

The activity of Aat and a related enzyme alanine aminotransferase (Alat E.C. 2.6.1.2) was determined from crude tissue homogenates of *L. saxatilis*, *L. arcana*, *L. littorea*, *L. obtusata* and sympatric small *L. saxatilis* and *L. neglecta* forms. In all the species Aat activity was inversely related to body wet weight and was greater than Alat activity. *L. saxatilis* (both forms) and *L. arcana* showed proportionally more Alat activity than the other species. The sympatric small *L. saxatilis* and *L. neglecta* forms showed no difference in Aat activity, but the *L. neglecta* form contained significantly less Alat activity than the small *L. saxatilis* (t-test, $P = 0.02$). Using ANOVA, we found a significant difference in mean enzyme activity between the species, Aat, $P = 0.031$ and Alat, $P = 0.001$.

After heat treatment at various temperatures Aat appears to be more heat labile than Alat. High shore *L. saxatilis* showed the greatest heat stability; how shore and small *L. saxatilis* were more heat stable than *L. arcana*, *L. littorea*, *L. obtusata* and *L. neglecta*. The enzymes were distributed throughout the body tissues, but the kidney of *L. saxatilis* contained at least twice the activity of both enzymes than was found in the kidneys of the other taxa (except in the case of *L. neglecta*, which has yet to be determined).

The rate of ammonia excretion correlated with Aat activity in *L. saxatilis*. Glutamate dehydrogenase levels were very low in all species, suggesting that the major route of catabolism of aspartate to ammonia is via the purine nucleotide cycle rather than the transdeaminase pathway (Sollock, Vorhaben & Campbell 1979).

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Dispersal and population expansion in a direct developing marine snail (*Littorina saxatilis*) following a severe population bottleneck

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The littorinid snail *Littorina saxatilis* (Olivi) has no pelagic larval phase and is therefore thought to be an organism of poor dispersal. Nevertheless, this species inhabits small intertidal skerries on the Swedish west coast, which are of a recent geological origin due to post-glacial land elevation. We report the effects of an extremely dense bloom of the toxic-producing flagellate (*Chrysochromulina polylepis*) in May 1988. During the bloom of this flagellate all *Littorina saxatilis* of intertidal skerries and nearly all individuals living in moderately to extremely wave exposed shores were killed in the study area (the south part of the Koster archipelago in the northern part of the Swedish west coast).

Almost all intertidal skerries visited before the flagellate bloom had populations of *Littorina saxatilis*. Exposed intertidal skerries had, however, more dense populations than protected intertidal skerries although the former category were more remote from the nearest islands than was the latter. The bloom eliminated the snail populations of all of 34 stu-

died skerries. Four years later four of the skerries had been successfully recolonized, and another five had received a few founder snails.

More than 99 % of the snail populations in island shores were also eliminated. But due to the fact that a small number of island individuals survived, densities of snails were restored over two to four years in these sites. Island populations expanded very rapidly in areas where a few snails had survived the bloom, and the snails dispersed at a rate of approximately 5 m per month into uninhabited pieces of shore.

We conclude that over a reasonably short time *Littorina saxatilis* is able to colonize all potential habitats of, for example, an archipelago as the one studied. Although we do not know the mechanism of dispersal we suggest that successful colonization of an island habitat may be accomplished by the dispersal of small founder groups, perhaps only one single fertilized female.

Morphological differentiation and genetic cohesiveness over a micro-environmental gradient in *Littorina saxatilis*

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The marine gastropod *Littorina saxatilis* has different ecotypes in shores only a few meters apart. This has both taxonomic and evolutionary implications. Here we report of an extreme type of within-shore dimorphism in shell characters (Johannesson *et al.*, in press). In the wave-exposed rocky shores in northwestern Spain, we found one form of *L. saxatilis* in the upper-level barnacle zone. It had a white, ridged shell, with black bands in the grooves. Another form confined to the lower-shore mussel belt had a smooth shell that was either white and tessellated or darkly colored. These two forms co-occurred in a narrow mid-shore zone together with individuals that had combined characters, but were present in low frequencies (11 - 29 %). We used principal component analysis of metric shell characters to study variation in shell size and shape. We found that the upper-shore form was larger than the lower-shore form. We also found small but significant differences in shell shape. Experiments in a common laboratory environment suggested the differences in shell ornamentation and color to be inherited, but the individuals did not develop the morph-specific characters until a shell height of about 3 mm. The occurrence of mainly two distinct forms may suggest two species being present that hybridize. An analysis of five polymorphic enzyme loci in populations of snails from three geographically separated sites indicated, however, that there was no positive correlation between morphological distances and genetic distances among populations on a geographic scale (tens of kilometres). Thus we rejected the hypothesis of two species. However, on a micro-geographic scale (meters), genetic differentiation between groups with the same form was less than differentiation between forms. This indicated a partial barrier to gene flow between the two forms, and mate choice data suggest this to be due to non-random mating in the mid-shore zone of overlap (Johannesson *et al.* in prep.).