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Body posturing in *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* (Mollusca: Gastropoda: Littorinidae): a behavioural response to reduce heat stress

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ABSTRACT

Field observations on posture positions adopted by two species of littorinids, *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* in response to environmental temperatures were investigated. The study was conducted at a rocky shore of Hospital Bay, North Stradbroke Island, Queensland, Australia, from 19–22 February 2005. Temperature difference between rock surface and the outer surface of the snail shell was used as the response variable to test the hypothesis that posturing in the littorinids was a behavioural response to reduce heat stress. There was no significant interaction between ‘species’ and ‘posture’ in the two-way ANOVA results for the first two days’ data; only ‘posture’ differed significantly in TempDiff (TempDiff_{flat} < TempDiff_{standing}) but not for ‘species’. Mean TempDiff for ‘flat’ and ‘standing’ postures, regardless of species, were $0.10 \pm 0.61^\circ\text{C}$ and $0.71 \pm 0.89^\circ\text{C}$ respectively. One additional posture was observed in *N. pyramidalis* on the third and fourth days: ‘lifted’ posture in which the opercular opening is closed and the shell slightly lifted off the rock surface but not entirely in the vertical/upright position. TempDiff for the three postures of *N. pyramidalis* was significantly different with TempDiff_{lifted} TempDiff_{flat} < TempDiff_{standing} (Tukey’s Test). Mean TempDiff for ‘lifted’, ‘flat’ and ‘standing’ postures for *N. pyramidalis* for the third and fourth days were $0.02 \pm 0.67^\circ\text{C}$, $0.02 \pm 0.52^\circ\text{C}$ and $1.07 \pm 0.73^\circ\text{C}$ respectively. The ‘standing’ posture significantly reduced the temperature of the snails and is thus, an effective adaptive strategy in overcoming heat stress for these two species of littorinids. □ *marine, intertidal, snail, behaviour, heat stress, Queensland, Moreton Bay*

Supralittoral marine organisms of an intertidal rocky shore must endure the physical stress of temperature and salinity fluctuations and are highly susceptible to desiccation (Vermeij 1972; Underwood 1973; Newell 1979; Little & Kitching 1996; Raffaelli & Hawkins 1996; Lang *et al.* 1998). Mechanical wave action may also be intense (Minton & Gochfeld 2001). Survival on the high shore may be enhanced by a combination of morphological, physiological or behavioural adaptations.

One highly successful group in this harsh environment is the littorinid snails. Comparative studies of gastropod thermal tolerance have shown that members of the superfamily Littorinoidea are generally the most heat tolerant animals on rocky shores (Fraenkel 1966, 1968; Stirling 1982; Cleland and McMahon 1990; McMahon 1990; Britton 1992). McMahon (2001) reported that the mean heat coma temperatures of littorinoids were higher than that of six other high shore superfamilies of molluscs. Being mobile

also helps as they are able to select particular microhabitats, such as pits and crevices, to alleviate thermal and desiccation stress (Garrity 1984; Britton 1992; Jones & Boulding 1999). Nevertheless, they are regularly subjected to prolonged sun and heat exposure when there is a lack of shelter.

How do these littorinids overcome such heat stress? The small species *Littorina striata* uses both its nodulose shell surface, and posture, to more effectively re-radiate absorbed incident radiant thermal energy by convection (Britton 1995). More typically, when ambient rock temperatures are too high or humidity is low, littorinids prevent desiccation by withdrawing into their shell and sealing the opercular opening. In addition, littorinids have been observed to attach themselves to the substratum by a dried mucous sheet at the outer apertural tip (termed a 'holdfast' by Bingham 1972) (see also Vermeij 1971a; Denny 1984; Garrity 1984; McMahon & Britton 1991; Wada & Ito 2000). The strength and stiffness of dehydrated mucous holdfasts (as little as 2–3

mm in thickness), allow littorinids to maintain their position with minimal effort while in repose (Denny 1984). One study found holdfast formation in *Littorina irrorata* to be dependent on relative humidity and salinity (Bingham 1972); while for *L. striata*, Britton (1995) observed that holdfasts were more frequently used by smaller individuals than larger ones.

More importantly, the holdfast minimises the area of contact between the gastropod and the heated substratum, reducing heat transfer by conduction (Vermeij 1971b). Vermeij (1971b) reasoned that a 'hanging' attachment increases the surface area exposed to convection currents and thus is more effective at removing heat; this is helped further if the gastropod is positioned under a shaded ledge as observed by Lang *et al.* (1998). Wada & Ito (2000) used an alternative term, 'tip-lip' attachment, as they observed *Nodilittorina radiata* more commonly using the holdfast on horizontal surfaces.

The term 'standing' is here used to describe the position in which the gastropod is held verti-

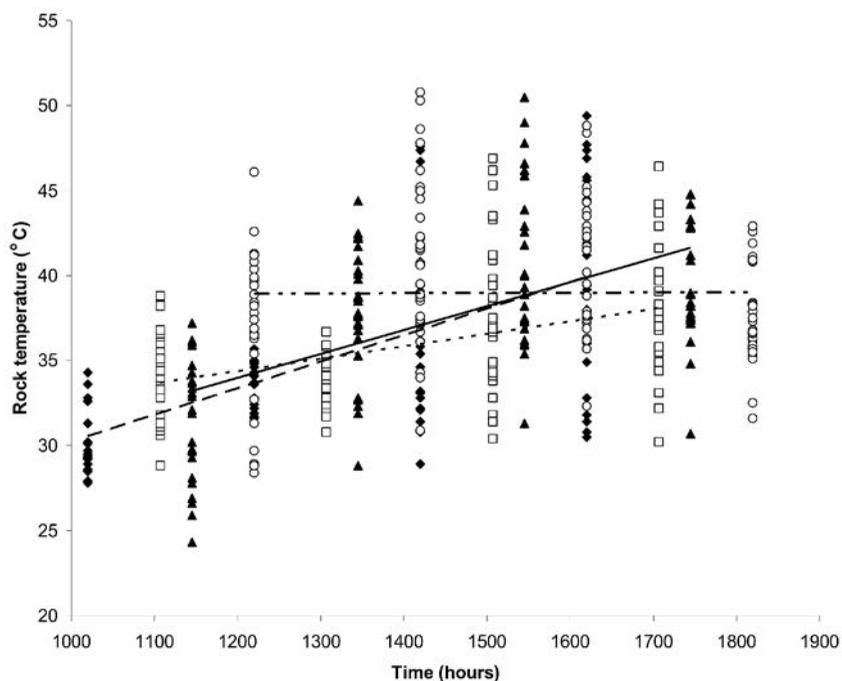


FIG. 1. Rock temperature profile taken at two-hour intervals for six-hour duration on the four consecutive days of 19–22 February 2005. First and last measurements were taken three hours before and after low tide respectively each day. ◆ 19 Feb.; □ 20 Feb.; ▲ 21 Feb.; ○ 22 Feb.

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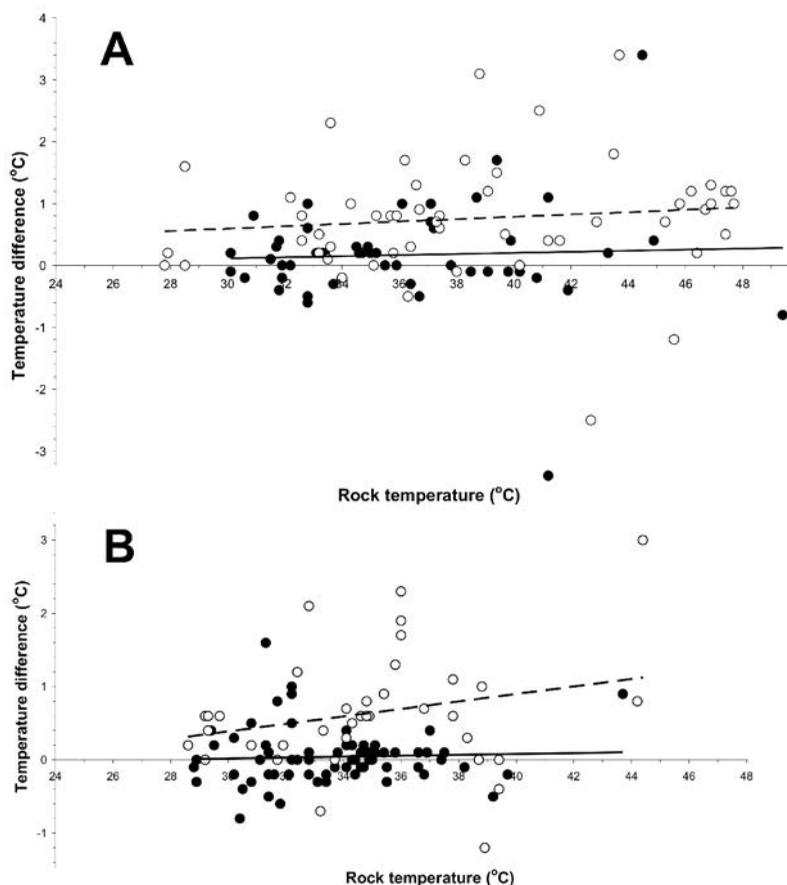


FIG. 2. Regressions of temperature difference between littorinid shell and rock surface against rock temperature for 'standing' and 'flat' postures in **A**, *Nodilittorina pyramidalis*; **B**, *Austrolittorina unifasciata*. ● = 'flat', ○ = 'standing'.

cally off the rock surface by its holdfast (Fig. 3A–C). During the present study *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* were observed to exhibit this 'standing' posture, with it being more common in *N. pyramidalis*. This behaviour has not been previously documented for either species, and thus it was decided to test whether they are also using such a 'standing' posture as an effective strategy to reduce heat stress.

MATERIALS AND METHODS

This study was conducted at the intertidal rocky shore off Hospital Bay adjacent to the Moreton Bay Research Station, Dunwich, North Stradbroke Island, Queensland. It has focussed on two species of littorinids: the larger, but less

common *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833), and the smaller, more abundant *Austrolittorina unifasciata* (Gray, 1826) (Fig. 4A, B). Field work was carried out over four days from 19 to 22 February 2005, for six hours each day. The topography of the shore was such that rocks on which the littorinids were sampled are entirely submerged at high tide. These rocks are only uncovered by the receding tide about four hours prior to the lowest tide each day. Hence, the first set of temperature measurements was taken three hours before the lowest tide, with subsequent readings recorded at two-hourly intervals. The lowest tide each day occurred at 1322 hrs, 1402 hrs, 1446 hrs and 1521 hrs respectively. Four sets of temperature measurements were recorded daily. The surface temperatures of the

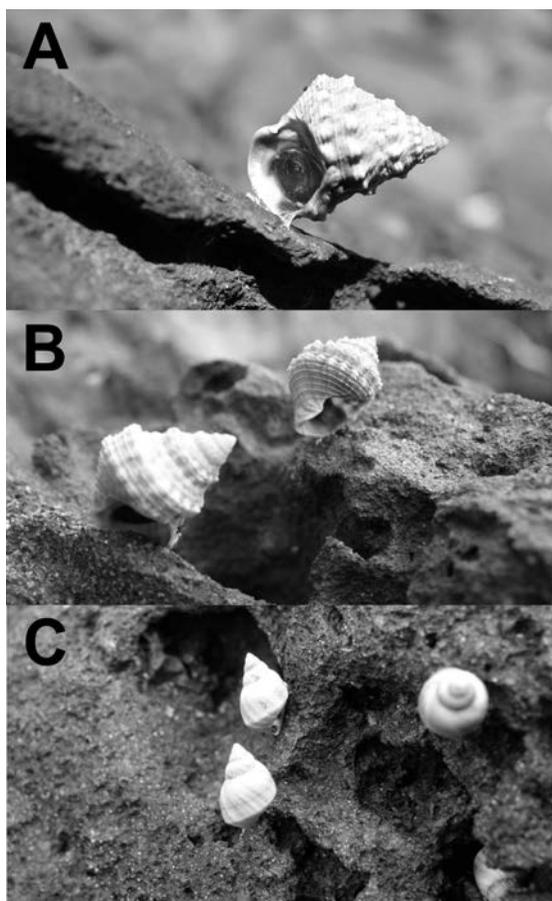


FIG. 3. **A**, thin holdfast of *Nodilittorina pyramidalis* securing it in the 'standing' posture; **B**, two individuals of *N. pyramidalis* in the 'standing' posture with spires pointing in the same direction; **C**, *Austrolittorina unifasciata* in the 'standing' position.

littorinid shells and the adjacent rock surface were measured ($\pm 0.1^{\circ}\text{C}$) with an infrared thermometer (Raynger® ST™).

During the first measurement period, all individuals of both species exhibiting the 'standing' posture were noted, and temperature measurements taken. Temperature readings were also taken for a similar number of individuals in the normal 'flat' posture in crevices or under shaded overhangs (see Fig. 4A, B).

Over the first two days 12–15 individuals for each species were sampled, but on the third and fourth days, there were respectively only two and three individuals of 'standing' *A. unifas-*

ciata, and also fewer 'standing' *N. pyramidalis*. Some *N. pyramidalis* were however in a 'lifted' position — one in which the opercular opening is closed, and though the shell is slightly lifted off the rock surface it is not in an obvious vertical/upright position (Fig. 5). However it is important to point out that (a) 'standing' posture was only observed in littorinids on exposed rock surfaces; (b) some individuals that were initially observed in the 'flat' posture subsequently adopted the 'standing' posture as the surface temperature of the rocks increased.

A General Linear Model (GLM) procedure on MINITAB (2003) was used to analyse the response variable, difference in temperature between the rock and shell temperatures ('TempDiff') with 'Species' and 'Posture' as the factors. When the interaction term, 'Species' x 'Posture' was not significant, the main factors were analysed using One-way ANOVAs. Only data for the first two days were used in this analysis as the sample sizes of 'standing' *A. unifasciata* individuals were too small for the third and fourth days. The variable, 'TempDiff' was regressed against 'Rock temperature' for the two postures, 'standing' and 'flat' in each species using MINITAB (2003). An analysis of covariance (ANCOVA) was performed using GLM (MINITAB 2003) with 'TempDiff' as the response variable, 'Posture' as the factor, and 'Rock temperature' as the covariate. This ANCOVA was applied to test for difference in slopes of the regressed lines between postures in each species. If the slopes were not found to be significantly different, a test of intercepts was undertaken; no test of intercepts would be carried out when slopes were significantly different.

Data for *N. pyramidalis* for the third and fourth day were analysed separately using One-way ANOVA with 'TempDiff' being the response variable and posture ('flat', 'standing' and 'lifted') as the factor, followed by Tukey's Test for multiple comparisons when the test results were significant. The behaviour of the littorinids in rock pools was also noted during the field work.

RESULTS

The time at which the lowest tide occurred influenced the temperature profiles of the rocks (Fig. 1). On 19 and 20 February, the temperatures

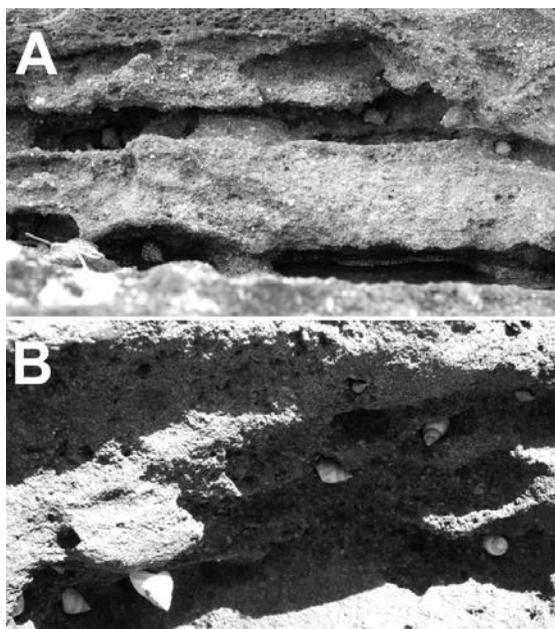


FIG. 4. Crevices and overhangs in rock boulders with sequestered individuals of: **A**, *Nodilittorina pyramidalis*; **B**, *Austrolittorina unifasciata*.

of the rocks at lowest tide (i.e., at the intersection of the regression line and the time of lowest tide) were less than 35°C. In contrast, surface temperatures of rocks on 21 and 22 February were above 35°C (Fig. 1), with maximum temperatures of the rocks exceeding 40°C. On the days when substrate surface temperatures were in excess of 35°C, no *A. unifasciata* individuals were in the 'standing' posture. These littorinids were generally not as active throughout the six hours of observation in these two days compared with the first two days of the study. It was observed that some *N. pyramidalis* individuals did not completely assume the 'standing' posture; their apertural openings were sealed with the operculum and the shells were lifted slightly off the rock surface.

Observations of littorinids' behaviour on the rock surfaces and in small tide pools as ambient temperature rose revealed some interesting behaviours. Individuals of *N. pyramidalis* that remained in the tide pools after the tide had receded (Fig. 6A) began leaving the 'hot water bath' to climb up the sides of the tide pool (Fig. 6B). Once out of the tide pools, the littorinids



FIG. 5. *Nodilittorina pyramidalis* in the 'lifted' position.

withdrew their foot, and then closed their apertural opening (Fig. 6C) before adopting the upright 'standing' posture on the rim of the apertural opening (Fig. 6D).

There was no significant interaction between the factors, 'species' and 'posture' ($p > 0.05$, Table 1) for the first two days' data. Subsequent One-way ANOVA tests showed that temperature difference was only significantly different for 'posture' ($\text{TempDiff}_{\text{flat}} < \text{TempDiff}_{\text{standing}}$) but not for 'species' (Table 1). Mean TempDiff for 'flat' and 'standing' postures, regardless of species, were $0.10 \pm 0.61^\circ\text{C}$ ($n = 125$) and $0.71 \pm 0.89^\circ\text{C}$ ($n = 91$) respectively. Analyses of covariance (ANCOVA) showed that there was no significant difference ($p > 0.05$) between the slopes and intercepts of the regression lines of Temp

Table 1. Results of Two-way ANOVA of the response variable, 'Temperature difference' (i.e., Rock temperature-Shell temperature) for the factors, 'Species' (i.e., *Nodilittorina pyramidalis* and *Austrolittorina unifasciata*) and 'Posture' (i.e. 'standing' and 'flat').

| | Source of variation | F | df ₁ , df ₂ | p | |
|--------------|---------------------|-------|-----------------------------------|-------|------|
| Full Model | Species | 1.56 | 1, 212 | 0.214 | |
| | Posture | 32.85 | 1, 212 | 0.000 | |
| | Species x posture | 0.00 | 1, 212 | 0.978 | n.s. |
| Main Factors | Species | 1.59 | 1, 213 | 0.208 | n.s. |
| | Posture | 33.07 | 1, 213 | 0.000 | |

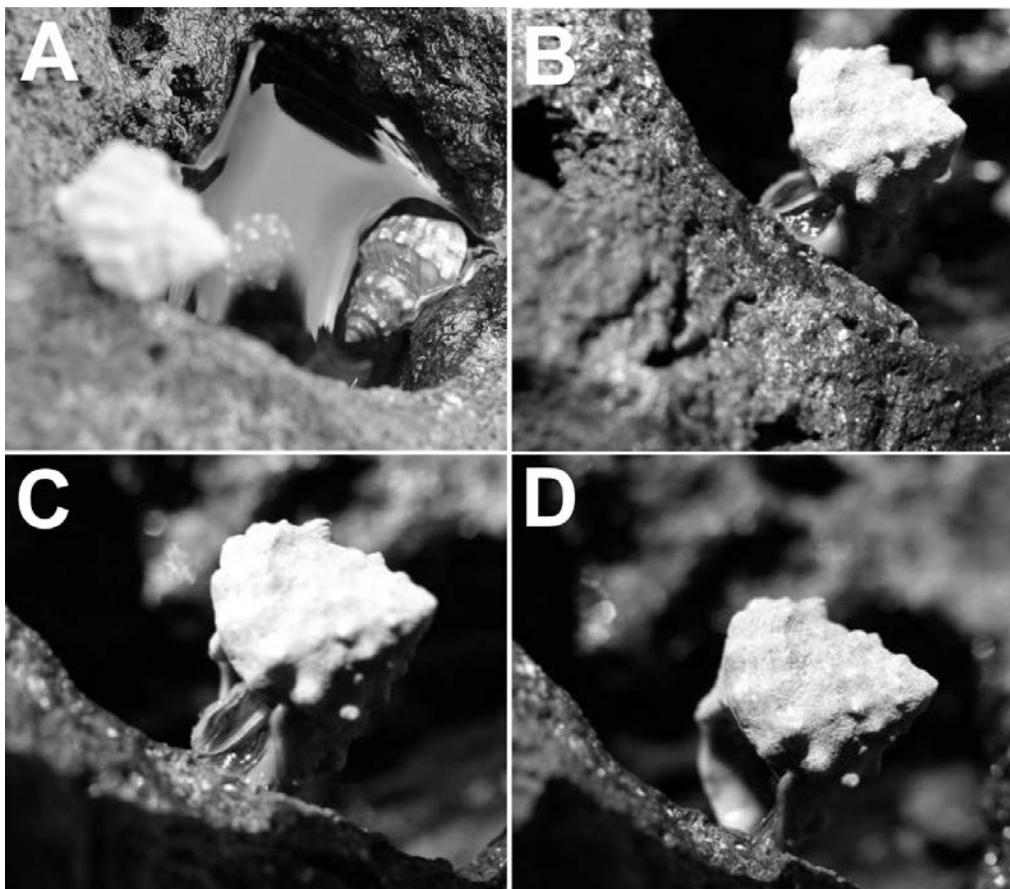


FIG. 6. A, two *Nodilittorina pyramidalis* individuals in a small tide pool; B, the larger of the two crawled up the side of the rock pool; C, gradual withdrawal of the foot; D, closed apertural opening and upright 'standing' posture attained.

Diff against rock temperature (Fig. 2A & B) for 'standing' and 'flat' postures in both species (Table 2).

Results of the One-way ANOVA for the *Nodilittorina pyramidalis* data for the third and fourth days showed that there was a significant difference in TempDiff for the three postures ($F_{2,130} = 33.80$, $p = 0.000$). Tukey's test showed that TempDiff_{standing} was significantly greater than both TempDiff_{flat} and TempDiff_{lifted} but there was no significant difference between the latter two TempDiffs (i.e., $\text{TempDiff}_{\text{lifted}} - \text{TempDiff}_{\text{flat}} < \text{TempDiff}_{\text{standing}}$). Mean TempDiff for 'lifted', 'flat' and 'standing' postures for *N. pyramidalis* for the third and fourth days were $0.02 \pm 0.67^{\circ}\text{C}$ ($n = 29$), $0.02 \pm 0.52^{\circ}\text{C}$ ($n = 75$) and $1.07 \pm 0.73^{\circ}\text{C}$ ($n = 29$) respectively.

DISCUSSION

Austrolittorina unifasciata rarely displayed 'standing' posture when rock surface temperature exceeded 35°C . On days when the low tide period occurred earlier in the day rock-surface temperatures were relatively lower ($< 35^{\circ}\text{C}$) (Fig. 1). It appears that the rate at which the temperature of the rocks rises is the key to whether they assume a 'standing' posture or sequester themselves in crevices. The threshold temperature for the onset of this response seems to be about 35°C – snails can still move around on their foot to seek crevices or gradually attain the 'standing' posture at this temperature. When the whole foot is in contact with the substratum, there is heat input by conduction as well as insolation. McQuaid & Scherman (1988) reported that body temper-

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Table 2. Results of ANCOVAs for the test of slopes and intercepts of regression equations of: *Nodilittorina pyramidalis*, 'Standing' versus 'Flat'; *Austrolittorina unifasciata*, 'Standing' versus 'Flat'. n.s. = not significant.

| | Predictor | P | |
|------------------------------------|----------------------------|-------|--------------------------------|
| <i>Nodilittorina pyramidalis</i> | Posture | 0.886 | n.s.: Intercepts not different |
| | Rock temperature | 0.435 | |
| | Posture x Rock temperature | 0.787 | n.s.: Slopes not different |
| <i>Austrolittorina unifasciata</i> | Posture | 0.391 | n.s.: Intercepts not different |
| | Rock temperature | 0.087 | |
| | Posture x Rock temperature | 0.178 | n.s.: Slopes not different |

atures of the paler *Littorina africana africana* using foot attachment to the substratum, were similar to those of *L. africana kynsnaensis*, a darker-shelled species, and this suggests that conductive heat gain may be just as important as insolation.

On the third and fourth days of the study, the snails were exposed later in the day when the ambient temperature was much hotter. As a result, rock temperatures rapidly rose past the crucial 35°C temperature. Very few of snails had the opportunity to assume the 'standing' posture before it became too hot. The 'lifted' posture could be the arrested/interrupted stage in the process of 'standing' in instances when heat stress becomes so extreme that it has to abort any attempt to become upright and close its operculum completely. This aspect of the heat response of these two species needs further investigation. It is also pertinent to note that during the first two days of the study, quite a lot of movement of snails was observed after the rocks were exposed. In contrast, there was hardly any snail that crawled on the rocks during the third and fourth day of the study. Further work is required to investigate the critical temperature at which the littorinids' foot is extended.

In Vermeij's (1973) discussion of dissipation of absorbed thermal energy by re-radiation and convection in littorinids, he emphasised the importance of a large shell surface area. He postulated that the increased surface area of nodulose shells means they are better radiators of absorbed thermal energy. Results of the present ANOVA showed that regardless of species, only the posture of snails significantly affected 'TempDiff', suggesting that even in pits or crevices, the nodulose *N.*

pyramidalis and the smooth-shelled *A. unifasciata* are similarly heated. This finding contrasts with both Vermeij's (1973) prediction and with Britton's (1995) report that both nodules and posture of *L. striata* aided to relieve thermal stress by re-radiation and convection. Lee (2003) reported similar TempDiff in individuals of the nodulose *Echinolittorina malaccana* (previously known as *Nodilittorina trochoides*) with intact shells and filed-shells (i.e., with nodules removed), thereby providing evidence that an increase in surface area due to shell ornamentation might not be responsible for heat dissipation. Radiation that falls on a body may be absorbed, reflected or transmitted (Jones 2000), hence, the more heat energy that is reflected, the less is absorbed and transmitted. Rough, nodulated shells reflect more heat (Nybakken 2001). Lee (2003) also observed that (1) the nodules of *E. malaccana* were of a much lighter colour than the rest of the shell and (2) filed-shells were darker in colour as compared with intact shells. She concluded that the shell ornamentation enhanced heat reflection. From the added evidence provided by this study, I suggest that when littorinids are sequestered in pits and crevices, nodules do not facilitate heat stress reduction as reflection is minimal in the shade.

The present results showed that *N. pyramidalis* individuals in the 'lifted' posture were not any cooler than those in the pits or crevices, indicating that perhaps the 'standing' posture offers the optimum heat reduction. McQuaid & Scherman (1988) reported that pits not only provide some shade from the sun but also offer

a substratum which may be 3–4°C cooler, resulting in lower body temperatures in *Littorina africana africana* and *L. africana knysnaensis*. ‘Standing’ posture, was, however, not reported in their paper to provide a comparison with present study. Lang *et al.* (1998) also reported that body temperatures of crevice occupants were cooler than those of individuals found on exposed areas in four Jamaican littorinids. Mineralogy of the substratum may account for large variations of the micro-environment (Britton *et al.* 1991). Although results of the ANCOVA test showed that the rate of change in the ‘TempDiff’ in response to rising rock temperature was similar for the two postures in both species of littorinids, it can be seen that ‘TempDiff’ for ‘standing’ snails was consistently higher than that of snails in the ‘flat’ posture in both species. This further substantiates the advantage of using the ‘standing’ posture as a strategy to overcome heat stress. The fact that *N. pyramidalis* crawls out of rock pools to assume the ‘standing’ posture (Fig. 6A–D) further reinforces that this is a better strategy than remaining in a ‘hot water bath’ that while it may prevent desiccation, must still reach an intolerable temperature.

Other behavioural adaptations have been suggested to help thermal regulation in high shore gastropods. Garrity (1984) noted that *Littorina aspera* and *L. modesta* used both holdfasts and orientation of the shell spire to minimise solar energy absorption. In contrast, no discernible pattern in the shell orientation was observed in seven species of Jamaican littorinid gastropods (Lang *et al.* 1998), and similarly *Littorina africana africana* and *L. a. knysnaensis* did not show any significant tendency for shell orientation (McQuaid & Schermann 1988). These contrasting observations suggest that behavioural adaptation may vary with local conditions, or with differences in the microenvironment, or may be species-specific. Shell spire-orientation in littorinid populations exhibiting ‘standing’ posture merits further study to determine whether the species involved is a thermal conformer or thermal regulator.

The present study showed that a ‘standing’ posture appears the most effective strategy for alleviating heat stress, but may be part of a complex response to various interacting factors

such as differences between individual species, substratum characteristics, length and timing of tidal exposure, and regional climatic regimes. Further studies will be necessary to better determine the factors that elicit the ‘standing’ posture.

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LITERATURE CITED

- Bingham, F.O. 1972. The mucus holdfast of *Littorina irrorata* and its relationship to relative humidity and salinity. *The Veliger* **15**: 48–50.
- Britton, J.C. 1992. Evaporative water loss, behaviour during emersion, and upper thermal tolerance limits in seven species of eulittoral-fringe Littorinidae (Mollusca: Gastropoda) from Jamaica. Pp. 69–83. *In*, Grahame, J., Mill, P.J. & Reid, D.G. (Eds), *Proceedings of the 3rd International Symposium on Littorinid Biology*. (The Malacological Society of London).
1995. The relationship between position on shore and shell ornamentation in two size-dependent morphotypes of *Littorina striata*, with an estimate of evaporative water loss in these morphotypes and in *Melarhaphé neritoides*. *Hydrobiologia* **309**: 129–142.
- Britton, J.C., McMahon, R.F. & Hart, J. 1991. Relationships between topography, substratum composition and surface temperature, and the spatial distribution of intertidal fauna on rocky shores of south-western Australia. Pp. 521–540. *In*, Wells, F.E., Walker, D.I., Kirkman, A.H. & Lethbridge, R. (Eds), *Proceedings of the 3rd International Marine Biological Workshop: the Marine Flora and Fauna of Albany, Western Australia*. Vol. II. (Western Australian Museum: Perth).
- Cleland, J.D. & McMahon, R.F. 1990. Upper thermal limit of nine intertidal gastropod species from a Hong Kong rocky shore in relation to vertical distribution and desiccation associated with evaporative cooling. Pp. 1141–1152. *In*, Morton, B. (Ed.) *The Marine Flora and Fauna of Hong Kong and Southern China*. II. Vol. 3. (Hong Kong University Press: Hong Kong).
- Denny, M.W. 1984. Mechanical properties of pedal mucus and their consequences for gastropod structure and performance. *American Zoologist* **24**: 23–36.

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- Fraenkel, G. 1966. The heat resistance of intertidal snails at Shirahama, Wakayama-Ken, Japan. *Publications of the Seto Marine Biological Laboratory* **14**: 185–195.
1968. The heat resistance of intertidal snails at Bihimi, Bahamas; Ocean Springs, Mississippi; and Woods Hole, Massachusetts. *Physiological Zoology* **41**: 1–13.
- Garrity, S.D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* **65**: 559–574.
- Jones, H.R.N. 2000. *Radiation Heat Transfer*. (Oxford University Press: New York). 83 pp.
- Jones, K.M. & Boulding, E.G. 1999. State-dependent habitat selection by an intertidal snail: the costs of selecting a physically stressful microhabitat. *Journal of Experimental Marine Biology and Ecology* **242**: 149–177.
- Lang, R.C., Britton, J.C. & Metz, T. 1998. What to do when there is nothing to do: the ecology of Jamaican intertidal Littorinidae (Gastropoda: Prosobranchia) in repose. *Hydrobiologia* **378**: 161–185.
- Lee, S.L. 2003. Distribution, modes of attachment and heat tolerances of *Nodilittorina* sp. and *Littoraria* sp. at Labrador Beach and Tanjong Chek Jawa. Honours Thesis. Nanyang Technological University, Singapore. 118 pp.
- Little, C. & Kitching, J.A. 1996. *The Biology of Rocky Shores*. (Oxford University Press: New York). 240 pp.
- McMahon, R.F. 1990. Thermal tolerance, evaporative water loss, air-water oxygen consumption and zonation of intertidal prosobranchs: a new synthesis. *Hydrobiologia* **193**: 241–460.
- McMahon, R.F. & Britton, J.C. 1991. The relationship between vertical distribution, rate of evaporative water loss, behaviour during emergence and morphometrics in six species of rocky shore gastropods from Princess Royal Harbour, Western Australia. Pp. 675–692. In, Wells, F.E., Walker, D.I., Kirkman, A.H. & Lethbridge, R. *Proceedings of the 3rd International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia, Vol. II*. (Western Australia Museum: Perth).
- McMahon, R.F. 2001. Acute thermal tolerance in intertidal gastropods relative to latitude, superfamily, zonation and habitat with special emphasis on the Littorinoidea. *Journal of Shellfish Research* **20**: 459–467.
- McQuaid, C.D. & Schermann, P.A. 1988. Thermal stress in a high shore intertidal environment: morphological and behavioural adaptations of the gastropod *Littorina africana*. Pp. 213–224. In, Chelazzi, G. & Vannini, M. (Eds), *Behavioural Adaptation to Intertidal Life*. (Plenum Press: New York).
- MINITAB, Inc., 2003. MINITAB User's Guide 2: Data analysis and quality tools. Release 14 for Windows. State College, PA, USA.
- Minton, D. & Gochfeld, D.J. 2001. Is life on a tropical shore really so hard? The role of abiotic factors in structuring a supralittoral molluscan assemblage. *Journal of Shellfish Research* **20**: 477–483.
- Newell, R.C. 1979. *Biology of Intertidal Animals*. (Marine Ecological Surveys Ltd., U.K.). 781 + ix pp.
- Nybakken, J.W. 2001. *Marine Biology: an Ecological Approach*. 5th edition. (Benjamin Cummings: San Francisco). 516 pp.
- Raffaelli, D. & Hawkins, S. 1996. *Intertidal Ecology*. (Chapman & Hall: New York). 356 pp.
- Stirling, H.P. 1982. The upper temperature tolerance of prosobranch gastropods of rocky shores at Hong Kong and Dar Es Salaam, Tanzania. *Journal of Experimental Marine Biology and Ecology* **63**: 133–144.
- Underwood, A.J. 1973. Studies on zonation of intertidal prosobranch molluscs in the Plymouth region. *Journal of Animal Ecology* **42**: 353–372.
- Vermeij, G.J. 1971a. Substratum relationships of some tropical Pacific intertidal gastropods. *Marine Biology* **10**: 315–320.
- 1971b. Temperature relationships of some tropical Pacific intertidal gastropods. *Marine Biology* **10**: 308–314.
1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology* **53**: 693–700.
1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Marine Biology* **20**: 319–346.
- Wada, S. & Ito, A. 2000. Preliminary observation on "tip-lip" attachment in the periwinkle *Nodilittorina radiata*. *Bulletin of Marine Science and Fisheries, Kochi University* **20**: 15–24.