In a comparison between the two seasons (one non-mating and one mating) we measured trail complexity of non-sexed snails with fractal dimension, the degree of mucous trail following (coincidence index of marker and tracker trails) and average movement speed of marker and tracker snails. We found no differences of fractal dimension and coincidence index of trails between the two seasons. Tracker snails moved significantly faster than marker snails during both seasons. This, however, could not be explained by trackers using the mucous trail deposited by the marker to increase their speed passively, since there was no correlation between coincidence index and tracker speed.

During the mating season we also conducted trail complexity-, trail following- and speed experiments comparing the behaviour of males and females. There was no difference between male and female speed, and between males and females in the fractal dimension of movement. Furthermore, males tracking other males, females tracking other females and females tracking males followed trails about equally long distances (i.e. coincidence indices did not differ). In contrast, males following female mucous trails (female marker-male tracker) showed a significantly higher degree of trail following than the other sex combinations. This new finding implies that females of *L. littorea* release pheromones in their mucous trails and that males are able to identify them.

Microgeografical variation in shell strength in the flat periwinkles *Littorina obtusata* and *L. mariae*

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The strength of molluscan shells has been shown to vary in adaptive ways in a number of species and one of the main factors thought to be involved is shell-crushing predators (Vermeij, 1978, Vermeij & Currey 1980). In a recent study (Lowell *et al.,* 1993) the sibling species of flat periwinkle *L. obtusata* and *L. mariae* were shown to show significant differences in the rates at which shell strength increased with size in specimens which had been collected from the same location, where the species were sympatric.

A comparative study of the two species from a number of localities around Milford Haven in Pembrokeshire, Wales showed that whilst the modal sizes (maximum shell diameter), heights (minimum shell diameter), and shell masses of the two species differed markedly there was relatively much less difference in strength. In order to facilitate study of the power law relationships which are usually involved in morphometric studies the natural logarithms of the data were analysed. As the animals grow shell mass increases isometrically with size in *L. obtusata* (i.e. mass increases in proportion to the cube of size), but it increases faster than isometrically in *L. mariae*. Thus at all but the smallest sizes the shell of *L. mariae* is more massive than that of a similar sized *L. obtusata.*

Shell strength, determined as the maximum force applied by a hydraulic tensile testing machine before the shell cracked, showed considerable variability, both geographically and between species. Strength increases at a rate not significantly different to the cube of size in both species in this study ; shell strength is thus strongly positively allometric since the isometric exponent is 2. *L. mariae* is markedly stronger than *L. obtusata* of similar sizes.

Strength varies significantly from shore to shore, and with the level on the shore from which the animals were collected. These differences become highly significant when allowance is made for variation in the sizes of the animals, which was effected using the model II (also termed reduced major axis or geometric mean) regression coefficients between ln(strength) and ln(shell size). Strength increases down the shore in both species. There is a very significant rank correlation between corrected strength of the shells and the exposure index of the shore in both species, but this does not fully account for shore-to shore variation. Furthermore the sign of the correlation differs between the species ; the corrected strength decreases with exposure in *L. mariae* but increases in *L. obtusata*.

The logarithm of shell strength is more closely correlated with ln(shell mass) than with ln(shell strength) in both species. However path analysis of the relationships between the natural logarithms of the measured variables indicates that a better predictor of ln(shell strength) is a parameter which is heavily positively loaded on ln(shell mass) and strongly offset by a negative loading on ln(shell size). Such a combination of ln(size) and ln(shell mass) with loadings of 2.3 and -1.3 times the respective model II regression coefficients accounts for 83 % of the variation in *L. mariae* compared with 62 % using ln(size) alone, and the remaining variation does not contain any significant dependence on the shore or on the zone and shows only a residual sexual dimorphism. Similar treatment accounts for 77 % of the variation in the strength of *L. obtusata* compared with under 50 % using ln(size) alone. The variation between shores and that between zones are reduced by more than 90 % (although they remain significant in this species), and the other identified sources of variation in this species, maturity and parasitism are similarly largely explained.

Thus most of the observed variation in strength from shore to shore and with tidal zone may be explained by the two measures, maximum shell size and shell mass used with appropriate loadings.

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Shape, size and enzymes : the problem of *Littorina neglecta*

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Among the rough periwinkles on European shores there occur small, barnacle-dwelling individuals. In many instances these may be simply juveniles of the three large species. However there are sexually mature individuals as well, and Reid (1993) has suggested that *Littorina saxatilis, L. arcana* and *L. nigrolineata* are all capable of producing forms which may mature at a small size. In view of this, Reid concluded that the evidence was consistent with *L. neglecta* being a barnacle-dwelling ecotype of *L. saxatilis*. In earlier work, Johannesson & Johannesson (1990) examined material from Wales, the Isle of Man, Iceland and Sweden, and concluded that *L. neglecta* was an ecotype of *L. saxatilis*, and that there was gene flow between the populations on any one shore.