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Inheritance of a shell-color polymorphism in the mussel

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SHELL-COLOR polymorphisms are known to exist in several molluscan species[2]. Most studied is probably the land snail, *Cepaea nemoralis*, which exhibits a few distinct morphs based on shell color and banding pattern[1]. These visual polymorphisms allow field populations to be characterized by their phenotypic frequencies. Populations from different geographical regions can therefore easily be compared with respect to observed morph frequencies. Such ecological genetic investigations have made a large contribution to the understanding of the mechanisms maintaining population polymorphisms under natural conditions.

Using shell-color morphs to study ecological genetics of molluscs implies an underlying genetic basis for the polymorphism. Environmental factors, such as diet, are known to influence shell color[7]. Circumstantial evidence, such as the color of newly repaired shells, has been used to indicate its genetic determinism[4]. But the best way to understand the genetics of any character obviously is through selected crosses and observation in the F_1 generation.

Shell color in the common mussel, *Mytilus edulis*, is predominantly black. The occurrence of a brown form, which actually ranges from pure brown to almost black, except for a small brown patch near the umbone (see cover), has been noted. A striped phenotype was also observed, where brown and black stripes of varying thickness run along the length of the shell. Information on the genetic basis of such a color polymorphism should be easily sorted out by performing the appropriate crosses.

Materials and Methods

Adult mussels were collected about the time of natural spawning from a single population located in a sheltered bay at Ostrea Lake, Nova Scotia. Observation of the phenotypes from this population showed black at a frequency of 0.95, brown 0.02 and various other individuals with a mixed brown and black shell color (including stripes) making up the remaining 0.03 (N = 1257).

Sexually mature mussels release large quantities of eggs or sperm into the surrounding water, allowing for multiple matings between separate individuals. Crosses were originally made for experiments designed to investigate the genetics of growth rate during the free-swimming larval stage[5]. Five half-sib families were produced by crossing a single female with five different males. A sixth family was produced by a cross between a second female and the fifth male in the first cross. These families were maintained under identical conditions in running sea water and regularly fed a suspension of algae (*Tetraselmis* sp.).

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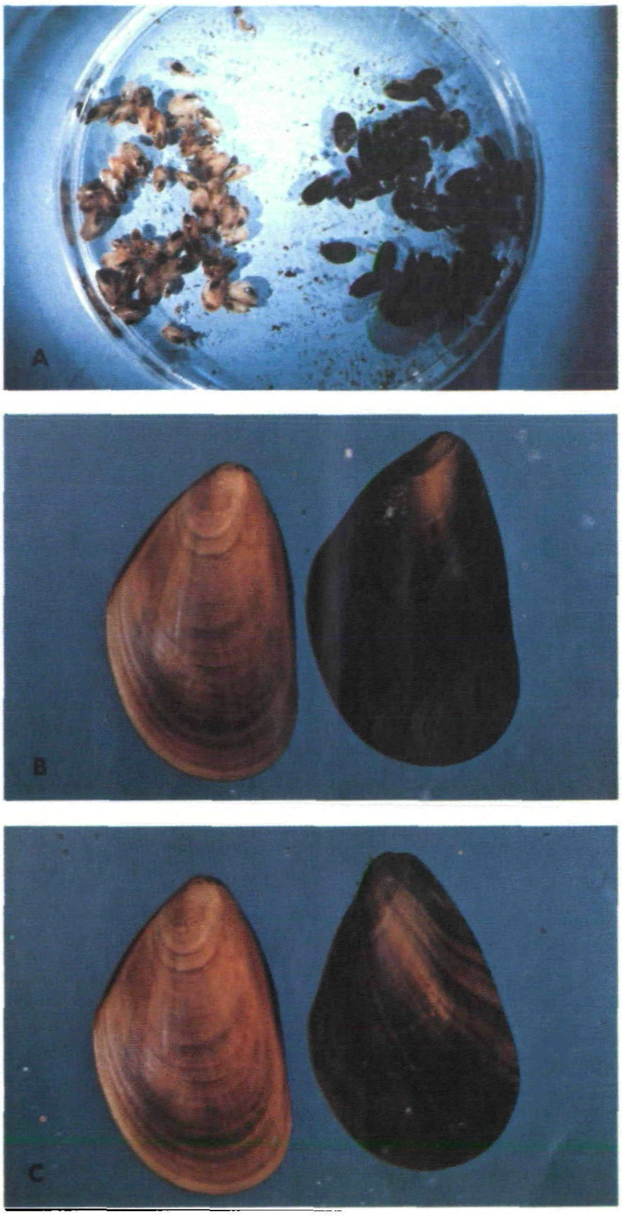

FIGURE 1—*A* shows 1:1 segregation of brown and black 5–10 mm mussels in family 3; *B*—mature brown and black mussels from family 3; mature brown and striped mussels from family 6.

Results and Discussion

After the larvae had settled as spat and grown to a size of about 5–10 mm, a clear-cut segregation of shell color was observed in each family (Figure 1). Table I summarizes the available data. These families were

The brown and black morphs are clearly a result of genotypic differences. Using the limited information from Table I, a single-gene two-allele model is proposed to explain the results, brown being dominant over black. If this is true, female 1 should have been brown (*Bb*), male 1 brown (*Bb*) and male 2 brown (*Bb*). The expected genotypes of males 3, 4, and 5 (*bb*, *bb*, *Bb*) conform to the observed shell colors. The cross between female 2 and male 5 produced approximately equal numbers of brown and striped progeny. If female 2 was brown with a *BB* genotype we would expect an all-brown family to conform to our model. The occurrence of a striped form may indicate a second gene that controls the striped phenotype.

Since large adults in the field exhibit various patterns of brown shell color, it is of interest to know if the individuals in our families that are brown when they are small remain pure brown as they grow larger. To test this, 10 individuals of each color from each family were placed in separate mesh bags and suspended in Ostrea Lake over the summer growing season. At the end of this period no modification of the original shell color was observed.

Summary

In populations of the mussel *Mytilus edulis* a brown shell phenotype occurs at a lower frequency than the common black phenotype. Crosses between individuals and observations on the shell color of the progeny indicate shell color appears to be the result of a single gene with the brown allele dominant over the black. The brown shell color may be modified by black stripes controlled by a second gene.

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Table I. Shell color of the F_1 generation of 6 families derived from 5 males crossed to a single female and a second female crossed to the fifth male. Observed counts and expected ratios assuming Mendelian inheritance of two alleles at the shell color locus

	Parental shell color		F_1 shell color				
	Female	Male	Brown	Black	Total no.	Expected ratio	χ^2†
1.		1*	154	62	216	3 : 1	0.8
2.		2*	59	24	83	3 : 1	0.7
3.	1*	3 Black	65	66	131	1 : 1	0.01
4.		4 Black	38	49	87	1 : 1	1.4
5.		5 Brown	143	55	198	3 : 1	0.8
6.	2*	5 Brown	29	22 striped	51	1 : 1	0.96

* Shell color unknown

† All χ^2 values not significant at $\alpha = 0.05$