

Lack of Metabolic Temperature Compensation in *Littorina saxatilis* and *L. obtusata*

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Two intertidal snails, *Littorina saxatilis* (Olivi, 1792) (upper eulittoral fringe/maritime zone) and *Littorina obtusata* (Linnaeus, 1758) (lower eulittoral) were collected from a boulder shore on Nobska Point, Cape Cod, Massachusetts, in July and were acclimated for 15-20 days at 4° or 21°C. Thereafter, O₂ consumption rate ($\dot{V}O_2$) was determined for subsamples of individuals (n = 11-15) at 4°, 11° and 21°C with silver/platinum oxygen electrodes. Plotting of animal dry tissue weight (DTW, X axis) against whole animal $\dot{V}O_2$ revealed a high degree of overlap of points between 4°C and 21°C acclimated individuals in both tested species at all test temperatures, indicating an apparent lack of capacity to temperature compensate metabolic rates. Multiple analysis of variance (MANOVA) of log₁₀ transformed values of whole animal $\dot{V}O_2$ with log₁₀ DTW values as a covariant revealed that test temperature significantly affected $\dot{V}O_2$ in both *L. saxatilis* (P<0.00001) and *L. obtusata* (P<0.00001) with increased test temperature resulting in an increased oxygen consumption rate. In contrast, MANOVA revealed that temperature acclimation did not affect $\dot{V}O_2$ in either *L. saxatilis* (P = 0.35) or *L. obtusata* (P = 0.095). Thus, neither species displayed a capacity for the typical metabolic temperature compensation (i.e., increase in $\dot{V}O_2$ at any one test temperature in individuals acclimated to a lower temperature) characteristic of most ectotherms.

Lack of capacity for typical metabolic temperature acclimation also has been reported for *Littorina littorea* (Linnaeus, 1758) and *Littoraria angulifera* (Lamarck, 1822), suggesting that it may be characteristic of intertidal littorinid species in general. Lack of capacity for respiratory temperature acclimation may reflect the extraordinary semi-diurnal temperature variation that littorinid snails are exposed to in their eulittoral and upper eulittoral fringe/maritime zone habitats where any metabolic benefits derived from longer-term temperature compensation are negated by extreme daily temperature variation. Instead, littorinid species have evolved other mechanisms of immediate metabolic regulation. In all littorinid snails examined to date, including *L. saxatilis* and *L. obtusata*, such adaptations appear to center on a unique ability for near instantaneous suppression of metabolic rate and entrance into short-term metabolic diapause at temperatures above 25-35°C. As such, typical seasonal respiratory compensation mechanisms may be of little adaptive value to littorinid species.

Community ecology of littorinid snails

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The Littorinidae is a cosmopolitan family of intertidal and shallow subtidal mesogastropod snails which are extremely abundant in many ecosystems. Most members of the family

fall into one of three feeding types and this paper synthesises the literature on the community ecology of the most intensively studied examples of each type.

Epilithic grazers feed directly off hard substrata, mainly eating microalgae, including the sporelings of macroalgae. They can also feed on ephemeral macroalgae. Low shore species have a stronger influence on the community, but the effects of grazing depend very much on snail density. Epilithic grazers affect perennial algae indirectly by removing ephemeral species and reducing competition for space or light. They also influence the recruitment of perennials as mature algae often represent sporelings which have "escaped" grazing and have grown to a size at which they are no longer vulnerable to grazers.

Macroalgal grazers live on, and eat perennial macroalgae. They affect canopy forming perennials directly by grazing and influence ephemeral algae indirectly by reducing canopy shading. Unlike epilithic grazers their effects on the community depend not as much on grazer density as on the fine details of the interaction between grazer and alga. These include the part of the plant which is eaten, the seasonality of grazing pressure and the population dynamics of both grazer and alga. Macroalgal grazers can devastate canopy species with subsequent effects on understory algae. But at similar densities the same grazer can have very little effect on another canopy species.

Epiphytic/detrital feeders live on macrophytic plants (usually angiosperms), but do not feed on them. They may graze epiphytes from their surface, or feed on dead, standing material rather than the living plant itself. They have no direct effect on plant abundance or distribution, but may reduce epiphytic shading and can have a very important role in the community through recycling nutrients and energy from detrital material.

Shape variation in *Littorina saxatilis* along the west coast of Britain.

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Previous work on shell shape in *Littorina saxatilis* (Grahame & Mill, 1989, 1992; Grahame, Mill & Brown, 1990) has indicated that, not only is there local adaptive variation in shape, but that there are geographical variations which may take the form of clines, and/or involve character displacement when the species is sympatric with *Littorina arcana*.

Data from 23 sites on the west coast of Britain, totalling 35 samples and 606 shells of female *L. saxatilis*, indicate strong correlations between the various measurements of aperture size (aperture width and length, and operculum area) as would be expected; also between columellar length and the width of the second whorl. Negative correlations occurred between lip length and aperture width, lip length and operculum area, apical angle and columella length, and apical angle and the width of the second whorl.

Principal Component analysis indicates that 81 % of the variation in the raw, log-transformed data can be accounted for primarily by size. However, the removal of size as a primary source of variation, by use of the geometric mean, has revealed some interesting trends. At the southern end of the range PC1 (which accounts for 38.6 % of the variation)