

Variability of growth rate in *Mytilus edulis* L. from the Chupa Inlet (the White Sea)

A. A. Sukhotin^{a,*}, N. V. Maximovich^b

^aThe White Sea Biological Station, Zoological Institute, Universitetskaya nab., 1, 199034 St. Petersburg, Russia; ^bBiological Faculty, St. Petersburg State University, St. Petersburg, Russia

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Abstract

Length growth of mussels *Mytilus edulis* L. was studied in the White Sea in four habitats after reciprocal transplantation during a one-year period (1987–1988) and summer period (1989). Mussels from different habitats, size and age groups were marked individually and put in net cages. The cages were located in intertidal zone, subtidal zone and on suspended aquaculture rafts. Habitat appeared to be the most important factor for growth of mussels. In spite of origin and age/length characteristics in intertidal zone, mussels grew approximately 2 times slower than in subtidal zone and 3–5 times slower than in suspended conditions. Age or length of mussels was the second most important growth factor. Type of habitat where the mussels came from (“origin”) appeared to have no influence on growth. Model of mussel growth in different habitats in relation to seasonal temperatures, molluscs age or length is given.

Key words: Aquaculture; Growth; Model; Mussel; *Mytilus edulis*; White Sea

1. Introduction

Growth rate is one of the most easily tested integral indicators of life conditions of bivalve molluscs. Environmental parameters influencing growth rate can be divided into factors of general action and those of local action. Factors of general action include water temperature and salinity, which may affect the rates of biochemical reactions within an organism in temperate latitudes. Local factors determining nutritional conditions can influence greatly the growth rate of marine bivalves. The most important among them are: particulate organic matter concentration and quality (Essink & Bos, 1985; Wilson, 1987; Brown, 1988; Thompson & Nickols, 1988), duration of air expo-

* Corresponding author.

sure (Savilov, 1953; Baird, 1966; Seed, 1969), population density (Broom, 1982; Peterson & Beal, 1989) and water current velocity (Harger, 1970; Soldatova, 1986; Grizzle & Morin, 1989). In addition, there are factors of “individual” action such as size, age, reproductive condition and genetic characteristics of specimens.

The main objective of this paper is to study the linear growth rate of the White Sea mussels (*Mytilus edulis* L.) as a response to the most significant factors:

- habitat as an integral index of growth conditions for molluscs from certain population
- origin as a possible influence of former life conditions
- size and age of mussels in the analyzed groups as the main characteristics of their initial growth possibilities
- seasonal changes of water temperature as a factor determining the phenology of biological processes in the White Sea (Kaufman, 1977).

2. Materials and methods

Mussels for the experiments were collected from two natural mussel beds and from a suspended mussel culture farm (Fig. 1) ($66^{\circ} 20' N$; $33^{\circ} 40' E$). Four local habitats were studied: 1, middle level of intertidal zone (+0.6 m) near Cape Kartesh; 2, middle level of intertidal zone (+0.7 m); 3, subtidal zone (−0.5 m) of Matrenin Island and

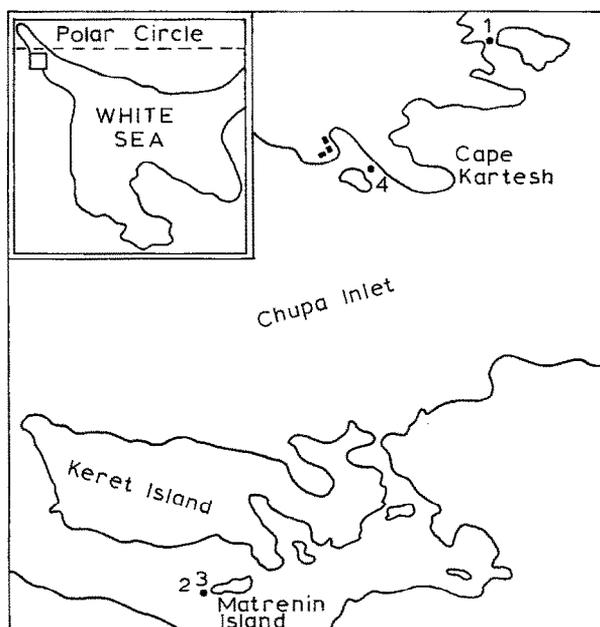


Fig. 1. Map of the area studied. Mussel sampling localities (see text).

4, artificial substrata of suspended mussel culture farm (≈ 1 m under the water surface) near Cape Kartesh.

Two growth experiments were performed:

(I) Mussels of different sizes from habitats 1 and 4 were maintained in net cages for a year (1 June 1987 to 1 June 1988). One hundred mussels from each habitat were collected, measured to the nearest 0.1 mm and marked individually. The mussels were put into net cages (50 specimens in each) and located in habitats 1 and 4. Thus, in each site there were two cages containing mussels from native and from another habitat. For studying seasonal dynamics of mussel growth, 13 control measurements of the mussels have been made throughout the year.

(II) Mussels of different sizes and ages from habitats 2, 3 and 4 were kept in net cages for three summer months (9 June to 9 September 1989). Mussel reciprocal transplantation was performed in the same way as in the experiment I, so that three cages containing 43–55 molluscs were located in each habitat. The net cages used in these two experiments differed slightly in their shape and in size of mesh (in the first experiment cages with 5-mm grid and in the second, 8-mm grid were used). Mortality of mussels in cages located in the intertidal zone and suspended from mussel culture rafts did not exceed 7%, while in subtidal cages (habitat 3) it was about 20%. In the latter case the cages were rather muddy at the end of the experiment.

Length growth of mussels was reconstructed by counting and measuring of the rings of winter growth delays on the shells. The data obtained were formalized using the von Bertalanffy equation

$$L_t = L_\infty (1 - \exp^{-k(t - t_0)}) \quad (1)$$

where L_t is shell length (mm) at time t (year), and L_∞ , k , t_0 are constants. Calculation of parameters was performed analytically (Maximovich, 1989a). Seasonal changes of growth rate were determined, taking into account the average monthly water temperature (Babkov, 1982). An annual sum of day-degrees in the region was 1932.2. In order to incorporate temperature into Eq. (1), accumulated values of corresponding sums of day-degrees were introduced instead of t (Ursin, 1965; Maximovich, 1989b)

$$L_D = L_\infty (1 - \exp^{-k'D - k't_0}) \quad (2)$$

where $k' = k/D_y$; D_y is an annual sum of day-degrees, D is a sum of day-degrees since growth began. It has been assumed that L_∞ does not depend on temperature. A temperature of -0.9°C was taken as the lowest level of temperature when mussel growth stops.

3. Results

One of the main principles allowing these experiments to be carried out is the initial difference of mussel growth in the chosen settlements/habitats. For each settlement the von Bertalanffy equation of mussel growth was obtained (Table 1). The studied habitats differed from one another in height on the shore, type of substratum (gravel

Table 1

Mean mussel length at winter growth stopping and parameters of growth Eqs. 1 and 2

<i>t</i>	Habitats			
	1	2	3	4
1	–	5.2	5.4	6.3
2	–	9.2	13.9	17.0
3	14.0	18.4	23.4	30.4
4	17.8	27.4	32.8	43.9
5	20.5	33.2	40.3	56.6
6	24.5	38.7	45.7	63.3
7	30.5	42.0	49.4	67.4
8	32.5	42.5	51.7	70.5
9	31.5	44.2	52.6	72.9
10	34.5	–	–	74.1
11	35.0	–	–	–
12	39.5	–	–	–
<i>k</i>	0.1187	0.1597	0.1866	0.1956
<i>k'</i>	$6.1 \cdot 10^{-5}$	$8.3 \cdot 10^{-5}$	$9.6 \cdot 10^{-5}$	$1.0 \cdot 10^{-4}$
L_x	51.254	63.245	69.841	92.945
t_0	0.3495	0.6395	0.6738	0.7414

Note: *t* is number of growth rings (symbolical age); *k*, L_x and t_0 are parameters of Eqs. 1 and 2; *k'* is parameter of Eq. 2. For descriptions of habitats, see text.

for settlements 1, 2, 3 and nylon net band for settlement 4), intensity of water dynamics (settlements 2 and 3 were constantly washed by rapid tidal currents). The corresponding growth curves differ significantly and confidence intervals ($p < 0.05$) of average length for mussels of the same age as a rule are not overlapping (Fig. 2). Increase of mussel growth rate in these habitats corresponds to gradients of improvement of growth conditions, i.e. (1) intertidal zone with low water current; (2) intertidal zone with high water current; (3) subtidal zone and (4) suspended culture.

The experiments have resulted in obtaining two data sets characterizing values of the mussel length growth increments in different growth conditions. For the ANOVA test these values were arranged as follows: (I) along the gradients of three factors, initial length (IL) (< 20; 20–30; 30–40 mm), origin (OR) and habitat (HAB) (symbolic grades: intertidal zone, subtidal zone, aquaculture) and (II) along the gradients of four factors, initial length (IL) (< 30; 30–40; 40–50; > 50 mm), age (AG) (3–4; 6–7; > 8 years), origin (OR) and habitat (HAB) (symbolic grades: intertidal zone, subtidal zone, aquaculture).

The results of ANOVA are given in Tables 2 and 3 and Figs. 3 and 4.

3.1. Habitat (HAB)

As follows from the divergence of growth curves (Fig. 2), the environmental conditions in investigated habitats largely determine the growth of mussels. In both experiments this factor primarily influenced the value of length increments of the mussels

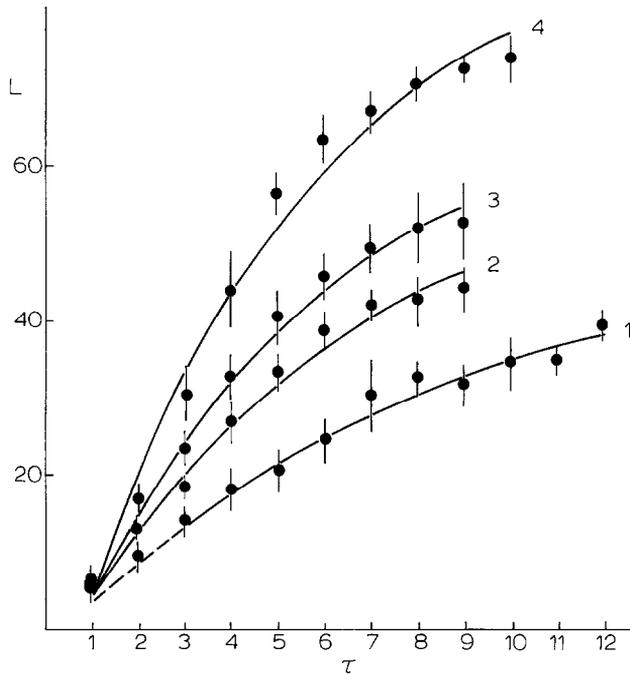


Fig. 2. Length growth curves of mussel from different settlements/habitats. Figures: number of settlements (see text). Y-axis: mean shell length (mm); X-axis: number of growth ring (years). Vertical bars: 95% confidence limits.

(Tables 2 and 3). In almost all cases, HAB was responsible for at least 40% of total complex deviance. The length increments of mussels located in the intertidal zone appeared to be almost half lower, that in the subtidal zone (habitat 3) and 20–30% than those of mussels from suspended culture (habitat 4) (Fig. 3).

Table 2
Analysis of variance for experimental complex I

Source of variance	SS	df	S ²	F	Sig. level	H (%)
Factors	2070.8	4	527.7	120.3	<0.001	84.6
IL	696.3	2	348.2	85.0	<0.001	29.6
HAB	1175.2	1	1175.2	286.8	<0.001	47.6
OR	113.8	1	113.8	27.8	<0.001	4.8
IL-HAB	82.0	2	41.0	10.0	<0.001	3.5
IL-OR	11.5	2	5.7	1.4	0.252	–
HAB-OR	0.3	1	0.3	0.1	0.777	–
Residual	376.9	92	4.1	–	–	–

Note: SS = deviance; S² = variance; F = F-ratio (p < 0.05); H = SS/ΣSS; IL = initial length; HAB = habitat; OR = origin.

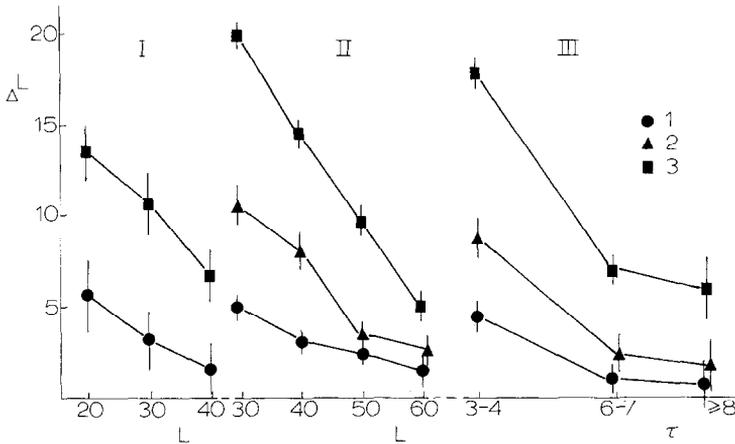


Fig. 3. Mean growth increments (mm per year for I and mm per 3 months for II and III) of mussels of different length and age class in different habitats: 1, intertidal zone; 2, subtidal zone; 3, suspended aquaculture. I, one-year exposition of cages (1987–1988), II and III, 3-months exposition of cages (summer 1989). X-axis: in I and II graphs, length classes (mm), and in III graph, age classes (years). Vertical bars: 95% confidence limits.

3.2. Initial length and age (IL and AG)

As IL and AG are correlated factors, their effects were analyzed in different ANOVA complexes. The effects of these factors on mussel growth rate were similar and explained about 30% of total deviance (Tables 2 and 3). Increase in both size and age causes the regular decrease in length increments of mussels regardless to site of cages location. The better growth conditions were, the more abruptly length increments decreased with increasing size and age of molluscs (Fig. 3).

3.3. Origin of mussels (habitat where the mussels come from) (OR)

In general, this factor significantly influenced the growth of mussels ($p < 0.05$) (Tables 2 and 3A,B). However, this effect was relatively small and explained only 1.5–4.8% of total deviance. In addition, the effect of OR was different in the two experiments. In the first experiment mean length increment of originally intertidal mussels in suspended conditions was lower than that of cultured mussels in the same habitat. On the contrary, in the second experiment the length increments of cultured mussels were lower (Fig. 4). We assumed that the effect of OR appears due to heterogeneity of mussel age and size characteristics in the experimental samples (Table 1). Standardization of the variants by age and size became possible only after considerable reduction of complex II. Mussels of one age group (3–4 years) and size class (30–40 mm) were found only among subtidal and cultured ones and involved into analysis. In such analysis the effect of OR was insignificant and 85% of total deviance was associated with the factor HAB (Table 3C).

Table 3
Analysis of variance for experimental complex II

Source of variance	SS	df	S^2	F	Sig. level	H (%)
<i>(A) Factors IL, HAB and OR:</i>						
Factors	12390.9	23	538.7	1.6	<0.001	87.7
IL	4728.7	3	1576.2	294.9	<0.001	33.5
HAB	5719.2	2	2852.5	535.0	<0.001	40.5
OR	225.2	2	112.5	21.0	<0.001	1.6
IL-HAB	864.9	6	144.2	27.0	<0.001	6.0
IL-OR	435.5	6	72.6	13.6	<0.001	3.1
HAB-OR	35.9	4	9.0	1.7	0.155	0.3
IL-HAB-OR	106.7	12	9.0	1.7	0.155	0.1
Residual	1742.4	326	5.3	–	–	–
<i>(B) Factors AG, HAB and OR:</i>						
Factors	11195.2	18	1865.9	340.5	<0.001	86.1
AG	4976.4	2	2488.2	454.0	<0.001	35.2
HAB	5278.1	2	2639.0	481.5	<0.001	37.3
OR	561.5	2	280.8	51.2	<0.001	4.0
AG-HAB	976.4	4	244.1	44.5	<0.001	6.9
AG-OR	70.1	4	17.5	3.2	0.013	0.5
HAB-OR	230.8	4	57.7	10.5	<0.001	1.6
AG-HAB-OR	225.8	8	28.2	5.2	<0.001	–
Residual	1814.0	331	5.5	–	–	–
<i>(C) Factors HAB and OR with standardized size and age distribution in ANOVA cells:</i>						
Factors	1430.0	5	286.0	84.3	<0.001	88.3
HAB	1380.0	2	689.0	152.8	<0.001	85.1
OR	1.7	1	1.7	0.4	–	0.1
HAB-OR	50.3	2	25.2	5.6	0.001	3.1
Residual	189.0	42	5.6	–	–	–

Note: SS = deviance; S^2 = variance; F = F -ratio ($p < 0.05$); H = SS/ESS ; IL = initial length; HAB = habitat; OR = origin; AG = age.

3.4. Factor interactions

Besides the main factors (HAB, IL, AG, OR), joint effects were shown in the experiments. This explained from 4 to 10% of total deviance (Tables 2 and 3). For example, factor HAB had a different influence on mussels of varying age and size. In small mussels from the intertidal zone and culture rafts the absolute values of growth increments had a greater difference than in larger ones. In other words, younger and smaller specimens responded more sharply to the changes of environmental conditions than older and larger specimens. However, relative values of length increments were found to be greater in older and larger mussels than in smaller and younger ones. Thus, while being transferred from intertidal zone to suspended culture (experiment II), 30 mm mussels increased their length increment 3.7 times (from 5.4 to 20.0 mm), 40 mm, 4.9 times (from 3.0 to 14.8 mm), 50 mm, 6.5 times (from 1.5 to 9.8 mm) and 60 mm, 9.8

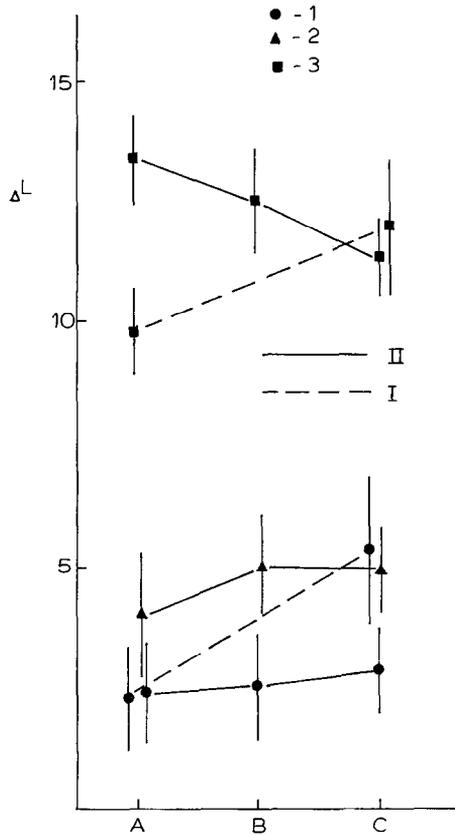


Fig. 4. Mean growth increments (mm per year for I and mm per 3 months for II) of mussels of different origin (A, intertidal zone; B, subtidal zone; C, suspended aquaculture) transplanted into: 1, intertidal zone, 2, subtidal zone, 3, suspended aquaculture. I, experiment 1 (1987–1988); II, experiment 2 (summer 1989).

times (from 0.5 to 4.9 mm). The same tendency was observed regarding not only size, but also age.

3.5. Temperature

Since the studied settlements were situated not far from one another, we assumed that seasonal temperature gradients equally affected the mussel growth in all of them. Monthly length increments of mussels from settlements 1 and 4 were compared with seasonal growth curves estimated using Eq. 2 (Fig. 5, Table 1). Generally the models corresponded with the observed changes in length of experimental mussels, though in settlement 4 the length of 2- and 3-year-old molluscs appeared to be considerably less than the theoretic values. Probably it is connected with the characteristics of the von Bertalanffy equation as a growth model (Theisen, 1973).

On the whole, the observed seasonal growth changes of cultured mussels better

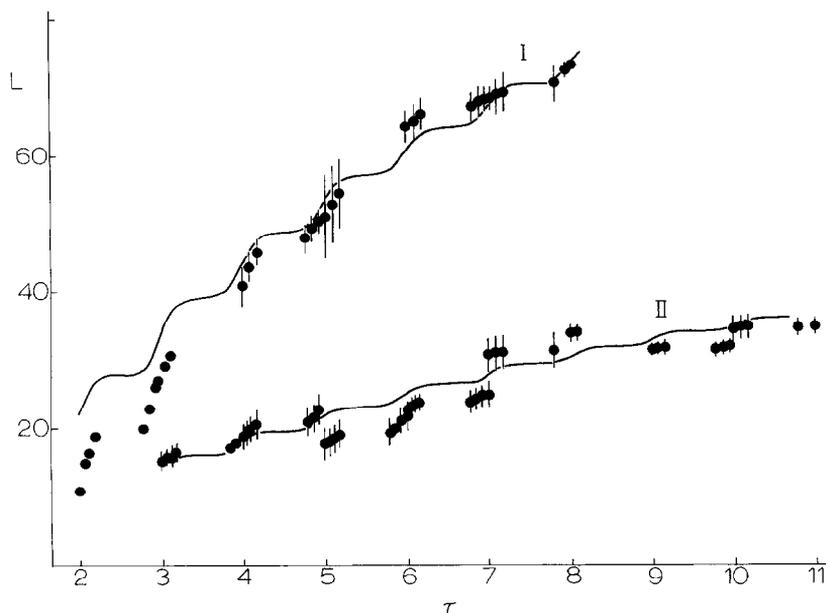


Fig. 5. Seasonal dynamics in length growth of mussels from suspended culture (I) and intertidal zone (II) (from Sukhotin et al., 1992). Y-axis: mean shell length (mm); X-axis: age (years). Vertical bars: 95% confidence limits.

corresponded to the model than those from the intertidal zone. It is important that in all 10 cases, changes in growth rate of experimental mussels coincided with model characteristics, regardless of absolute values.

4. Discussion

The results of the study show that the mussels from intertidal zone, subtidal zone and suspended aquaculture in the White Sea have significantly different average growth rates. The observed trend in growth rate changes is well known. Decreasing growth rate with increasing air exposure has been demonstrated in different populations of bivalves (Savilov, 1953; Dehnel, 1956; Seed, 1969, 1973; Peterson & Black, 1988). It is also well known that maximal growth rate is typical for mussels from fouling communities, living above the bottom (Baird, 1966; Soldatova et al., 1985; Fréchette & Bourget, 1985; Sukhotin & Kulakowski, 1992). Moreover, even within the single tidal level (settlements 1 and 2), the characteristics of hydrodynamics can cause significant differences in mussel growth rate. Changes in mussel growth rate depend on the significance and range of the main growth factor variation (Baird, 1966; Seed, 1968; Kautsky et al., 1990), but can appear in habitats with similar environmental conditions (Dickie et al., 1984; Mallet et al., 1987).

Similar growth rates observed in mussels from different areas, but similar habitats,

are probably caused by resemblance in food conditions. At the investigated sites, the main indirect indices of food conditions were the duration of air exposure and the intensity of water exchange. These aspects can be expressed quantitatively by the following: in the obtained data (Tables 2 and 3) factor HAB accounted for about 40–50% of total deviance; the average growth increments of mussels from intertidal zone were 2–5 times lower than of those from suspended culture and 1.5–2 times lower than of those from subtidal zone. A very similar value of site effect on growth (40% of total variance) was observed for *Mytilus edulis* from Nova Scotia (Canada) (Mallet et al., 1987) and (50% of non-error variance) for *Mercenaria mercenaria* from the Atlantic coast of the USA (Rawson & Hilbish, 1991). It is worth noting that in Killary Harbour (Ireland) *Mytilus edulis* from intertidal zone grew approximately 4 times slower than in aquaculture conditions (Rodhouse et al., 1984).

The influence of the factor OR is considered by many authors as a manifestation of genetic differences of mussels from separate sites, which cause differences in growth rate (Tedengren & Kautsky, 1986; Peterson & Beal, 1989; Rawson & Hilbish, 1991), filtration rate and net growth efficiency (Widdows et al., 1984), mortality (Dickie et al., 1984; Kautsky et al., 1990). On the other hand, OR may reflect differences in “pre-experimental” life of mussels and serve as a characteristic of “ecological memory” of specimens, i.e. the ability to keep invariable or change growth parameters while the life conditions alter (Mallet et al., 1987). In this case, the effect of this factor is already involved in the initial length and age heterogeneity of the experimental sample. Mallet and colleagues (1987) found the effect of “stock” (origin) on *Mytilus edulis* length increments to be about 27% of total variance. In contrast, mussels from subtidal populations and from suspended collectors (Denmark) transplanted to subtidal zone demonstrated similar growth rates (Kristensen and Hoffman, 1991). In the present study, this question remains open since, after standardizing of mussels by age and length, the effect of OR on growth was not proved. In the above-mentioned experiments any genetic factor was probably completely masked by the influence of such strong factors as HAB, IL and AG.

The importance of size and age on mollusc growth rate is well known. According to the data obtained, IL (or AG) appears to be the second most important factor (of those tested) of mussel growth. It explains more than 30% of total deviance in data complexes (Tables 2 and 3).

Mean length increments of mussels of different size groups within one year (1987–1988) and within three summer months in 1989 may be considered as comparable. Probably it is because of the differences in cage construction and environmental conditions of two growth seasons. This makes it possible to carry out a comparative analysis of results obtained in both experiments. It is obvious that mussel growth is determined by only three factors: habitat, initial length and age. Within the investigated time period, these relations are non-linear (correlation coefficient not least 0.75) and can be fitted with multiple regression equations, where IL and AG, as correlated factors, are taken separately. These models, to a great extent, are of local importance. Their parameters are similar and express a notable effect of all three factors in the investigated range of variation. In practice, the models allow the prediction of mussel length increment using both IL and AG. Thus, the regression model of changing of mean

annual length increments of mussels as a function of length (age) and habitat can be estimated. "Habitat" here was taken in accordance to symbolic scale of six values. These values meant the improvement of growth conditions along the gradient and were proportional to the minimal difference in mean growth rate of mussels (populations 2 and 3) (Fig. 2). Therefore, the site/settlement 1 had value 1, the site/settlement 2 had value 3, the site/settlement 3 had value 4 and the site/settlement 4 had value 6. Seasonal changes of length increments of mussels of different size can be predicted using the following equations:

$$\Delta L = D/D_y (5.11 - 0.16 * L_o + 1.59 * \text{Habitat}), r^2 = 0.67, \quad \text{SE} = 2.208 \quad (3)$$

$$\Delta L = D/D_y (8.14 - 0.91 * \text{Age} + 0.57 * \text{Habitat}), r^2 = 0.56, \quad \text{SE} = 2.559 \quad (4)$$

where D_y is an annual sum of day-degrees; D is a sum of day-degrees since growth began; L_o is the initial length (mm).

These models can be used successfully for mussels from suspended culture, because in this habitat seasonal growth model has the best fit with observed data. Obviously the effect of temperature on mussel growth in intertidal zone to the great extent can be hidden by the influence of such a stress factor as air exposure.

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