Respiratory Adaptation in *Littoraria angulifera*

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Littoraria angulifera (Lamark, 1822), inhabiting mangrove trees well above the extreme high tide mark, is rarely submersed by high tides. Emersed individuals remain inactive for extended periods and feed only during very high relative humidity or when tree trunks and branches are moistened by condensation, rainfall or wave splash. When moistened, snails begin grazing within minutes on bark epiphytic lichens and algae. Littorinids inhabiting high rocky shores display a number of respiratory adaptations to prolonged emersion, including suppression of O_2 uptake at elevated temperatures and during emersion. In contrast, the respiratory adaptations of mangrove littorinids are unknown. Therefore, the respiratory responses of *L. angulifera* to emersion, submersion, temperature variation and hypoxia were examined.

Specimens of *L. angulifera* were collected from mangrove trees at New Pass, 20 km North of Naples, in southwestern, Florida, USA. They were returned overnight to the University of Texas at Arlington and maintained in 57 % artificial sea water (20 ppt) for > 14 days at either 15 °C or 25 °C. After acclimation, the O_2 consumption rate ($\overset{\circ}{V}O_2$) of 15 individuals was determined in air (emersed) or water (submersed in 20 ppt seawater) at 10, 15, 20, 25, 30, 35, 40 and 45 °C with oxygen electrodes. $\overset{\circ}{V}O_2$ was also determined for six snails from each acclimation group in 20 ppt seawater at 15 ° and 25 °C during progressive hypoxia.

Multiple Analysis of Variance (MANOVA) indicated no correlation between dry tissue weight and weight specific $\overset{\circ}{V}O_2$ ($\mu l\ O_2\ mg^{-1}h^{-1}$) (P = 0.415). $\overset{\circ}{V}O_2$ was depressed in emersed individuals (P = 0.0037). Temperature also significantly effected $\overset{\circ}{V}O_2$ (P<0.00001). $\overset{\circ}{V}O_2$ in submersed and emersed individuals increased with temperature up to 30 °C. Above 30 °C, $\overset{\circ}{V}O_2$ was regulated, with little further increase in $\overset{\circ}{V}O_2$ recorded over 30-45 °C. Regulation of $\overset{\circ}{V}O_2$ above 30 °C is characteristic of littorinid snails, allowing conservation of energy stores during prolonged exposure to elevated temperatures in upper eulittoral fringe/maritim habitats.

MANOVA indicated that emersed snails acclimated to 25 °C had elevated $\overset{\circ}{V}O_2$ relative to 15 °C acclimated snails (P = 0.0001), a metabolic response termed "reverse acclimation". A similar tendency (P = 0.10) occurred in submersed individuals. Reverse acclimation is believed to allow cold acclimated individuals to conserve energy stores during prolonged winter inactivity.

$\overset{\circ}{V}O_2$ values over progressive hypoxia were standardized as ratios of the rate at full air $\overset{\circ}{V}O_2$ saturation. MANOVA of these values indicated that neither acclimation temperature (P = 0.133) or test temperature (P = 0.231) significantly effected ability to regulate standardized $\overset{\circ}{V}O_2$ with progressive hypoxia. Standardized $\overset{\circ}{V}O_2$ values (dependent variable) were fitted to a quadratic equation against PO_2 (Torr) (independent variable) for each tested individual. The quadratic

coefficient or b_2 value (i.e., Standardized $\mathring{V}O_2 = a + b_1(PO_2) + b_2(PO_2)$ becomes increasingly negative as capacity for regulation of $\mathring{V}O_2$ increases. MANOVA of $b_2 \times 10^3$ values suggested that acclimation to 25 °C significantly increased capacity to regulate $\mathring{V}O_2$ (P = 0.053). However, overall capacity of *L. angulifera* for O_2 regulation is not exceptional, average $b_2 \times 10^3$ values indicating nonregulation to good regulation over tested conditions. Lack O_2 regulation of $\mathring{V}O_2$ is characteristic of littorinid snails (McMahon, 1992), reflecting the essentially aerobic nature of their upper eulittoral fringe/maritime zone habitats.

The phylogenetic relationships of *Littorina striata* as deduced from allozyme data

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Recently, Backeljau & Warmoes (1992) assessed the phylogenetic relationships of ten Atlantic Littorinidae using two tree making methods (UPGMA and Distance Wagner) applied on three genetic distances inferred from allozyme data. It was concluded that (1) *Melarhaphe* and *Littorina* are only distantly related, (2) *Littorina striata* clusters with *Littorina*, (3) the generally accepted relationships between *L. littorea, L. obtusata* complex and *L. saxatilis* complex are supported and (4) *L. saxatilis* is a sister group to *L. arcana* + *L. nigrolineata*. In addition, it appeared that the Distance Wagner method, which is free of molecular clock constraints, performed better than UPGMA (which relies on a molecular clock).

In the present contribution we use the data set of Backeljau & Warmoes (1992) to evaluate in how far other evolutionary rate independent tree making methods support these conclusions. These methods include (programs used in parentheses) : Neighbor-joining (NEIGHBOR), Fitch & Margoliash (FITCH), Maximum Likelihood (CONTML) and Parsimony (MlX, PENNY, IE* + BB*) as implemented by the algorithms of PHYLIP 3.4 and HENNIG86. Parsimony trees were bootstrapped to place confidence limits on the branching points. We also assessed to what extent different data input orders affected tree topologies, including those obtained by UPGMA. This latter was tested using a data set published by Janson (1985).

Following observations were made : (1) different genetic distances provoke different topologies, even when subjected to the same tree making method ; (2) none of the methods used recovered completely the topology of the Distance Wagner tree presented by Backeljau & Warmoes (1992) ; (3) parsimony analysis confirmed the "traditional" branching pattern within the *L. saxatilis* complex (*L. nigrolineata* is sister taxon to *L. saxatilis* + *L. arcana)*, but placed *L. striata* at the base of the tree ; (4) the maximum likelihood tree did the same, but confirmed the Distance Wagner tree with respect to the relationships within the *L. saxatilis* complex ; (5) both Neighbor-joining and Fitch & Margoliash trees yielded a wide array of tree topologies, but only when Cavalli-Sforza's chord distance was