# Growth and size structure in a Baltic Mytilus edulis population

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# Growth and Size Structure in a Baltic *Mytilus edulis* Population

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## Abstract

Since *Mytilus edulis* L. has very few predators and competitors for space, it has become a biomass dominant in the Baltic proper covering hard substrates from the water surface to more than 30 m depth. In order to investigate the factors controlling size and production in a Baltic *M. edulis* population, growth was studied by the analysis of annual growth rings, measurements of caged individuals and the analysis of size classes in the population, and on settlement ropes. The total number of mussels in a representative mussel bed at 4 m depth varied between 36 000 and 158 000 ind · m$^{-2}$ during the year, mainly due to variations in very small mussels (< 2 mm), whereas the abundance of mussels ≧ 2 mm was rather constant between about 17 000 and 28 000 ind · m$^{-2}$. Maximum numbes of mussels < 2 mm, amounting to 132 000 ind · m$^{-2}$, were found after settlement in summer, but still half a year later in spring, 65 000 ind · m$^{-2}$ < 2 mm were registered, due to very strong intraspecific competition for food and space leading to the competitive suppression of small individuals and large variations in growth rates. Due to the special size-structure of the population only the analysis of annual growth rings could be used to estimate natural shell growth. From being very low in the smallest mussels, growth was linear between about 2–10 yr of age, corresponding to about 3–20 mm length, after which it decreased with a $L_\infty = 32$ mm. Over the linear interval, growth in the populations from 3–6 m and 10–15 m depth was 3.1 and 2.2 mm · yr$^{-1}$, respectively. Meat growth showed strong annual variations mainly due to gonad production. Starving mussels could, however, while utilizing energy reserves, survive losses of up to 78% of their meat biomass. This ability of *M. edulis* to "respire away its own biomass" and its apparent tolerance of weight loss has important implications. It will drastically reduce the energy flow to destruents from mussels dying naturally, which is of special significance in the Baltic, where predators and scavengers are scarce. It enables the mussels to endure bad food conditions and buffer strong seasonal variations in food abundance, maintaining the strongly food- and space-limited Baltic *M. edulis* population at the carrying capacity of the area.

## Introduction

Only a few marine species have managed to adapt to the reduced salinities in the Baltic Sea, with *Mytilus edulis* being one of the most tolerant. Due to the absence of major predators and competitors, this species has been able to colonize nearly all hard substrates from the water surface down to more than 30 m depth (Kautsky, 1981a) and is also an important faunal component on coastal sandy bottoms (Ankar and Elmgren, 1976). Since physical factors like ice and storm abrasion influence only a minor fraction of the mainly sublittoral Baltic *M. edulis* population, intraspecific competition for food and space will be the main factor controlling this species. This leads to the population size and biomass being kept fairly constant, near the carrying capacity of the area with regard to food and space (Kautsky, 1981b, 1982).

The lowered salinities in the Baltic have a detrimental effect on the growth rate of *Mytilus edulis,* and the mussels reach a maximum length of only 40 mm at 4–5‰ S (Remane and Schlieper, 1971). This results in very dense populations of dwarfed mussels that completely dominate the hard bottoms, often making up more than 80% of the animal biomass (as ash free dry weight) in the Baltic proper (Jansson and Kautsky, 1977).

Despite its importance there is little quantitative information on the growth of *Mytilus edulis* in the Baltic proper. Data are available only from the more saline waters of the Western Baltic (e.g. Schütz, 1964; Boje, 1965; Samtleben, 1973, 1977). This study attempts to elucidate the factors controlling size and production in a *M. edulis* population from 6.5 to 7‰ S in the Baltic proper. Esti-

mates of growth rates were obtained using several methods, such as analysis of annual growth rings, measurements on caged individuals and size class analysis.

## Material and Methods

### Study Area

This study was made in a relatively unpolluted archipelago on the Swedish Baltic coast, near the Askö Laboratory, about 70 km south of Stockholm. The Baltic is atidal and the salinity of the area is rather stable, with values around 7‰ S in the upper 25 m. The water temperature has a yearly mean of 6 °C in depths down to 25 m, with large annual variations from −0.5 °C in winter, and generally 1–2 months of ice cover, to about 20 °C in summer (Fig. 1). About half of the bottom area above 25-m depth is covered by hard bottom communities (Jansson and Kautsky, 1977; Kautsky, 1981 b).

Most of the material was collected at 4-m depth outside the islet of Vrångskär, close to the laboratory. The bottom consists of rock and boulders with a dense population of *Mytilus edulis* and a flora mainly of the red algae *Furcellaria lumbricalis* (Huds.) Lamour., *Phyllophora truncata* (Pallas) Newroth and Taylor and *Ceramium tenuicorne* (Kütz.) Waern.

### Cage Experiments

Two types of cage were used to monitor growth. A larger "box-type" cage 16×12×12 cm, with the vertical sides covered by ∼ 1.5-mm mesh plastic net, and a smaller spherical cage type (Φ 10 cm) made of 1.5-mm plankton net. During 1973–1974, the larger type of cage was used in which 120 mussels belonging to four different size classes were kept. This cage was placed on the bottom in the *Mytilus edulis* bed at 4-m depth. During 1974–1975 the smaller type of cage was used in order to follow growth of individual mussels. Four to five mussels belonging to different size classes were placed in a total of 30 cages of

this type. No taggings were made since tests had shown them to be detrimental to the small, thin-shelled Baltic mussels. The small cages were suspended in the water at 4- and 15-m depths outside Vrångskär. At intervals of 1–2 months the mussels were brought to the laboratory and the shell lengths were measured with calipers.

During 1975 an experiment was designed to investigate the effect of increasing mussel densities on growth. Fifteen 5-mm mussels were placed in each of 3 cages of the small type. To two of the cages, 16 and 30 large mussels (∼ 30 mm) respectively, were added. The growth rates of the small mussels in the cages were then compared from June 5 to December 12.

### Calculations of Specific Growth Rate

Since the growth data obtained in the cages were derived from different time periods and size classes, the data had to be normalized to facilitate comparisons and the analysis of factors controlling growth. To do this the daily length-specific growth rate ($C_l$) of each individual was first calculated by the formula

$$C_l = \frac{{}^{10}\log L_2 - {}^{10}\log L_1}{\Delta t},$$

according to Winberg (1971), where $L_1$ and $L_2$ denote lengths at the start and end of the growth period ($\Delta t$). $C_l$ was then plotted against ${}^{10}\log L_{mean}$ during the period and straight lines were fitted by least squares. In this way estimates of the specific growth rate of mussels of any size during the different periods could be obtained. The equations from 4 m in 1974 and 15 m in 1974–1975 were also used in a computer program allowing the integration of *Mytilus edulis* shell growth from any starting date and size.

### Growth of Juveniles

The growth of juvenile mussels after settlement was followed on roughened 5-mm polyester ropes hanging from a supporting system outside Vrångskär. The mean
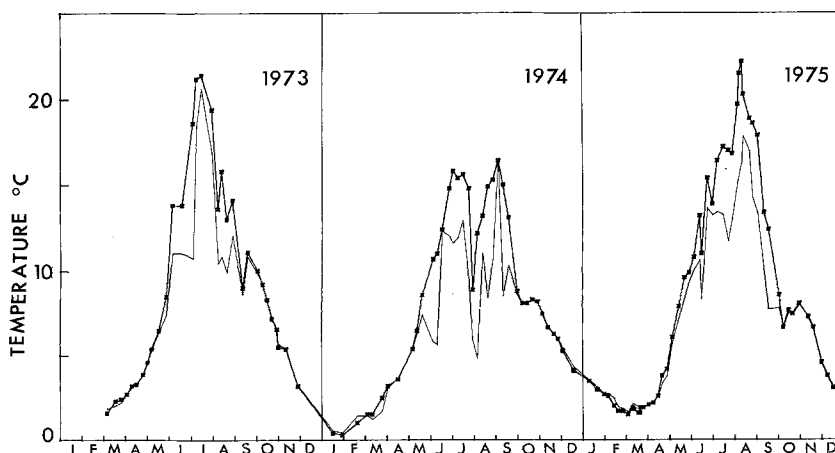


Fig. 1. Annual variation in water temperature at 4 (-■-) and 15 m (—) during 1973 – 1975

growth of the cohorts at 3 m in 1973 and at 3, 6, 11, and 15 m in 1975 were registered at weekly to monthly intervals. A further description of the material and methods used as well as a discussion of settlement variation and intensity is given in Kautsky (1982).

## Cohort Analysis

Size frequency diagrams of natural populations were constructed from quantitative samples taken during different seasons at 4 to 4.5-m depth outside Vrångskär, with a single additional sample taken further out at 13-m depth from a boulder bottom. Sampling was performed by divers using a 15 × 15 cm sampling frame with one side replaced by a 0.1 mm net bag (Dybern *et al.*, 1976, p. 91). The samples were sieved through a 0.1 mm mesh screen and the mussels were sorted out. All mussels larger than ~ 5 mm were measured to the nearest 0.05 mm with calipers while the smaller mussels were generally subsampled to ⅕ and measured under a stereo microscope.

Additional size-frequency diagrams were constructed from selected samples originating from a random sampling survey of the 160-km² research area (Jansson and Kautsky, 1977). Here a 1-mm sieve was used, thus largely excluding the size fraction < 2 mm. Small mussels clinging to algae and not loosening when shaken in water are, however, included.

**Table 1.** *Mytilus edulis.* Least-squares regressions of daily length-specific growth rate $(C_l)$ against $^{10}$log $L_{mean}$ for different growth periods obtained from cage growth data at 4- and 15-m depth during 1974 and 1975. a and b are parameters fitted to the equation $y = a\ ^{10}\log x + ^{10}\log b$, where y is the daily length-specific growth rate $(C_l)$ and x is the mean length $(L_{mean})$ of the individual mussel during the growth period. The correlation coefficient (r) and the number of mussels are also given

| Period | Depth | a | b | r | n |
|---|---|---|---|---|---|
| 74 02 20 – 74 04 22 | 4 | 0.02621 | – 0.01775 | 0.76 | 78 |
| 74 04 22 – 74 05 23 | 4 | 0.11167 | – 0.07728 | 0.83 | 77 |
| 74 05 23 – 74 06 22 | 4 | 0.30462 | – 0.20910 | 0.87 | 76 |
| 74 06 22 – 74 07 22 | 4 | 0.34450 | – 0.22097 | 0.77 | 75 |
| 74 07 22 – 74 08 19 | 4 | 0.28731 | – 0.17799 | 0.73 | 70 |
| 74 08 19 – 74 10 01 | 4 | 0.17609 | – 0.09896 | 0.51 | 66 |
| 74 10 01 – 74 11 20 | 4 | 0.09821 | – 0.05743 | 0.57 | 28 |
| 74 11 20 – 75 01 07 | 4 | 0.01504 | – 0.00749 | 0.27 | 32 |
| 75 03 27 – 75 06 03 | 4 | 0.13765 | – 0.09353 | 0.94 | 44 |
| 75 06 03 – 75 07 19 | 4 | 0.31580 | – 0.20388 | 0.90 | 41 |
| 75 07 19 – 75 08 27 | 4 | 0.29083 | – 0.18749 | 0.70 | 41 |
| 75 08 27 – 75 10 09 | 4 | 0.10714 | – 0.05659 | 0.34 | 42 |
| 75 10 09 – 75 12 10 | 4 | 0.12252 | – 0.07824 | 0.71 | 43 |
| 75 12 10 – 76 02 18 | 4 | 0.00335 | – 0.00072 | 0.07 | 32 |
| 74 08 06 – 74 10 01 | 15 | 0.16696 | – 0.10948 | 0.89 | 36 |
| 74 10 01 – 74 11 20 | 15 | 0.09286 | – 0.05894 | 0.84 | 36 |
| 74 11 20 – 75 01 07 | 15 | 0.01414 | – 0.00837 | 0.47 | 39 |
| 75 01 07 – 75 03 27 | 15 | 0.01397 | – 0.00899 | 0.68 | 35 |
| 75 03 27 – 75 06 03 | 15 | 0.10377 | – 0.06796 | 0.92 | 44 |
| 75 06 03 – 75 07 27 | 15 | 0.29511 | – 0.19629 | 0.92 | 41 |
| 75 07 27 – 75 08 27 | 15 | 0.21556 | – 0.13834 | 0.76 | 40 |
| 75 08 27 – 75 10 07 | 15 | 0.13629 | – 0.08421 | 0.87 | 41 |
| 75 10 07 – 75 12 10 | 15 | 0.09131 | – 0.05813 | 0.88 | 46 |
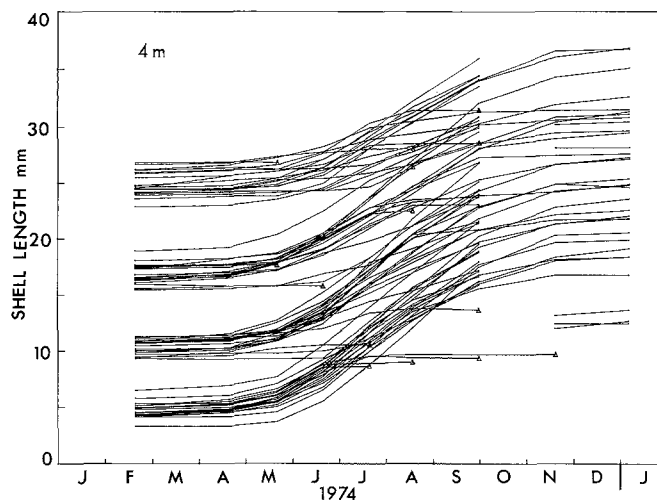


**Fig. 2.** *Mytilus edulis.* Growth of individual mussels in small cages at 4 m during 1974. Triangles (△) indicate mussels dying during the experiment
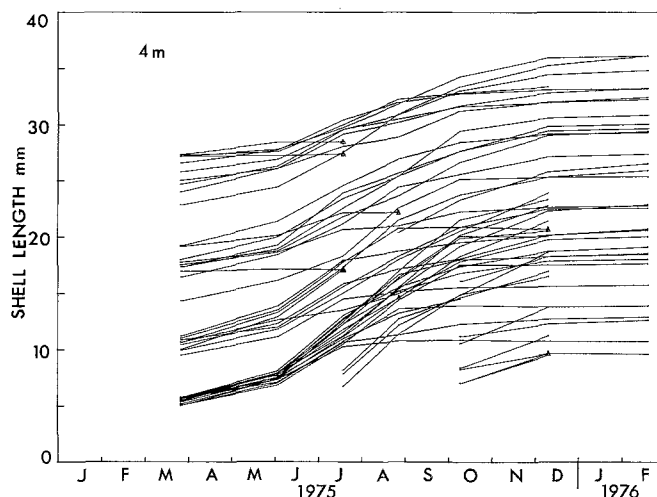


**Fig. 3.** *Mytilus edulis.* Growth of individual mussels in small cages at 4 m during 1975. Triangles (△) indicate mussels dying during the experiment
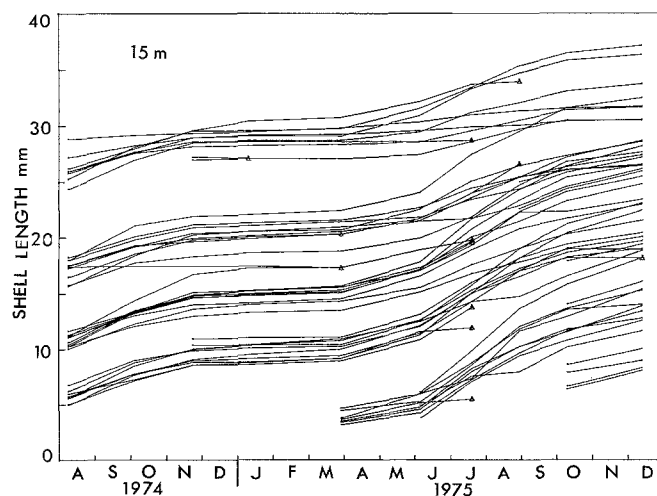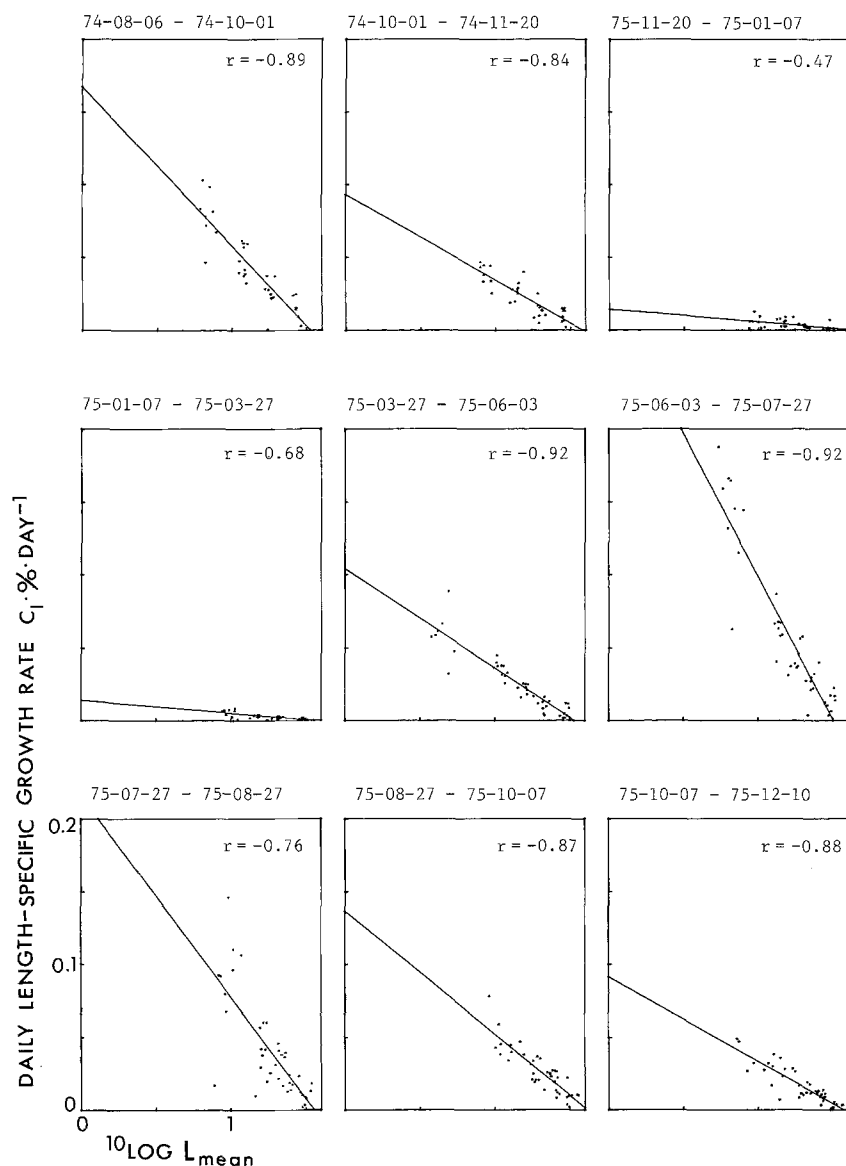


**Fig. 4.** *Mytilus edulis.* Growth of individual mussels in small cages at 15 m during 1974–1975. Triangles (△) indicate mussels dying during the experiment

**Fig. 5.** *Mytilus edulis*. Regressions of daily length-specific growth rate $(C_l)$ vs $^{10}$log $L_{mean}$ during different seasons. Example from 15-m growth cage during 1974 – 1975. The correlation coefficient (r) is given. The equations are presented in Table 1

## Analysis of Growth Rings

Growth rings in bivalve shells have in several cases been shown to be formed annually (review in Seed, 1976). The rings are laid down when shell growth is disturbed, e.g. due to adverse temperature conditions, reproduction or variations in food availability (Seed, 1976). Generally they seem to be most distinct if the annual growth pattern shows pronounced variations. Sometimes several rings are formed annually (Seed, 1976; Ankar, 1980).

The fact that *Mytilus edulis* in the Northern Baltic proper seems to have only one reproductive period (Kautsky, 1982) immediately following the winter growth minimum, supports the assumption that the growth rings here are formed only once per year. However, no further tests were performed to verify this.

Some of the samples from the random sampling survey, representing the 3 to 6-m and 10 to 15-m depth intervals were selected. The dried mussels were soaked in water and the meat was scraped away. When held against a lamp, growth marks could generally be clearly seen in the wet shells. These were counted and the length of the mussel was measured to the nearest 0.1 mm by means of calipers. Beyond about 3–4 mm from umbo it is most likely that the observed growth marks were annually formed since they were generally very distinct and occurred at regular intervals. In smaller mussels age determination was more difficult and the growth rings were often found at close or irregular intervals, indicating varying growth conditions. Most of these rings were distinct but in some cases presumed weak "disturbance" rings were also detected, especially when the shells were examined under a stereo microscope.

In the largest mussels the shells were sometimes eroded near the umbo, making age determination uncertain or impossible. All rings that could be classified as growth rings were counted. Since the collected material was sieved through a 1-mm screen, mussels <2 mm were not collected quantitatively and are omitted in the age determinations.
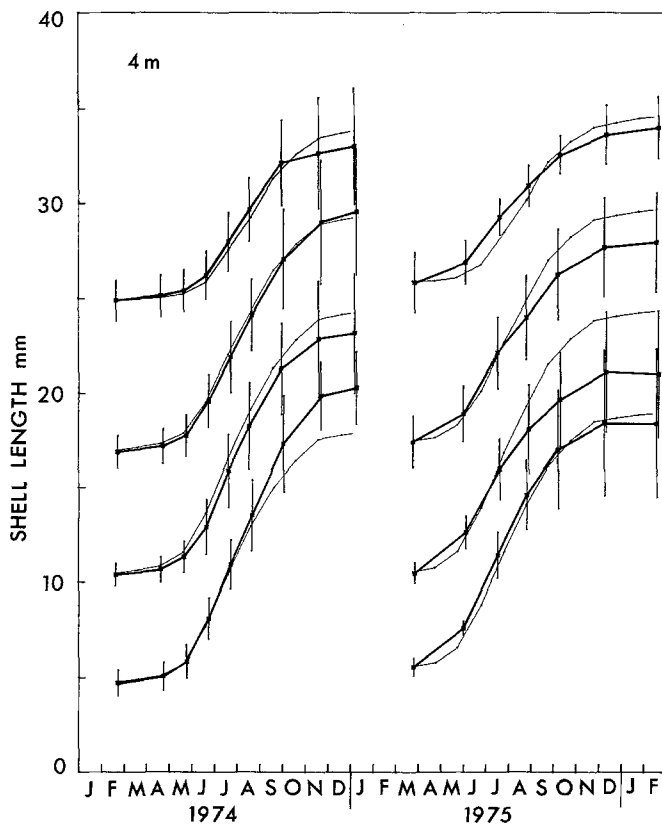
**Fig. 6.** *Mytilus edulis.* Calculated mean growth ± SD of different size classes of 4-m mussels in 1974 and 1975 cages together with growth curves calculated from the length-specific growth rate regressions obtained in 1974
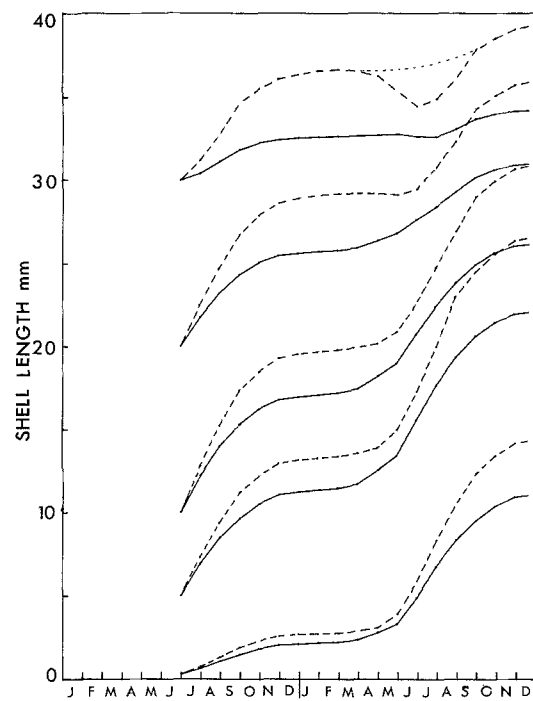
**Fig. 8.** *Mytilus edulis.* Comparison of growth at 4-m (---) and 15-m (—) depth in mussels of different initial lengths. Curves computed from the length-specific growth rate regressions given in Table 1
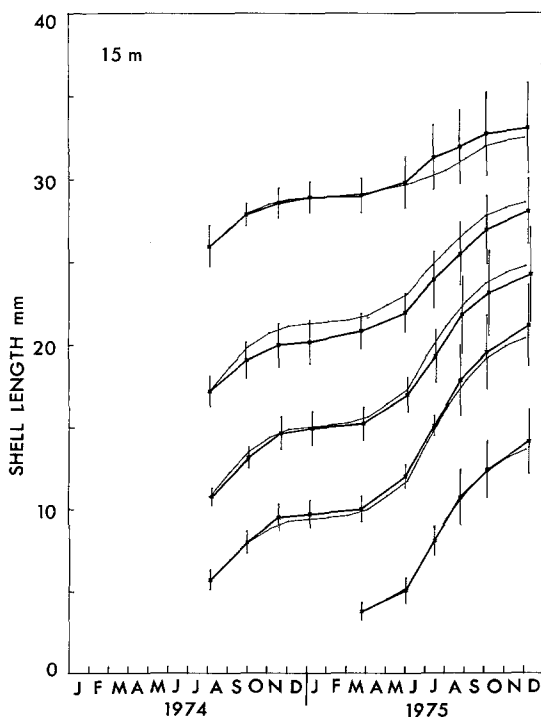
**Fig. 7.** *Mytilus edulis.* Calculated mean growth ± SD of 15-m cage mussels belonging to different size classes together with growth curves calculated from the length-specific growth rate regressions
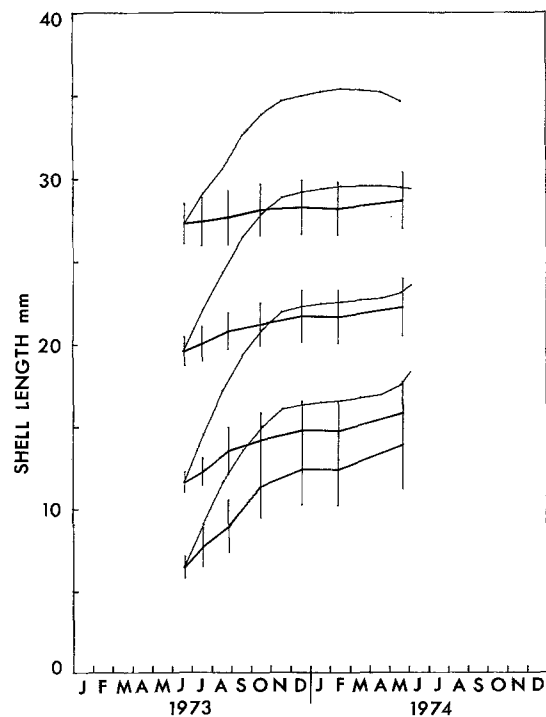
**Fig. 9.** *Mytilus edulis.* Mean growth ± SD of mussels in the large cage compared with growth calculated from the length-specific growth rate regressions of small cages in 1974
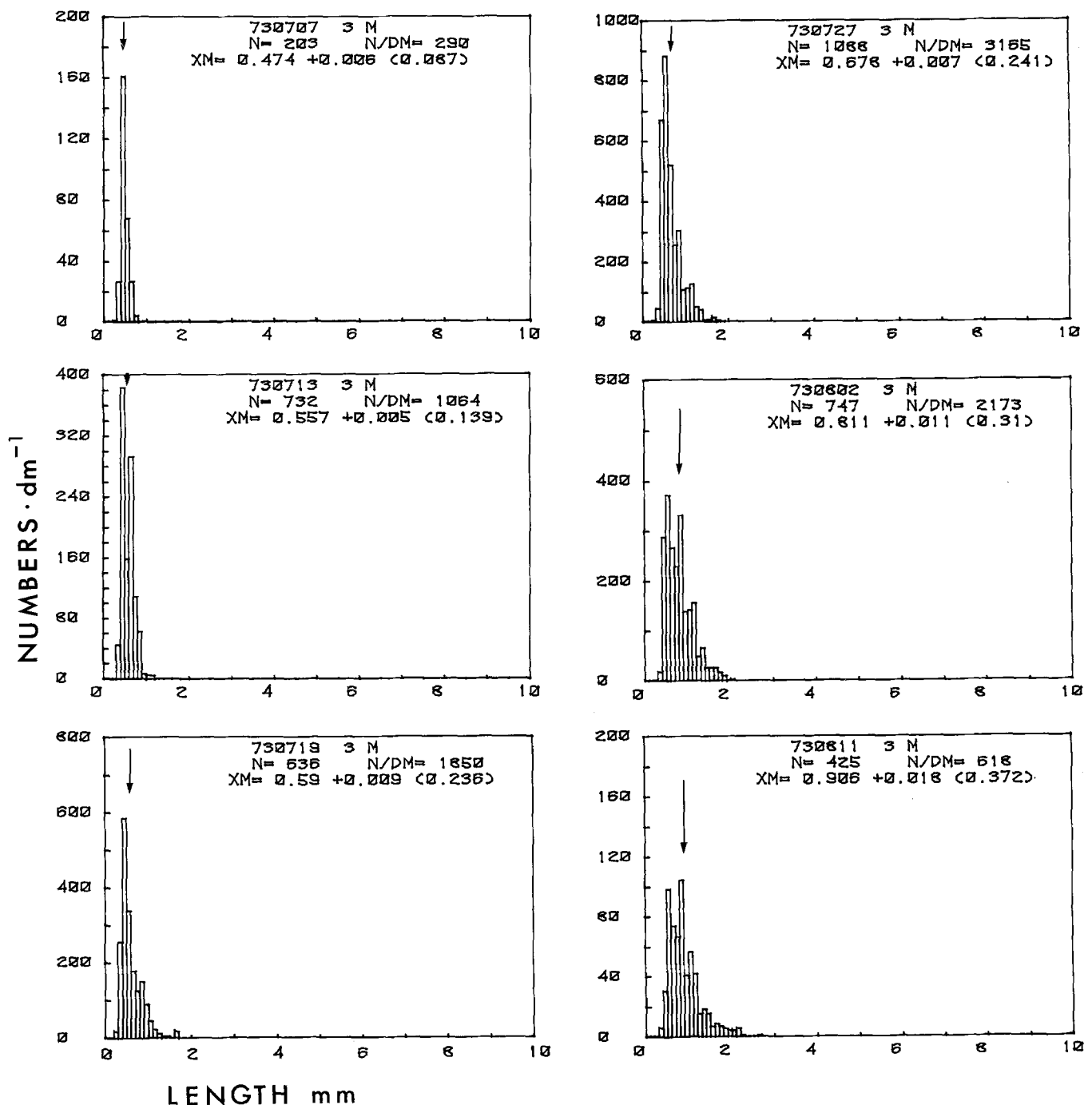
**Fig. 10.** *Mytilus edulis.* Changes of size-frequency on successive dates of accumulated settlement and growth of *M. edulis* larvae on long-term ropes. Example from 3 m in 1973. Sampling date, number of measured individuals (N), numbers per dm of rope (N/DM) and mean length (indicated by an arrow) (XM) ± SE (SD) are given

## Results

### Cage Experiment

In Figs. 2–4 the growths of individual mussels from the small cages are given for 4-m depth during 1974 and 1975, respectively, and for 15-m depth during 1974–1975. For mussels dying during the experiment, growth often slowed down or stopped long before death. For each growth period the individual length-specific growth was calculated

and plotted against $^{10}$log of the individual mean length during the period. Mussels which were found dead at the end of the period were not included. The calculated linear regressions are given in Table 1 and an example of the changes in slope during the season is shown in Fig. 5. Figs. 6 and 7 show the calculated mean growth ± SD of mussels belonging to the different size classes which were present from the start of the experiments together with the curves calculated from the specific growth rate estimates. The jump in the mean growth curve on October 1, 1974

NUMBERS · dm⁻¹

LENGTH mm
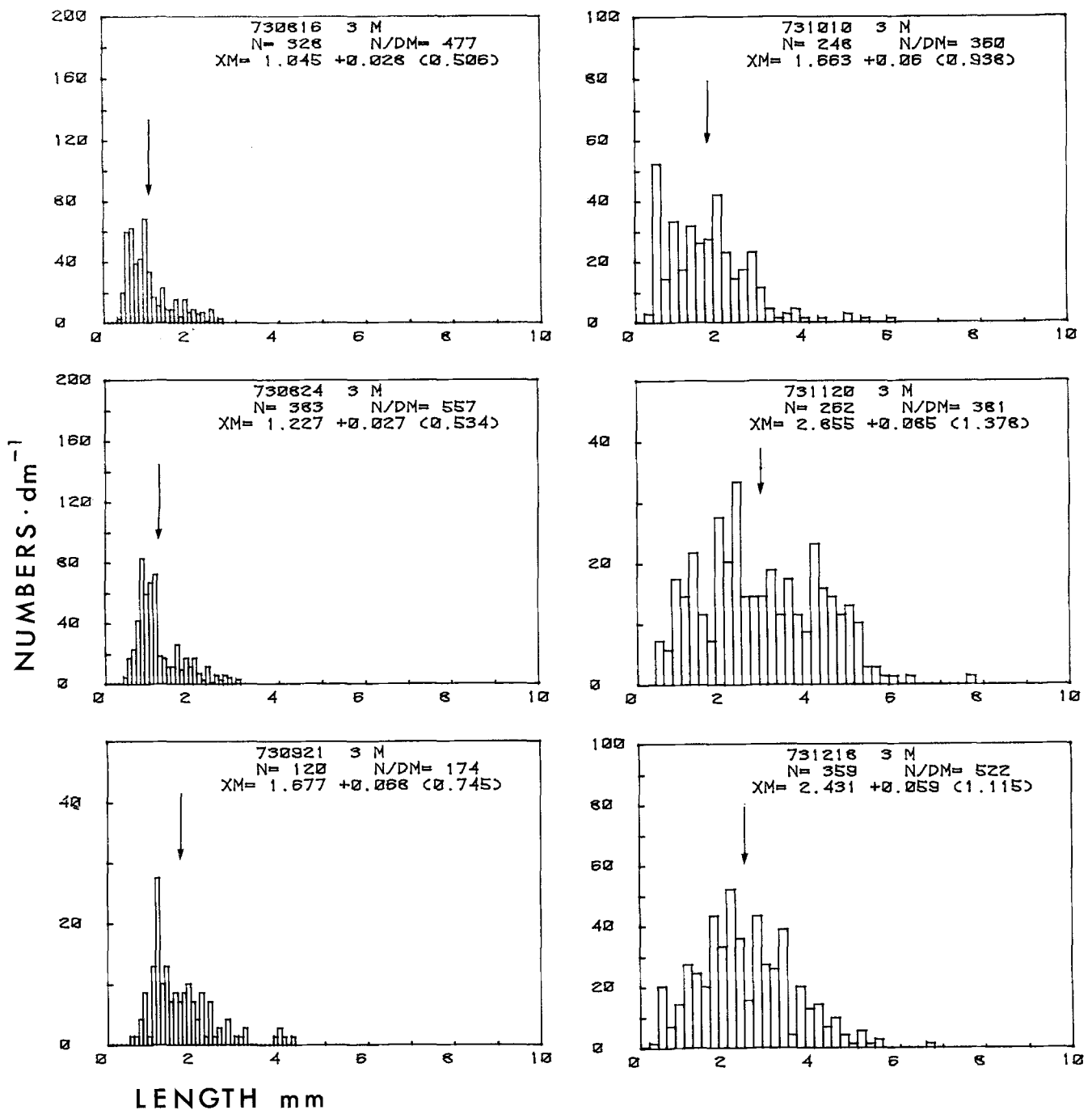
(Fig. 6), most clearly visible in the largest size class, is due to the removal of mussels for use in other experiments. Death of mussels could cause similar jumps, although this was not significant with the large material used here. The addition of new mussels to the cages, as e.g. on November 15, 1974 at 4 m and October 10, 1975 at 4 and 15 m (Figs. 2–4), however, does not influence the mean growth of the size class since these mussels were omitted in the calculations of mean growth in Figs. 6–7 and were used only in the specific growth rate equations. As can be seen there is

a rather good fit between the mean growth and the curve calculated from the specific growth rates although the accumulated error at the end of the year may in some cases be significant.

The calculated growth curves for the 4- and 15-m populations, based on the estimated length-specific growth rates (Fig. 8), clearly show reduced growth rates at 15 m. A comparison of the observed growth at 4 m during 1975 with the calculated growth based on the 1974 data (Fig. 6) indicates higher actual growth rates during spring in 1975
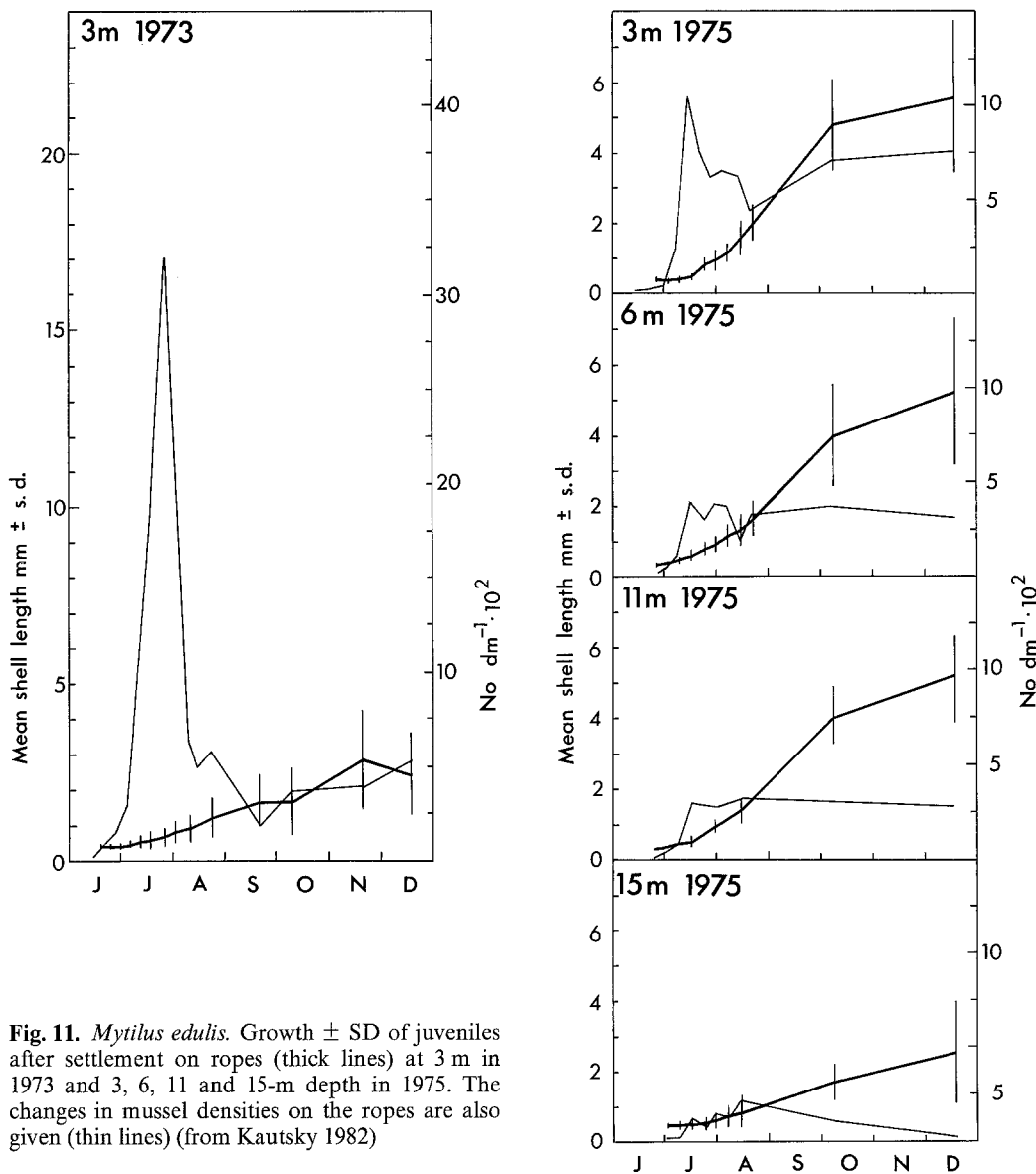
**Fig. 11.** *Mytilus edulis.* Growth ± SD of juveniles after settlement on ropes (thick lines) at 3 m in 1973 and 3, 6, 11 and 15-m depth in 1975. The changes in mussel densities on the ropes are also given (thin lines) (from Kautsky 1982)

but lower rates during summer and autumn, resulting in a lower total growth that year.

In Fig. 9 the mean growth of mussels in the large cage used in 1973–1974 is compared with the growth rates obtained from the small cages in 1974. It can be seen that the growth in the large cage that was standing on the bottom is considerably lower than in the small cages hanging freely in the water.

## Growth of Juveniles

The growth of juvenile mussels was calculated from changes with time in the size distribution of mussels after settlement on ropes. An example of the diagrams obtained is given in Fig. 10.

In Fig. 11 the changes in mean size ± SD at 3-m depth in 1973 and 3-, 6-, 11- and 15-m depth in 1975 and variations in mussel density are summarized. The highest growth rate was observed at 3-, 6- and 11-m depth in 1975

when by December the mussels had reached a mean length of 5.6, 5.2 and 5.2 mm, respectively.

At 15 m in 1975 the increments in mean size were very low until the end of July because of a prolonged settlement period. Also after that, however, the growth rate was significantly lower than at 3 and 6 m and a maximum size of only 2.5 mm was attained during the autumn. At 3 m in 1973 the increase in the mean length also seems to have been delayed due to prolonged settlement, with the maximum settling intensity not observed until July 27, about 2 wk later than in 1975. In 1973 the maximum density of spat on the ropes was about 3 times higher than in 1975 (Kautsky, 1982), and the mean length reached by November 1973 was only 2.8 mm or about half that reached in 1975.

## Size-Frequency Analysis of the Natural Population

The annual variation in size-frequency distribution at 4-m depth as well as the size distribution in a sample from 13-m
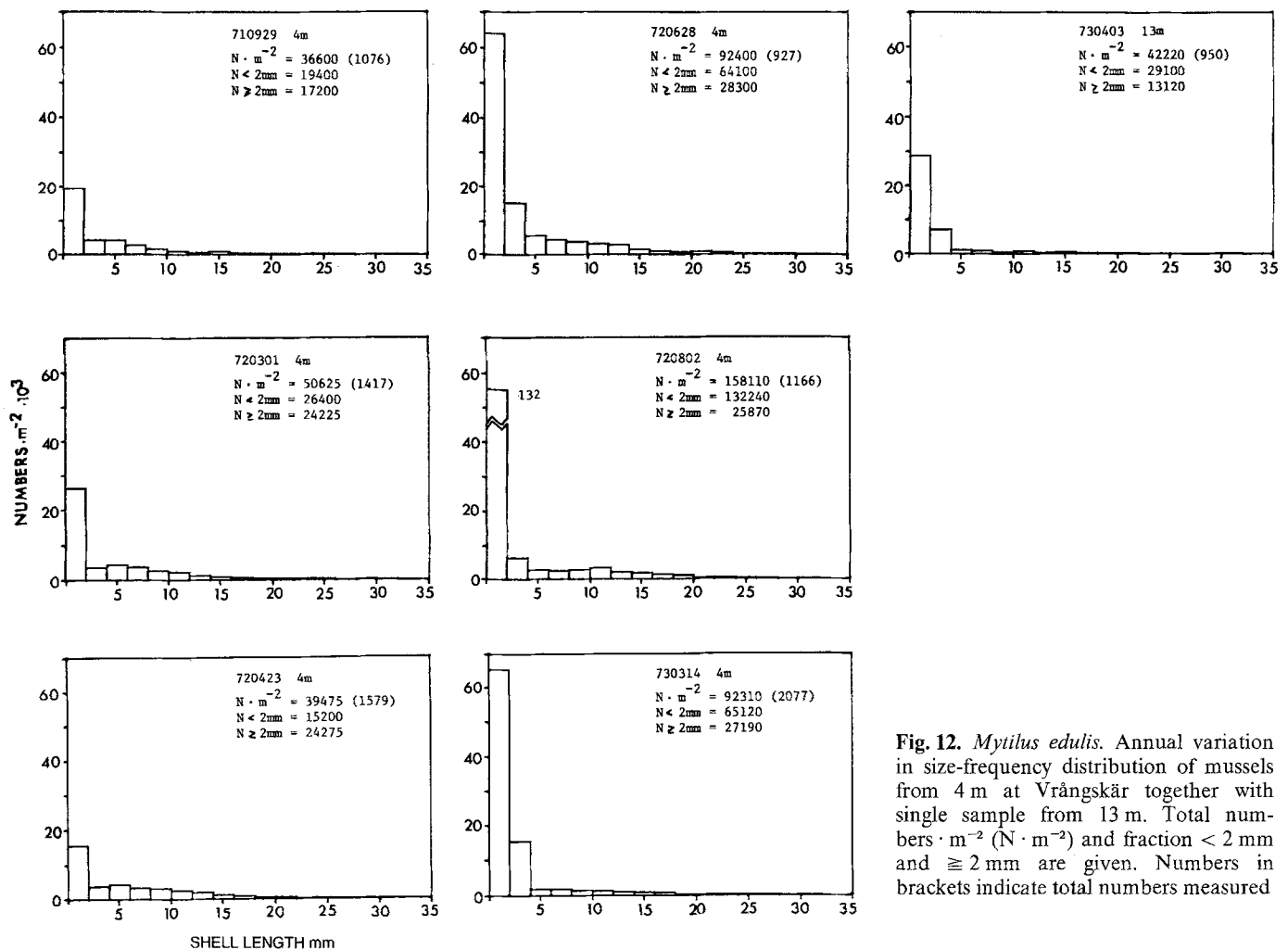
Fig. 12. *Mytilus edulis.* Annual variation in size-frequency distribution of mussels from 4 m at Vrångskär together with single sample from 13 m. Total numbers · m⁻² $(N \cdot m^{-2})$ and fraction < 2 mm and ≧ 2 mm are given. Numbers in brackets indicate total numbers measured

depth is given in Fig. 12. A typical pattern can be observed all year round with a high peak in abundance of mussels in the 0–2 mm size class and a smooth decline in numbers with increasing size. No further peaks indicating cohorts can be discerned. The same peak in abundance of small mussels can also be observed in the spring sample from 13-m depth at Vrångskär.

The total numbers vary between 36 000 and 158 000 individuals · m⁻². This is mainly due to variations in the abundance of very small mussels < 2 mm whereas the number of mussels ≧ 2 mm is fairly constant during the year, between about 17 000 and 28 000 individuals · m⁻². The maximum numbers in the size class < 2 mm were found on August 2 with 132 000 individuals · m⁻² after the settlement of juveniles in July (Kautsky, 1982) but still in spring, more than half a year after settlement, small mussels could be found abundantly with e.g. 65 000 individuals · m⁻² < 2 mm registered on March 14.

The maximum peak in abundance of mussels < 2 mm observed in August is most probably due to the settlement of juveniles. The variation in numbers found during the rest of the year, however, is probably caused by irregularities on the bottoms due to stones, pebbles and algae. Especially variations in the cover of the partially annual

species of *Ceramium tenuicorne,* which is readily used as substrate by the juveniles, would cause such variations.

In Fig. 13 the mean variation of size distribution with depth is given as obtained from a random sampling over the research area. Since these samples were sieved through a 1-mm mesh screen they largely exclude mussels < 2 mm. A rather similar size-frequency pattern over the 2- to 15-m depth interval can also be observed here with a smooth decline in numbers with increasing size. The overall numbers of mussels ≧ 2 mm are lower here than obtained at Vrångskär, since the randomization also included stations with less dense communities.

Analysis of Growth Rates

In Figs. 14 and 15 the number of observed growth rings is plotted against shell length for mussels in the natural population from 3–6 and 10–15 m depth. The mean length of each age class is connected by a line. A similar pattern can be observed at both depths with large variations in length at a given age.

A tentative growth curve for the populations based on the data is indicated. Since the mussels < 2 mm, which
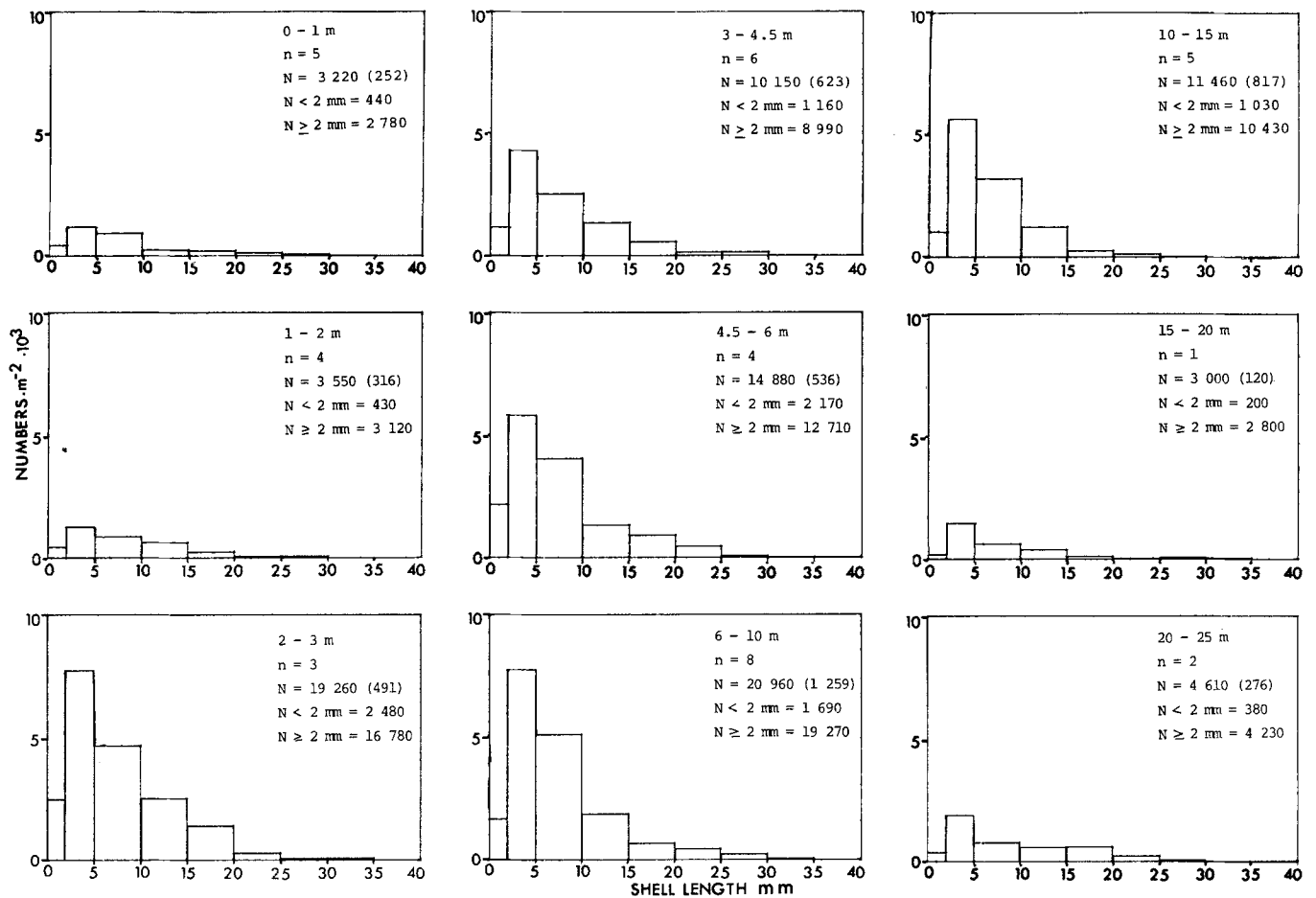
**Fig. 13.** *Mytilus edulis.* Size-frequency distribution in different depth intervals from samples randomized over Askö primary research area. Number of samples (n), total abundance of *M. edulis* · m$^{-2}$ (N), numbers < 2 mm and $\geqq$ 2 mm are given. Number of mussels measured are given within brackets



**Fig. 14.** *Mytilus edulis.* Shell length plotted against number of growth rings for mussels > 2 mm from 3 to 6-m depth. Line indicates mean length at given age. Broken line is a tentative growth curve (see text). Number of observations (n) are given
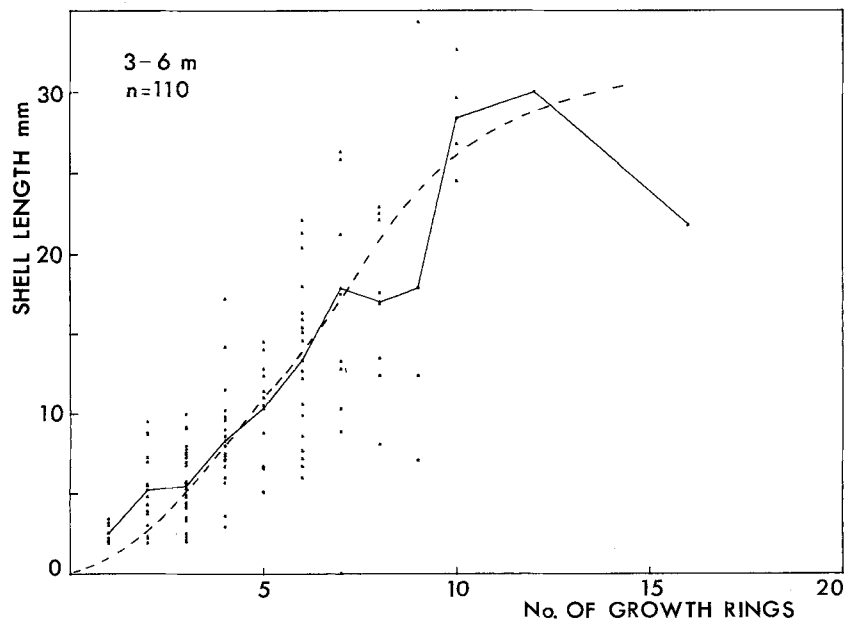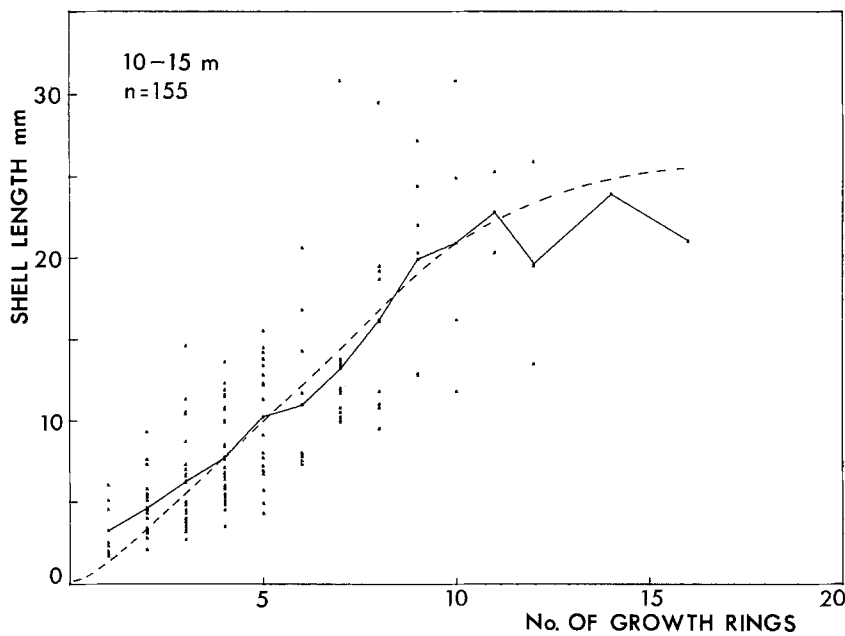
**Fig. 15.** *Mytilus edulis.* Shell length plotted against number of growth rings for mussels > 2 mm from 10 to 15-m depth. Line indicates mean length at given age. Broken line is a tentative growth curve (see text). Number of observations (n) are given
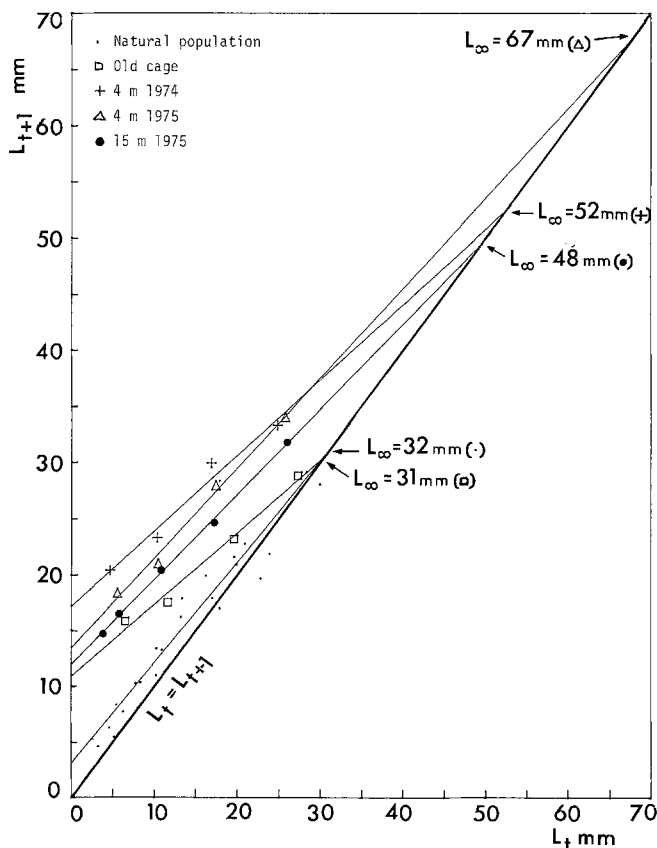


**Fig. 16.** *Mytilus edulis.* Comparison of annual growth increments in different cages and natural population. Initial mean length of size class ($L_t$) vs mean length attained after one year ($L_t + 1$). The asymptotic length ($L_\infty$) is estimated by "Walford" plots
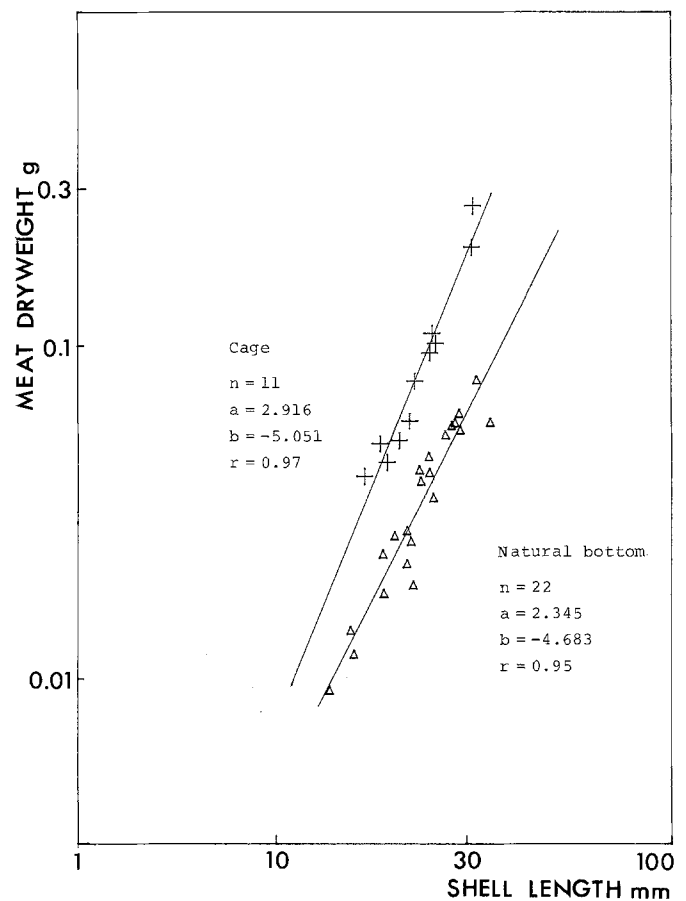


**Fig. 17.** *Mytilus edulis.* Comparison of meat content in mussels kept one year in cages (+) at 4 m and mussels taken from natural bottom (△) at 4 m. a and b are parameters fitted to the equation $^{10}\log y = a\,^{10}\log x + ^{10}\log b$ where y is the dry weight of the tissue and x is the shell length. The correlation coefficient (r) and the number of observations (n) are also given
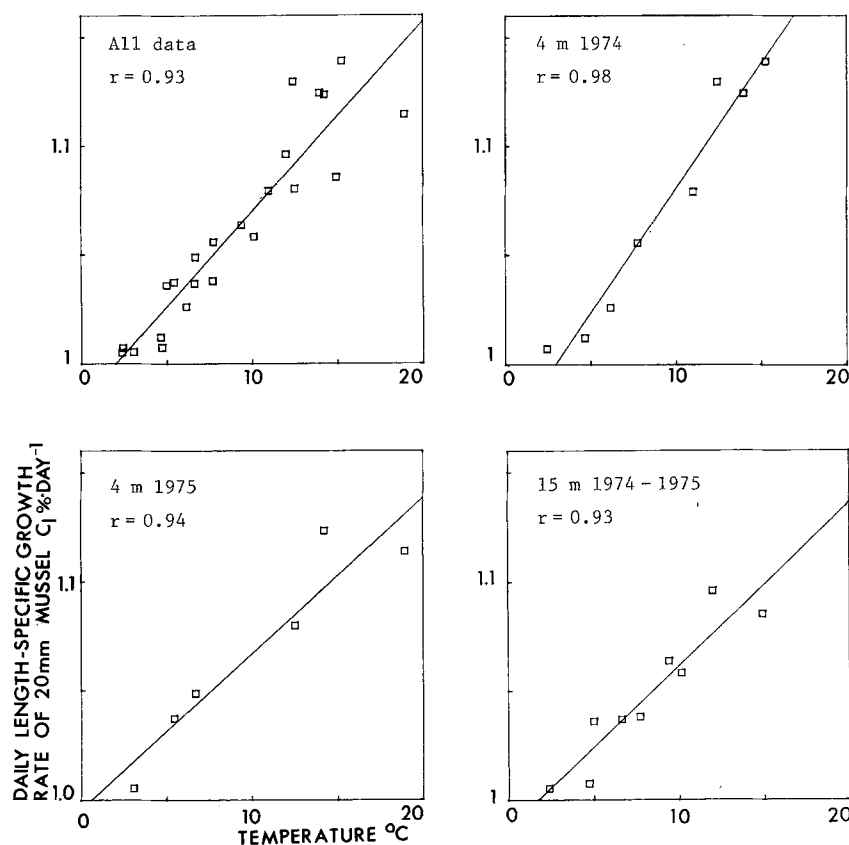
**Fig. 18.** *Mytilus edulis*. Regressions of daily length-specific growth rate of a 20-mm mussel vs. mean water temperature during growth period for 4- and 15-m depth during 1974 and 1975 and for the pooled observations. The correlation coefficients (r) for the regressions are also given

dominate in abundance, were not analysed, the mean length of the age classes up to about 3 yr are probably overestimated as indicated by the first part of the tentative growth curve. Between about 2–10 yr of age corresponding to about 3–20 mm length, a nearly linear or even slightly exponential increase in shell growth rate with age, can be observed. Over this interval growth was somewhat higher at 3- to 6-m depth with 3.1 mm · yr$^{-1}$ compared to 2.2 mm at 10- to 15-m depth.

## Comparison of Growth Estimates

In Fig. 16 the annual growth increments in the different cages and on the natural bottoms, as obtained from the growth ring analysis are compared by "Walford" plots (Walford, 1946). In the figure the initial mean length of a size-class is plotted against the length attained after one year. To cover a full year the last month's growth in the cages at 4 m in 1974 and 1975 and in the old cage was calculated from the specific growth rate regressions (Table 1) and added to the growth actually observed over 11 months in the cages. The regressions show that growth is much higher in the cages compared to the bottoms, being highest at 4 m in 1974, followed by 4 m in 1975, 15 m in 1974–1975 and 4 m in the old cage of 1973. Whereas in the natural population a mussel of 10-mm length would only grow by 2–3 mm during one year, it would double its length reaching 17–24 mm in the cages. The extrapolation of the regression lines gives an asymptotic length (L$_\infty$) of

32 mm in the natural population compared to 31 mm in the mussels from the old cage, while in the other cages values of L$_\infty$ amounting to 48–67 mm are obtained.

The improved growth conditions in the cages were further confirmed in a prolonged cage experiment, where the 6 largest mussels removed from the 4-m cage of October 1, 1974 increased from an initial mean length of 31.67 ± 2.57 mm to 39.72 ± 3.75 mm by December 10, 1975. Three of the mussels were over 42 mm in size with the largest individual being 43.9 mm.

The favourable growth conditions in the cages can also be observed in mussels kept one year in the small cages. These mussels showed a significantly higher ratio of meat weight : shell length than the population from which they originated (Fig. 17). Microscopic examination (Kautsky, 1982) revealed that the cage mussels were nearly ripe on January 7, thus contrasting with the natural population that was only beginning to develop gonads. This would probably explain most of the meat weight differences found. It also indicates that feeding conditions are much better in the cages, with higher growth rates and sufficient food for gonad development in autumn, compared to the natural population where gonad buildup does not start until the spring bloom in March (Kautsky, 1982).

## Factors Controlling Growth Rates in the Cages

In Figs. 18 and 19 the annual variation in length-specific growth rate calculated for a 20-mm mussel is plotted
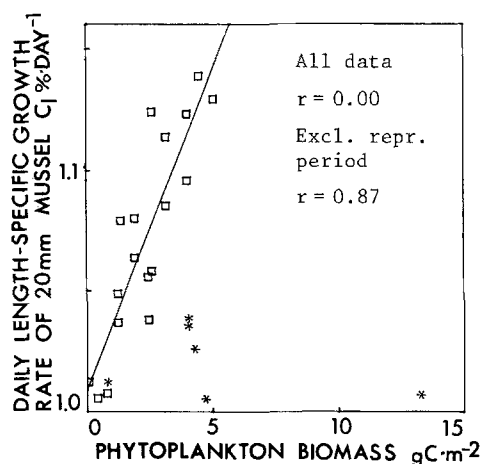
Fig. 19. *Mytilus edulis*. Regression of daily length-specific growth rate of a 20-mm mussel vs, mean phytoplankton biomass during growth period and excluding observations during "reproductive period" (*) (see text). The data for 4- and 15-m depth during 1974 and 1975 are pooled
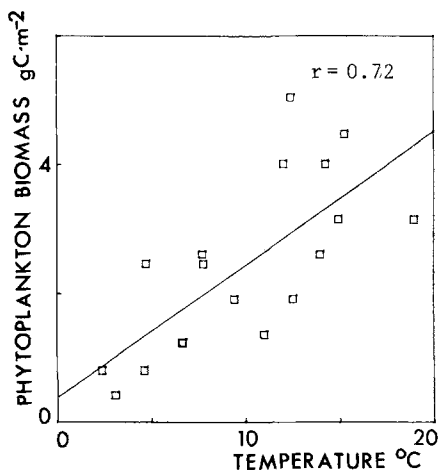


Fig. 20. Plot showing covariance between mean temperature and mean phytoplankton biomass in data outside the "reproductive period" (see text)

against mean temperature and mean food abundance (phytoplankton biomass) during the different experimental periods. Good correlations were obtained between shell growth and temperature with the regressions for 4 and 15 m during 1975 being very similar but with growth at 4 m in 1974 being somewhat higher at corresponding temperatures (Fig. 18).

No correlation at all was obtained between growth rate and food abundance expressed as phytoplankton biomass in the pooled material from the different years (Fig. 19). However, after excluding the spring values representing the reproductive period of the mussels (March 1–June 10), when gonad buildup occurs (Kautsky, 1982), a good correlation was obtained. Outside the reproductive period, however, a large degree of covariance was found between temperature and food (Fig. 20).

The effects of increasing mussel densities on growth can be seen in the competition cages (Fig. 21). Whereas

growth in the cage with small mussels only is normal, growth of small mussels amongst 16 larger ones was lowered by about 10% and by about 50% in the cage with 30 large mussels.

Meat Growth

A linear relationship can generally be established between [10]log shell length and [10]log meat dry weight for a given time during the year with the "condition" (slope) changing during the season relative to the reproductive status of the mussels (Kautsky, 1982). The meat growth pattern in the natural population could thus be predicted by applying length : weight regressions calculated for different seasons to the estimates of shell growth obtained from the age ring analysis. In Fig. 22 the shell and meat growth pattern over the 12 yr following settlement is compared between 4- and 15-m depth. The shell growth data were derived from the age ring analysis, assuming the annual length increments of 3.1 and 2.2 mm · yr$^{-1}$ respectively being constant over the entire life cycle. The interannual variations in shell growth rate were obtained from the cage data, and the meat growth curves were obtained by incorporating length : dry weight regression data from Kautsky (1982).

The peaks in meat growth, occurring just at the start of each year's shell growth, are due to the buildup of gonads.
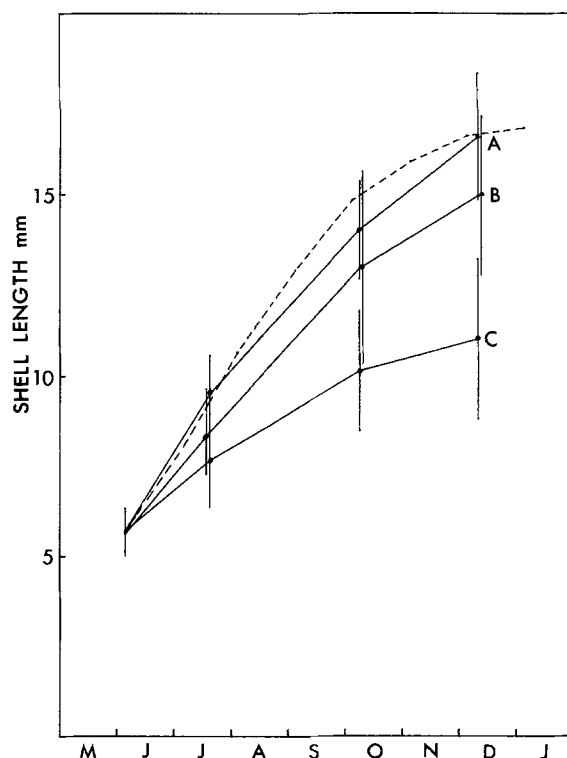


Fig. 21. *Mytilus edulis*. Mean growth ± SD of small mussels in "competition" cages with increasing amounts of large mussels. Compared to "normal" growth curve (broken line) calculated from length specific growth rate regressions. (A) Only small mussels in cage. (B) Small mussels + 16 large mussels in cage. (C) Small mussels + 30 large mussels in cage
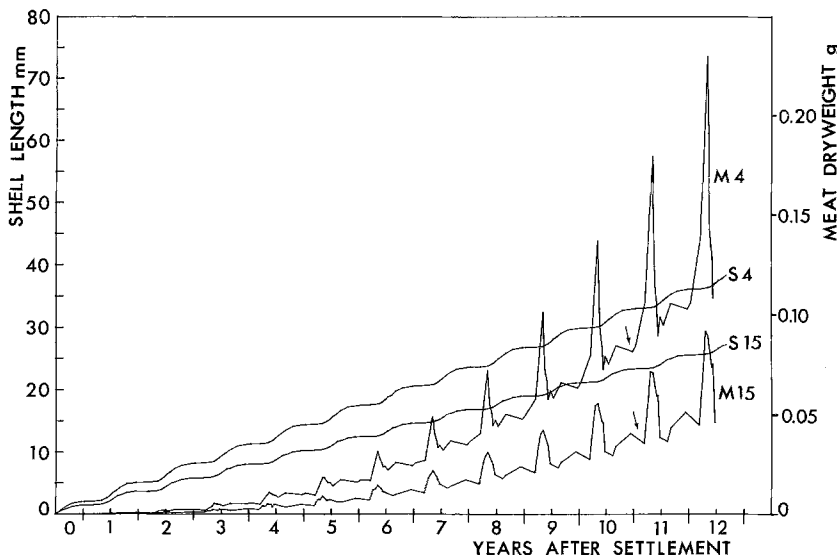
**Fig. 22.** *Mytilus edulis.* Model of shell (S 4, S 15) and meat (M 4, M 15) growth pattern over 12 yr after settlement at 4- and 15-m depth. Shell growth data from age ring analysis assuming constant annual length increament of 3.1 and 2.2 mm · yr$^{-1}$ respectively for 4 and 15 m. Interannual variations obtained from cage data. Meat growth curves obtained by incorporating shell length:meat weight regression data from Kautsky (1982). Arrows indicate examples of periods of negative meat growth before gonad buildup in winter (see text)

This peak is followed by strong "negative growth" due to spawning of the mussels. Also in winter, during the period immediately before gonad buildup, meat growth may be slightly negative.

Although in the plots of meat weight to shell length it was generally observed that most individuals fitted the regressions well, single mussels could occasionally be found having significantly lower meat weight than the average. In Fig. 23 a length:weight analysis of mussels taken from the exhibition aquarium at the Askö Laboratory is shown. In this aquarium it is very difficult to keep mussels during the summer and they often die within a few months, probably due to a combination of lack of

food, high temperature and air supersaturation. The analysis showed that many of the mussels had meat contents 30–50% lower than those found in the field. One extreme individual had 78% lower meat weight, although still living, as evidenced by ciliary movements.

## Discussion

### Factors Influencing Shell Growth

The factors governing growth of molluscs have been reviewed by Seed (1976).

In the present investigation growth rates were found to vary from 2.2–3.1 mm · yr$^{-1}$ in the natural community up to 15 mm · yr$^{-1}$ under optimal conditions in growth cages. Even the maximum values found here are, however, much lower than the maximum growth rates measured under optimal food and salinity conditions in other areas, exceeding 50 mm over 18 months (reviews in Seed, 1976; Bayne and Worral, 1980). Minimum mussel growth in other areas is generally reported from high density populations exposed to harsh physical conditions as e.g. in the high littoral zone of the British coasts where mussels of 20–30 mm length can be up to 15–20 yr old (Seed, 1969).

As mentioned earlier the main factor affecting growth rate and maximum size in the Baltic is salinity. Schütz (1964) gave an exemple of this in a comparison of first year's growth of juvenile mussels in a salinity gradient in the Schwentine river mouth area in the western Baltic. Following settlement in early August the mussels in the river mouth (14–16‰ S) had already attained a size of 16–18 mm by mid September, after only about 6 wk of growth, and by April the following year they were 20–23 mm long. At the innermost station close to the freshwater outlet (∼ 3–5‰ S), growth was considerably lowered with most of the mussels having reached only 2–3 mm by April. In Kiel Bight (> 18‰ S) *Mytilus edulis* could grow to more than 30 mm during their first year of life, at-
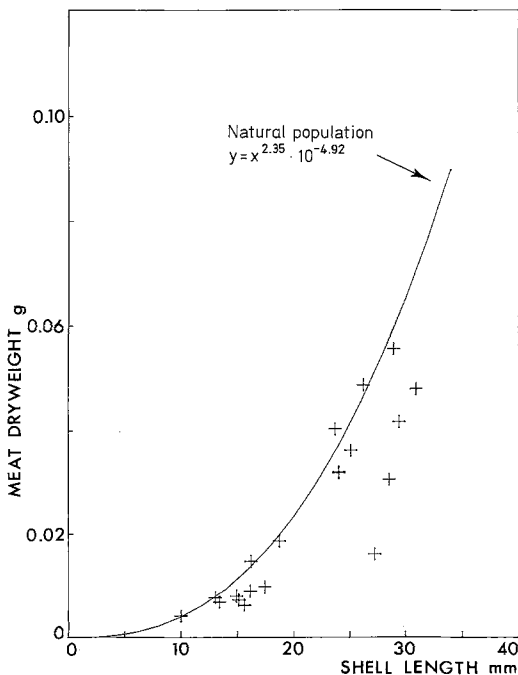


**Fig. 23.** *Mytilus edulis.* Meat content in starved mussels from the exibition aquarium (+) compared with average curve for natural population at 4 m (from Kautsky 1982)

taining a maximum length of up to 90 mm after about 5 yr.

Thus the mean growth of juveniles at 6–7‰ S obtained on the ropes in the present investigation (Fig. 11) ranging from 2.5–5.6 mm before winter growth stoppage, compare rather well with the growth rates obtained at corresponding salinities by Schütz.

Within a salinity regime, temperature is generally acknowledged as an important factor controlling growth rate and linear relationships between shell length and day-degrees (D°) can often be established (Boëtius, 1962; Ursin, 1963; Theisen, 1973; Bayne and Worrall, 1980). Several other factors interact with temperature, however, such as food supply, wave exposure, light, population structure etc., making it very difficult to isolate the effect of single factors.

In the small cages good correlations were obtained between growth and temperature (Fig. 18) and as the regressions for 4 and 15 m in 1975 are nearly identical the growth differences between depths found that year may very well be explained by the different temperature levels. In 1974 the regression was somewhat different, indicating that other factors also differed between the years.

The most important single factor in determining growth rate, however, is probably the food supply, since if food is scarce growth will be retarded regardless of all other conditions (Seed, 1976). Under special circumstances Wallace (1980) even found that *Mytilus edulis* close to a fish-farming station could maintain their summer growth rates throughout the long Arctic winter in northern Norway despite 0 °C water temperatures, probably while feeding on microscopic particles of fish food.

While at first analysis of the cage material no correlation at all was found between growth rate and phytoplankton biomass, a good correlation was obtained after the spring values from the reproductive period were excluded. This is probably due to the energy supplied during the reproductive period being canalized more or less directly into gonad growth (Kautsky, 1982), resulting in low shell growth despite abundant food (Figs. 19 and 22). Caution must, however, be taken in further interpreting the data from outside the reproductive period since temperature and food abundance were strongly correlated (Fig. 20).

With increasing size the growth rate declines due to reduced relative metabolic activity in larger mussels (e.g. Seed, 1976) and a reduced rate of water transport, i.e. of food uptake (Jørgensen, 1976). Age, however, is not always the primary cause of reduced growth, since transplantation of old nongrowing mussels to more favourable situations can often result in renewed growth (Mossop, 1922; Seed, 1968). Thus the growth characteristics and maximum sizes attained in different populations may reveal the resource limiting environmental conditions of their habitat (Seed, 1968). This could clearly be observed in the cages where the favourable growth conditions resulted in estimated $L_\infty$ of 48–67 mm and actual maximum lengths of 43.9 mm. Such sizes were never found in the natural population at Vrångskär, where the maximum lies around 35 mm. In

the eutrophic receiver of the Trosa river, however, mussels of 46 mm have been found (Jansson *et al.*, 1980), despite the fact that salinities are somewhat lowered there. Similarly large mussels can also be found in the innermost part of the eutrophic Bay of Himmerfjärden, north of Askö, probably due to improved food conditions. In these more sheltered areas competition is also lowered by the thinning out of the populations since settlement and survival of juveniles is low due to the rocks being covered by thin layers of fine sediment (Kautsky, unpublished data).

Detrimental effects of high mussel densities on growth have been shown by e.g. Wilson and Hodgkin (1967) and Seed (1969). This effect was clearly seen in the competition experiment where growth decreased with increasing densities, probably due to reduced food availability, but possibly also from the accumulation of metabolites. This is probably also the reason for the lower growth rate observed in the "old" cage, but here the food availability may have been further diminished by the smaller water exchange close to the bottom. Competition is suspected to be the reason also for the lowered growth of juveniles observed on the ropes in 1973, when mussel densities were about 3 times higher than in 1975.

## Aspects of Growth in the Natural Population

In dense mussel clumps, growth may be slow in the majority of the individuals – especially amongst those ensnared in the byssus threads of larger ones – which will frequently result in populations containing an abundance of small mussels (e.g. Richards, 1928; Madsen, 1940; Raymont, 1955; Sadykhova, 1967; Reynolds, 1969; Harger, 1970; Seed, 1976). Whedon (1936), Bouxin (1956) and Seed (1976) drew attention to the fact that small (though not necessarily young?) individuals could persist in the population throughout the year.

In the western Baltic Samtleben (1977) observed irregular growth in the smallest size-classes of the mussels. In the dense populations of the northern Baltic proper these effects are further enhanced and can be observed on a really large scale, since, due to the nearly complete absence of predators and competitors for space, intraspecific competition is likely to be the main factor controlling the mussel population (Kautsky, 1981 a, b, 1982).

This will result in the size-frequency distribution observed with a peak in mussels < 2 mm all year round, even in spring more than half a year after settlement. In the cages or on the ropes, where competition is less intense, these mussels would have grown to more than 5 mm.

These small mussels may be competitively suppressed since they do not reach as far into the water as the larger ones while at the same time having a higher metabolic demand per unit of biomass. Possibly, these mussels are even confined to deposit feeding (Theisen, 1972) on pseudofeces and feces, matter with low energy content. This strong competition will give very slow and differen-

tiated growth rates, depending on the position of the individual mussel, resulting in size frequency diagrams such as those observed, with no discernable modes indicating cohorts.

The analysis of growth marks also indicate strong competition. Generally mussel shell growth, as in the cages, reaches its maximum in young rather small individuals, to decline with increasing size (age) (e.g. Seed, 1976). As indicated in Figs. 14–15, shell growth rates in the natural Askö population seem to be very low in the smallest mussels, rising to a constant or even slightly increasing rate over a large size interval from about 3- to more than 20-mm length, and declines in the largest mussels only. The low growth rates in the smallest mussels assumed at the start in Figs. 14 and 15 are supported by the results from size-frequency analysis. The constant or even increasing growth rates, however, indicate that the larger mussels may also suffer from competition, obtaining more and more advantage with increasing size as they can reach further out into the water. This increasing advantage may thus partly compensate for the normal physiologically induced decline in growth rates with size, thus explaining the observed pattern.

The large scatter in the observed growth rates is probably due to more or less favourable positions of individual mussels with regard to food availability, although large genetic variability in growth rate and mortality is also to be expected in *Mytilus edulis* populations (Milkman and Koehn, 1977; Innes and Haley, 1977; Gartner-Kepkay *et al.*, 1980).

As already discussed, shell growth may be drastically reduced in the natural population due to competition. During severe food shortage, when demands for the basal metabolism are not met by food uptake, the mussel will have a "negative scope for growth" (Warren and Davis, 1967; Bayne *et al.*, 1976) and will utilize its stored energy reserves. This will result in the negative meat growth observed in the starving aquarium mussels (Fig. 23) and in the natural population before gonad buildup in winter (Fig. 22). Molluscs seem to be very tolerant of weight loss, as observed in the aquarium, where losses of up to 78% of the meat weight were registered. The results obtained e.g. by Bayne and Thompson (1970) that unfed *Mytilus edulis* declined by 57% in weight over 90 d at 15 °C and those of von Brand *et al.* (1957) that snails of the genus *Australorbis glabratus* could metabolize 50–60% of their organic material before death also confirm this. Such negative growth will probably also occur if food uptake is lowered e.g. by strong competition, senility, parasites or disease.

In the cages shell growth was often found to slow down and stop long before death (Figs. 2–4), indicating that it is inhibited during the periods of declining meat weight. Thus in most cases of death, predation excluded, a substantial decline in biomass due to the utilization of energy reserves seems probable. In the Atlantic such weakened individuals would probably be quickly removed by predators. In the Baltic, however, where predators are scarce, these mussels may respire away most of their biomass

before death, which, if it is a common occurrence, as supposed here, will result in a considerably reduced energy input to the decomposers of the ecosystem (Kautsky, 1981 a).

Conversely, if mussels in bad condition are supplied with food they can recover and grow normally again. Such a capacity to grow and shrink as a function of food supply is known also e.g. from anemones (Muscatine, 1961), sea urchins (Ebert, 1968) starfish (Mead, 1901; Menge, 1972) and nudibranchs (Paine, 1965).

The special structure of Baltic *Mytilus edulis* populations with a majority of competitively suppressed individuals and the ability of the mussels to survive periods of low food abundance will stabilize the population and give it a high capacity to buffer the large annual variations in food availability. During food shortage the mussels will utilize their energy reserves and while food is abundant, e.g. during the spring bloom period, even otherwise competitively suppressed individuals, may get enough for gonad buildup and growth (Kautsky, (1982). Furthermore, as death of an "established" mussel in the population will immediately result in a competitively suppressed mussel taking its place, recruitment will be possible all year round (Kautsky, 1982), which will further stabilize the population, keeping it at the carrying capacity of the area with regard to food and space availability (Kautsky, 1981 b, 1982).

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