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Selection, ecology and evolutionary adjustment within bivalve mollusc populations

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Distributional and experimental studies of protein polymorphisms of bivalve populations permit considerations of the rôles of migration and selection in evolution. Minimal variation in west coast North American *Mytilus californianus* populations, relative to greater geographic differentiation in east coast *M. edulis*, correlates with the relatively steep latitudinal thermal gradient of the east coast. Among-locality differences are probably due to local selection and differences in the genetic composition of larval immigrants. Ecological influences are indicated by correlations of genetic structure with intertidal height, hydrographic structure, and greater among-locality differentiation of the eurytopic *M. edulis* relative to the stenotopic *M. californianus* in the same region. Problems in determining experimentally the relative contributions of migration and selection are highlighted by a genetic difference in *M. edulis* within and outside Long Island Sound, U.S.A. A dramatic cline in allele frequency occurs over a distance easily traversed by the planktotrophic larval stage. The large amount of selection indicated, however, is not confirmed through shock-mortality experiments in the laboratory or among-genotype measures of physiological response such as growth. The within-sound populations may be more isolated than we now suppose, either through the estuarine flow of the sound or by the existence of physiological races of ecotypes. The establishment of such isolation would permit genetic difference to accumulate slowly.

Introduction

Adaptation in bivalve mollusc populations occurs against a background of changing environments and genetic variation in natural populations. Genetic polymorphism provides the spectrum upon which natural selection can operate and varying environments constantly shift the fitness of given genotypes. It is usual for the morphology of a bivalve mollusc, particularly the form of the bivalve shell, to be regarded as the culmination of a series of evolutionary events bringing bivalve form into equilibrium with environmental requirements. Similarly, patterns of diversity and species occurrence are thought to be indicators of environmental and evolutionary processes regulating speciation and extinction. The factors governing such evolutionary adjustments can only be elucidated with a thorough knowledge of the ecological and genetic context within which such evolutionary events occur.

Surveys of bivalves as different as *Tridacna maxima* (Ayala, Hedgecock, Zumwalt & Valentine 1973) and *Mytilus edulis* (Levinton & Koehn 1976) reveal high levels of genetic polymorphism, typical of most species surveyed to date (see Powell 1975). Ranging as high as 63.3 % polymorphism of all the examined loci and 20.2 % of the loci heterozygous per individual in *T. maxima*, such polymorphism is surprising in the light of traditional expectations of field populations consisting of wild-type genotypes, with little or no genetic variation. The explanation for the maintenance of such high genetic variability has been couched in two alternate hypo-

theses. The *neutralist* theory asserts that genetic variants at biochemical loci are selectively neutral and are maintained in populations as a balance among mutation, genetic drift and migration (Kimura & Ohta 1971). The *selectionist* theory asserts that functional differences among the isoenzymes provides the adaptive variation to maintain polymorphisms in natural populations. Heterozygote superiority or disruptive selection in a patchy and heterogeneous environment have been suggested as mechanisms for maintenance of biochemical polymorphisms (see Levinton (1973, 1975) and Levinton & Fundiller (1975) for discussion).

Support for the selectionist hypothesis in marine species comes from several types of circumstantial evidence. (1) Clines, or spatially autocorrelated changes of allele frequency with concomitant geographic variation of physical parameters such as sea temperature (Johnson 1971; Schopf & Gooch 1971 a). A local reversal in a geographic trend of sea temperature coincided with a reversal of allele frequency in a haemoglobin polymorphism of the clam *Anadara transversa* in eastern Australia (O'Gower & Nicol 1967). (2) Correlations of polymorphism with microgeographic physical gradients or environmental heterogeneity (Levinton 1973; Levinton & Fundiller 1975; Koehn, Turano & Mitton 1973; Mitton, Koehn & Prout 1975; Boyer 1974; Balegot 1971). The lack of diminished polymorphism in deep sea species (Schopf & Gooch 1971 b; Valentine & Ayala 1975), lack of repeatability of microgeographic variation (Balegot 1971) and among-locus differences in environmental correlation (Levinton 1975) complicate this picture. (3) Among-locus discordance in patterns of geographic variation (Christiansen & Frydenberg 1974; Koehn, Milkman & Mitton 1976; Williams, Koehn & Mitton 1974). Along the east coast of North America, *Mytilus edulis* shows smooth linear clines, discordant step clines, and no variation at all, depending upon the individual locus. Such among-locus differences cannot be accomodated by any model of isolation or genetic drift. (4) Clines in areas of presumed high gene flow, and differences in allele frequencies between juveniles and adults, implying selective mortality (Koehn *et al.* 1976; Boyer 1974; Levinton & Koehn 1976). None of these lines of evidence conclusively suggests the exact mechanism of selection because systematic variation may be ascribed to linkage with other loci responding to selection or may be correlated with environmental variation owing to indirect interactions with isolation and mixing processes. Only a functional relation between biochemical differences among the allozymes, and fitness differences among allozyme phenotypes, can explain the selective basis of such a polymorphism (see Koehn (1977) for some preliminary work on *M. edulis*). Thus, a superficially superior source of genetic data is plagued with methodological and theoretical difficulties.

Excluding genetic drift in large bivalve mollusc populations, geographic variation in allele frequencies must be explained as a balance of migration and selection. The process of selection in an environmental gradient enhances genetic differentiation, whereas migration tends to dilute such incipient divergence. Population structure, as manifested in different marine invertebrate dispersal modes, can influence geographic differentiation. Species with planktotrophic larvae tend to show less geographic differentiation than those with reduced dispersal (Berger 1973; Snyder & Gooch 1973). But despite a planktotrophic dispersal stage of 3–7 weeks (Seed 1976) *Mytilus edulis* shows pronounced geographic variation over short distances. A dramatic cline (figure 4) occurs at an enzyme locus over a distance of only 30 km (Koehn *et al.* 1976; H. H. Lassen & F. T. Turano, unpublished), at the transition from open marine to estuarine waters of Long Island Sound, New York, U.S.A. This variation superficially indicates strong selection at this enzyme locus, given the dispersal stage of *M. edulis*.

In this discussion, we shall highlight patterns and significance of geographic variation in allozyme polymorphisms of the mussels *Mytilus edulis* L. and *Mytilus californianus* Conrad to examine magnitudes of geographic differentiation along the east and west coasts of North America. Given the similar modes of dispersal of the two species, the relative steepness of the latitudinal gradient of water temperature on the Atlantic coast compared with the Pacific can be used as a test case for an expected increase of differentiation due to selection. Second, we contrast magnitudes of among-locality genetic similarity and genetic polymorphism between the two mussel species living sympatrically in the Strait of Juan de Fuca region, Washington, U.S.A. *M. californianus* is a relatively stenotopic mussel occurring only on exposed coasts of open marine salinity (Ricketts, Calvin & Hedgpeth 1968; Harger 1972; Paine 1974; T. H. Suchanek, unpublished). By contrast, *M. edulis* occurs in a variety of bay, estuarine and exposed coast habitats (Harger 1972; Levinton & Suchanek 1978). The wider variety of habitats exploited by *M. edulis* suggests an expected greater among-locality differentiation and poly-morphism. Finally we focus on the cline mentioned above, and discuss a series of physiological and genetic experiments designed to determine the extent of strong selection at the estuary–open-marine transition of eastern Long Island Sound. These latter results provide a means of understanding the dynamic aspects of selection in an area of strong genetic change.

Methods

Characterization of differentiation in *M. edulis* and *M. californianus* is based on intertidal collections along the east and west coasts of North America and on sampling of mainly sympatric occurrences of the two species in the Strait of Juan de Fuca region, Washington, U.S.A. (see Levinton & Suchanek (1978) for details). We report on levels of differentiation at several geographic scales in *M. californianus* and differences in among-localty genetic similarity between the two species at the leucine aminopeptidase (*LAP-1*, L-leucyl peptide hydrolase: E.C. 3.4.1.1) and glucose phosphate isomerase (*GPI*, D-glucose-6-phosphate ketoisomerase: E.C. 5.3.1.9) loci.

Collections of intertidal populations of *M. edulis* were also made in the Long Island Sound region, focusing on the *LAP-1* (more anodal LAP) locus. In open marine waters from Cape Cod to Virginia the frequency of the common *LAP*[94] (we refer to the locus simply as *LAP* below) allele remains within the range 0.47–0.60 (Koehn *et al.* 1976; Levinton & Lassen 1978). However, the frequency decreases to 0.1–0.2 over a distance of 30 km into the Long Island Sound estuary (Lassen & Turano, unpublished) and over shorter distances in other estuaries south of Cape Cod (Boyer 1974; Koehn *et al.* 1976). We performed physiological tolerance, growth and shock-mortality experiments on one population with open marine allele frequencies and two others with estuarine frequencies (see Levinton & Lassen (1978) for details).

Sample preparation, starch block electrophoresis, and classification of LAP allozyme pheno-types of *M. edulis* follows Koehn *et al.* (1976). Details on *M. californianus* electrophoresis and terminology are in Levinton & Koehn (1976) and Levinton & Suchanek (1978). We characterize among-locality genetic similarity with two indices. The Hedrick index, *H*, (Hedrick 1971) estimates genetic similarity between pairs of populations from genotypic frequencies. We calculated matrices of pairwise similarities, using arcsin transformations to normalize the data. Higher values of *H* indicate greater genetic similarity. *F*-statistics (inbreeding coefficients) also estimate the magnitude of spatial heterogeneity (Wright 1940; Neel & Ward 1972). Treating

a set of localities as a single gene pool from which samples are drawn, F_{ST}, the standardized variance estimates allele frequency variation over k samples as:

$$F_{ST} = \sigma^2_{p_i}/\bar{p}(1-\bar{p}),$$

where $\sigma^2_{p_i} = \Sigma\,(\bar{p}-p_i)^2/k$, and $\bar{p}$ is the weighted mean allele frequency. Higher values of F_{ST} indicate greater amounts of geographic differentiation. F_{ST} can be directly related to the χ^2 statistic and tests for significant among-locality heterogeneity follow the procedures of Snedecor & Irwin (1933).

TABLE 1. AMONG-LOCALITY GENOTYPIC SIMILARITY (HEDRICK COEFFICIENT, H) AND STANDARDIZED ALLELIC VARIANCE (F_{ST}) FOR SAMPLES OF *M. CALIFORNIANUS* TAKEN AT DIFFERENT GEO-GRAPHIC SCALES

(Data from Levinton & Suchanek (1978); see text for details. Standard error and number of two-way comparisons (in parentheses) are indicated for H.†)

scale/m	$\bar{H}_{GPI}$	$\bar{H}_{LAP}$	$F_{ST}GPI^{m}$	$F_{ST}LAP^{m}$
10^0: rocky point	80.7 ± 0.8 (15)	82.9 ± 1.1 (15)	0.004	0.003
10^2–10^3: island	79.4 ± 0.4 (55)	74.0 ± 1.0 (55)	0.002	0.018‡
10^5: strait	79.3 ± 0.4 (105)	73.9 ± 0.8 (105)	0.013‡	0.009
10^6: North American Coast	78.0 ± 0.7 (36)	78.8 ± 0.8 (36)	0.002	0.002

† Higher values of $\bar{H}$ indicate greater similarity; higher values of F_{ST} indicate greater allelic variance.
‡ $p < 0.05$.

PATTERNS OF VARIATION

Variation in Mytilus californianus *at different geographic scales*

Magnitudes of among-locality differentiation at the *LAP* and *GPI* loci were investigated in sample sets taken from a rocky point (scale of metres between sites), an island (scale of 10^2–10^3 m between sites), a strait (10^2 km) and along the west coast of North America (10^3 km; see Levinton & Suchanek (1978) for details). At the *GPI* locus, among-locality genetic similarity is similar at all scales (table 1), except for some allele frequency heterogeneity in the strait. At the *LAP* locus genetic similarity is high in both the North American coast and rocky point sample sets. But similarity is *less* in the strait and island sample sets. This anomalous observation is explained at least in the island sampling scheme which purposefully included a great range of mussel environments. Levinton & Fundiller (1975) estimated relative intertidal height of the island sampling sites and found a correlation of allele frequency and genotypic frequencies with mean shell length and intertidal height. If ecologically marginal samples are subtracted from the island sample set then differentiation approximates outer coast variation (Levinton & Suchanek 1978). Outer coast samples were all collected in the mid-intertidal zone, indicating an ecological control of genetic variation. However, Tracey, Bellet & Gravem (1975) found no intertidal differentiation at the *LAP* locus.

Differentiation in M. californianus *and* M. edulis

Table 2 shows comparative among-locality genetic similarity in the Strait of Juan de Fuca region for the two mussel species. *M. edulis* shows greater differentiation in genotypic frequencies at both the *LAP* and *GPI* loci. Allelic variance (F_{ST}) is greater in the *LAP* but not the *GPI* locus. The amount of polymorphism within populations is also greater at both loci in *M. edulis* (figure 1). Thus the broader ecological occurrence of *M. edulis* is reflected in

Table 2. Comparison of among-locality genotypic similarity and allelic variance in the eurytopic *M. edulis* and the stenotopic *M. californianus* in localities from the Strait of Juan de Fuca region, Washington, U.S.A.

(a) Hedrick coefficient

locus	species	$\bar{H}$	no. of paired locality comparisons
GPI	M. edulis	69.2 ± 0.6	136
GPI	M. californianus	79.3 ± 0.4	105
LAP	M. edulis	68.0 ± 0.8	136
LAP	M. californianus	73.9 ± 0.8	105

(b) Allelic variance

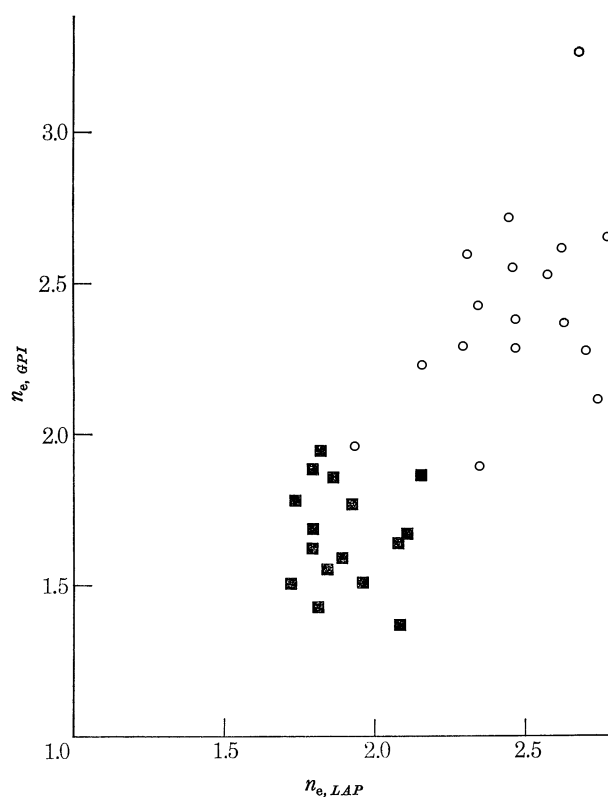| allele	species	F_{ST}	k
GPI^m	M. edulis	0.013†	16
GPI^m	M. Californianus	0.013†	14
LAP^m	M. edulis	0.019‡	16
LAP^m	M. californianus	0.009	14

† $p < 0.05$.   ‡ $p < 0.01$.

Figure 1. Polymorphism in *M. californianus* (■) and *M. edulis* (○) at two enzyme loci as estimated by the effective number of alleles, n_e (reciprocal of the sums of the squares of the allele frequencies). Data from Levinton & Suchanek (1978).

greater among-locality genetic differentiation and higher levels of polymorphism than in *M. californianus* (see Levinton & Suchanek (1978) for more evidence). However, we find no difference in H for populations of *M. edulis* sympatric with *M. californianus* and populations that are allopatric (arcsin of H, $\bar{H}$, $= 68.2 \pm 2.0$, $N = 28$ for sympatric samples, $\bar{H} = 67.2 \pm 1.4$, $N = 36$ for allopatry).
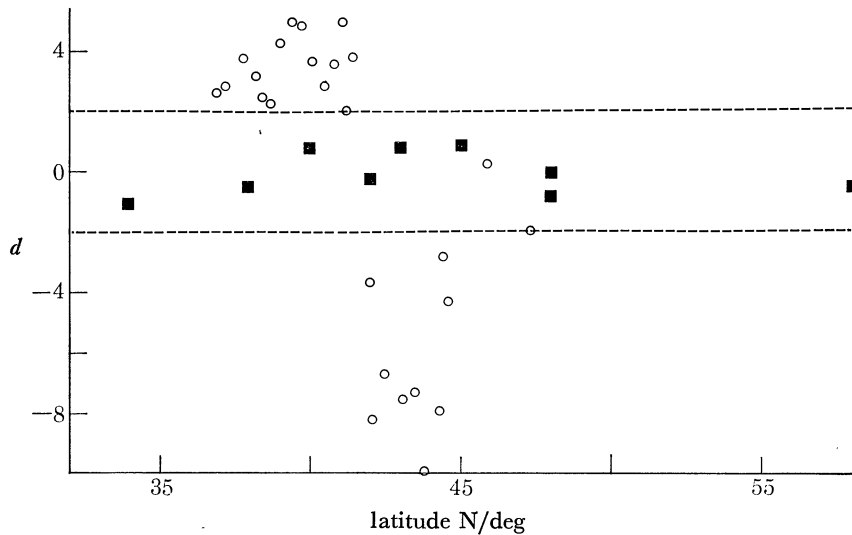

FIGURE 2. Diagram (freddiegram) showing standardized deviation of samples from an overall mean *LAP* allele frequency for *M. edulis* (O) on the east coast of North America and *M. californianus* (■) on the west coast.
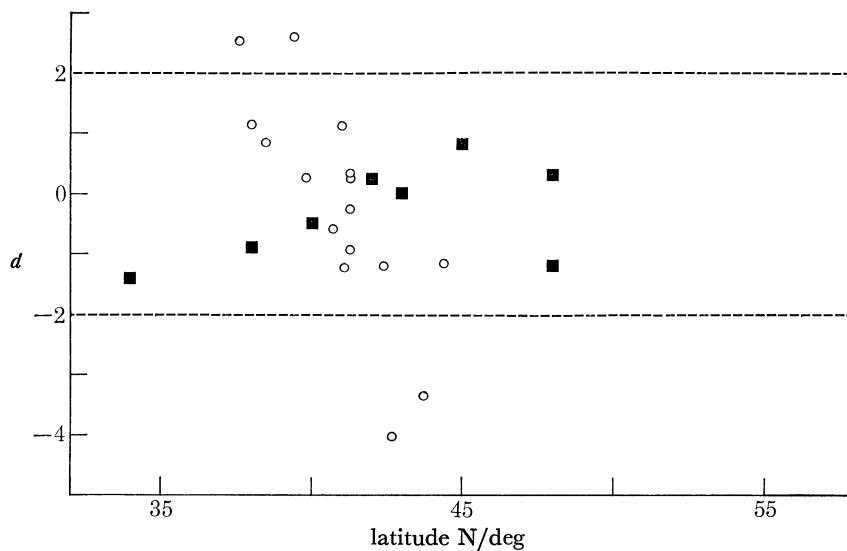

FIGURE 3. Freddiegram for the *GPI* locus. Same symbols as in figure 2.

Figures 2 and 3 show differentiation of *M. edulis* along the east coast of North America (data from plotted localities of Koehn *et al.* (1976) and *M. californianus* along the west coast of North America for the *LAP* and *GPI* loci. The frequencies of common alleles are plotted as standardized deviations from a grand mean calculated from all the samples. If the grand mean is p_0, and all samples come from a statistically homogeneous source, then the frequency deviation of a sample i is

$$d_i = (p_i - p_0) \sqrt{(2X_i/p_0 q_0)},$$

and is approximately normally distributed with zero mean and unit variance (X_i is the sample size, $q_0 = 1 - p_0$; Christiansen, Frydenberg, Hjorth & Simonsen 1976). With a series of samples taken from a homogeneous source, 95 % of the sample points would be expected to fall in the interval -2 to $+2$. The expected preponderance of samples within this range is found for *M. californianus* but in *M. edulis* the differentiation is clearly too pronounced to be considered as random variation around a mean allele frequency. The greater magnitude of coastal differentiation in the east coast *M. edulis* is consistent with the steeper latitudinal thermal gradient of the Atlantic relative to that of the Pacific. Unfortunately, we do not have similar data for Pacific coast *M. edulis*. However, the recent discovery of widespread outer coast *M. edulis* makes this comparison feasible with future work (see Suchanek 1978).
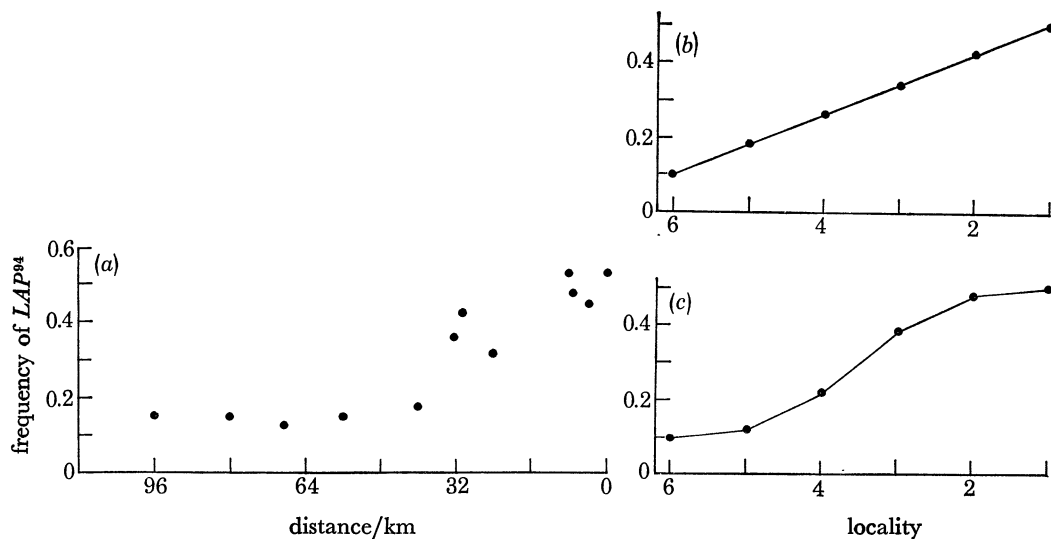

FIGURE 4. (a) Cline in the frequency of the LAP^{94} allele with distance into Long Island Sound (kilometres west of New London, Connecticut). (b) Hypothetical cline generated if two end member larval swarms are mixed with linear dilution of a swarm as one goes from one end of the cline to the other (see text). (c) Hypothetical cline generated if dilution occurs, as well as increasing mortality with distance from the source of the respective swarm. In these two cases, a swarm with a LAP^{94} frequency of 0.5 starts at locality 1, and is mixed to the left. Another swarm with frequency of 0.1 is mixed to the right from locality 6. The same number of larvae start in each swarm.

LAP cline in Long Island Sound

Figure 4 shows the clinal change of the LAP^{94} allele with increasing distance into Long Island Sound. This change occurs along both shores over a distance of 30 km. Paskausky & Murphy (1976) showed that surface floats may traverse this distance in less than 2 weeks and probably in a still shorter period. Surface movement, however, is estuarine and floats leave the Sound. A possible inference is that the cline must be generated by strong selection at the *LAP* locus, and that functional differences among the *LAP* phenotypes are manifested in differential survival. We have explored the following hypotheses to understand the dynamics of the polymorphism and the differential physiological context within which selection must operate in the two environments: (1) that estuarine (Long Island Sound) and open marine populations have different physiological reactions to the same stress; (2) that among-LAP phenotype differences result in differential physiological response, as manifested in growth; and (3) that

low-salinity shock experiments shift *LAP*[94] allele frequencies of open marine populations towards those of estuarine populations.

Between-habitat physiological response

Mussels were collected from both open marine and estuarine habitats and maintained in aquaria for 3–4 weeks at 32‰ and temperatures approximating field conditions. Figure 5 shows patterns of between-habitat mortality of these populations when placed in different salinities at 20 °C for 24 h. Long Island Sound mussels suffered no mortality whereas open marine mussels showed increasing mortality with decreasing salinity. In another experiment done at 32 °C (Levinton & Lassen 1978), estuarine and open marine mortality curves diverged with decreasing salinity. At 32 °C, 32‰, estuarine and open marine mortality curves approximately coincided, indicating that the differential response is salinity and not temperature based. Although these results show a differential physiological response of open marine and estuarine mussels, transplants of open marine mussels into Long Island Sound resulted in no mortality (Levinton & Lassen 1978).
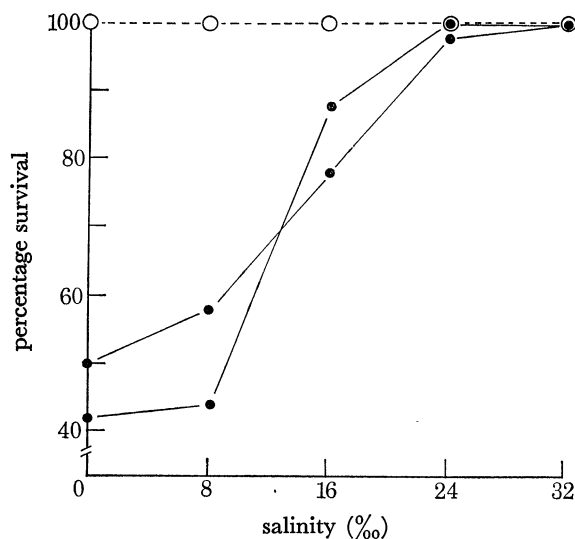

FIGURE 5. Differential response of open marine (●) and estuarine (○) *M. edulis* to low salinity shock, at 20 °C (after Levinton & Lassen 1977).

Genotype-specific growth

Mussels 14–17 mm long were collected in open marine and estuarine localities and transplanted to intertidal cages in Long Island Sound. After several months, growth and LAP genotype were determined for each individual. Within each population no genotypic differences in growth were observed (table 3), indicating that hypothetical differences among *LAP* genotypes are not manifested in an integral physiological response such as growth.

Allele frequency in mortality experiments

A pilot study showed that low salinity and high temperature effectively act as a source of high mussel mortality. The effects of low salinity are diminished with decreasing temperature (Levinton & Lassen 1977). Figure 6 shows changes in *LAP*[94] frequency of laboratory populations

when 65–70 % mortality was imposed on open marine populations with high temperature (25–30 °C) and low salinity (usually 16‰) conditions. Changes in genotypic frequency were significant ($p < 0.05$) in nine of the sixteen experiments, while changes in LAP^{94} frequency were significant in six. Random variation cannot explain the frequency of significant genotypic or allele frequency changes (Levinton & Lassen 1977). But two other important points emerge. In no case is there an allele frequency change of the magnitude of that observed along the Long Island Sound cline. Second, LAP^{94} frequency changes do not show a consistent

TABLE 3. AMONG-LAP GENOTYPE GROWTH RATES (millimetres per week) OF OPEN MARINE AND LONG ISLAND SOUND $M.$ $EDULIS$ TRANSPLANTED TO LONG ISLAND SOUND CAGES (Levinton & Lassen 1977)

(One way analyses of variance show no significant growth differences. Sample size in parentheses.)

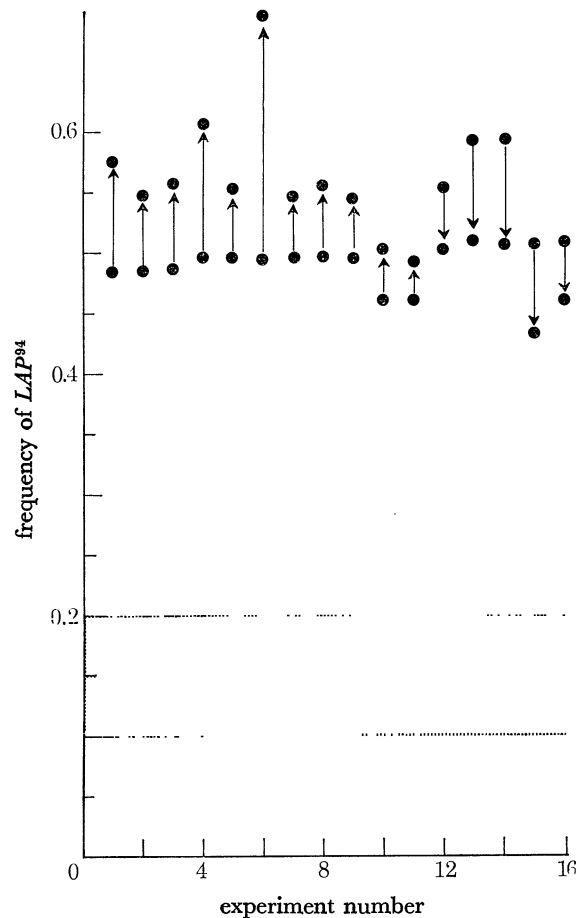| LAP genotype	94/94	94/96	96/96	96/98	98/98	94/98
Long Island Sound	0.95 (16)	1.07 (63)	1.06 (151)	1.05 (217)	1.05 (237)	1.02 mm/week (79)
open marine	0.66 (300)	0.65 (162)	0.64 (45)	0.65 (80)	0.65 (85)	0.66 mm/week (231)

FIGURE 6. Changes in the frequency of LAP^{94} after 65–70 % mortality resulting from low salinity, high temperature shock. Shaded area indicates expected frequencies if change conformed to hypothesis of salinity-induced mortality among LAP genotypes. See text.

trend towards those of Long Island Sound. In fact, an increase in frequency seems to be associated with experiments done on controls collected in January.

In January 1976, a warm spell (over 12 °C) following a prolonged cold period resulted in mass intertidal mortality of *M. edulis*. We followed LAP^{94} frequencies at an open marine locality and observed a progressive increase from 0.47 to 0.60 (see Levinton & Lassen (1977) for details). The direction of change was the same in shock mortality experiments done on population with low LAP^{94} frequencies associated with winter collections. But even during this period, where 50–100 % mortality occurred in Long Island localities (both estuarine and open marine), the total LAP^{94} change was less dramatic than that observed along the cline. A similar mass mortality in January 1977 showed no change in LAP^{94} frequency.

DISCUSSION

Patterns of observed differentiation between *M. edulis* and *M. californianus* suggest that natural selection is the ultimate agent which maintains the level and geographic distribution of the polymorphisms. The greater among-locality differentiation of *M. edulis* reflects its greater niche width. Furthermore, the strong latitudinal differentiation in *LAP* and *GPI* allele frequencies of east coast *M. edulis* contrasts with the homogeneity of distribution of allele frequencies at the same loci in west coast *M. californianus*. However, these differences provide no compelling evidence that fitness differences among allozyme genotypes can be ascribed to differential function of kinetic characteristics of the respective allozymes. Linkage with other genes involved in selection can also generate such patterns. Genes that are effectively neutral may 'hitch-hike' along with others and thus be markers of an unknown selection process (Maynard-Smith & Haigh 1974). Given genes might also be organized with certain ecotypes constituting a series of isolated gene pools composing the species. Thus, although selection must almost certainly be implicated in our data the estimation of natural selection at a locus, or the contribution of a given allozyme to fitness may be effectively masked.

A study of geographic variation in the American eel, *Anguilla rostrata*, almost certainly points to selection within a single generation at some loci (Williams *et al.* 1973). Larvae originate as a presumed panmictic gene pool in the Sargasso Sea with subsequent shoreward migration as the swarm moves northward in the Gulf Stream. Clines at several loci have been observed in newly arrived elvers collected in shore localities. The possibility that temperature-selective ecotypes migrate inshore upon reaching a given latitude should not be excluded, but seems unlikely.

The steepness of the LAP^{94} cline of *M. edulis* at the entrance of Long Island Sound suggests similar short-term selection, given the 3–7 week dispersal stage and current structure. This would suggest strong selective mortality among *LAP* genotypes. As the cline is also found for juveniles of 10 mm length (Lassen & Turano, unpublished) selection must occur in the planktonic larval stage or around the time of settlement and metamorphosis. Given such strong among-genotype mortality we would predict that fitness differentials would also be reflected in different growth rates as well. Growth is a reflexion of a mussel's energetic surfeit, given the metabolic demands of specific temperature, salinity and ration conditions (see Bayne, Thompson & Widdows 1976). The concentration of *LAP* in the brush border of the digestive gland suggests a digestive function for the enzyme. However, a function related to the dissolved amino acid pool and osmoregulation cannot be excluded and acclimation of *LAP* activity to

different salinities can be accomplished (Koehn 1977). But we can detect no among-*LAP* genotype growth differences when either Long Island Sound or open marine mussels are placed in Long Island Sound cages. Given our sample sizes, we conclude that there is either no such growth difference, or one too small to reasonably imply a dramatic differential mortality at the *LAP* locus as previously implied for the Long Island Sound cline.

Our shock mortality experiments similarly have resulted in allele frequency changes too small in magnitude to explain the cline. Moreover, the direction of change of *LAP*[94] was sometimes opposite to that predicted by the expected effect of low salinity. But allele and genotype frequency changes are too strong to be explained by chance alone. Further, shock experiments on populations with lower *LAP*[94] frequencies shifted allele frequencies in a manner similar to that observed in a natural population following a mass mortality. But even a mass mortality only shifted the frequency of *LAP*[94] by 0.13; far less than the 0.4 change along the cline. We therefore conclude that among-genotype differential mortality of post-settlement mussels is not a likely explanation for the clinal distribution of *LAP*[94] in Long Island Sound.

In June 1976 we discovered mussels 5–6 mm long in cages of much larger open marine mussels that had been transplanted to Long Island Sound in April. Because such small mussels were not found anywhere in the vicinity of the cages and it is unlikely that planktotrophic larvae would remain in the cages, these mussels were probably plantigrades (newly settled individuals) that settled among byssal threads the previous autumn at the source locality of the transplant. They had then been transplanted for 2–3 months. We do not know the magnitude of juvenile mortality associated with the transplant, but *LAP* allele frequencies were within the range typically observed for adjacent open marine populations ($LAP^{94} = 0.515$, $N = 132$).

With these points in mind, the following hypotheses might explain the *LAP* cline:

(1) Selection in the larval stage among genotypes occurs as larvae enter or leave the Sound, or just after metamorphosis. Larval experiments are now in progress.

(2) Isolation is more pronounced at the entrance of Long Island Sound than we now suspect. Long Island Sound is an estuary with a net outwards flow. Larvae may therefore leave the Sound and are diluted by enormous numbers of larvae of open marine origin, with little influx of the latter larvae into the Sound.

(3) Long Island Sound and adjacent open marine populations are different physiological races. The basis may be genetic or due to differences in long-term acclimation. When open marine larvae enter the Sound, their intolerance to lowered salinity results in high mortality. An effective isolation would be accomplished. This hypothesis is plausible because *M. edulis* larvae from open marine environments (30–32‰) show retardation of growth at 24‰ and cessation at 19‰. Larvae of mussels from a lower salinity environment show normal growth at 14‰ (Bayne 1965).

Such an isolation permits the establishment of a cline with no selection among genotypes at the *LAP* locus. Figure 4*b* shows the distribution of *LAP*[94] with distance if the fraction of open marine larval migrants contributing to any locality ranges from 1.0 to 0.0 on going from the entrance of Long Island Sound to the point where 'true' estuarine frequencies are first obtained. The estuarine contribution of larvae is the reverse. A linear dilution of the two populations generates a linear cline. If larval mortality increases linearly with distance from the source (estuarine or open marine) the cline is accentuated (figure 4*c*). In both these hypothetical constructions the dilution of two end member populations generates a cline with no mortality among *LAP* genotypes, independent of source population.

It seems likely that some selective mechanism originally generated and now maintains the estuarine differentiation we now observe. The effective isolation generated by physiological races or another isolating mechanism would allow the *LAP* differentiation to accumulate more slowly than in a single generation. Given some isolation, very small among-genotype fitness differences could eventually result in shifts of allele frequencies. Such shifts could occur episodically, as after a mass mortality, or through gradual accumulated change.

The genetic differentiation observed allows us to speculate on a model of bivalve speciation only in partial agreement with proposals of rapid and peripheral species origin, as suggested by Eldredge (1971) and later by Stanley (1975). Eldredge expands the framework of Mayr (1963) proposing that marine species originate rapidly in peripheral (shoreward) sites, with subsequent rapid spread of the new species over broad shallow water areas. Speciation events are visualized as rapid events with subsequent stable periods involving little change in the daughter species (Eldredge & Gould 1972). However, although ecologically peripheral sites are logical places for the accumulation of genetic difference, genetic change could occur very slowly and in rather large populations, not fitting Mayr's characterization of a peripheral isolate undergoing a genetic revolution. The rapid establishment of isolation would permit a large peripheral population to accumulate genetic difference. Thus isolation has permitted extensive genetic divergence in substantially large populations of the eel pout, *Zoarces viviparus*, in the Baltic relative to the North Sea (Christiansen & Frydenberg 1974). Although peripheral locations are often ecologically marginal and a stimulant to speciation, the speciation process itself in the sea may be slow and not in founder populations small enough to be affected by genetic drift.

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