Genotypic and phenotypic differences between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal transplantations. I. Growth and morphology

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ABSTRACT: Growth rate and maximum size of *Mytilus edulis* is much lower in the Baltic Sea (7 ‰ S) than in the North Sea (28 ‰ S). Reciprocally transplanted mussels grew at rates similar to those of native mussels at each site, indicating that this variation can largely be explained by physiological differences due to environmental salinity. Initial survival of Baltic mussels was very high after transfer to the marine environment both in 1984 and 1986, but was followed by very high mortality in the following late summer. In contrast immediate mortality was over 90 % among North Sea mussels transferred to the Baltic Sea with only some of the smallest mussels surviving. These, however, suffered no further excessive mortality. These different survival rates probably have mainly genetic causes. Genetic factors also seem to explain morphological differences, since these were to a large extent maintained even more than 1 yr after transplantation. Native North Sea mussels had 24 % larger volume and 9 % greater shell height than transplanted Baltic mussels of the same length (48 mm), while shell width differed little. Total dry weight and shell weight were about 2 times larger in North Sea than in transplanted mussels, and weights of meat and posterior adductor muscle were 1.6 times and 3.3 times larger, respectively. However, in mussels of Baltic origin more biomass was allocated to meat (14.7 % of total dry wt) relative to shell and adductor muscle, than in North Sea mussels (11.2 %). Predation experiments with *Asterias rubens* showed that Baltic mussels grown for 12 mo in the North Sea were more readily attacked and more easily opened than equal-sized North Sea mussels. We suggest that the lack of thick shells and large adductor muscles is caused by low predation pressure in the Baltic which does not select for such protective characters. Relatively more of the available energy instead seems to be allocated to reproduction.

INTRODUCTION

The blue mussel *Mytilus edulis* is a highly variable species or a species complex (cf. Johannesson et al. 1990 – companion article), and populations frequently differ in growth rate and size as well as in the morphology of shell and soft parts. A large part of this variation may be a result of environmental factors such as temperature, salinity and food abundance (review in Seed 1976), although genetic differentiation in growth rate and morphological traits has been observed in several mussel populations (e.g. Koehn & Gaffney 1984, Mitton & Grant 1984, Diehl et al. 1985, Rodhouse et al. 1986).

The Baltic Sea represents a very stable low-saline environment. It has existed for some 7000 yr and very few true brackish water species have evolved – most species are of either marine or freshwater origin (Remane & Schlieper 1971). The Baltic Sea is also species-poor and only about 100 invertebrate species are found in the northern Baltic proper compared to some 2000 species on the Swedish Skagerrak coast (cf. Jansson 1972). Some species like herring and certain molluscs have dwarf forms in the Baltic Sea compared to marine environments, and many marine species are known to increase their depth distribution and/or feeding niches due to the reduced competition (Remane & Schlieper 1971).

It is a well-documented fact that *Mytilus edulis* in the Baltic Sea have a much lower growth rate and reach a maximum size of only about 1/3 that of North Sea

mussels (e.g. Remane 1934, 1971, Kautsky 1982a). Other morphological characters such as thin and more elongated shell, and a smaller posterior adductor muscle, have also been reported for Baltic mussels (Remane & Schlieper 1971, Theisen 1978, 1982, Kautsky 1981, 1982a). Tedengren & Kautsky (1986) suggested that the low growth rate and small size of Baltic mussels are mainly due to physiological adaptations to the low salinity, while the thinner shell has been attributed to lower calcium content (Schlieper 1971) and temperature (Remane 1971) in the Baltic, but as Schlieper (1971) pointed out this could only be verified by long-term breeding experiments in artificially prepared brackish water of varying calcium content and temperature.

Theisen (1982) found large variation in the size of gills, labial palps, and posterior adductor muscle in samples from different parts of Danish waters. He suggested that the differences in gill and palp size can be explained by adaptations to waters of different turbidity, and that most of the variation in adductor muscle size is related to differential predation by *Asterias* (cf. also Hancock 1965). However, since large genetic differences had earlier been observed between the populations (Theisen 1978), it was concluded by Theisen (1982) that it remained to be ascertained whether these morphological differences are phenotypic adaptations or whether they are related to genetic differences between populations.

Reciprocal transplantations could be one way to examine the extent to which population differences in growth and morphology may be environmentally induced (non-genetic variation), or inherited (genetic variation). In this paper we compare growth rate and morphology in reciprocally transplanted mussels from Baltic and North Sea populations with that of their native populations. Enzyme variability and physiological differences between the 2 populations are discussed in Parts II and III of this series (Johannesson et al. 1990, Tedengren et al. 1990).

MATERIAL AND METHODS

Reciprocal transplantations and growth comparisons. About 10 000 mussels (age 15 mo; mean size 20.0 ± 1.2 mm (SE), n = 40), collected from ropes at 9 m depth at Askö in the northern Baltic proper (58° 49' N, 19° 39' E; 6 to 7 ‰ S), were transferred to Tjärnö in the North Sea (58° 53' N, 11° 09' E; 20 to 30‰ S) in September 1984. Stepwise acclimatisation took place in aerated 50 l tanks by increasing salinity by about 4 ‰ per day over 1 wk in the laboratory by adding seawater until a salinity level of 28‰ S was attained. The mussels were then put into cages at 9 m depth, side by side

with rope-cultured native North Sea mussels of the same size, although no more than 2 to 3 mo old. All Baltic mussels survived this treatment. Growth rate (shell length) of transferred mussels was measured at intervals and compared with reference mussels left in the Baltic. All growth measurements were carried out on subsamples of 40 mussels taken from the populations.

About 600 mussels from 1 to 40 mm in length (mean 21 mm) from Tjärnö in the North Sea were transferred to Askö in the Baltic at the end of September 1984. During 2 wk of stepwise acclimatisation to the low salinity by lowering salinity about 2‰ S per day through addition of brackish water to the aerated tanks, only 22 of the smallest mussels survived (range 1 to 4 mm; mean 2.0 ± 0.2 mm, n = 22), and were put out.

In July 1986 another batch of 40 000 Baltic mussels growing on ropes (age 12 mo; mean size 4.0 ± 1.5 mm, n = 40) were transferred and suspended at the North Sea site. Growth of a subsample was measured and compared to rope-cultured native North Sea mussels of the same age but of a larger size (10.0 ± 2.0 mm, n = 40) and to reference mussels remaining in the Baltic (4.0 ± 1.5 mm, n = 40). Tentative growth curves between the measurements were calculated from regressions of daily length-specific growth rates established for the same locality in the Askö area by Kautsky (1982a) and calculated from data of Loo & Rosenberg (1983) for a nearby locality in the Tjärnö area.

Morphology. A number of morphological characteristics were assessed in the transfered Baltic mussels and in the native North Sea mussels after 12 mo of growth in the North Sea. A sample of 12 mussels was randomly selected from the population. Length, height and width were measured with calipers to the nearest 0.1 mm, and the displacement volume in water was determined for the whole mussel. Weight of shell, the posterior adductor muscle and of meat excluding the adductor muscle were determined separately after drying at 70 °C. The $CaCO_3$ content of the shell was determined by decalcification with diluted HCl and subsequent dry weight determination of the residues.

Predation experiment. Susceptibility to predation by the asteroid *Asterias rubens* was compared in the laboratory between transplanted Baltic and native North Sea mussels. Ten 1-yr-old mussels from the North Sea population (mean length 35.2 ± 1.0 mm) and 10 Baltic mussels of similar size transplanted to the North Sea 12 mo earlier (35.4 ± 1.2 mm), were placed in each of ten 40 l aquaria with running seawater. Two *A. rubens* of similar size (42 to 48 g wet weight) were placed in each of 8 aquaria; the remaining 2 aquaria were used to estimate non-predatory mortality The starfish were kept in the aquaria for 4 d without food to adapt to experimental

conditions and standardise hunger levels. The experiment was terminated in each aquarium after 10 mussels had been eaten, and the ratio between Baltic and North Sea mussels consumed was determined.

RESULTS

Growth

The growth rate of Baltic mussels transplanted to the North Sea in September 1984 increased compared to the control population in the Baltic, and approached that of North Sea mussels (Fig. 1). The rapid increase in growth rate after transfer resulted in characteristic growth marks in the shells although the general shell shape of the Baltic mussels remained (Fig. 2). After 1 yr of quite low mortality all transplanted Baltic mussels died in September 1985.

The North Sea mussels transplanted to the Baltic in September 1984 showed a high initial mortality (> 95 %) and only 22 small individuals survived (mean length 2.0 ± 0.2 mm, n = 22). The growth of these was slow and by July 1986 they had attained a size of 22.0 ± 1.9 mm (n = 22), similar to that reached over the same time period by native Baltic mussels of the same initial size.

Baltic mussels transplanted to the North Sea in July 1986 showed a similar growth rate to those transplanted in 1984 (Fig. 3). The mortality of transplanted mussels in 1986 was also similar to that of mussels transplanted in 1984, i.e. mortality was low until the end of August 1987 when suddenly 99.5 % of the population died. Some 200 mussels survived and continued growing until August 1988 when 74 of them were sampled for genetic analysis (cf. Johannesson et al. 1990). Some 100 mussels of the 1986 transplants were still living in August 1989, but as mortality was very

Fig. 1. *Mytilus edulis*. Growth of mussels transplanted from the Baltic to the North Sea (AS–TJ) and from the North Sea to the Baltic (TJ–AS) compared to native Baltic (AS) and North Sea (TJ) populations. The mussels were of the same initial size in September 1984 but Baltic mussels were about 14 mo and North Sea mussels 2 to 3 mo old. The initial decline in size of the TJ–AS mussels is due to high mortality of large mussels (see text). Mean values ± SE of means are given. The broken lines between measurements are estimated from growth equations given in Kautsky (1982a) and using growth data given in Loo & Rosenberg (1983)
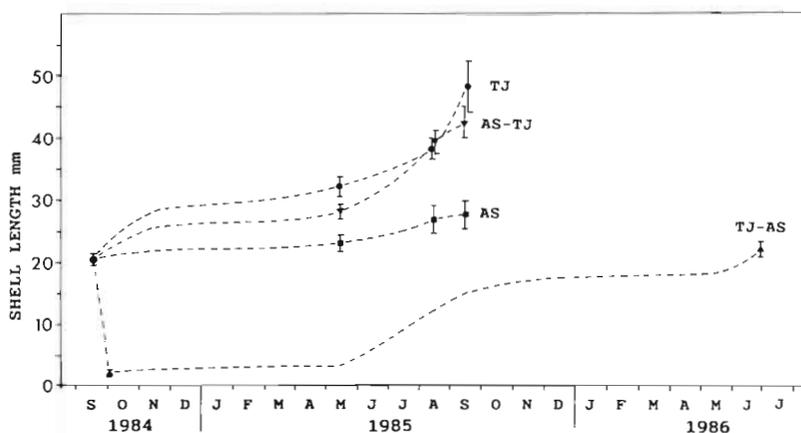

Fig. 2. *Mytilus edulis*. Shell form in North Sea mussels (left), Baltic mussels transplanted to the North Sea (middle), and Baltic mussels (right). Size at transfer is revealed by growth marks and it can be seen that the characteristic shell shape of Baltic mussels is maintained after transplantation
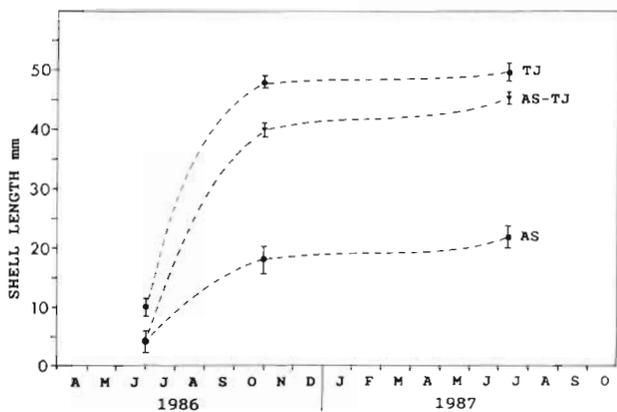
Fig. 3. *Mytilus edulis.* Growth of Baltic mussels transplanted to the North Sea (AS–TJ) compared to mussels of the Baltic (AS) and the North Sea (TJ) populations. The mussels were of the same age, i.e. about 12 mo old in July 1986 (cf. Fig. 1)

selective with mainly North Sea genotypes surviving (Johannesson et al. 1990), these mussels were not used for further experiments.

Morphology

The morphological characteristics of Baltic mussels, 1 yr after transplantation, and native North Sea mussels are plotted against shell length in Fig. 4. A curve of best fit was calculated for the data, using linear regression for width and height, and power functions for volume and weight characteristics. Significant differences between the populations were found for all parameters except shell width (Fig. 4F). For an average-sized mussel (48 mm) total volume was 24 % larger in North Sea mussels than in Baltic mussels ($p < 0.05$) (Fig. 4G). Shell height was 9 % larger in North Sea mussels ($p < 0.05$) (Fig. 4E). Size-specific dry weight of the whole mussel (Fig. 4A) and dry weight of the shell (Fig. 4D) were 100 % ($p < 0.001$) and 108 % ($p < 0.001$) higher, respectively, in North Sea than in transplanted Baltic mussels, while dry meat weight (excl. adductor muscle) was 56 % ($p < 0.001$) higher in North Sea compared to transplanted Baltic mussels (Fig. 4B), and dry weight of the posterior adductor muscle was 230 % ($p < 0.001$) higher in North Sea mussels (Fig. 4C).
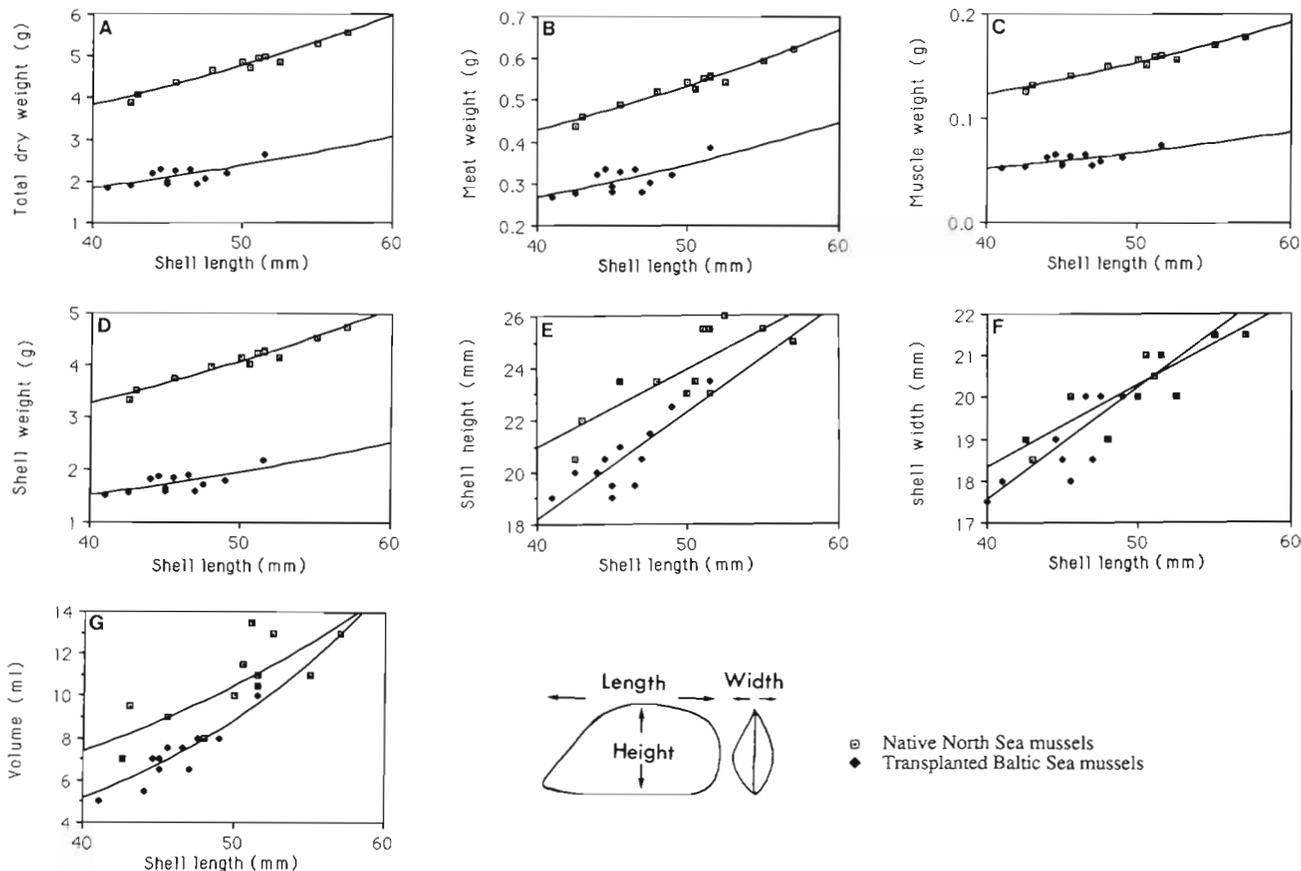

Fig. 4. *Mytilus edulis.* Regressions of different morphological characters against length compared between transplanted Baltic mussels and native North Sea mussels. (A) Total mussel dry weight ($p < 0.001$). (B) Meat dry weight ($p < 0.001$). (C) Posterior adductor muscle dry weight ($p < 0.001$). (D) Shell dry weight ($p < 0.001$). (E) Shell height ($p < 0.05$). (F) Shell width (ns). (G) Volume ($p < 0.05$)

The proportion of biomass allocated to shell, meat and adductor muscle in the 2 populations is given in Table 1. One-tailed t-tests showed that all differences recorded between the populations are significant ($p < 0.05$). In North Sea mussels, shell constituted on average 85.6 % of the total dry weight compared to 82.5 % in transferred Baltic mussels. Relatively more biomass was allocated to the posterior adductor muscle (3.2 % of total dry wt, 22.4 % of shellfree dry wt) in the North Sea compared to transferred Baltic mussels (2.8 % of total dry weight, 16.2 % of shellfree dry weight) while transferred Baltic mussels contained more meat (14.7 % of total dry wt, 83.8 % of shellfree dry wt) than North Sea mussels (11.2 % and 77.6 % respectively).

A comparison of $CaCO_3$ and organic content in shells of Baltic mussels, North Sea mussels and mussels 1 yr after transplantation from the Baltic to the North Sea, is given in Table 2a. The $CaCO_3$ content of the shell was generally lower in native Baltic mussels than in native North Sea mussels with intermediate values for the transplanted mussels. While $CaCO_3$ content decreased with size in Baltic and transferred mussels it increased in North Sea specimens. The organic content varied in the opposite way and was lower in North Sea and transplanted specimens. A randomised block analysis (Table 2b) showed that the $CaCO_3$ content is dependent on origin, but not on size. A few determinations of shell ash content also showed higher values in North Sea mussels.

Predation experiment

In 4 aquaria the 10 mussels first opened by *Asterias rubens* were all of Baltic origin (ratio 10 : 0), while in the remaining aquaria the ratios were 9:1, 8:2, 8:2 and 7:3.

Table 1. *Mytilus edulis*. Percentage of total and shellfree dry weight allocated to shell, posterior adductor muscle and meat excluding adductor muscle in Baltic mussels 1 yr after transplantation to the North Sea and of native North Sea mussels of the same size (ca 50 mm). SE of means are given. One-tailed t-test showed that all differences between the populations are significant ($p < 0.05$)

		Muscle	Meat	Shell
Transplanted to North Sea	% of total dry wt	2.8 ± 0.2	14.7 ± 1.3	82.5 ± 1.4
	% of shellfree dry wt	16.2 ± 1.4	83.8 ± 1.4	–
North Sea	% of total dry wt	3.2 ± 0.2	11.2 ± 0.7	85.6 ± 0.8
	% of shellfree dry wt	22.4 ± 1.7	77.6 ± 1.7	–

Table 2a. *Mytilus edulis*. Comparison of $CaCO_3$ and organic content in shells of Baltic mussels, North Sea mussels and mussels 1 yr after transplantation from the Baltic to the North Sea, after treatments with diluted HCl. SE of means are given

		Size (mm)		
		10–25	25–40	40–60
Baltic Sea	Organic %	7.8 ± 0.8	9.3 ± 0.8	–
	$CaCO_3$ %	92.2 ± 0.8	90.7 ± 0.8	–
Transplanted to North Sea	Organic %	5.5 ± 0.6	7.1 ± 0.6	7.6 ± 0.6
	$CaCO_3$ %	94.5 ± 0.6	92.9 ± 0.6	92.4 ± 0.6
North Sea	Organic %	6.7 ± 1.1	4.8 ± 1.1	2.8 ± 1.1
	$CaCO_3$ %	93.3 ± 1.1	95.2 ± 1.1	97.2 ± 1.1

Table 2b. Randomised block analysis of data in Table 2a. Degree of freedom (df), sum of square (SS) and mean square (MS) are given. H_0:$CaCO_3$ independent of origin $= 0.005 > p > 0.001$; H_0:$CaCO_3$ independent of size $= 0.25 > p > 0.1$; H_0:$CaCO_3$ independent of origin/size interaction $= 0.25 > p > 0.1$

Source of variation	df	SS	MS
Between seas (origin)	2	35.1	17.6
Between sizes (size)	2	8.8	4.4
Interaction	3	13.5	4.5
Residual	8	12.0	1.5
Total	15	69.4	

Thus, the transferred Baltic mussels were clearly more susceptible to predation by *A. rubens* than were North Sea mussels. Through direct visual observation of the aquaria it was also noted that the starfish more readily attacked the Baltic mussels, even though there could be North Sea mussels closer at hand. It took between 1 and 4 d for *A. rubens* to open 10 mussels, and during this period no mortality occurred in the 2 control aquaria without predators. The longest time (3 to 4 d) for eating 10 mussels was recorded in the experiments with most North Sea mussels consumed, which indicates that these are more difficult to open. Most shells (90 %) of the Baltic mussels were broken by the predator, while all North Sea mussels eaten were opened without damaging the shells.

DISCUSSION

Shell length in the transplanted mussels from both the Baltic and North Sea populations approached that of the native populations, and this suggests that growth in length is to a major extent regulated by non-genetic factors. The most important environmental factors influencing growth rate are likely to be salinity, temperature and food supply (see reviews in Seed 1976, Kautsky 1982a). Only few comparable measurements of primary production exist for the areas. Aertebjerg et al. (1981) (in Rosenberg et al. 1986) gives a mean annual primary production of 105 g C m^{-2} yr^{-1} for the period 1968 to 1977 in the Kattegatt, while Larsson & Johansson (1988) give a slightly higher average value of 129 g C m^{-2} yr^{-1} for the Askö area during 1976 to 1987. The annual mean water temperature calculated from monthly measurements at 5 m depth at the 2 sites was very similar during the experimental period; 1985, Askö 6.3 °C, Tjärnö 7.6 °C; 1986, Askö 7.2 °C, Tjärnö 7.6 °C; 1987, Askö 6.6 °C, Tjärnö 6.8 °C. Thus, since the differences in primary production and temperature are minor between the Baltic and North Sea sites, salinity is probably the main cause of growth and size differences between the 2 areas.

Although low salinity may reduce ciliary activity in mussels (Schlieper 1955, Schlieper & Kowalski 1957, Lagerspetz & Sirkka 1959), filtration rate is only influenced to a minor degree by lowering salinity (Theede 1963), and direct comparisons of filtration rates from the 2 populations have given even slightly higher values for Askö mussels (6.6 ± 1.8 l g^{-1} h^{-1}) than for Tjärnö mussels (4.1 ± 0.5 l g^{-1} h^{-1}) (Gilek & Tedengren unpubl.). Thus we conclude that the main reason for the much lower growth rate is likely to be a salinity-dependent change in amino acid metabolism and nitrogen excretion resulting in a less favorable energy balance in low saline areas (Tedengren

& Kautsky 1986) (cf. also discussion in Tedengren et al. 1990).

Enzyme analysis by Johannesson et al. (1990) showed that the high initial mortality of North Sea mussels transplanted to the Baltic was selective in some enzyme loci and that only North Sea mussels of Baltic Sea genotype survived. Also the sudden mortality of Baltic mussels in late summer 1 yr after transplantation to the North Sea seems to be due to genetic factors, as it was very selective against Baltic genotypes (Johannesson et al. 1990). While the North Sea mussels were probably killed by direct salinity effects after transfer, a possible mechanism for death of the Baltic genotypes may be a genetically determined low resistance to diseases in Baltic mussels (cf. Tedengren et al. 1990).

Thus, our general results, indicating that growth and maximum size are determined by salinity and that the observed mortalities seem to be genetically induced, are in accordance with Dickie et al. (1984), who found that site differences were the major determinants of variation in growth in populations of *Mytilus edulis*, while population differences were chiefly responsible for variation in mortality. Similar conclusions have also been drawn for the oyster *Crassostrea virginica* by Mallet & Haley (1983).

Although after 1 yr in the North Sea environment shell length and width of the transferred Baltic mussels were similar to those of North Sea mussels, major differences in shell height gave the Baltic mussels a more narrow and elongated shape. As a consequence total volume, shell weight and meat weight of the transferred Baltic mussels were lower than for North Sea mussels of the same length. Although the size-specific amount of meat was significantly less in the transferred Baltic mussels, these had significantly more meat relative to shell and adductor muscle biomass.

The $CaCO_3$ content in shells was also higher in North Sea mussels and they appeared thicker having a blue-white coloration, while Baltic and transferred mussels were thinner with brown, translucent shells. Since the shells of transferred Baltic mussels were furthermore easily cracked by *Asterias rubens* in the predation experiment, this confirms a weaker shell structure.

Schlieper (1971) found that while dry weight and calcareous content of *Mytilus edulis* shells of equal size at 6 ‰ S were only 34 % of those at 30 ‰ S, the organic content was only reduced to 55 %. Since the amount of organic matter (conchiolin, periostracum) does not diminish to the same degree as the calcium content, the percentage of organic matter in the shell will increase. This explains the generally slightly higher proportion of organic matter observed in the Baltic and in the transferred mussels.

The observation by Almeda-Villela (1984) that the

process of calcification and shell deposition is depressed at salinities below 12.8 ‰ S may explain part of the differences in shell thickness existing between Baltic and North Sea mussels in their natural habitats (cf. also Schlieper 1957, Malone & Dodd 1967). However, the fact that these differences were also maintained in Baltic mussels that had been transplanted 1 yr earlier would indicate that there are also genetic causes.

The other morphological differences remaining more than 1 yr after transplantation (e.g. meat weight, muscle size, shell height, total volume), are also likely to be genetically induced. The alternative to a genetic explanation would be the possibility of a slow acclimatisation process. This, however, seems unlikely as the mussels increased in length from 4 to 43 mm and more than 100 times by weight over the time period. Differences in the reproductive cycle are also not likely to be the cause as this is similar in the 2 populations (Kautsky 1982b), and as transplantations were made in July, before the buildup phase of the gonads, and sampling was carried out after spawning the following year.

Although grown in the North Sea for 12 mo and having reached the same length as North Sea mussels, the Baltic mussels in our experiments were much more susceptible to predation from *Asterias rubens*. This higher susceptibility to predation of Baltic mussels seems to be mainly due to the recorded morphological differences, such as thinner shells and smaller adductor muscles, but visual observations of starfish behaviour indicated that there may be also differences in attractiveness through the release of chemical stimuli or repellants from the mussels into the water.

Muscle size would normally determine susceptibility to predation by *Asterias rubens*, which usually opens the shells by exhausting the adductor muscle (cf. Hancock 1965, Theisen 1982). However, as most shells of mussels originating in the Baltic were broken by the starfish, the weakest point in these seems rather to be the shell structure.

Asterias rubens represents only one type of a mussel predator, and it is clear that the thin shells would also be much easier to break for the shore crab *Carcinus maenas*. Furthermore, the much smaller size of mussels in the Baltic would increase susceptibility to predators which swallow their prey whole, e.g. some fish and eider ducks.

Nonetheless, despite being poorly equipped with protective characters, *Mytilus edulis* is extremely successful in the Baltic proper where it constitutes 80 to 90 % of the total animal biomass in coastal areas (Jansson & Kautsky 1977, Kautsky 1988). The main reason for this dominance has been attributed to an almost complete absence of mussel predators (Kautsky 1981). Mussel-predating invertebrates (e.g. *Asterias rubens, Carcinus maenas*) are lacking completely and those

remaining (i.e. diving birds and some fish) have been estimated to annually consume less than 1 % of the standing stock in the northern Baltic proper (Kautsky 1981). We suggest that this lack of predation pressure may be the reason for low selection favouring genes promoting characteristics such as thick shells and large adductor muscles in the Baltic Sea.

Since maturity in *Mytilus edulis* is determined by age rather than size (Seed 1969, Kautsky 1982b), there would also be little selection pressure for increasing size in Baltic mussels for this purpose. This means that relatively more of the energy available can be allocated to gamete production, which is shown by the fact that the fecundity of mature but small Baltic mussels (25 mm) is similar to that of adult mussels (60 mm) from marine areas (Kautsky 1982b). This is also consistent with our data showing that the Baltic mussels have significantly more meat relative to shell and adductor muscle biomass than North Sea mussels, and that these differences remain even more than 1 yr after transplantation. If these differences had been solely environmentally induced, they should have disappeared. This therefore suggests that the fecundity of Baltic mussels is partly genetically determined.

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