

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*

Kerstin Johannesson¹, Bo Johannesson¹ and Emilio Rolán-Alvarez²

1) Tjärnö Marine Biological Laboratory, S 452 96 Strömstad, Sweden

2) Departamento de Biología Fundamental, Facultad de Biología,
Universidad de Santiago de Compostela, Santiago de Compostela, Spain

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.).

REFERENCES

- JOHANNESSON, K., B. JOHANNESSON and E. ROLÁN-ALVAREZ. Morphological differentiation and genetic cohesiveness over a micro-environmental gradient in the marine snail *Littorina saxatilis*. *Evolution* (in press).
- JOHANNESSON, K., E. ROLÁN-ALVAREZ, E. and A. EKENDAHL. Incipient reproductive isolation between two sympatric morphs of the intertidal snail *Littorina saxatilis* (in prep.).

A morphometric and genetic comparison between *Littorina obtusata* (L.) from the UK and the high-spired form *Littorina palliata* (Say) from Iceland

R. I. Lewis¹ and Gray A. Williams²

1) University College of Swansea, School of Biological Sciences, Singleton Park, Swansea, SA2 8PP, UK

2) Dept. of Botany and Swire Marine Laboratory, University of Hong Kong, Cape d'Aguilar, Hong Kong

In intertidal gastropods which do not disperse larvae in the plankton, shell shape is often highly variable. Many factors have been shown to influence shell morphology, such as predation, exposure, pollution, heritability, parasitism, and growth rate.

Over its range in the northern Atlantic *Littorina obtusata* (L.) shows geographic variation in shell morphology. Some authors have referred to high-spired northern forms as *L. palliata* (Say) (e.g. Thorson 1941, Hubendick & Warén 1975), whilst others have considered them as variants of *L. obtusata* (e.g. Colman 1932, Knudsen 1949, Seeley 1986).

During the summer of 1989, samples of high-spired forms were collected from Grótta, Seltjarnarnes Cape, Iceland (64°10'N, 22°03'W), and S.W. Borgarnes, Iceland (64°33'N, 21°53'W). Low-spired forms were collected from St. Michael's Island off the Isle of Man (54°05'N, 4°33'W). Morphological differences between sites were investigated using a multivariate discriminant function analysis. The shell parameters length, height, and aperture width (after Goodwin & Fish 1977) were chosen as function variables. Genetic variability was also assayed using standard starch gel electrophoresis techniques (e.g. Ferguson 1980) at 13 allozyme loci. The discriminant analysis showed almost complete morphological separation among the three samples. A Chi-square test based on the transformed Wilks' Lambda statistic (for all functions) was highly significant ($P < 0.001$) indicating that mean values for discriminant scores were highly heterogeneous between the three samples. The shell parameter with the highest correlation with discriminant function scores for function 1 (which accounted for approximately 90 % of total between groups variance in discriminant scores) was aperture width, indicating that this is the most diagnostic of the three variables.

Genetic analysis revealed that the most distant relationship (between the Grótta and Isle of Man samples) was surprisingly close (Nei's (1972) $I = 0.983$). Thus we have no evidence in this study to suggest that the northern high-spired *L. palliata* form from Iceland is not conspecific with *L. obtusata* from the UK.

REFERENCES

- COLMAN, J., 1932. *Biol. Bull. mar. biol. Lab. Woods Hole* 62 : 223-243.
- FERGUSON, A., 1980. Biochemical systematics and evolution (Glasgow, Blackie).
- GOODWIN, B. J. & J.D. FISH, 1977. *J. molluscan Stud.* 43 : 241-251.
- HUBENDICK, B. & A. WARÉN, 1969-76. *Framgållade Snäckor från Svenska Västkusten. Göteborg Naturhistoriska Museum.* 36-43.
- KNUDSEN, J., 1949. *Vidensk. Meddr. dansk. naturh. Foren.* 111 : 247-255.
- NEI, M., 1972. *Am. Nat.* 106 : 283-292.
- SEELEY, R.H., 1986. *Proc. Nat. Acad. Sci. USA.* 83 : 6897-6901.
- THORSON, G., 1941. in *The Zoology of Iceland*, Vol. 4 : 1-150.