P., and J. R. Spotila. 1992.** Consider a spherical lizard: animals, models, and
467 approximations. *Am. Zool.* **32**: 179-193.

468 **Ohgaki, S.-i. 1988.** Rain and the distribution of *Nodilittorina exigua* (Dunker) (Gastropoda:
469 Littorinidae). *J. Exp. Mar. Biol. Ecol.* **122**: 213-223.

470 **Paine, R. T. 1974.** Intertidal community structure - experimental studies on relationship between
471 a dominant competitor and its principal predator. *Oecologia* **15**: 93-120.

472 **Pardo, L. M., and L. E. Johnson. 2005.** Explaining variation in life-history traits: growth rate,
473 size, and fecundity in a marine snail across an environmental gradient lacking predators.
474 *Mar. Ecol. Prog. Ser.* **296**: 229-239.

475 **Phifer-Rixey, M., M. Heckman, G. C. Trussell, and P. S. Schmidt. 2008.** Maintenance of
476 clinal variation for shell colour phenotype in the flat periwinkle *Littorina obtusata*. *J.*
477 *Evol. Biol.* **21**: 966-978.

478 **Porter, W. P., and D. M. Gates. 1969.** Thermodynamic equilibria of animals with environment.
479 *Ecol. Monogr.* **39**: 228-244.

480 **Porter, W. P., and M. Kearney. 2009.** Size, shape, and the thermal niche of endotherms. *Proc.*
481 *Natl. Acad. Sci. U.S.A.* **106**: 19666-19672.

482 **Porter, W. P., J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973.** Behavioral
483 implications of mechanistic ecology: thermal and behavioral modeling of desert
484 ectotherms and their microenvironment. *Oecologia* **13**: 1-54.

485 **R Development Core Team 2010.** R: A language and environment for statistical computing. R
486 Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>

487 **Rasband, W. S. 1997-2010.** ImageJ. U. S. National Institutes of Health, Bethesda, Maryland,
488 USA. <http://rsb.info.nih.gov/ij/>

489 **Reid, D. G. 1987.** Natural selection for apostasy and crypsis acting on the shell color
490 polymorphism of a mangrove snail, *Littoraria filosa* (Sowerby) (Gastropoda:
491 Littorinidae). *Biol. J. Linn. Soc.* **30**: 1-24.

492 **Reid, D. G. 1996.** *Systematics and Evolution of Littorina*. The Dorset Press, Dorchester, UK.

493 **Reid, D. G. 2002.** Morphological review and phylogenetic analysis of *Nodilittorina*
494 (Gastropoda: Littorinidae). *J. Molluscan Stud.* **68**: 259-281.

495 **Reimchen, T. E. 1979.** Substratum heterogeneity, crypsis, and colour polymorphism in an
496 intertidal snail (*Littorina maria*). *Canadian Journal of Zoology* **57**: 1070-1085.

497 **Rochette, R., and L. M. Dill. 2000.** Mortality, behavior and the effects of predators on the
498 intertidal distribution of littorinid gastropods. *J. Exp. Mar. Biol. Ecol.* **253**: 165-191.

499 **Schmidt-Nielsen, K., C. R. Taylor, and A. Shkolnik. 1971.** Desert snails: problems of heat,
500 water and food. *J. Exp. Biol.* **55**: 385-398.

501 **Schmidt-Nielsen, K., C. R. Taylor, and A. Shkolnik. 1972.** Desert snails: Problems of
502 survival. Pp. 1-13 in *Comparative Physiology of Desert Animals*, G. M. O. Maloiy, ed.
503 Academic Press, London.

504 **Seeley, R. H. 1986.** Intense natural selection caused a rapid morphological transition in a living
505 marine snail. *Proc. Natl. Acad. Sci. U.S.A.* **83**: 6897-6901.

506 **Sergievsky, S. O. 1992.** A review of ecophysiological studies of the colour polymorphism of
507 *Littorina obtusata* (L.) and *L. saxatilis* (Olivi) in the White Sea. Pp. 235-245 in
508 *Proceedings of the Third International Symposium on Littorinid biology*, J. Grahame, P.
509 J. Mill and D. G. Reid, eds. The Malacological Society of London, London.

510 **Sokolova, I. M., and H.-O. Pörtner. 2003.** Metabolic plasticity and critical temperatures for
511 aerobic scope in a eurythermal marine invertebrate (*Littorina saxatilis*, Gastropoda:
512 Littorinidae) from different latitudes. *J. Exp. Biol.* **206**: 195-207.

513 **Somero, G. N. 2002.** Thermal physiology and vertical zonation of intertidal animals: Optima,
514 limits, and costs of living. *Integr. Comp. Biol.* **42**: 780-789.

515 **Stearns, R. E. C. 1877.** On the vitality of certain land mollusks. *Am. Nat.* **11**: 100-102.

516 **Stephenson, T. A., and A. Stephenson. 1972.** *Life between tidemarks on rocky shores*. W. H.
517 Freeman and Company, San Francisco.

518 **Stevenson, R. D. 1985.** The relative importance of behavioral and physiological adjustments
519 controlling body temperature in terrestrial ectotherms. *The American Naturalist* **126**:
520 362-386.

521 **Stirling, H. P. 1982.** The upper temperature tolerance of prosobranch gastropods of rocky shores
522 at Hong Kong and Dar ES Salaam, Tanzania. *J. Exp. Mar. Biol. Ecol.* **63**: 133-144.

523 **Struhsaker, J. W. 1968.** Selection mechanisms associated with intraspecific shell variation in
524 *Littorina picta* (Prosobranchia: Mesogastropoda). *Evolution* **22**: 459-480.

525 **Tomanek, L. 2010.** Variation in the heat shock response and its implication for predicting the
526 effect of global climate change on species' biogeographical distribution ranges and
527 metabolic costs. *J. Exp. Biol.* **213**: 971-979.

528 **Trussell, G. C. 1997a.** Phenotypic plasticity in the foot size of an intertidal snail. *Ecology* **78**:
529 1033-1048.

530 **Trussell, G. C. 1997b.** Phenotypic selection in an intertidal snail: Effects of a catastrophic
531 storm. *Mar. Ecol. Prog. Ser.* **151**: 73-79.

- 532 **Trussell, G. C. 2000.** Predator-induced plasticity and morphological trade-offs in latitudinally
533 separated populations of *Littorina obtusata*. *Evol. Ecol. Res.* **2**: 803-822.
- 534 **Trussell, G. C. 2002.** Evidence of countergradient variation in the growth of an intertidal snail in
535 response to water velocity. *Mar. Ecol. Prog. Ser.* **243**: 123-131.
- 536 **Trussell, G. C., and M. O. Nicklin. 2002.** Cue sensitivity, inducible defense, and trade-offs in a
537 marine snail. *Ecology* **83**: 1635-1647.
- 538 **Vermeij, G. J. 1971a.** Substratum relationships of some tropical Pacific intertidal gastropods.
539 *Mar. Biol.* **10**: 345-320.
- 540 **Vermeij, G. J. 1971b.** Temperature relationships of some tropical Pacific intertidal gastropods.
541 *Mar. Biol.* **10**: 308-314.
- 542 **Vermeij, G. J. 1972.** Intraspecific shore level size gradients in intertidal mollusks. *Ecology* **53**:
543 693-700.
- 544 **Vermeij, G. J. 1973.** Morphological patterns in high-intertidal gastropods: adaptive strategies
545 and their limitations. *Mar. Biol.* **20**: 319-346.
- 546 **Wada, S., and A. Ito. 2000.** Preliminary observation on "tip-lip" attachment in the periwinkle
547 *Nodilittorina radiata*. *Bull. Mar. Sci. Fish. Kochi Univ.* **20**: 15-24.
- 548 **Wethey, D. S. 2002.** Biogeography, competition, and microclimate: The barnacle *Chthamalus*
549 *fragilis* in New England. *Integr. Comp. Biol.* **42**: 872-880.
- 550 **Williams, S. T., D. G. Reid, and D. T. J. Littlewood. 2003.** A molecular phylogeny of the
551 Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological
552 parallelism, and biogeography of the Southern Ocean. *Molecular Phylogenetics and*
553 *Evolution* **28**: 60-86.

554 **Wilson, D. P. 1929.** A habit of the common periwinkle (*Littorina littorea* Linn). *Nature* **124:**

555 443.

556

557

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

563 *Model verification*

564 The heat-budget model predicted temperatures for silver-epoxy-filled shells from all five
565 species and for live *L. keenae* deployed in the field that were typically within 1.5°C of the
566 measured temperatures at each time point, while predictions for the hottest 1% of time points
567 were within 0.64 °C of measured temperatures (Table 3, Figure 2). The largest deviations
568 between predicted and measured temperatures occurred during foggy conditions at night because
569 our weather records do not record the incidence of fog. The altered long-wave heat-flux during
570 foggy periods should keep snails slightly warmer than predicted by our model. Temperature
571 predictions for the live *L. keenae* measured in the temperature-controlled wind tunnel agreed
572 closely with measured temperatures. The difference between measured and predicted
573 temperatures was $0.18\text{ °C} \pm 0.27$ (mean \pm SD) while the snail was actively crawling, and was
574 $0.02\text{ °C} \pm 0.40$ when the foot was withdrawn and the shell rested on the substratum.

575 *Effect of foot position*

576 The effect of withdrawing the foot into the shell and leaving only portions of the shell in
577 contact with the substratum was estimated by calculating the average temperature difference
578 between the foot-out and foot-withdrawn positions during the hottest 1% of all 10-minute time
579 periods in the 10 yr dataset ($n = 5260$). Snails modeled with the foot withdrawn were 2.3 – 3.2

580 °C cooler on average during these hot periods than snails that kept the foot attached to the
581 substratum, with a maximum difference of 5.4 °C for the smallest species, *L. plena* (Figure 3A).
582 When the foot was left in contact with the surface, the maximum predicted temperature at HMS
583 for all five species was between 40.4 and 40.7 °C. When the foot was withdrawn into the shell
584 during low tide, the maximum temperature experienced by the five modeled species during the
585 10 yr model run ranged from 38.4 to 39.0 °C. The smallest snail modeled, *L. plena*, stayed the
586 coolest, and the largest species, *L. keenae*, reached the highest temperatures. The daily maximum
587 body temperature for each day in the 10 year time series (n = 3652) was generally higher for a
588 snail with its foot in contact with the rock, as shown for *L. keenae* (Figure 4A).

589 *Effect of shell position*

590 Standing the shell on edge yielded body temperatures that were on average 1.5 to 2.3 °C
591 cooler during the hottest 1% of time points when compared to the same shell sitting down against
592 the substratum with the foot withdrawn (Figure 3B). For all species, the maximum temperature
593 difference between the two shell orientations was between 2.2 and 3.5 °C. While snails in either
594 orientation generally start from similar body temperatures in the pre-dawn hours, the difference
595 in temperatures grows through the day and typically becomes largest during the hottest part of
596 the day. Maximum temperatures reached by snails with the shell elevated off the substratum
597 ranged from 36.9 °C (*L. plena*) to 37.8 °C (*L. keenae*). Daily maximum body temperature for
598 every day in the 10 year time series was higher for snails that left the shell on the substratum,
599 except during occasional cooler periods when the elevated shells became warmer (Figure 4B).

600 *Latitudinal comparison*

601 During 2007-2009, *L. scutulata* was predicted to reach the highest maximum
602 temperatures near the edges of its latitudinal distribution (Figure 5), both in the north at Friday
603 Harbor, WA (42.9 °C, 6 days > 40 °C) and Toke Point, WA (40.7 °C, 2 days > 40°C), and in the
604 south in Los Angeles (41.9 °C, 2 days > 40 °C) and La Jolla, CA (42.7 °C, 4 days > 40 °C). In all
605 cases, a snail with the foot in contact with the rock reached the highest temperatures, while
606 removing the foot from the rock reduced the predicted maximum temperature by 1.18 ± 0.53 °C
607 (mean \pm SD), and elevating the shell reduced maximum temperature by an additional 1.56 ± 0.34
608 °C.

609 *Effect of shell color*

610 For black vs. white comparisons, the model predicted average temperature differences of
611 0.38 to 0.54 °C during the hottest 1% of times in the data set, with maximal differences of 0.8 °C
612 (Figure 3C). Black shells were always predicted to be warmer than white shells when exposed to
613 the sun, while brown and green shells fell closer to black shells. The magnitude of the
614 temperature difference between shell color morphs was influenced by conductive heat flux
615 through the shell or foot, and greater conductive flux with the rock tended to homogenize body
616 temperatures (Figure 6). At colder environmental temperatures, a similar pattern in temperature
617 differences between black and white shell color morphs was maintained. For daylight low tides
618 when air temperatures were less than 15 °C, black morphs of *L. keenae* were 0.44 ± 0.2 °C
619 (mean \pm 1SD, for all seasons, $n = 80,476$ time points) warmer than white morphs when snails
620 were modeled elevated off the substratum (Figure 7A), and for snails modeled with the foot
621 always in contact with the substratum, the average predicted difference between black and white
622 morphs was reduced to 0.03 ± 0.03 °C across all seasons (Figure 7B).

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

628

629 *Effect of shell sculpture*

630 The influence of shell sculpturing of *E. natalensis* on body temperature during warm
631 periods was minimal. The heat transfer coefficient was greater for the nodulose *E. natalensis*
632 shell compared to the smooth-shelled *L. scutulata*, but the convective flux difference was
633 greatest at high wind speeds (Figure 8A), which rarely occur during the hottest days (see Denny
634 and Harley, 2006, materials and methods for the calculation of the heat transfer coefficient). On
635 calm, hot days, the small difference in heat transfer coefficient resulted in an average predicted
636 body temperature for *L. scutulata* 0.2 ± 0.3 °C (mean \pm SD, $n = 5260$) warmer than a similarly-
637 sized and identically-colored *E. natalensis* shell modeled in the same weather conditions (Figure
638 8B).

639 **Discussion**

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

645 species exerting grazing control over algal communities (Norton *et al.*, 1990; McQuaid, 1996b).
646 The behavioral and morphological traits of these species, combined with their physiological
647 tolerance to heat and desiccation stress, permits them to occupy these habitats and survive
648 extreme weather conditions.

649 Most rocky intertidal gastropods must keep their foot attached to the substratum to
650 maintain their position on the shore, but this comes at the expense of increasing conductive heat
651 flux between the foot and a potentially hot substratum (Denny and Harley, 2006). The propensity
652 for littorinid snails to anchor their shell to the rock with mucus and withdraw the foot into the
653 shell provides a reduction in body temperature not available to most other intertidal gastropods
654 (Vermeij, 1971a, 1973; McQuaid and Scherman, 1988), and results in body temperatures for the
655 five species studied here that can be 3-5°C lower than when the foot is left in contact with the
656 rock. Withdrawing the foot into the shell has the added benefit of allowing the snail to seal the
657 operculum, thereby reducing water loss (McMahon and Britton, 1985; Britton and McMahon,
658 1986). As a result, littorinid snails typically have very slow evaporative water loss rates,
659 permitting survival of multi-day aerial exposures (Broekhuysen, 1940; Cleland and McMahon,
660 1986; Britton, 1995; Marshall *et al.*, 2010). The use of a mucus holdfast does, however,
661 introduce a trade-off in terms of stability and attachment strength relative to the snail foot
662 (Miller, 1974; Denny, 1984; Ohgaki, 1988), increasing the chance of dislodgement. However,
663 survival of dislodged snails is typically high and they are commonly able to navigate back to
664 their preferred high shore habitats (Evans, 1961; Bock and Johnson, 1967; Miller *et al.*, 2007).

665 Reorienting the shell so that only the outer lip of the shell is in contact with the
666 substratum further enhances littorinid snails' ability to minimize body temperature on warm
667 days. Although we lack quantitative data on the frequency of this behavior in the field, the shell-

668 lifting behavior has been observed in all five species discussed here (L. Miller, personal
669 observations), as well as in numerous other littorinid snail species (Garrity, 1984; Britton, 1995;
670 Lang *et al.*, 1998; Wada and Ito, 2000). Lifting the shell from the substratum further reduces the
671 surface area in contact with the substratum over the initial reduction achieved by pulling the foot
672 into the shell (Table 1), but also changes other important heat flux components. The reoriented
673 shell exposes a greater surface area to the surrounding air, increasing the rate of convective heat
674 exchange, which cools a snail that is warmer than the air, as is often the case on hot days
675 (Marshall *et al.*, 2010), while also lifting the shell higher into faster-flowing air in the boundary
676 layer over the rock. Together, the reduction in conduction and increase in convection help
677 minimize body temperature, as has been shown in many terrestrial organisms (Stevenson, 1985).
678 Changing shells' orientation could also change the projected area facing the sun, potentially
679 minimizing absorption of shortwave radiation. Although some species of littorinid snails have
680 been shown to orient parallel to the sun when resting against the substratum (Muñoz *et al.*,
681 2005), there is no evidence that the species studied here consistently orient the shell spire
682 towards the midday sun (Miller, 2008).

683 The role of shell morphology in avoiding high body temperatures is relatively small.
684 Within the range of shell colors tested, the reduction in body temperature created by having a
685 white *versus* a dark shell is on average less than 0.5 °C, both for model snails of all five species
686 and for live *L. keenae*. The complementary hypothesis—that dark shells should be advantageous
687 in cool conditions by helping to warm these ectothermic animals—also receives minimal support
688 (Jones, 1973; Phifer-Rixey *et al.*, 2008). Due to the substantial influence of conductive heat flux
689 between the snail foot and the rock substratum, an actively grazing littorinid snail does not
690 deviate from the substratum temperature appreciably, so that differences in short-wave

691 absorptivity between shell colors result in temperature differences of less than 0.5 °C in the
692 model, while the range of reported temperature differences between color morphs of other
693 species of intertidal snails is on the order of 0 – 2 °C (Markel, 1971; Cook and Freeman, 1986;
694 Reid, 1987; Phifer-Rixey *et al.*, 2008), with differences of 3 – 5 °C in some larger snails species
695 on certain substrata (Etter, 1988). The high thermal conductivity and heat capacity of seawater
696 effectively homogenizes temperatures in the intertidal zone during high tide and when waves
697 splash during rising and ebbing tides, removing any effect of shell color on body temperature
698 during these periods. Thus, while thermal melanism may be important for warming the body in
699 some terrestrial organisms (Kingsolver, 1996; Clusella-Trullas *et al.*, 2007), the importance to
700 gastropods in intertidal systems is less clear. Differences in shell colors among intertidal snail
701 populations could be driven by other factors such as visual predation by crabs and fishes
702 (Reimchen, 1979; Hughes and Mather, 1986; Reid, 1987; Johannesson and Ekendahl, 2002;
703 Manríquez *et al.*, 2009).

704 The functional significance of shell shape in intertidal snails has received substantial
705 attention. Shell shape and size influence drag forces imposed by waves during high tide (Denny
706 *et al.*, 1985; Boulding and Van Alstyne, 1993; Trussell, 1997a; Denny and Blanchette, 2000;
707 Pardo and Johnson, 2005) determine the volume of fluid retained in the shell during emersion
708 (Vermeij, 1973; Britton and McMahon, 1986), and provide protection from predators (Seeley,
709 1986; Trussell, 2000; Trussell and Nicklin, 2002; Johannesson, 2003). The importance of shell
710 shape for mitigating stress due to exposure to extreme high temperatures in these small species is
711 less clear. We have shown that when comparing *L. scutulata* and *E. natalensis*, the addition of
712 nodules on the outer surface of *E. natalensis* shells produces a negligible reduction in body
713 temperature on hot days. These results mirror the minor contribution of shell sculpture to

714 convective cooling found in intertidal limpet species (Harley *et al.*, 2009). Additionally,
715 estimated temperatures for the globose, ribbed *L. sitkana* do not differ markedly from the other
716 high-spired species examined here. Despite the relatively small effect of shell shape and shell
717 sculpturing on body temperature in the temperate climate conditions used here, the trend within
718 tropical intertidal gastropods, and particularly littorinids, is generally towards increased
719 sculpturing and higher-spired shells at higher shore heights (Vermeij, 1973). The nodulose
720 littorinids such as *E. natalensis* are primarily found in tropical or sub-tropical regions, so the
721 importance of these characteristics to controlling body temperature may take on a greater
722 importance at low latitudes where the frequency of high temperature exposures is greater.

723 Though body temperature changes created by the behavioral choices and color
724 differences described here are only a few degrees, they may be sufficient to help littorinid snail
725 populations avoid substantial mortality due to thermal stress. The reported physiological thermal
726 tolerances of *L. keenae* and *L. scutulata* (> 42-44°C, Somero, 2002) exceed the body
727 temperatures predicted for snails in the field at HMS, but snails at other sites along the coast may
728 approach or exceed these temperature limits. The frequency and severity of thermal stress events
729 are driven by the timing of the tides and the coincidence of calm, warm weather conditions with
730 midday tides (Helmuth *et al.*, 2002; Helmuth *et al.*, 2006; Denny *et al.*, 2009; Mislán *et al.*,
731 2009). Our model predicts that littorinids living throughout the species' latitudinal ranges could
732 occasionally experience prolonged aerial emersion at midday during weather conditions hot
733 enough to push body temperatures close to 42 °C. Under these circumstances, the additive
734 benefits of removing the foot from the rock, reorienting the shell, and having lighter shell colors
735 could keep body temperatures several degrees below those lethal temperatures and help limit
736 sublethal temperature stress. Work on the physiology of related littorinid snails has shown that as

737 temperatures approach lethal limits, there is often an attendant decrease in aerobic respiration,
738 increases in anaerobic metabolism, and eventual heart failure (McMahon and Russell-Hunter,
739 1977; Sokolova and Pörtner, 2003; Marshall *et al.*, 2010), along with the added energetic cost
740 of repairing cellular-level damage through avenues such as heat shock protein expression
741 (Tomanek, 2010).

742 Although lighter shell colors help avoid temperature stress, the native snail populations in
743 many of the warmer sites on the west coast of North America highlighted here contain a
744 substantial fraction of dark-colored individuals (L. Miller, personal observations). All of the
745 *Littorina* species discussed here, except *L. sitkana*, have a pelagic larval dispersal phase (Reid,
746 1996, 2002), so that mixture among populations may counteract any selection for lighter shell
747 colors at hot sites. In sub-tropical and tropical habitats the role of shell color may be more
748 important, as evidenced by experiments with black-painted littorine snails in South Africa that
749 demonstrated that darker colors did result in acute thermally-induced mortality on hot days
750 (McQuaid, 1992). At sites with higher peak air and substratum temperatures, the small reduction
751 in body temperature created by a light colored shell may make the difference between survival
752 and death on hot days, especially after the more effective behavioral options have been
753 exhausted.

754 Based on the long-term weather records for our central California coast site, it appears
755 unlikely that acute high temperature exposures regularly cause significant mortality in *Littorina*
756 populations at HMS. However, when considered over the lifetime of an organism, the cumulative
757 benefits of the small temperature reductions afforded by the behavioral and morphological traits
758 examined here could be important for allowing littorinids to exploit high littoral habitats. Sub-
759 lethal temperatures will still incur metabolic costs that can be partially mitigated by having a

760 lighter colored shell or minimizing conductive heat flux from a hot substratum. The attendant
761 reduction in desiccation stress provided by these traits may also help contribute to the success of
762 littorinids in the high intertidal zone (Chow, 1989). While these behaviors or shell morphologies
763 may have little effect on the occurrence of single-day thermal mortality events at HMS, on other
764 shores, particularly tropical shores and sites where mid-day low tides frequently coincide with
765 warm weather, these traits may be key in allowing littorinids to avoid thermally-induced
766 mortality.

767 **Acknowledgements**

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

782

783 **References**

- 784 **Behrens Yamada, S. 1989.** Are direct developers more locally adapted than planktonic
785 developers? *Mar. Biol.* **103**: 403-411.
- 786 **Behrens Yamada, S. 1992.** Niche relationships in northeastern Pacific littorines. Pp. 281-291 in
787 *Proceedings of the Third International Symposium on Littorinid Biology*, J. Grahame, P.
788 J. Mill and D. G. Reid, eds. The Malacological Society of London.
- 789 **Bock, C. E., and R. E. Johnson. 1967.** The role of behavior in determining the intertidal
790 zonation of *Littorina planaxis* Phillipi, 1847, and *Littorina scutulata* Gould, 1849.
791 *Veliger* **10**: 42-54.
- 792 **Boulding, E. G., and K. L. Van Alstyne. 1993.** Mechanisms of differential survival and growth
793 of two species of *Littorina* on wave-exposed and on protected shores. *J. Exp. Mar. Biol.*
794 *Ecol.* **169**: 139-166.
- 795 **Branch, G. M., C. L. Griffiths, M. L. Branch, and L. E. Beckley. 2002.** *Two Oceans: A Guide*
796 *to the Marine Life of Southern Africa*. David Philips Publishers, Cape Town.
- 797 **Britton, J. C. 1995.** The relationship between position on shore and shell ornamentation in two
798 size-dependent morphotypes of *Littorina striata*, with an estimate of evaporative water
799 loss in these morphotypes and in *Melarhaphe neritoides*. *Hydrobiologia* **309**: 129-142.
- 800 **Britton, J. C., and R. F. McMahon. 1986.** The relationship between vertical distribution
801 evaporative water loss rate behavior and some morphometric parameters in four species
802 of rocky intertidal gastropods from Hong Kong. Pp. 1153-1171 in *Proceedings of the*
803 *Second International Marine Biological Workshop: The Marine Flora and Fauna of*
804 *Hong Kong and Southern China, Hong Kong, 1986*, B. Morton, ed. Hong Kong
805 University Press, Hong Kong.

806 **Broekhuysen, G. J. 1940.** A preliminary investigation of the importance of desiccation,
807 temperature and salinity as factors controlling the vertical distribution of certain intertidal
808 marine gastropods in False Bay, South Africa. *Trans. R. Soc. S. Afr.* **28:** 255-291.

809 **Campbell, G. S., and J. M. Norman. 1998.** *An Introduction to Environmental Biophysics.*
810 Springer-Verlag, New York.

811 **Castenholz, R. W. 1961.** Effect of grazing on marine littoral diatom populations. *Ecology* **42:**
812 783-794.

813 **Chapman, M. G. 1995.** Spatial patterns of shell shape of three species of co-existing Littorinid
814 snails in New South Wales, Australia. *J. Molluscan Stud.* **61:** 141-162.

815 **Chow, V. 1989.** Intraspecific competition in a fluctuating population of *Littorina plena* Gould
816 (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* **130:** 147-165.

817 **Cleland, J. D., and R. F. McMahon. 1986.** Upper thermal limit of nine intertidal gastropod
818 species from a Hong Kong rocky shore in relation to vertical distribution and desiccation
819 associated with evaporative cooling. Pp. 1141-1152 in *Proceedings of the Second*
820 *International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong*
821 *and Southern China, Hong Kong, 1986* B. Morton, ed. Hong Kong University Press,
822 Hong Kong.

823 **Clusella-Trullas, S., J. H. van Wyk, and J. R. Spotila. 2007.** Thermal melanism in ectotherms.
824 *J. Therm. Biol.* **32:** 235-245.

825 **Connell, J. H. 1961.** Effects of competition, predation by *Thais lapillus*, and other factors on
826 natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* **31:** 61-104.

827 **Connell, J. H. 1972.** Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol.*
828 *Syst.* **3:** 169-192.

829 **Cook, L. M., and P. M. Freeman. 1986.** Heating properties of morphs of the mangrove snail
830 *Littoraria pallescens*. *Biol. J. Linn. Soc.* **29**: 295-300.

831 **Dayton, P. K. 1975.** Experimental evaluation of ecological dominance in a rocky intertidal algal
832 community. *Ecol. Monogr.* **45**: 137-159.

833 **Denny, M. W. 1984.** Mechanical properties of pedal mucus and their consequences for
834 gastropod structure and performance. *Am. Zool.* **24**: 23-36.

835 **Denny, M. W. 2006.** Ocean waves, nearshore ecology, and natural selection. *Aquat. Ecol.* **40**:
836 439-461.

837 **Denny, M. W., and C. A. Blanchette. 2000.** Hydrodynamics, shell shape, behavior and
838 survivorship in the owl limpet *Lottia gigantea*. *J. Exp. Biol.* **203**: 2623-2639.

839 **Denny, M. W., T. L. Daniel, and M. A. R. Koehl. 1985.** Mechanical limits to size in wave-
840 swept organisms. *Ecol. Monogr.* **55**: 69-102.

841 **Denny, M. W., and C. D. G. Harley. 2006.** Hot limpets: predicting body temperature in a
842 conductance-mediated thermal system. *J. Exp. Biol.* **209**: 2409-2419.

843 **Denny, M. W., B. Helmuth, G. Leonard, C. D. G. Harley, L. J. H. Hunt, and E. K. Nelson.**
844 **2004.** Quantifying scale in ecology: lessons from a wave-swept shore. *Ecol. Monogr.* **74**:
845 513-532.

846 **Denny, M. W., L. J. H. Hunt, L. P. Miller, and C. D. G. Harley. 2009.** On the prediction of
847 extreme ecological events. *Ecol. Monogr.* **79**: 397-421.

848 **Etter, R. J. 1988.** Physiological stress and color polymorphism in the intertidal snail *Nucella*
849 *lapillus*. *Evolution* **42**: 660-680.

850 **Evans, F. 1961.** Responses to disturbance of the periwinkle *Littorina punctata* (Gmelin) on a
851 shore in Ghana. *Proceedings of the Zoological Society of London* **137**: 393-402.

852 **Garrity, S. D. 1984.** Some adaptations of gastropods to physical stress on a tropical rocky shore.
853 *Ecology* **65**: 559-574.

854 **Gates, D. M. 1980.** *Biophysical Ecology*. Springer-Verlag, New York, USA.

855 **Harger, J. R. E. 1972.** Competitive coexistence among intertidal invertebrates. *Am. Sci.* **60**:
856 600-607.

857 **Harley, C. D. G. 2008.** Tidal dynamics, topographic orientation, and temperature-mediated mass
858 mortalities on rocky shores. *Mar. Ecol. Prog. Ser.* **371**: 37-46.

859 **Harley, C. D. G., M. W. Denny, K. J. Mach, and L. P. Miller. 2009.** Thermal stress and
860 morphological adaptations in limpets. *Funct. Ecol.* **23**: 292-301.

861 **Hawkins, S. J., and R. G. Hartnoll. 1983.** Grazing of intertidal algae by marine invertebrates.
862 *Oceanography and Marine Biology: an Annual Review* **21**: 195-282.

863 **Heath, D. J. 1975.** Colour, sunlight, and internal temperatures in the land-snail *Cepaea*
864 *nemoralis* (L.). *Oecologia* **19**: 29-38.

865 **Heller, J. 1981.** Visual versus climatic selection of shell banding in the landsnail *Theba pisana*
866 in Israel. *Journal of Zoology* **194**: 85-101.

867 **Helmuth, B., B. R. Broitman, C. A. Blanchette, S. E. Gilman, P. M. Halpin, C. D. G.**
868 **Harley, M. J. O'Donnell, G. E. Hofmann, B. A. Menge, and D. Strickland. 2006.**
869 Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate
870 change. *Ecol. Monogr.* **76**: 461-479.

871 **Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A.**
872 **Blanchette. 2002.** Climate change and latitudinal patterns of intertidal thermal stress.
873 *Science* **298**: 1015-1017.

874 **Hidalgo, F. J., F. N. Firstater, E. Fanjul, M. C. Bazterrica, B. J. Lomovasky, J. Tarazona,**
875 **and O. O. Iribarne. 2008.** Grazing effects of the periwinkle *Echinolittorina peruviana* at
876 a central Peruvian high rocky intertidal. *Helgol. Mar. Res.* **62:** S73-S83.

877 **Huey, R. B. 1991.** Physiological consequences of habitat selection. *The American Naturalist*
878 **137:** S91-S115.

879 **Hughes, J. M., and P. B. Mather. 1986.** Evidence for predation as a factor in determining shell
880 color frequencies in a mangrove snail *Littorina* sp. (Prosobranchia: Littorinidae).
881 *Evolution* **40:** 68-77.

882 **Johannesson, B. 1986.** Shell morphology of *Littorina saxatilis* Olivi: the relative importance of
883 physical factors and predation. *J. Exp. Mar. Biol. Ecol.* **102:** 183-195.

884 **Johannesson, K. 2003.** Evolution in *Littorina*: ecology matters. *J. Sea Res.* **49:** 107-117.

885 **Johannesson, K., and A. Ekendahl. 2002.** Selective predation favouring cryptic individuals of
886 marine snails (*Littorina*). *Biol. J. Linn. Soc.* **76:** 137-144.

887 **Johannesson, K., B. Johannesson, and E. Rolán-Alvarez. 1993.** Morphological differentiation
888 and genetic cohesiveness over a microenvironmental gradient in the marine snail
889 *Littorina saxatilis*. *Evolution* **47:** 1770-1787.

890 **Johnsen, S., and E. A. Widder. 1999.** The physical basis of transparency in biological tissue:
891 ultrastructure and the minimization of light scattering. *J. Theor. Biol.* **199:** 181-198.

892 **Jones, J. S. 1973.** Ecological genetics and natural selection in mollusks. *Science* **182:** 546-552.

893 **Judge, M. L., R. Duell, L. Burriesci, and W. Moarsi. 2009.** Life in the supralittoral fringe:
894 microhabitat choice, mobility and growth in the tropical periwinkle *Cenchritis*
895 (= *Tectarius*) *muricatus* (Linnaeus, 1758). *J. Exp. Mar. Biol. Ecol.* **369:** 148-154.

896 **Kearney, M., R. Shine, and W. P. Porter. 2009.** The potential for behavioral thermoregulation
897 to buffer "cold-blooded" animals against climate warming. *Proc. Natl. Acad. Sci. U.S.A.*
898 **106:** 3835-3840.

899 **Kingsolver, J. G. 1996.** Experimental manipulation of wing pigment pattern and survival in
900 western white butterflies. *The American Naturalist* **147:** 296-306.

901 **Kronberg, I. 1990.** Heat production in *Littorina saxatilis* Olivi and *Littorina neritoides* L.
902 (Gastropoda: Prosobranchia) during an experimental exposure to air. *Helgol. Wiss.*
903 *Meeresunters.* **44:** 125-134.

904 **Lang, R. C., J. C. Britton, and T. Metz. 1998.** What to do when there is nothing to do: The
905 ecology of Jamaican intertidal Littorinidae (Gastropoda: Prosobranchia) in repose.
906 *Hydrobiologia* **378:** 161-185.

907 **Lewis, J. R. 1964.** *Ecology of Rocky Shores.* English Universities Press, London.

908 **Machin, J. 1967.** Structural adaptation for reducing water-loss in three species of terrestrial
909 snail. *Journal of Zoology* **152:** 55-65.

910 **Manríquez, P. H., N. A. Lagos, M. E. Jara, and J. C. Castilla. 2009.** Adaptive shell color
911 plasticity during the early ontogeny of an intertidal keystone snail. *Proc. Natl. Acad. Sci.*
912 *U.S.A.* **106:** 16298-16303.

913 **Markel, R. P. 1971.** Temperature relations in two species of tropical west American littorines.
914 *Ecology* **52:** 1126-1130.

915 **Marshall, D. J., C. D. McQuaid, and G. A. Williams. 2010.** Non-climatic thermal adaptation:
916 implications for species' responses to climate warming. *Biology Letters* **6:** 669-673.

917 **McMahon, R. F. 1990.** Thermal tolerance evaporative water loss air-water oxygen consumption
918 and zonation of intertidal prosobranchs: a new synthesis. *Hydrobiologia* **193:** 241-260.

919 **McMahon, R. F., and J. C. Britton. 1985.** The relationship between vertical distribution,
920 thermal tolerance, evaporative water loss rate, and behavior on emergence in six species
921 of mangrove gastropods from Hong Kong. Pp. 563-582 in *The Malacofauna of Hong*
922 *Kong and Southern China. II, Vol. 1 and 2. Second International Workshop: Hong Kong,*
923 *Hong Kong, Apr. 6-24, 1983.,* B. Morton and D. Dudgeon, eds. Hong Kong University
924 Press, Hong Kong.

925 **McMahon, R. F., and W. D. Russell-Hunter. 1977.** Temperature relations of aerial and aquatic
926 respiration in six littoral snails in relation to their vertical zonation. *Biol. Bull.* **152:** 182-
927 198.

928 **McQuaid, C. D. 1992.** Stress on the high shore: a review of age-dependent causes of mortality
929 in *Nodilittorina knysnaensis* and *N. africana*. Pp. 85-89 in *Proceedings of the Third*
930 *International Symposium on Littorinid Biology,* J. Grahame, P. J. Mill and D. G. Reid,
931 eds. The Malacological Society of London, London.

932 **McQuaid, C. D. 1996a.** Biology of the gastropod family Littorinidae. I. Evolutionary aspects.
933 *Oceanography and Marine Biology: an Annual Review* **34:** 233-262.

934 **McQuaid, C. D. 1996b.** Biology of the gastropod family Littorinidae. II. Role in the ecology of
935 intertidal and shallow marine ecosystems. *Oceanography and Marine Biology: an Annual*
936 *Review* **34:** 263-302.

937 **McQuaid, C. D., and P. A. Scherman. 1988.** Thermal stress in a high shore intertidal
938 environment: morphological and behavioural adaptations of the gastropod *Littorina*
939 *africana*. Pp. 213-224 in *Behavioral Adaptation to Intertidal Life,* G. Chelazzi and M.
940 Vannini, eds. Plenum Press, New York.

941 **Menge, B. A., and G. M. Branch. 2001.** Rocky Intertidal Communities. Pp. 221-251 in *Marine*
942 *Community Ecology*, M. D. Bertness, S. D. Gaines and M. E. Hay, eds. Sinauer
943 Associates, Inc., Sunderland, Massachusetts.

944 **Miller, L. P. 2008.** Life on the edge: morphological and behavioral adaptations for survival on
945 wave-swept shores, PhD Thesis, Biology, Stanford University.

946 **Miller, L. P., C. D. G. Harley, and M. W. Denny. 2009.** The role of temperature and
947 desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia*
948 *gigantea*. *Funct. Ecol.* **23**: 756-767.

949 **Miller, L. P., M. J. O'Donnell, and K. J. Mach. 2007.** Dislodged but not dead: survivorship of
950 a high intertidal snail following wave dislodgement. *J. Mar. Biol. Assoc. U. K.* **87**: 735-
951 739.

952 **Miller, S. L. 1974.** Adaptive design of locomotion and foot form in prosobranch gastropods. *J.*
953 *Exp. Mar. Biol. Ecol.* **14**: 99-156.

954 **Mislan, K. A. S., D. S. Wethey, and B. Helmuth. 2009.** When to worry about the weather: role
955 of tidal cycle in determining patterns of risk in intertidal ecosystems. *Global Change*
956 *Biology* **15**: 3056-3065.

957 **Muñoz, J. L. P., G. R. Finke, P. A. Camus, and F. Bozinovic. 2005.** Thermoregulatory
958 behavior, heat gain, and thermal tolerance in the periwinkle *Echinolittorina peruviana* in
959 central Chile. *Comparative Biochemistry and Physiology, Part A* **142**: 92-98.

960 **Newell, G. E. 1958.** The behaviour of *Littorina littorea* (L.) under natural conditions and its
961 relation to position on the shore. *J. Mar. Biol. Assoc. U. K.* **37**: 229-239.

962 **Newell, R. C. 1976.** Adaptations to intertidal life. Pp. 1-82 in *Adaptation to Environment: Essays*
963 *on the Physiology of Marine Animals*, R. C. Newell, ed. Butterworths, London, UK.

964 **Norton, T. A., S. J. Hawkins, N. L. Manley, G. A. Williams, and D. C. Watson. 1990.**
965 Scraping a living: a review of littorinid grazing. *Hydrobiologia* **193**: 117-138.

966 **O'Connor, M. P., and J. R. Spotila. 1992.** Consider a spherical lizard: animals, models, and
967 approximations. *Am. Zool.* **32**: 179-193.

968 **Ohgaki, S.-i. 1988.** Rain and the distribution of *Nodilittorina exigua* (Dunker) (Gastropoda:
969 Littorinidae). *J. Exp. Mar. Biol. Ecol.* **122**: 213-223.

970 **Paine, R. T. 1974.** Intertidal community structure - experimental studies on relationship between
971 a dominant competitor and its principal predator. *Oecologia* **15**: 93-120.

972 **Pardo, L. M., and L. E. Johnson. 2005.** Explaining variation in life-history traits: growth rate,
973 size, and fecundity in a marine snail across an environmental gradient lacking predators.
974 *Mar. Ecol. Prog. Ser.* **296**: 229-239.

975 **Phifer-Rixey, M., M. Heckman, G. C. Trussell, and P. S. Schmidt. 2008.** Maintenance of
976 clinal variation for shell colour phenotype in the flat periwinkle *Littorina obtusata*. *J.*
977 *Evol. Biol.* **21**: 966-978.

978 **Porter, W. P., and D. M. Gates. 1969.** Thermodynamic equilibria of animals with environment.
979 *Ecol. Monogr.* **39**: 228-244.

980 **Porter, W. P., and M. Kearney. 2009.** Size, shape, and the thermal niche of endotherms. *Proc.*
981 *Natl. Acad. Sci. U.S.A.* **106**: 19666-19672.

982 **Porter, W. P., J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973.** Behavioral
983 implications of mechanistic ecology: thermal and behavioral modeling of desert
984 ecotherms and their microenvironment. *Oecologia* **13**: 1-54.

985 **R Development Core Team 2010.** R: A language and environment for statistical computing. R
986 Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>

- 987 **Rasband, W. S. 1997-2010.** ImageJ. U. S. National Institutes of Health, Bethesda, Maryland,
988 USA. <http://rsb.info.nih.gov/ij/>
- 989 **Reid, D. G. 1987.** Natural selection for apostasy and crypsis acting on the shell color
990 polymorphism of a mangrove snail, *Littoraria filosa* (Sowerby) (Gastropoda:
991 Littorinidae). *Biol. J. Linn. Soc.* **30**: 1-24.
- 992 **Reid, D. G. 1996.** *Systematics and Evolution of Littorina*. The Dorset Press, Dorchester, UK.
- 993 **Reid, D. G. 2002.** Morphological review and phylogenetic analysis of *Nodilittorina*
994 (Gastropoda: Littorinidae). *J. Molluscan Stud.* **68**: 259-281.
- 995 **Reimchen, T. E. 1979.** Substratum heterogeneity, crypsis, and colour polymorphism in an
996 intertidal snail (*Littorina maria*). *Canadian Journal of Zoology* **57**: 1070-1085.
- 997 **Rochette, R., and L. M. Dill. 2000.** Mortality, behavior and the effects of predators on the
998 intertidal distribution of littorinid gastropods. *J. Exp. Mar. Biol. Ecol.* **253**: 165-191.
- 999 **Schmidt-Nielsen, K., C. R. Taylor, and A. Shkolnik. 1971.** Desert snails: problems of heat,
1000 water and food. *J. Exp. Biol.* **55**: 385-398.
- 1001 **Schmidt-Nielsen, K., C. R. Taylor, and A. Shkolnik. 1972.** Desert snails: Problems of
1002 survival. Pp. 1-13 in *Comparative Physiology of Desert Animals*, G. M. O. Maloiy, ed.
1003 Academic Press, London.
- 1004 **Seeley, R. H. 1986.** Intense natural selection caused a rapid morphological transition in a living
1005 marine snail. *Proc. Natl. Acad. Sci. U.S.A.* **83**: 6897-6901.
- 1006 **Sergievsky, S. O. 1992.** A review of ecophysiological studies of the colour polymorphism of
1007 *Littorina obtusata* (L.) and *L. saxatilis* (Olivi) in the White Sea. Pp. 235-245 in
1008 *Proceedings of the Third International Symposium on Littorinid biology*, J. Grahame, P.
1009 J. Mill and D. G. Reid, eds. The Malacological Society of London, London.

1010 **Sokolova, I. M., and H.-O. Pörtner. 2003.** Metabolic plasticity and critical temperatures for
1011 aerobic scope in a eurythermal marine invertebrate (*Littorina saxatilis*, Gastropoda:
1012 Littorinidae) from different latitudes. *J. Exp. Biol.* **206**: 195-207.

1013 **Somero, G. N. 2002.** Thermal physiology and vertical zonation of intertidal animals: Optima,
1014 limits, and costs of living. *Integr. Comp. Biol.* **42**: 780-789.

1015 **Stearns, R. E. C. 1877.** On the vitality of certain land mollusks. *Am. Nat.* **11**: 100-102.

1016 **Stephenson, T. A., and A. Stephenson. 1972.** *Life between tidemarks on rocky shores.* W. H.
1017 Freeman and Company, San Francisco.

1018 **Stevenson, R. D. 1985.** The relative importance of behavioral and physiological adjustments
1019 controlling body temperature in terrestrial ectotherms. *The American Naturalist* **126**:
1020 362-386.

1021 **Stirling, H. P. 1982.** The upper temperature tolerance of prosobranch gastropods of rocky shores
1022 at Hong Kong and Dar ES Salaam, Tanzania. *J. Exp. Mar. Biol. Ecol.* **63**: 133-144.

1023 **Struhsaker, J. W. 1968.** Selection mechanisms associated with intraspecific shell variation in
1024 *Littorina picta* (Prosobranchia: Mesogastropoda). *Evolution* **22**: 459-480.

1025 **Tomanek, L. 2010.** Variation in the heat shock response and its implication for predicting the
1026 effect of global climate change on species' biogeographical distribution ranges and
1027 metabolic costs. *J. Exp. Biol.* **213**: 971-979.

1028 **Trussell, G. C. 1997a.** Phenotypic plasticity in the foot size of an intertidal snail. *Ecology* **78**:
1029 1033-1048.

1030 **Trussell, G. C. 1997b.** Phenotypic selection in an intertidal snail: Effects of a catastrophic
1031 storm. *Mar. Ecol. Prog. Ser.* **151**: 73-79.

- 1032 **Trussell, G. C. 2000.** Predator-induced plasticity and morphological trade-offs in latitudinally
1033 separated populations of *Littorina obtusata*. *Evol. Ecol. Res.* **2**: 803-822.
- 1034 **Trussell, G. C. 2002.** Evidence of countergradient variation in the growth of an intertidal snail in
1035 response to water velocity. *Mar. Ecol. Prog. Ser.* **243**: 123-131.
- 1036 **Trussell, G. C., and M. O. Nicklin. 2002.** Cue sensitivity, inducible defense, and trade-offs in a
1037 marine snail. *Ecology* **83**: 1635-1647.
- 1038 **Vermeij, G. J. 1971a.** Substratum relationships of some tropical Pacific intertidal gastropods.
1039 *Mar. Biol.* **10**: 345-320.
- 1040 **Vermeij, G. J. 1971b.** Temperature relationships of some tropical Pacific intertidal gastropods.
1041 *Mar. Biol.* **10**: 308-314.
- 1042 **Vermeij, G. J. 1972.** Intraspecific shore level size gradients in intertidal mollusks. *Ecology* **53**:
1043 693-700.
- 1044 **Vermeij, G. J. 1973.** Morphological patterns in high-intertidal gastropods: adaptive strategies
1045 and their limitations. *Mar. Biol.* **20**: 319-346.
- 1046 **Wada, S., and A. Ito. 2000.** Preliminary observation on "tip-lip" attachment in the periwinkle
1047 *Nodilittorina radiata*. *Bull. Mar. Sci. Fish. Kochi Univ.* **20**: 15-24.
- 1048 **Wethey, D. S. 2002.** Biogeography, competition, and microclimate: The barnacle *Chthamalus*
1049 *fragilis* in New England. *Integr. Comp. Biol.* **42**: 872-880.
- 1050 **Williams, S. T., D. G. Reid, and D. T. J. Littlewood. 2003.** A molecular phylogeny of the
1051 Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological
1052 parallelism, and biogeography of the Southern Ocean. *Molecular Phylogenetics and*
1053 *Evolution* **28**: 60-86.

1054 **Wilson, D. P. 1929.** A habit of the common periwinkle (*Littorina littorea* Linn). *Nature* **124:**

1055 443.

1056

1057

1058 Table 1. Measured shell parameters for the five littorinid species used in this study.

Parameter	Units	<i>Littorina</i>	<i>Littorina</i>	<i>Littorina</i>	<i>Littorina</i>	<i>Echinolittorina</i>
		<i>keenae</i>	<i>scutulata</i>	<i>plena</i>	<i>sitkana</i>	<i>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

1059

1060 Table 2. Sites on the west coast of North America used to model maximum body temperature for
 1061 *L. scutulata* from August 2007 to August 2009. The relevant NOAA tide monitoring station ID
 1062 from which data were obtained is given for each site, except La Jolla, CA, where data were
 1063 obtained from the Scripps Institute of Oceanography archive. Maximum water level is the
 1064 highest measured tide height during the survey period, referenced to mean lower low water.

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

1065

1066 Table 3. Comparison of measured temperatures of epoxy-filled shells and live snails in the field
 1067 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>L. keenae</i> 1	-0.56 (± 1.50)	-0.06 (± 0.86)
<i>L. keenae</i> 2	-1.00 (± 1.50)	0.17 (± 0.29)

1068

1069

1070 Table 4. Summary of temperatures of three pairs of similarly-sized live black-shelled and white-
 1071 shelled *Littorina keenae* deployed on a high intertidal rock during a heat wave on May 14 – 16,
 1072 2008. Temperature differences between each black and white pair are calculated for times from
 1073 one hour after sunrise to one hour before sunset, and during the four hottest hours of the day.

Temperature difference (°C)						
black – white shell						
6:00 – 18:00	Pair 1		Pair 2		Pair 3	
Average ± 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	
Temperature difference (°C)						
black – white shell						
11:00 – 15:00	Pair 1		Pair 2		Pair 3	
Average ± 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, May 14-16	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 (hr)	18.7	18.5	19.2	19.1	19.4	19.1
Time above 40°C (hr)	1.5	1.25	2.05	1.47	2.38	2.0

1074

1075 **Figure legends**

1076 Figure 1. Littorinid snails can often be found (A) with the foot withdrawn into the shell and the
1077 shell glued to the substratum, or (B) with the shell elevated up off the substratum, perched on the
1078 outer lip of the shell aperture. C) Representative shells of the five species used in the heat-budget
1079 model. From left to right: *Littorina keenae*, *L. scutulata*, *L. plena*, *L. sitkana*, *Echinolittorina*
1080 *natalensis*.

1081 Figure 2. Measured vs. predicted temperatures for silver-epoxy-filled shells set out in the field.
1082 The left column shows the relationship when the shells were positioned with the aperture down
1083 against the substratum. The right column shows data for the same shells re-oriented up onto the
1084 edge of the shell lip. Data were collected during April 23-29 and June 3-7, 2007, at HMS.

1085 Figure 3. Mean temperature differences (± 1 SD) between modeled snails during the hottest 1%
1086 of all time periods in the 10 yr weather data set ($n = 5620$). Maximum differences are denoted by
1087 the + symbol above each bar. A) Comparison of snails modeled with the foot always on the rock,
1088 or withdrawn into the shell during hot periods. Snails with the foot in contact with the rock reach
1089 higher temperatures. B) Comparison of snails modeled with the foot withdrawn into the shell,
1090 and the snail either resting aperture-down on the substratum or perched on the outer lip of the
1091 shell. Leaving the shell resting on the substratum results in higher body temperatures. C)
1092 Temperature differences between a black shell and alternate shell color morphs. Each color
1093 morph was modeled with the foot withdrawn and shell perched on the outer lip of the shell.
1094 Black shells are always warmer than the alternate color morphs.

1095 Figure 4. A) Predicted daily maximum body temperatures for a black *L. keenae* modeled with the
1096 foot out in contact with the substratum at all times or withdrawn into the shell during low tide. B)

1097 Predicted daily maximum body temperatures for the same *L. keenae* with the foot withdrawn and
1098 the shell sitting down on the substratum or with the shell tipped up on the edge of the aperture
1099 lip. Temperatures were predicted using environmental data for HMS from 1999-2009 (n = 3652
1100 days). The snail was modeled on horizontal substratum at 2.0 m above mean lower low water. A
1101 line of unity is plotted in both panels.

1102 Figure 5. Maximum predicted body temperatures for a black *L. scutulata* at eleven sites along the
1103 west coast of North America, using environmental data from 1 August 2007 through 1 August
1104 2009. Temperatures are given for the same snail in three positions: with the foot out on the rock
1105 at all times, with the foot withdrawn into the shell at low tide, and with the shell tipped up on
1106 edge during low tide. All models were run with the snail sitting on a horizontal surface at the
1107 height of the maximum still tide level for each site.

1108 Figure 6. Maximum predicted body temperatures for a black snail shell (solid line) and white
1109 snail (dashed line) modeled with a range of contact areas on the substratum, using environmental
1110 data from HMS for 1999-2009. The shaded areas represent the typical range of contact areas for
1111 littorinid snails with only the lip of the shell glued to the substratum (1 point), resting on the lip
1112 and main whorl of the shell (2 points), or attached by the foot. As contact area increases,
1113 conductive heat flux reduces the effect of shell color differences on body temperature.

1114 Figure 7. Temperature differences between black and white morphs of *L. keenae*, for all daytime
1115 low tide periods when air temperature was less than 15 °C. A) Temperature differences for snails
1116 modeled with the foot withdrawn and the shell elevated up onto the outer lip of the aperture.
1117 Black shells were warmer than white shells. B) Temperature differences for black vs. white
1118 snails modeled with the foot always in contact with the substratum. Comparisons were made for

1119 each meteorological season using weather data from HMS for 1999-2009. The center line in each
1120 box represents the median temperature difference between the two color morphs at each time
1121 point, and the upper and lower bounds of each box denote the 1st and 3rd quartiles, respectively.
1122 Crosses above a boxplot represent outliers. Box width represents the relative sample size in each
1123 season (Spring = 29,918 samples in both panels). Sample size varies between seasons due to the
1124 timing of low tides, wave action, and day length.

1125 Figure 8. A) Calculated heat transfer coefficients for similarly-sized *E. natalensis* (black line)
1126 and *L. scutulata* (gray line). Higher values increase the convective heat exchange with the
1127 surrounding air. Values are calculated for 25°C air temperature and shells sitting with the
1128 aperture against the substratum. B) Predicted body temperatures for a representative hot day, for
1129 brown snails of each species modeled with the foot withdrawn and shell resting on the
1130 substratum. The sculptured shell of *E. natalensis* was 0.2°C cooler on average compared to the
1131 smooth shell of *L. scutulata* under identical weather conditions. The wind speed on this day was
1132 $1.2 \pm 0.6 \text{ m s}^{-1}$ (mean \pm 1SD).

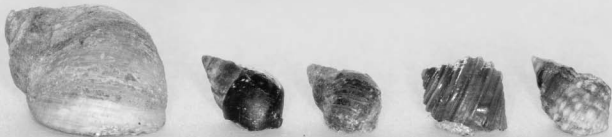
A)



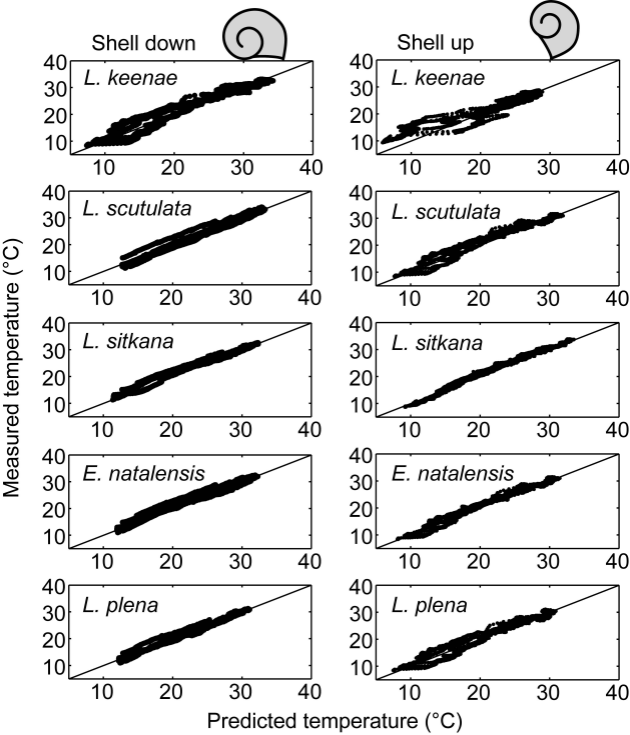
B)

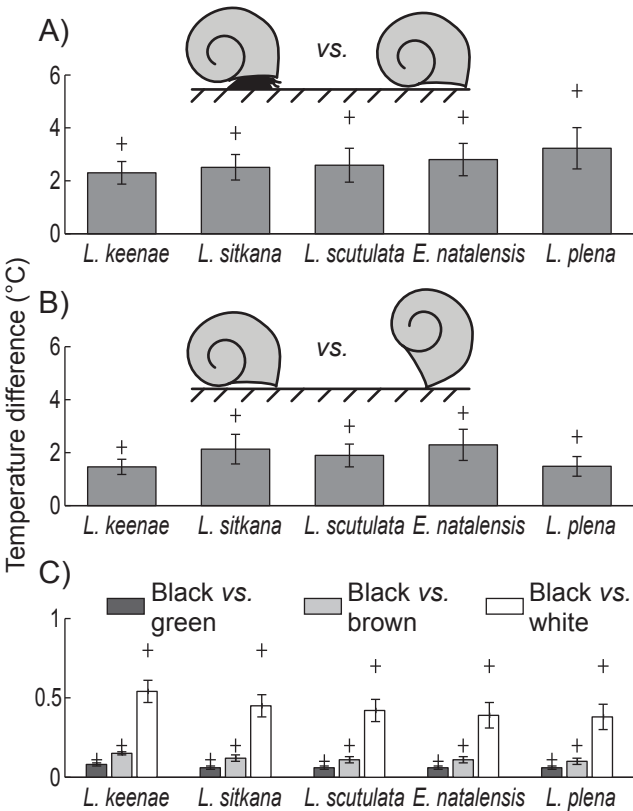


C)

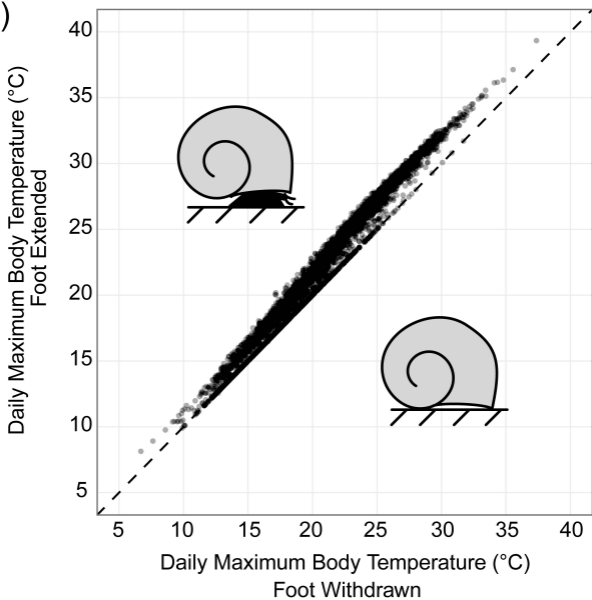


— 5 mm

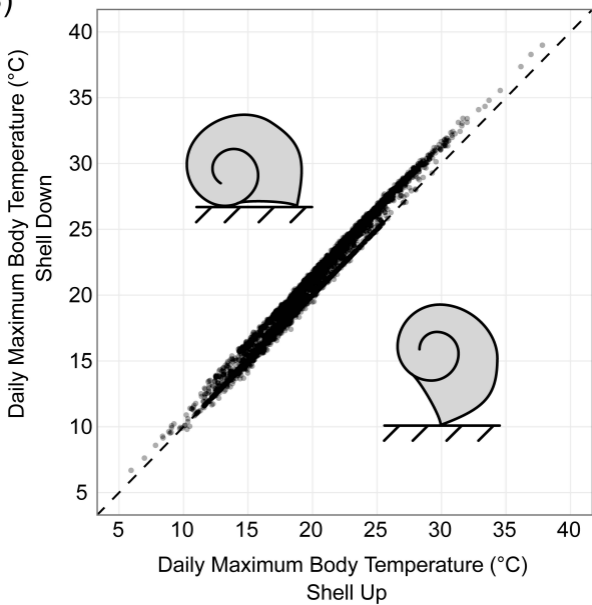




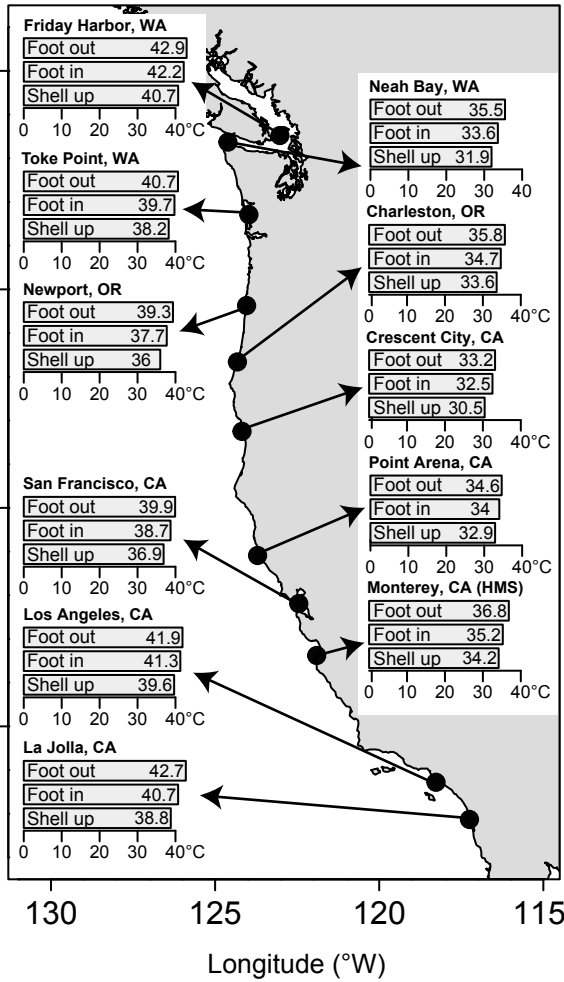
A)

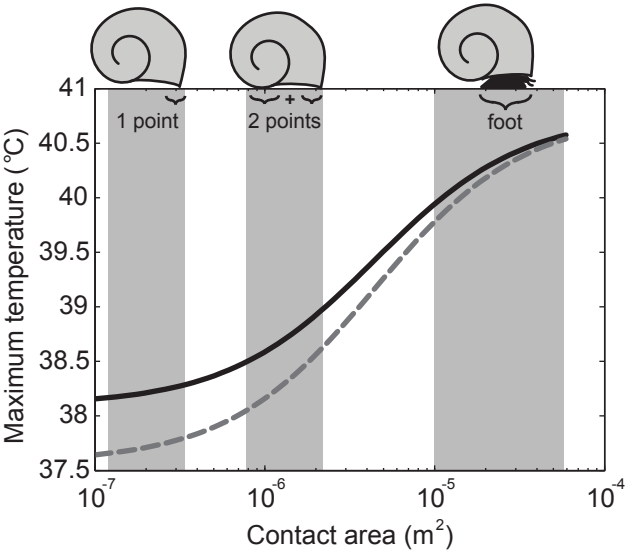


B)

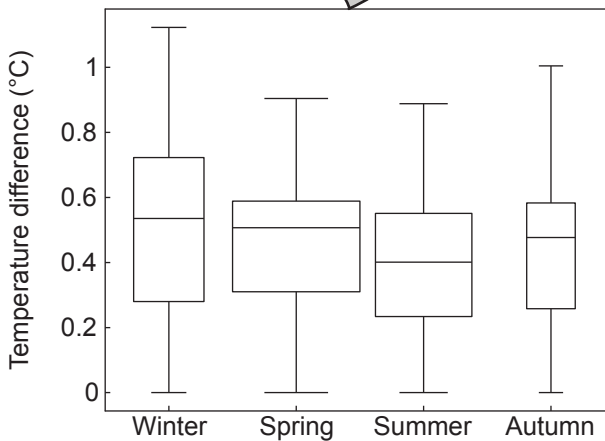


Latitude (°N)





A)



B)

