Vol. 67: 309–310, 1990 | MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published November 1

NOTE

Allozyme differentiation – a reply to Väinölä

Kerstin Johannesson[1], Nils Kautsky[2], Michael Tedengren[2]

[1] Tjärnö Marine Biological Laboratory, Pl. 2781, S-452 00 Strömstad, Sweden
[2] Askö Laboratory, Institute of Marine Ecology and Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden

In a series of papers (Kautsky et al. 1990, Johannesson et al. 1990, Tedengren et al. 1990) we presented morphological, genetic and physiological results of blue mussels *Mytilus edulis*, reciprocally transplanted between one Baltic (6 to 7 ‰ S) and one North Sea (Swedish west coast, 20 to 30 ‰ S) site. The genetic paper also included allele frequency distributions from several other populations along the Swedish west coast. Our results indicated that differences in many of the morphological and physiological characters distinguishing Baltic and North Sea populations were due to phenotypic plasticity, although some characters were affected by a more direct genetic component.

Some of the transplanted populations suffered from very high mortality rates and the genetic composition of the surviving populations were heavily affected at the 2 loci *Pgm* and *Pgi*. We interpreted this as a result of heavy selection upon the transplanted populations.

In a critical comment on our genetic paper Väinölä (1990) argues for an alternative interpretation. He concludes that the observed allele frequencies following the mortality events are most likely due to contamination by local recruits and not to selective mortality within the transplanted populations. Although this may seem a probable interpretation we will argue that although we cannot reject the possibility of contamination in the transplants from the Baltic to the North Sea we can do so in the North Sea to Baltic experiment.

We admit that the design of the genetic part of the experiment was 'ad hoc', that is, we did not expect the outcome of the experiment. Thus, for example, we did not label the transplanted mussels individually.

The Baltic population transplanted to the North Sea consisted of about 40 000 individuals hanging on ropes (AS86* in Johannesson et al. 1990). As these mussels were placed in the North Sea after a week of acclimatisation in the laboratory when they were still very small (4.0 ± 1.5 mm), the risk of contamination by native recruits seems obvious. However, at the actual depth of 9 m settling rate is generally very low (Romare et al. 1982) (this was why we placed the mussels at such a great depth). The weekly inspection dives during the summer and irregular inspection dives over the winter period showed that there was no settling at all on the empty parts of the rope which suggest no settling at all of native recruits. A few very small individuals were found at the inspections; they were removed, although it is most likely that these mussels were only poorly developed mussels of a Baltic origin. Late settlement (October onwards), as proposed by Väinölä (1990) as a possible source of contamination, would have produced mussels of a much smaller size than the transplanted mussels which at that time had grown from an initial size of 4.0 to between 35 and 40 mm (Kautsky et al. 1990).

Of the estimated 40 000 Baltic mussels in the AS86* sample only some 200 survived a period of heavy mortality in September the following year. The surviving mussels were very similar in allele frequencies at the 2 loci *Pgi* and *Pgm* to North Sea populations, despite a large amount of differentiation between unselected Baltic and North Sea stocks. Väinölä (1990) made back-calculations based on the number of transplanted mussels, number of survivors and allele frequencies in selected and unselected samples. He concluded that the results showed 'that the transplanted mussel batches could not have contained sufficient genetic diversity to yield the observed selection responses' (Väinölä 1990). A problem with this kind of calculation is, however, that estimates of frequencies of rare alleles may be influenced by sampling error unless sample sizes are very large. We observed the frequency of the pooled North Sea allele of *Pgi* to be 0.003 (one heterozygote out of 161 individuals) while a frequency of 0.06 would have been required to explain the observed frequency of Baltic homozygote genotype

0171-8630/90/0067/0309/$ 03.00

after the selection event. Besides sampling errors we may have underestimated the size of the transplanted population, perhaps up to 2 or 3 times, as no direct count was actually made.

Obviously we cannot fully rule out the possibility suggested by Väinölä (1990) of contamination of local recruits to the surviving sample of AS86*. However, unless nearly all individuals of the AS86* sample were in fact North Sea contaminants, selection must be invoked to explain the striking similarity at *Pgi* and *Pgm* between the AS86* sample and North Sea stocks.

Contamination of local recruits to the sample of North Sea mussels transplanted to the Baltic seems nearly impossible. In this case the mortality took place during the acclimatisation period in the laboratory. During this period the mussels were held in an aerated aquarium in water brought from the North Sea. The salinity was reduced through dilution with filtered brackish water. Of the 600 transferred mussels only 22 (2.0 ± 0.2 mm) survived. These were placed in the sea in October in suspended net cages with a mesh size of 0.8 mm. No settling was ever observed on these cages and settlement of blue mussel larvae does not generally take place in October or later (Kautsky 1982).

The genetic analyses of the survivors of this transplant suggest selection in the direction of the Baltic genotype at *Pgi* which is compatible with a 100 % contamination hypothesis indicated by Väinölä (1990). However, this is obviously not the case as the resulting allele frequencies at *Pgm* deviate both from Baltic and North Sea stock distributions. In fact, the distribution pattern of *Pgi* and *Pgm* taken together is not even compatible with a mixing of unselected North Sea individuals and Baltic contaminants. That is, the interpretation of these data has to invoke selection in some form. Also in this case Väinölä (1990) performed a back-calculation and found that the results would imply that the selection was exclusively based on the *Pgi* phenotype; practically all the BB homozygotes, and no others, survived'. He further remarked that as the surviving mussels were smaller than average 'this size class would have initially contained only a couple of BB individuals'. Another possibility is, however, that genotype distribution within this sample varied with size. That is, homozygotes of BB may have been smaller than average, which indeed seems likely as the mortality was highly size dependent.

Two samples of North Sea mussels deviated significantly from the other North Sea samples. Both were from the estuarine site Idefjord. ID83 deviated significantly in *Pgi* from both the North Sea and the Baltic stocks, while ID87 deviated from North Sea and Baltic stocks in *Pgm*. Although the salinity range is wide the Idefjord is on average less saline than the other North Sea sites examined in Johannesson et al. (1990). The possibility of this population being a mixture of *Mytilus edulis* and *'Mytilus trossulus'* may, however, be ruled out since the tidal water exchange of the small and narrow fjord replaces the surface water of the fjord within 1 to 2 wk, while to retain a local population of *M. trossulus* would require that the estuarine water is not replaced over about 4 wk or more.

Väinölä (1990) pointed out a shortcoming of the genetic part of our investigation. However, the results are not compatible with his interpretation of local contamination either. One way to resolve this conflict would be to repeat the transplant experiment with labeled mussels or complete it in the laboratory.

LITERATURE CITED

Johannesson, K., Kautsky, N., Tedengren, M. (1990). Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. II. Genetic variation. Mar. Ecol. Prog. Ser. 59: 211–219

Kautsky, N. (1982). Quantitative studies of gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. Mar. Biol. 68: 143–160

Kautsky, N., Johannesson, K., Tedengren, M. (1990). Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. I. Growth and morphology. Mar Ecol. Prog. Ser. 59: 203–210

Romare, P., Håkansson, M., Rosenberg, R. (1982). Fastsättning och efterföljande spridning av blåmusslan *Mytilus edulis* L. vid svenska västkusten. Medd. Havsfiskelab. Lysekil 285: 1–16 (in Swedish)

Tedengren, M., André, C., Johannesson, K., Kautsky, N. (1990). Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. III. Physiology. Mar Ecol. Prog. Ser 59: 221–227

Väinölä, R. (1990). Allozyme differentiation between Baltic and North Sea *Mytilus* populations: a reassessment of evidence from transplantations. Mar. Ecol. Prog. Ser 67: 305–308

Manuscript received: June 6, 1990