

excess of homozygosity has repeatedly been observed in species of marine molluscs, including *Crassostrea*, *Littorina*, *Macoma*, *Modiolus* and *Mytilus*. Possible explanations for such an observation fall in four categories: inbreeding, presence of null alleles, Wahlund effect and selection. Species are in general dioecious with external fertilization and therefore avoid inbreeding. An excess of homozygosity has been observed for a number of enzyme loci. The presence of many common null alleles on all these randomly selected polymorphic loci is not likely. Aspects of the Wahlund effect (a consequence of sampling over populations which behaves as a separate Mendelian population), and selection are presented using data on *Crassostrea*, *Macoma* and *Mytilus*. The data on excess of homozygosity, presented here, has three special features: (1) The degree of excess is dependent on age and stage of development, with individuals of younger than of older age groups; (2) the degree of homozygosity has a negative correlation with growth rate and with metabolic efficiency; and (3) slow growing molluscs have a higher post-settlement mortality rate. Such an observation could not be explained by the Wahlund effect. These observations permit us to offer an hypothesis for the origin and persistence of excess homozygosity observed in these species with pelagic larvae. Depending on the species the larval period may range from three to four weeks after which they settle to form spat and grow to maturity. Further, the time to first spawning tends to be a function of size at settlement age, and individuals continue to reproduce after spawning as long as they stay in the population. This could be viewed as a form of balancing selection, where the relative fitness of homozygotes and heterozygotes is different during the pelagic larval phase from stages following settlement. Differential fitness based on development has been reported in other organisms.

#### POSSIBLE EXPLANATIONS OF HETEROZYGOTE DEFICIENCY IN MARINE MOLLUSCS. E. Zouros and D. W.

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Many studies of natural populations of marine molluscs have shown heterozygote deficiency at enzyme loci. This phenomenon is prevalent in an oyster population that we have studied for the last five years (Singh and Zouros, 1978; Zouros et al., 1980). Elsewhere, we have presented arguments against the hypothesis of inbreeding (Zouros et al., 1980) and population mixture (Zouros et al., submitted). We examine selection models that may generate heterozygote deficiency without genetic differentiation. In particular we consider the following three models. (1) Viability selection is reversed from the planktonic to the post-settlement stage. Under this model, heterozygote deficiency may appear in the population is scored after settlement but before selection is completed. The condition for this situation to occur is that the gene selected against in the larval stage be dominant (in its selective effect) over the gene selected for. Therefore, underdominance is not a necessary condition for heterozygote deficiency. (2) Viability selection is confined to the larval stage and is compensated by differential fecundity

in the adult stage. This model may generate post-settlement heterozygote deficiency and, again, for this event to occur there is no need for underdominance in larval viabilities. (3) This model considers genotype-dependent spawning time. When homozygotes spawn at different times than heterozygotes, there will occur in a population a heterozygote deficiency whose equilibrium value depends on the gene frequency and the coefficient of overlap between the spawning times of homozygotes and heterozygotes. Overdominance for fecundity will enhance the effect of genotype-dependent spawning. The models are based on the observation that in the American oyster, heterozygotes attain larger size, thus producing more gametes than homozygotes, and may also have lower postsettlement mortality rates. The genotypic and phenotypic data from a large one-year-old oyster cohort are used to test the plausibility of the models.

#### POPULATION GENETICS AND TAXONOMIC INFERENCE.

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Methods developed by molecular geneticists to separate isoenzymes have made available for study a large number of genetic loci. The appropriate population genetic analyses of these loci and their use in making taxonomic inferences is reviewed using specific examples.

Although there is a correlation between divergence at these loci and taxonomic divergence in well-studied groups, there is a high variance associated with measures of genetic divergence that limits the utility of these data in making taxonomic inferences concerning allopatric populations. Isoenzyme data are still of some use for classification of allopatric populations below the generic level. In these cases, the application of isoenzyme data generally follows criteria similar to those used for measures of morphological divergence. Description of allopatric species or subspecies based solely on isoenzymes can rarely be justified.

Different criteria are appropriate for making taxonomic inferences from isoenzyme data for sympatric populations of possible sibling species. In these cases, population genetic analyses of deviations of genotype frequencies from Hardy-Weinberg equilibrium expectations and maximum likelihood analyses of multilocus genotypes are appropriate.

#### GENETIC RELATIONSHIPS AMONG NORTH AMERICAN PLEUROBEMINI AND AMBLEMINI (BIVALVIA: UNIONIDAE) WITH EMPHASIS ON *ELLIPTIO*, *UNIOMERUS*, *ELLIPTOIDEUS*, AND *QUINCUNCINA*. George M. Davis, Academy of Natural Sciences of Philadelphia, Pennsylvania.

Allozyme analyses over 14 loci were used to assess the molecular genetic relationships among 39 populations pertaining to 24+ species. The distribution of species per genus was: *Elliptio*(14+), *Fusconaia*(2), *Uniomerus*(3), *Elliptoideus*(1), *Quincuncina*(1), *Megaloniais*(1), *Quadrula*(1). The outgroup comparator was *Lampsilis*(1; tribe Lampsilini). A matrix of Nei's genetic distances was used in multivariate procedures to produce a two dimensional diagram of OTU

projections on the first two Principle Components following 3D scaling; a Prim network was used.

The purposes of these analyses were: 1) to determine the relationships among species of *Elliptio* where several populations of lanceolate taxa with different shell phenotypes were involved; 2) to determine the relationships between *Uniomerus* and *Elliptio*; 3) to determine the relationships of *Elliptioideus* and *Quincuncina* to genera assigned to the tribes Pleurobemini and Amblemini (in: Davis and Fuller, 1980). No. 3 was done because of uncertainty of these relationships following immuno-electrophoretic studies (Davis and Fuller, 1980). Individual heterozygosity (H) and frequencies of polymorphism (P) were assessed in relationship to species and higher taxa. *Uniomerus* is divergent from *Elliptio* yet clearly in the same tribe, the Pleurobemini. The amount of genetic divergence among species of *Uniomerus* approximates the greatest divergence among species of *Elliptio*. *Elliptioideus* and *Quincuncina* group with other genera of the Amblemini. There appear to be three separate clades of lanceolate *Elliptio*. *Fusconaia succissa* and *F. flava* clearly belong in different genera.

Parameter H has high variance among species. Variance within a species is seen for *Elliptio complanata*;  $\bar{X} = .146 \pm .032$  (.119 - .214; N = 8). Lanceolate taxa of *Elliptio* had  $\bar{X}$  H of  $.096 \pm .047$  (.021 - .173). Topotype *E. lanceolata* had the lowest H, 0.021. Highest values of H were found in the *E. crassidens* group of related taxa:  $E_{Cr}^5$ , .212;  $E_{c28}$ , .214.

#### USE OF MOLECULAR GENETICS TO DISTINGUISH SPECIES OF THE GASTROPOD GENUS *CREPIDULA*.

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Populations of *Crepidula convexa* and *C. plana* were collected in mangroves near Ft. Pierce, Florida. They were found to differ from New England populations in the mode of larval development, although this character is not known to vary intraspecifically in the genus. Allozyme studies were conducted to assess the genetic differences between the Ft. Pierce and northern populations. Horizontal starch gel electrophoresis resolved 24 loci for about 100 individuals of each population. Two populations each of the Floridian *C. convexa* and *C. plana* were compared with three each of the same species from New England. To assess the typical amount of genetic difference within and between species, seven populations of *C. fornicata* and one each of Californian *C. onyx* and Brazilian *C. protea* were electrophoresed. The populations of *C. fornicata* clustered tightly, with Nei's distance values (D) of .003-.016. The two Floridian *C. convexa*

were separated by  $D = .008$  while the average separation of three populations of northern *C. convexa*'s was .054. The two groups coalesced at .745, using a simple unweighted averaging technique. For southern and northern *C. plana*, D values were .045 and .081, respectively; the groups coalesced at .393. *C. convexa* greater difference between regions is due to fixation of alternate alleles at 46% of the loci. *C. plana* is characterized more by large differences in allele frequencies; only 21% of the loci are fixed for alternate alleles. In both cases, many alleles are unique to one geographical region. These data demonstrate reproductive isolation between the Ft. Pierce and northern populations of both species, especially *C. convexa*. Because the populations are allopatric, electrophoretic data alone cannot conclusively delineate species. D values over .30 are strong indicators of speciation based on data from other taxa, but in this study, divergence between known species of *Crepidula* (e.g. *C. fornicata* and *C. plana*) was greater than that between either of the potential sibling species pairs being tested. Calculations based on Robers' distance gave similar results.

#### GENETIC POPULATION STRUCTURE AND BREEDING SYSTEMS IN TERRESTRIAL SLUGS OF THE FAMILIES ARIONIDAE, LIMACIDAE (MOLLUSCA: PULMONATA).

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Genetic variation detected by electrophoresis of enzymes was surveyed in populations of nine arionid species and seven limacid species of terrestrial slugs in Great Britain, Ireland, and France. In each family, average individual heterozygosity ( $\bar{H}_o$ ) varied widely across species, from zero to some (*Arion circumscriptus*, *A. silvaticus*, *A. intermedius*) 0.19 (*A. distinctus* and *Deroceras reticulatum*). Whereas no limacid slug studied to date has been found to lack genetic heterozygosity, our research indicates that four arionid species consist of monogenic (homozygous) strains (*A. intermedius*, *A. circumscriptus*, *A. fasciatus*, and *A. silvaticus*). This result suggests that self-fertilization is a less frequent breeding system in the Limacidae than in the Arionidae. The amount of heterogeneity in allele frequency among geographic samples of a species was not correlated with heterozygosity, but it was associated with breeding system. facultatively-selfing slugs (*A. ater*, *A. subfuscus*, and *A. laevis*) exhibit higher levels of allele frequency heterogeneity than do outcrossing species. In both the Limacidae and the Arionidae, the highly heterozygous species are major agricultural pests, whereas those with lower levels of heterozygosity occur in agricultural habitats less frequently or not at all.