

vicariant (large-subdivision) type. This contrasts with the peripheral isolation mode, widely believed to predominate on land. Most littorinids have planktotrophic larvae and are presumably widely dispersed, perhaps explaining why peripheral isolation is relatively rare. Island endemics are found only on the most isolated islands, such as Hawaii, Easter and Juan Fernandez.

There is no clear evidence for parapatric speciation ; stepped clines which may precede this process have not been described in littorinids, and sister species are rarely distributed parapatrically. Sympatric speciation remains a possibility, particularly in direct-developing species. Two theoretical models of sympatric speciation along an exposure gradient have been produced, but have only suggested that stable polymorphisms can be achieved (Boulding, 1990 ; Johannesson & Sundberg, 1992). In fact, sympatric sister species do not generally show the habitat differentiation that this mechanism is expected to produce. The high frequency of sympatry among sister-species pairs may be the result of dispersal following speciation in allopatry.

The only well-documented cases of speciation in Littorinidae concern the trans-Arctic migration of *Littorina* species from the Pacific to the Atlantic following the opening of the Bering Strait 3.5-4 My ago (see Rumbak, Reid & Thomas, this volume).

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## The contribution of mating behaviour to the reproductive isolation : the example of the Galician *L. saxatilis* populations

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Mating is usually one of the main behaviours capable of producing prezygotic reproductive isolation between incipient species. Mating behaviour mechanisms which may contribute to productive isolation can be partitioned in three additive and independent components : mating success for males (male sexual selection), mating success for females (female sexual selection), and assortative mating (sexual isolation) (Spieth & Ríngo, 1983). These three components can present different contributions and can be caused by different biological mechanisms.

Two different morphs of *L. saxatilis* coexist in different vertical habitats of Galician exposed shores. However, both pure morphs overlap with hybridization in midshore areas. Disruptive selection acting on the original population has probably caused the distribution of these two pure morphs (Johannesson *et al.*, in press).

The mating behaviour of *L. saxatilis* was studied in natural populations of upper, mid and lower shore areas (Johannesson *et al.*, in preparation). Copulating mating pairs and non-copulating snails surrounding the former were sampled in order to estimate the three different mating behavioural components. A conspicuous assortative mating between both

pure morphs was found in the two sampling areas. However, both pure morphs mated at random with the hybrid morph. A female hybrid sexual disadvantage also contributed to the incipient reproductive isolation between both pure morphs, but no such trend was found in males. The assortative mating behaviour and the female sexual selection components were probably caused by different biological phenomena.

These results confirm the conspecific status of the *L. saxatilis* Galician morphs, but also suggest the possibility of a further evolving towards complete speciation. The division of mating behaviour in three independent components represents a useful tool for the study of the reproductive isolation between incipient species.

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## Phylogenetic reconstruction of the genus *Littorina* using mitochondrial DNA sequence data

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A gene phylogeny of eighteen of the nineteen known species of *Littorina* was reconstructed using sequence data from three mitochondrial genes (small ribosomal RNA gene, large ribosomal RNA gene and cytochrome *b* gene). Using the sister genus *Nodilittorina* as the outgroup, the monophyly of the genus *Littorina* was supported. The problematical species *L. striata* was resolved in a basal position within *Littorina*, supporting classification in this genus. Data from one species of the enigmatic tropical genus *Mainwaringia* showed that it was not closely related to *Littorina*. Within *Littorina*, the terminal pairings of *L. brevicula* and *L. mandshurica*, *L. squalida* and *L. littorea*, *L. sitkana* and *L. horikawai* were resolved, as was the monophyly of the species of the subgenus *Neritrema* in the Atlantic. However, the branching sequence in the middle region of the tree was poorly resolved, suggesting that perhaps a short period of rapid cladogenesis may have taken place at this point in the phylogenetic history of the group. The phylogenetic trees generated from the sequence data are consistent with a revised morphological cladogram for the genus (Reid, 1990a and in prep.). The molecular phylogeny shows that the northern Atlantic species were derived from a minimum of two Pacific ancestors, supporting the hypothesis of trans-Arctic migration of this genus (Reid, 1990b).

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## Researches on the demecology of two species of Pacific *Littoraria* (Gastr. Pros.)

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