

Population structure, growth and reproduction of the common mussel (*Mytilus edulis* L.) off the Island of Seili (SW Finland)

Alexander E. Antsulevich¹⁾, Nikolay V. Maximovich¹⁾ and Ilppo Vuorinen²⁾

¹⁾ Department of Hydrobiology and Ichthyology, St. Petersburg State University, 16 linia, 29, St. Petersburg 199178, Russia.

²⁾ Archipelago Research Institute, University of Turku FIN-20014 Turku, Finland.

Antsulevich, A. E., Maximovich, N. V. and Vuorinen, I. 1999. Population structure, growth and reproduction of the common mussel (*Mytilus edulis* L.) off the Island of Seili (SW Finland). *Boreal Env. Res.* 4: 367–375. ISSN 1239-6095

We studied the reproduction, population structure and growth of the common mussel (*Mytilus edulis* L.) off the Island of Seili in summer 1996. The discharge of gametes occurred from 26 July to 2 August. The breeding period was short and repeated spawning was not found. Density of mussels ranged from 1 250 to 16 730 ind. m⁻² and biomass from 250 to 2 100 g m⁻². Size of individuals (shell length) ranged from 0.6 mm (spat) to 44.0 mm (nine years old). The distribution of age groups in the mussel population demonstrates the stability of recruitment over several previous years. The most rapidly growing individuals (reaching up to 41 mm at the end of the seventh year) were registered at the depth of 8 m. The average growth rate of molluscs from different habitats did not vary. A Bertalanffy model of ontogenetic growth, based on seasonal changes in the water temperature, was constructed for the “average individual” of this population.

Introduction

The common mussel (*Mytilus edulis* L.) is one of the most important invertebrates on the rocky and gravel bottoms of the eastern and northern Baltic Sea. On these bottoms it accounts for more than 80% of the total invertebrate biomass (Jansson and Kautsky 1977, Kautsky 1989). Mussels have an important role in the recycling of nutrients and other mineral and organic matter (Kautsky 1981). The importance of mussels has been recognized in a number of papers (Tulkki 1960, Heinonen 1961,

Bagge *et al.* 1965, Sunila 1981, Elmgren *et al.* 1984, Laihonon *et al.* 1985, Vuorinen *et al.* 1986, Öst and Kilpi 1997), but there still is a lack of data for comparative studies or for the monitoring of mussel populations in Finland. In particular, there is a need for data on long-term changes in individual abundance (Öst and Kilpi 1997) and on changes in the structure of mussel populations. The purpose of this study was to estimate the current state of the common mussel population in the vicinity of the Island of Seili, and to evaluate its structural parameters and dynamics of reproduction.

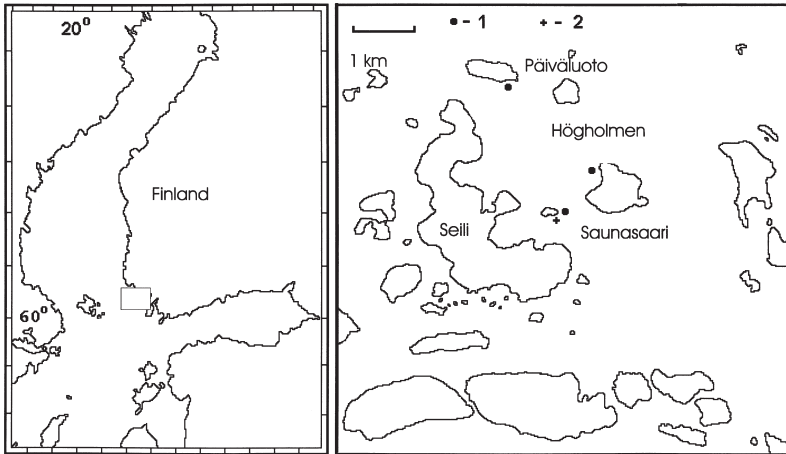


Fig. 1. Map of studied area: 1 = localities where common mussels were sampled, 2 = site of artificial reef location.

Material and methods

The material was collected during 17 July–10 September 1996 from typical mussel habitats by the small rocky islands of Saunasaari, Högholmen and Päiväluoto, near the Island of Seili (Fig. 1). For a preliminary timing of the reproduction period of the common mussel some field experiments were done on the spat forming on artificial substrata in 1995.

Investigated localities present typical common mussel habitats in SW Finland. The bottom angle in those habitats is about 30–40°. The bottom usually changes from rock covered by filamentous algae at a depth of 1–3 m to barren separated boulders and stones (with sand and gravel in-between) at a depth of 4–10 m. At depths greater than 10 m the hard substrate gradually disappears beneath the layer of sand and fine sediments, and the mussel aggregations become rarer and more scattered. Common mussels were found down to the depth of 12 m. Quantitative samples were collected by SCUBA-diving at a depth interval of 3–8.5 m, where also the mussel settlements were most dense. Because of evident differences in the vertical distribution of different sized mussels, noticed visually, three vertical levels were studied separately (depths of 3 m, 6–6.5 m and 8–8.5 m). Three localities were investigated: Saunasaari (samples taken from the depths of 3, 6 and 8 m (the last one for gonads investigation only)), Högholmen (6.5 m) and Päiväluoto (8.5 m).

Studies of reproduction

For the analysis of the sexual cycle mussels were collected weekly by towing a triangular bottom drag at the depth of 8–8.5 m close to the Saunasaari. Condition of the reproductive glands was evaluated visually and examined on microscopic slides from 20–30 adult individuals from weekly samples (length > 25 mm). Gametogenesis is a continual process, but for the convenience of description it can be divided into several stages. The greatest interest lies in the period of spawning of the mussel settlement as a whole. The subdivisions of the sexual cycle proposed by Chipperfield (1953) and Lubet (1959) were applied in this work to the analysis of gonad development. In this scheme the summer periodicity of *M. edulis* gametogenesis can be briefly described as follows (Maximovich 1985):

Stage II: The active gametogenesis.

Stage III: The maturity and spawning. Several separate phases or sub-stages can be distinguished within this stage, such as:

- IIIA1: when the follicles occupy most of the gonadal section, IIIA2, which occurs immediately before the spawning condition,
- IIIB: with partial or complete discharge of the gametes,
- IIIC: with the restoration of the gonad tissue after non-completed discharge of gametes, and

IIID: with repeated or completed discharge of the gonads

Stage 0: The period of gonad restoration.

The reproduction of mussels can as well be traced out by its final result, the spat forming. For this reason an artificial reef, consisting of a network of nylon ropes, was deployed and monitored off the Saunasaari (Fig. 1) in summer season of 1995.

Studies of population structure and growth

The structural characteristics of the population were studied on 10 September 1996, after the settling of the larvae. Mussels were collected in plastic bags with a help of a diver-operated collecting frame of 0.1 m² (two frames were from each depth). The structure of every local settlement was studied separately. All the data were later integrated in the population modelling. All the mussels in the quantitative samples were counted, weighed (g, wet weight) and measured to the nearest 1 mm, the spat of current season and juveniles to 0.1 mm. Individual age was identified by analysing the external shell morphology. For this reason variation in the position of the first growth ring were preliminarily investigated in selected well-distinguishable rings from mussels of the previous generation (with age of 1+ years). The length of the mussels during each winter, when their growth is suspended (later referred to as the winter stop-of-growth period), was measured from the yearly growth rings. A total of approximately 500 individuals were studied in this way.

The data on individual ontogenetic growth were summarised for each study locality. The growth rate dynamics of the mussels were studied by reconstructing their ontogenetic linear growth. These data were equalised using a linear modification of the Bertalanffy equation (Bertalanffy 1938) as follows:

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

where L_∞ , k and t_0 are parameters, L_t = shell length (mm), t = age (years). Evaluation of these equation parameters and the comparison of growth

curves were done with analysis of residual dispersion values (Allen 1976) with specially elaborated original software at the Department of Hydrobiology of St. Petersburg State University (Maximovich 1989).

Modelling of seasonal changes in the growth rate was carried out by inserting the sum of day-degrees in the Bertalanffy equation (Ursin 1965). The equation then looks as follows (Sukhotin and Maximovich 1994):

$$L_D = L_\infty \left(1 - \exp^{-(k'D-kt_0)}\right) \quad (2)$$

where L_D = mussel's shell length (mm) at age D (D = sum of day-degrees in mussel ontogenesis), $k' = k/D_y$ (D_y = annual sum of day-degrees). Mussel growth was considered to stop at 0 °C.

Results

The abundance of mussels varied by one order of magnitude: density ranged from 1 250 to 16 730 ind. m⁻² and biomass from 250 to 2 100 g m⁻² (Table 1).

Reproduction

Investigations of gonad tissues revealed some regularities in reproduction. The stage II (active gametogenesis) was already passed by the beginning of our research. The gonads of all mussels had reached maturity (stage IIIA1) by the middle of July (Fig. 2). Ten days later, the gonads of about one half of all individuals appeared to be in pre-spawning condition, and one week later they were in after-spawning condition. Up to 8 August, observation showed either gonad restoration (mainly in males, stage IIIC) or development of the after-spawning condition (stages IIIB and IIID). One week later (16 August) some individuals appeared with gonads corresponding to stage 0. Stage 0 was registered by the end of August in almost half (45%) of the mussels studied, and by the 10 of September in most of them (95%) (Fig. 2). Thus, in 1996 the discharge of gametes in the settlement of the common mussel occurred in the period from 26 July to 2 August. During this short

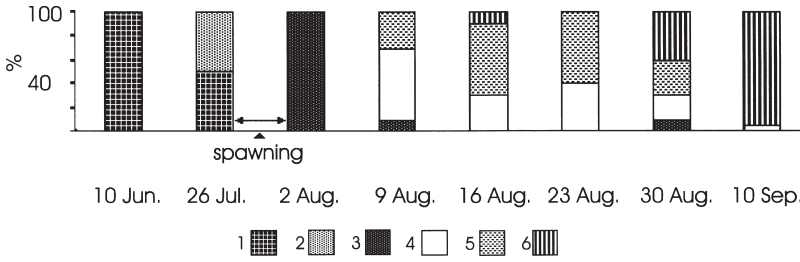


Fig. 2. Percentage of *M. edulis* individuals in different stages (1-III A1, 2-III A2, 3-III B, 4-III C, 5-III D, 6-0) of the gonad development in July–September 1996 by the Island of Saunasaari, at the depth of 8–8.5 m.

period, substantial warming of the water (from 14 to 17 °C) was registered at the depth of 5–10 m.

Judging from these findings, the discharge of gametes was a short-term and single event. Only 30% (seven from 24) of individuals investigated actually discharged their gametes completely. In others, the gonads contained remnants of partially non-discharged sexual products. In September, we observed the autolysis of gametes, the development of conjunctive tissue and a proliferation of spermatogenesis elements (in males). These observations give no reason to suggest repeated spawning during the season studied.

The season of 1996 was characterized by abnormally low temperatures during the first half of the summer, in other years, the spawning of the common mussel in the area may occur one to three weeks earlier. In 1995, the mass settling of common mussels spat on artificial reef at the Saunasaari was registered on 18 July, which corresponds to the spawning period not later than at the beginning of July.

Age structure

The range of individual sizes (shell length) was from 0.6 mm (spat) to 44.0 mm (9 years old) (Fig. 3). The largest, oldest (33–44 mm, 9 years old) and most rapidly growing mussels were found at the depth interval of 6–8.5 m, but these are rather rare in the populations studied. The distribution of age groups was different for each sampling location (Table 1). Spat of the current season was found only at a depth of 3 m (Saunasaari), and never deeper. The first growth ring was 0.8–1.9 mm from the tip of shell.

There is a density-difference in the vertical distribution of various age groups. The density of spat at the depth of 3 m was 256 ind. m⁻². The main part of the settlement there (80%) was represented by juveniles of age 1+. On the same site at the depth of 6 m the mussels in the age of three to five years were predominant, and young, one-year-old mussels represented only 18% of the total number. A rather peculiar situation was ob-

Table 1. Structure of *M. edulis* settlements at different depth and sites nearby the Island of Seili (SW Finland) in summer–autumn 1996. *L* = average shell length (mm), *N* = density (ind. m⁻²), *B* = biomass (g m⁻²).

Depth (site)	3 m (Saunasaari)			6 m (Saunasaari)			6.5 m (Högholmen)			8 m (Päiväluoto)		
	<i>L</i>	<i>N</i>	<i>B</i>	<i>L</i>	<i>N</i>	<i>B</i>	<i>L</i>	<i>N</i>	<i>B</i>	<i>L</i>	<i>N</i>	<i>B</i>
Age												
0+	0.9	256	0.02	–	–	–	–	–	–	–	–	–
1+	4.0	7 348	44.70	3.8	220	1.1	3.4	11 920	44.3	4.0	3 950	24.0
2+	9.9	960	91.90	9.2	80	6.1	10.2	1 580	165.6	10.3	2 030	219.2
3+	13.9	232	62.30	15.9	310	125.3	15.4	1 950	715.1	15.4	2 130	781.1
4+	18.2	24	14.60	20.0	420	340.9	20.2	1 120	937.0	20.6	160	142.1
5+	–	–	–	25.0	150	239.9	23.7	130	176.8	23.6	270	362.5
6+	25.3	24	39.80	28.1	50	114.1	26.2	30	55.3	28.9	50	124.3
7+	–	–	–	29.4	10	26.2	–	–	–	30.8	50	150.8
8+	–	–	–	37.6	10	55.3	–	–	–	33.4	50	192.9
Total		9 156	253.40		1 250		909.0	16 730	2 094.0		5 450	1 996.8

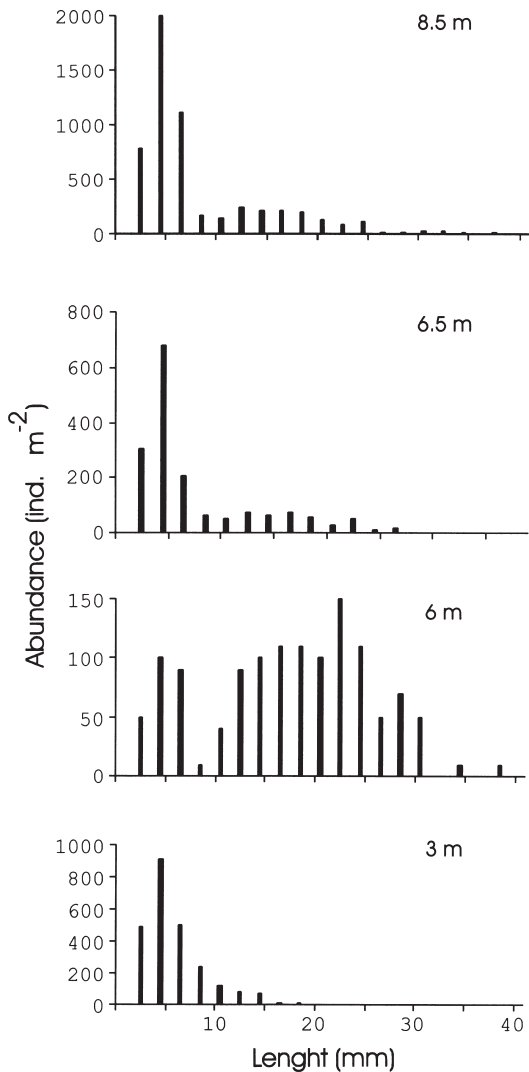


Fig. 3. Size (class interval 2 mm) frequency distribution of *M. edulis* (number of individuals m⁻²) in different depths nearby the Island of Seili.

served at Högholmen, where the bottom at the depth of 5–8 m was completely covered with a mat of detached green algae (mainly *Cladophora* spp.) An extremely high density (11 920 ind. m⁻², 71% of total number) of young mussels of the previous year's generation (1+) was discovered in association with these mats. Evidently these mussels had formerly been settled on *Cladophora* thallus at lower depths, and sank later together with their detached substrate. On 10 September, at the depth of 6.5 m, all mussels settled inside and under the mats were alive.

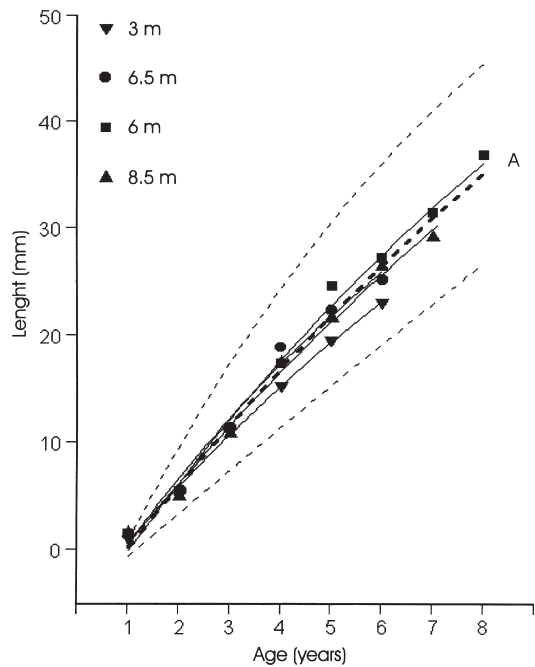


Fig. 4. Bertalanffy models of group linear growth of *M. edulis* settlements nearby the Island of Seili. Outer dotted lines show range of individual growth rate. Solid lines show average shell length during the winter stop-of-growth period in different habitats. Bold dotted line (curve A) is the general growth curve (Eq. 3).

Linear growth

Individual differences in the growth rate of the mussels are considerable as shown by the range of variation around the general growth curve (Fig. 4). The range of shell length variation among equally aged mussels can be as high as 20 mm in the later ontogenetic stages. On the other hand, mussels of equal size can differ in age by as much as four years. The most rapidly growing individuals (up to 41 mm at the end of the seventh year) were registered at the depth of 8 m. The most slowly growing mussel (20 mm, 6 years old) was found at the depth of 3 m.

The residual variances (Table 2) demonstrated that no differences in average growth rate of mussels from different habitats could be distinguished. Thus individuals of age from two to seven years in every habitat are considered to have a reasonably similar linear growth. The model of a general growth curve for all the mussels measured is described by the equation:

$$L_t = 140.6(1 - \exp^{-0.0404(t-0.87)}) \quad (3)$$

In creating the model of seasonal growth, the annual changes in the average sea water temperature (in °C) were grouped, according to regular measurements at the Island of Seili, as follows: Jan-0.7, Feb and Mar-0., Apr-2, May-6, Jun-13.2, Jul-17.3, Aug-17.5, Sep-14, Oct-10.3, Nov-5.5, Dec-2.5. Thus the sum of annual day-degrees (D_y) is 2 726. Incorporating this into (3), the rewritten model of seasonal mussel growth yields:

$$L_t = 140.6(1 - \exp^{-(0.0000148D-0.035)}) \quad (4)$$

In order to transform the temporal scale into a real-time scale, mussel growth after the winter stop-of-growth was assumed to co-occur with the intensive warming of the water. First April was arbitrarily chosen as the starting point. This yielded a curve of the ontogenetic growth of the average individual of *M. edulis* (Fig. 5). It is important to note that the seasonal changes in the growth rate forecast by this model coincide fairly closely with the average sizes of various aged individuals. Thus the model does in fact adequately reflect the multi-year dynamics of the mussels' linear growth.

Discussion

The reproductive period

The spawning of mussels at the depth of 5–10 m occurred in 1996 at the end of July. Heinonen (1961) and Sunila (1981) have noted that the main

spawning activity of the common mussel in the Archipelago Sea occurs during the two first summer months. In 1960 the spawning of mussels at the town of Naantali (inner archipelago) and at the Island of Lohm (outer archipelago) was registered from the end of May to the end of July at temperatures of 12–15°C (Heinonen 1961). In 1978, near the Tvärminne Biological Station (S coast of Finland), the peak of the spawning of common mussel was observed in July (Sunila 1981). This is in agreement with our data and supports the view of a regular mussel reproductive cycle also in other populations of the Baltic Sea and in nearby areas of the North Sea (Chipperfield 1953, Seed 1969, Kautsky 1982a).

Evidently in this part of the Baltic Sea the beginning of the mussels' reproductive period can vary depending on the annual hydrological conditions. For example Heinonen (1961) found remarkable differences (up to one month) in mussel spawning in various habitats in the SW Finland. A similar variability is known for the common mussel population of the Kandalaksha Bay in the White Sea (Savilov 1953, Maximovich 1985). Because of the external fertilization of mussels maximal success of reproduction within each local settlement is only possible when spawning is synchronized. In the boreal zone the synchronous discharge of gametes is triggered by temperature (Nelson 1928, Chipperfield 1953, Lubet 1959, Kaufman 1974, Maximovich 1985). Essential conditions for such discharge include not only a certain minimal temperature but also a certain rate and amplitude of temperature change. An additional factor, responsible for the local synchronization of gamete discharge, is biochemical sexual stimulation (Chipperfield 1953, Lubet 1959, Hrs-Brenko 1973, Seed 1969, 1976).

The spawning of common mussels in the way described is also evident from our data, and from the material of Heinonen (1961). The data of Sunila (1981) are not suitable for an adequate study of the spawning process, due to the insufficiently frequent sampling (once a month). However, a similar spawning pattern can be traced in these data on the basis of a sudden change in the gonad index of the mussels in the period from 10 June to 4 July (Sunila 1981). Only one cycle of gametogenesis was found in the northern Baltic common mussels by Kautsky (1982b). There is thus

Table 2. Analysis of residual variances in the average values of *Mytilus edulis* shell length (in mm from top of shell to winter stop-of-growth marks) in growth curves (Fig. 4).

Source of variation	df	SD	S ²	F	F _{kr} (α < 0.05)
Separate equations	15	20.23	1.349		
Common equation	24	48.94	2.039	1.51	2.29

Note: df = degrees of freedom ($\sum_{i=1}^m (n_i - 3)$), where m = number of growth curves, n_i = data number for different equation parameters), SD = standard deviation, S² = variance, F = F-ratio.

every reason to consider that in the Baltic Sea populations of *M. edulis* (as well as in the White Sea populations) in females only one generation of oocytes exists during the annual cycle of gametogenesis.

It is clear that morphological variation in the condition of the mussel gonads, as observed during the season of 1996, does not indicate the prolongation or repetition of spawning. We consider this to be a general feature of the life cycle of the northern Baltic Sea common mussel population.

Population structure

The structural parameters of the mussel populations studied are typical for the northern Baltic Sea, mussels in the size range of 15–20 mm and the age of 1–3 years predominate the populations (Kautsky 1982b, Sunila 1981, this study). The presence of juveniles (0+) only at low depths (above 3 m) is usual for the spat of the common mussel in the Baltic Sea. Juveniles use the green filamentous algae as a substrate. This substrate is not suitable for attachment of larger mussels because of too fine structure of the filaments and their ephemeral nature. The filamentous green algal environment is short-lived and seasonal only. Probably the detachment of green algae from the rocks in the autumn and winter also removes the spat of mussels sitting on them. By the next season, those mussels which were associated the previous year as a spat with the green algae belt become the 1+ mussels associated with green bottom-dwelling and decaying algae mats. This may explain the high density of young (1+) molluscs found in September within, upon and beneath the layer of detached green algae at the Island of Hög-holmen.

A decrease in average and maximal size and even in the coverage and biomass of the common mussel have been reported from several areas in the NW part of the Gulf of Finland (Hario *et al.* 1992, Hollmen *et al.* 1996, Öst and Kilpi 1997). It was suggested that the reason for the observed change in mean mussel size may be long-term salinity changes affecting the growth rate, maximal size and recruitment of mussels. No anomalies in size-frequency distribution (which could demonstrate an elimination of older and bigger mussels)

were found in our study despite the fact that a decrease of salinity has also been found in the same area (Vuorinen *et al.* 1998).

The comparability of fragmentary data collected over long periods of time from various localities and by different methods is a separate and important problem. It seems incorrect to compare quantitatively samples collected with bottom grabs, with a triangular scraper and by SCUBA-diving quantitative techniques (this study). It can only be mentioned that the size frequency distribution and maximal sizes of common mussels in population from the Seili area are very similar to ones in Hango peninsula area in 1992–1994, but differs from situation there described in 1996, as it was reported by Öst and Kilpi (1997). The population from the Seili area by now can be characterized by normal size frequency distribution and regular recruitment with the juveniles.

Growth

The basis for the linear growth model was the annual periodicity of the growth rings. The experimental investigations by Kautsky (1982 b) confirm the suitability of the method. The most common cause of systematic mistakes in bivalve age determination are the difficulties in finding the stop-of-growth mark of the first winter. According to our results, juveniles reach a length of 1–3.5 mm by the end of the first season, this is in agreement with the experimental data of Kautsky (1982b) for the Swedish coast of the Baltic Sea.

The average linear growth rate of mussels from the Seili area on the basis of reconstructing the general growth curve (35 mm after eight years, Fig. 4) is fairly similar, although slightly higher, to that of mussels from the Tvärminne area (31 mm after nine years, Sunila 1981) and about 1.5 times as high as that found on the Swedish coast of the Baltic Sea (Kautsky 1982b). It is evident that there is a substantial difference between the growth rates of mussels in SW Finland and on the Swedish coast, despite the approximately equal thermal conditions of these areas. Such a difference may result from the feeding conditions of the mussels. Kautsky (1982b) has noted a considerable increase in the growth rate in individuals placed in suspended cages, i.e. in optimal feeding

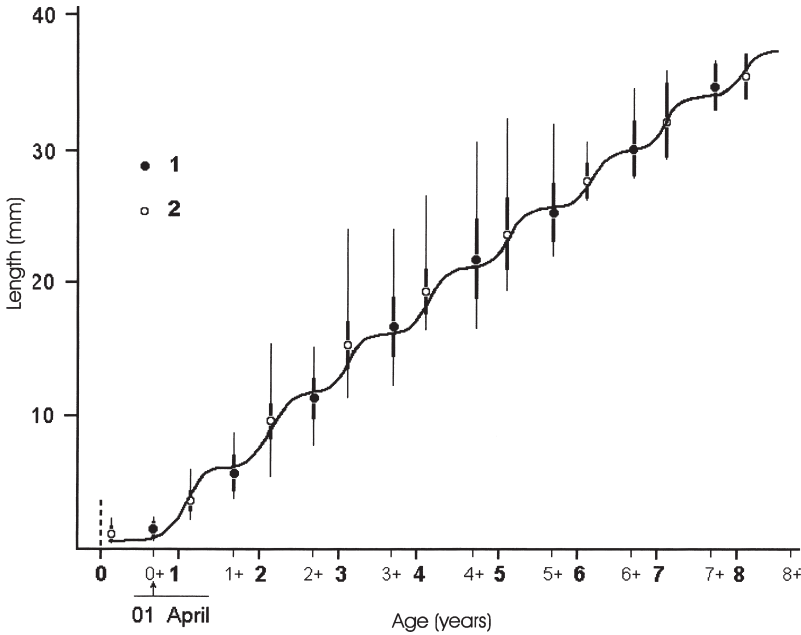


Fig. 5. Model of seasonal linear growth of *M. edulis* nearby the Island of Seili. Starting point of the settling arbitrarily set as first of August (dotted vertical line). 1 = average length of shells in winter, 2 = length of shells 10 of September 1996. Vertical lines: amplitude of variation between equally aged mussels. Thickness of lines indicates position of 95% confidence limit. The first of April marks the beginning of mussel growth after a winter pause.

conditions. However, the interesting fact of such a rapid growth rate of mussels in the south-eastern Gulf of Bothnia needs to be confirmed by additional experimental work.

One important finding is the lack of differences in the growth of mussels from different depths and habitats. Thus, in spite of the observed significant natural variability of equally-aged molluscs, the populational characteristics of their ontogenetic growth can be predicted on the basis of the dynamic of growth of an average individual. Analogous observations have been made on the populations of common mussels in the White Sea (Sukhotin and Maximovich 1994). However, it is important that a good correspondence is achieved between the seasonal dynamics of linear growth and a convenient and easily measured environmental parameter such as the water temperature.

The practical importance of this model lies in the possibility of predicting the main structural parameters of local populations of common mussels without separate studies. These prognoses could be improved by including in the model data on regional average temperatures collected since 1966 by the Island of Seili, and data on the average growth rate collected by reconstruction of the individual mussel growth rate (approximately 500 individuals aged from zero to nine years) over the last nine years.

For prognoses of mussel production characteristics (biomass, production, annual harvest), accurate monitoring data on the mussel abundance and its dynamics should be added to the model.

This particular model (Fig. 5) has regional application, it can be applied to natural settlements of the common mussel in SW Finland, as well as — without substantial changes — to neighboring areas of the Baltic Sea, characterized by similar temperature conditions. The approach itself seems to be a universally applicable one. The basic requirements of the model are: use of Bertalanffy equation as the model for growth, high correlation of the mussel growth rate with the annual temperature changes, and reliability of mussel age determination by annual rings. Using this approach similar regional models can be calculated for every area in the boreal zone where considerable seasonal gradients of environmental parameters are normal (Sukhotin and Maximovich 1994).

Acknowledgements: This research was carried out in the framework of the Program of Collaboration between the Universities of St. Petersburg and Turku. The study was also partly funded by the EU in the BASYS project of the MAST programme (contract MAS3-CT96-0058). The authors are grateful to Ms. Nina Heikkilä, Marja-Liisa Leinonen and Mr. Tapani Ranta for assistance in the field work and Dr. Ellen Valle for linguistic corrections.

References

- Allen R.L. 1976. Method for comparison fish growth curves. *N.Z.J. Mar. Freshwater Res.* 10: 687–692.
- Bagge P., Jumppanen K., Leppäkoski E. & Tulkki P. 1965. Bottom fauna of the Finnish southwestern archipelago. III. The Lohm area. *Ann. Zool. Fennici* 2: 38–52.
- Bertalanffy L. 1938. A quantitative theory of organic growth. *Human Biol. Baltimore* 10: 181–213.
- Field J.A. 1922. Biology and economic value of the sea mussel *Mytilus edulis*. *Bull. U.S. Bur. Fish* 38: 127–259.
- Chipperfield P.N.J. 1953. Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *J. Mar. Biol. Ass. U.K.* 32: 449–476.
- Elmgren R., Rosenberg R., Andersin A., Evans S., Kangas P., Lassig J., Leppäkoski E. & Varmo R. 1984. Benthic macro- and meiofauna in the Gulf of Bothnia (Northern Baltic). *Finn. Mar. Res.* 250: 3–18.
- Hario M., Selin K. & Soveri T. 1992. Loisten osuudesta haahkan lisääntyvyyden heikkenemisessä. *Suomen Riista* 38: 23–33.
- Heinonen A. 1961. Reproduction of *Mytilus edulis* L. in the Finnish southwestern archipelago in summer 1960. *Arch. Soc. Zool. Bot. Fenn.* "Vanamo" 16: 137–143.
- Hollmen T., Hario M. & Lehtonen. T. 1996. Haahkanpoikasten massakuolema ja loisepidemia Söderskärilla 1995. *Suomen Riista* 42: 32–39.
- Hrs-Brenko M., 1973. Gonad development, spawning and rearing of *Mytilus* sp. larvae in the laboratory. *FAO Cons. gen. peches. Mediter.* 52: 53–65.
- Jansson A.-M. & Kautsky N. 1977. Quantitative survey of hard bottom communities in a Baltic archipelago. In: Keegan B.F., Ceidigh P.O. & Boaden P.J.S. (eds.), *Biology of benthic organisms, 11th Europ. Symp. Mar. Biol., Perg. Press, Oxford*, pp. 359–366.
- Kaufman Z.S. 1974. Sexual cycles and gametogenesis of invertebrates from the White Sea. In: *Exploration of the Fauna of the Sea., XIII (XXI), Nauka, Leningrad*, pp. 191–271. [In Russian with English summary].
- Kautsky, H. 1989. Quantitative distribution of plant and animal communities of the phytobenthic zone in the Baltic Sea. *Contrib. Askö Lab., Univ. Stockholm, Sweden* 35: 1–80.
- Kautsky, N. 1981. On the trophic role of the common mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of the organic matter produced by the mussels. *Kieler Meeresforsch., Sonderh.* 5: 454–461.
- Kautsky N. 1982a. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. *Mar. Biol.* V68: 143–160.
- Kautsky N. 1982b. Growth and size structure in a Baltic *Mytilus edulis* population. *Mar. Biol.* 68: 117–133.
- Laihonen P., Lietzen E. & Vuorinen I. 1985. Fouling ilmiön esiintyminen ja torjunta Suomen voimaloissa 1984 [Occurrence and control of fouling in Finnish power plants 1984]. *Turun yliopiston biologian laitoksen julkaisuja n:o 10*: 1–69. [In Finnish with English summary].
- Lubet P. 1959. Recherches sur le cycle sexuel et l'émission des gamètes chez les Mytilidae et les Pectinidae (Mollusca Bivalves). *Rev. Trav. Inst. Peches Marit.* 23: 389–548.
- Lukanin V.V., Naumov, A.D. & Fedyakov. V.V. [Луканин В.В., Наумов, А.Д. & Федяков, В.В.] 1986. [Size structure dynamics of recolonization in the middle White Sea]. In: Lukanin V.V. & Fedyakov V.V. [Луканин В.В. & Федяков, В.В.] (eds.), [Ecological investigations of bottom organisms of the White Sea], ZIN AN SSSR, Leningrad, pp. 50–63. [In Russian].
- Maximovich N.V. [Максимович Н.В.] 1985. [Reproductive cycle of *M. edulis* in the inlet of Chupa]. In: Lukanin V.V. [Луканин В.В.] (ed.), [Investigations of mussels of the White Sea], ZIN AN SSSR, Leningrad, pp. 22–35. [In Russian].
- Maximovich N.V. 1989. Statistical comparison of growth curves. *Vestnik Leningr. Univ.* 3(4): 18–25. [In Russian with English summary].
- Nelson T.C. 1928. On the distribution of critical temperatures for spawning and for ciliary activity in bivalve molluscs. *Science* 67: 220–221.
- Savilov A.I. [Савилов А.И.] 1953. [Growth and its variability in invertebrates of the White Sea. *Mytilus edulis*, *Mya arenaria* i *Balanus balanoides*]. *Tr. Inst. Okeanologii* 7: 198–256. [In Russian].
- Seed R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchia) on exposed rocky shores. 1. Breeding and settlement. *Oecologia* 3–4: 227–316.
- Seed R. 1976. Ecology. In: Bayne B.L. (ed.), *Marine mussels: Their ecology and physiology*. Cambridge, London, New York, Melbourne, pp. 13–66.
- Sukhotin A.A. & Maximovich N.V. 1994. Variability of growth rate in *Mytilus edulis* L. from the Chupa Inlet (the White Sea). *J. Exp. Mar. Biol. Ecol.* 176: 15–26.
- Sunila I. 1981. Reproduction of *Mytilus edulis* L. (Bivalvia) in a brackish water area, the Gulf of Finland. *Ann. Zool. Fennici* 18: 121–128.
- Tulkki P. 1960. Studies on the bottom fauna of the Finnish southwestern archipelago. I. Bottom fauna of the Airisto Sound. *Ann. Zool. Soc.* "Vanamo" 21: 1–26.
- Ursin E. 1965. On the incorporation of temperature in the von Bertalanffy growth equation. *Medd. Dan. Fisk. Havunders.* 4: 1–16.
- Vuorinen I., Laihonen P. & E. Lietzen. 1986. Distribution and abundance of invertebrates causing fouling in power plant on the Finnish coast. *Mem. Soc. Fauna Flora Fennica* 62: 123–125.
- Vuorinen I., Hänninen J., Viitasalo M., Helminen U. & Kuosa H. 1998. Proportion of copepod biomass declines together with decreasing salinity in the Baltic Sea. *ICES J. Mar. Sci.* 55: 767–774.
- Öst M. & M. Kilpi. 1997. A recent change in size distribution of common mussels (*Mytilus edulis*) in the western part of the Gulf of Finland. *Ann. Zool. Fennici* 34: 31–36.