

Spatial distribution and growth of the common mussel *Mytilus edulis* L. in the archipelago of SW-Finland, northern Baltic Sea

Ilppo Vuorinen¹⁾, Alexander E. Antsulevich²⁾ and
Nicolay V. Maximovich²⁾

¹⁾ Archipelago Research Institute, University of Turku, FIN-20014 Turku, Finland

²⁾ Department of Hydrobiology and Ichthyology, St. Petersburg State University, 16 linia 29, St. Petersburg 199178, Russia

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Abundance, biomass, size distribution and growth of the common mussel, *Mytilus edulis* L. along a transect extending through the SW archipelago of Finland, northern Baltic Sea are described here for the first time. The parameters studied were found to vary according to environmental gradients extending from the inner to the outer archipelago. The lowest densities and biomass were found in the innermost archipelago. Most of the populations here consisted of small individuals between 4 to 6 mm (antero-posterior length), while in the middle and outer archipelago areas modal size was approximately twice as large. The average growth rate of mussels in the middle archipelago was higher than in all other areas. Very slow growing, or “dwarf” mussels were found in all areas studied, but these were most common in the outer archipelago.

Introduction

To date, the common, or blue mussel, *Mytilus edulis* L. has been studied little in the Finnish coastal areas despite their predominant role as a temporary storage of carbon and nutrients in the rocky sea bottom (J. Kotta, unpubl.); their role as filters at the base of the food chain (Laiho-nen *et al.* 1996, Antsulevich *et al.* 2000), and subsequently as food to the eider duck (*Somateria mollissima*), one of the most common birds

in the Baltic Sea (Öst and Kilpi 1998).

The taxonomy and biogeography of the *Mytilus edulis* species complex is subject to discussion due to the distinction of three component species (*M. edulis*, *M. galloprovincialis* and *M. trossulus*) by molecular techniques used in systematics (Varvio *et al.* 1988, Bulnheim and Gosling 1988, McDonald *et al.* 1991, Väinölä and Hvilson 1991, Gosling 1992, Seed 1992). Baltic *M. trossulus* and Atlantic *M. edulis* overlap and hybridise in the region of the Danish

Straits. The *Mytilus* specimens in our study may thus be referred to as *trossulus*. However, our intention is not to take a stand in this discussion, and thus we decided to follow Seed and Suchanek (1992) in retaining the specific names as used by authors in the primary citations in order to avoid any unnecessary confusion.

Populations of the blue mussel are a common element of the sublittoral landscape in the northern and north-western Baltic Proper, because the bottom substrata are predominated by rocks and boulders (Granö *et al.* 1999). The species is most abundant in the depth interval from 3 to 12 m (Bagge *et al.* 1965, Öst 1995, Öst and Kilpi 1997), but it can occur in considerably deeper waters, if suitable hard substrate is present (Tulkki 1960, Jansson and Kautsky 1977). General characteristics of mussel vertical distribution, reproduction and growth rate were described for some populations situated in the central part of the Archipelago Sea near the Island of Seili (Antsulevich *et al.* 1999). Results of this study showed that the breeding period was short and repeated spawning did not occur. The distribution of age groups in the mussel population around the island of Seili demonstrated the stability of recruitment over several previous years. The most rapidly growing individuals were found at a depth of 8 m while the average growth rate of molluscs did not vary between different habitats around the Seili area.

The goal of this study is to describe and compare abundance, biomass, size and age distribution and growth rates of common mussels over a larger area, i.e. the inner, middle and outer parts of the Archipelago Sea, SW Finland, where environmental conditions (gradients of temperature, salinity, exposure etc.) may vary substantially.

Materials and methods

Area of investigation

The Archipelago Sea (59°45'–60°45'N, 21°00'–23°00'E) (Fig.1) is located between the Gulf of Finland, the Gulf of Bothnia and the Baltic Proper. It is characterised by an

enormous topographic complexity, incorporating about 25 000 islands (there are some 73 000 islands on the Finnish coast) (Granö *et al.* 1999). Due to the vast number of islands the total length of the shoreline is 14 356 km in the SW Archipelago alone (not including the Åland Islands) (Granö *et al.* 1999). The total area of the Archipelago Sea is 9436 km², but the water volume is not more than 213 km³ as the average water depth is only 23 m, and the deepest trench reaches 146 m. The area is characterised by a strong seasonality, the average annual salinity range is between 5‰ and 6‰, and the temperature between slightly sub zero and 22 °C (Haapala and Alenius 1994). During the winter months the sea is covered with ice and permanent ice cover may last for over 100 days (Seinä and Peltola 1991). The sea is non-tidal, and the water level fluctuates irregularly up to one meter due to air pressure and prevailing winds.

As a starting point, we took the general environmental heterogeneity found in the Archipelago Sea. General characteristics and the geological and biological subdivisions of the Archipelago Sea range gradually from the more shallow, sheltered inner archipelago to the more open and deeper outer archipelago. This is due to slow postglacial land uplifting (about 0.5 cm a⁻¹) of a tilting coastal plain. As a result the area is ecologically, hydrographically and dynamically characterised by gradients of nutrients, salinity, temperature, oxygen, exposure etc. (Helminen *et al.* 1998, Hänninen *et al.* 2000, Vahteri *et al.* 2000). For practical reasons both biologists and geographers often divide the archipelago into three zones: the inner archipelago (the ratio of land/sea > 1), the intermediate zone (land/sea ≈ 1) and, finally the outer archipelago (land/sea < 1) (Häyrén 1900, Jaatinen 1960, Numers and van Maarel 1998, Granö *et al.* 1999). Hänninen *et al.* (2000) and Vahteri *et al.* (2000) studied this zonation in terms of nutrients and filamentous algae. They point out that despite the general decrease of nutrient concentrations with increasing distance from the mainland there may be local deviations such that in the middle archipelago local high concentrations may occur e.g. in areas of intensive fish farming.

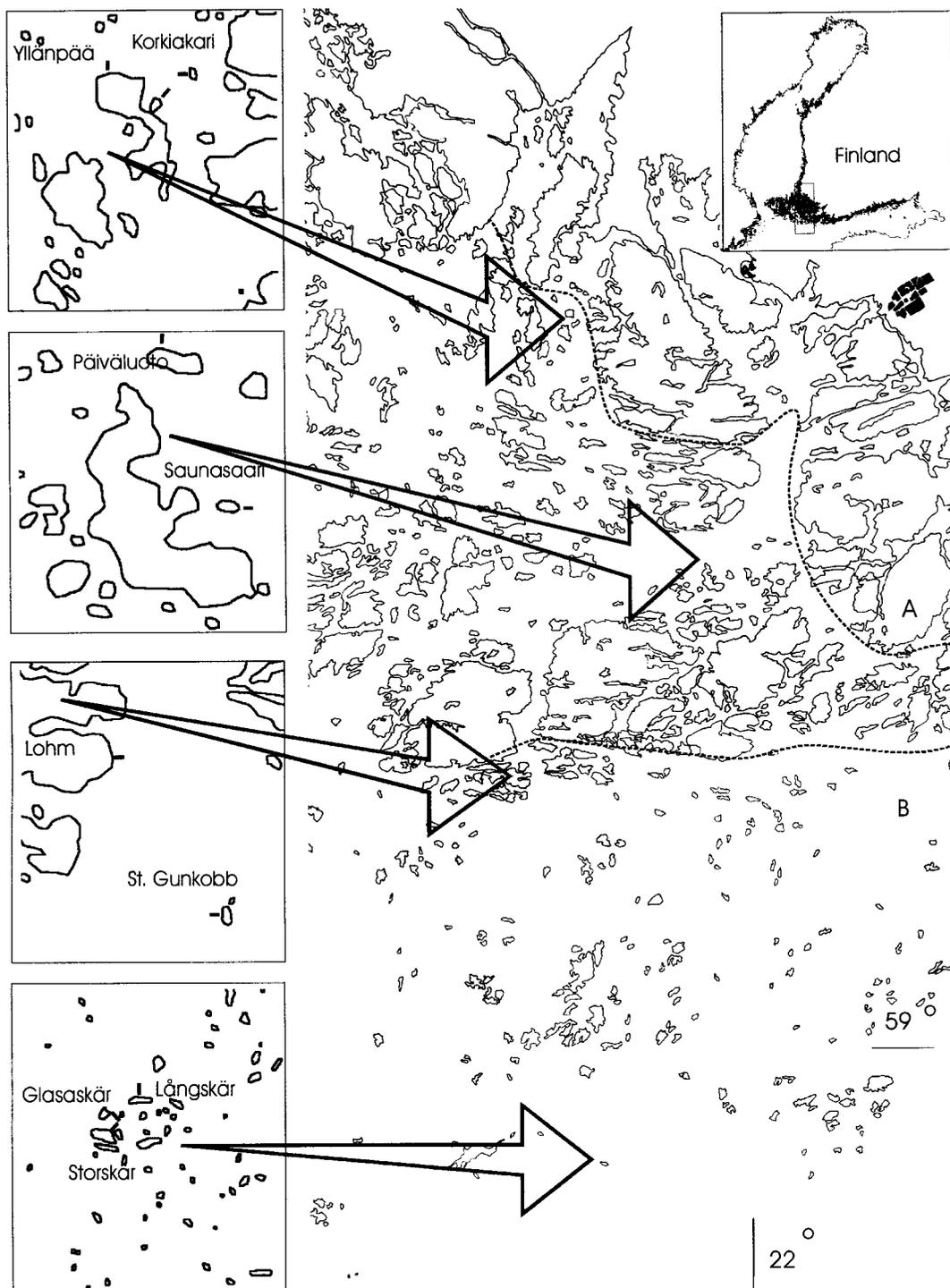


Fig. 1. Sampling locations of *Mytilus edulis* in the Archipelago Sea, northern Baltic in 1996. Sampling locations representing the inner archipelago zone (A) situated at the Islands of Yllänpää, Yllänpää-Korkiakari, and Korkiakari, the middle archipelago was sampled at Päiväluoto, Saunasaari, Lohm (collected in 1993), and St. Gunkobb, and the outer archipelago (B) at Storskär, Glasaskär, and Långskär

Sampling

Sampling for abundance and biomass was done from 16 July to 10 September 1996 at nine localities evenly distributed among the three archipelago zones (Fig. 1). Sampling locations were selected in order to find comparable sampling sites with rocky substrata and a minimum depth of 12 meters at a distance of around 50 meters from the shoreline.

The sampling was carried out by scuba diving. First, a 50 m rope with one meter markings was stretched perpendicularly to the shoreline. At each of the sampling locations, depths of 3, 6, 9 and 12 meters were sampled except in the innermost archipelago where only 3, 6 and 9 metres were sampled due to a lack of suitable substrata, i.e. soft sea-floor, at greater depths. Three replicate samples were collected from each depth. Sampling was done by scraping all mussels within a 20 × 20 cm aluminium frame into a nylon net attached to one side of the frame. Samples were preserved in 4% buffered formalin solution.

Laboratory analyses and statistics

In the laboratory, the mussels were counted, and their lengths and biomass (wet weight) were measured. Differences in abundance and biomass among the archipelago zones and the depths were tested with SPSS 8.0.1 software (SPSS Inc. 1989–1997), with $\log_{10}(x + 1)$ transformed data and applying General Linear Models (GLM) as well as a two way ANOVA (with Tukey's honestly significant difference (HSD) test as a posterior test). In case the variances remained heterogeneous after transformation (Levene's test), the Kruskal-Wallis non-parametric ANOVA or the Mann-Whitney *U*-test were used. In order to test the differences among the archipelago zones and among the depths, the GLM Contrasts (SPSS Inc. 1997) were specified for each factor level.

A total of 846 individuals were studied and about 2350 measurements made for the growth and size frequency analyses. In order to achieve comparability we used samples from the depth of 9 meters from four locations, with increasing distance from the inner archipelago: the islands

of Korkiakari, Saunasaari, St. Gunkobb and Långskär (Fig. 1).

Age structures of mussel populations in different parts of the archipelago were compared by identifying separate age groups in different locations, their maximal life duration, and the variability of modal sizes of individuals within the age groups. Age was estimated with a binocular microscope as follows: the mussel lengths during each winter were measured from the narrow external rings which are formed between the proper growth rings when the growth is retarded in winter. Only full cyclical rings between growth rings were accepted. Finally, the annual increase in size was calculated for each locality. The localities studied for mussel growth are listed above and include the island of Lohm. Exceptionally, sampling at the latter site was done in the summer of 1993, nevertheless these results were included for comparative purposes.

The growth rate of mussels was studied by reconstructing their ontogenetic linear growth by a linear modification of the von Bertalanffy equation (von Bertalanffy 1938) as follows:

$$L_t = L \left(1 - e^{-k(t-t_0)} \right) \quad (1),$$

where L = shell length (mm), k = growth constant, and t = mussel age (years).

The comparison of growth curves was done by analysing the residual dispersion (Allen 1976). The ratio F/F_{cr} (F_{cr} = F critical) (at significance level $\alpha < 0.05$) was used as an index of distance in a dendrogram according to Maximovich (1989). This was due to the fact that F_{cr} itself cannot be used because of the necessity to determine its value repeatedly according to degrees of freedom. As a result, all values of the index $F/F_{cr} < 1$ show that (at selected level of accuracy, here $\alpha = 0.05$) the differences between compared age curves are random (Maximovich 1989).

Results

Abundance and biomass

Horizontal distribution of *Mytilus* abundance and biomass were seen to increase broadly sea-

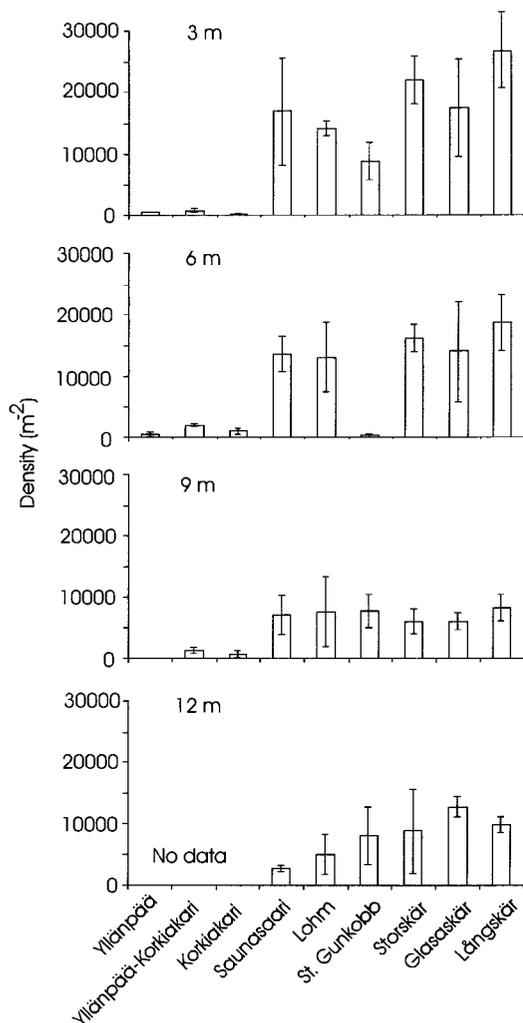


Fig. 2. Abundance of common mussels in the different locations in the Archipelago Sea, northern Baltic Sea in 1996.

wards from the inner study area towards the outer archipelago. There were clear differences among sampling locations in the abundance of the mussels (Figs. 2 and 3). Except for the innermost area, the abundance of mussels varied between 8000 and 26000 ind. m^{-2} at shallower depths (from 3 to 6 meters) and between 3000 and 12000 ind. m^{-2} at greater depths. Maximal densities were at the depth of 3 m in the three outermost locations, i.e. the Islands of Storskär, Glasaskär and Långskär (Fig. 2). The innermost area (sampling locations at Yllänpää, Yllänpää-

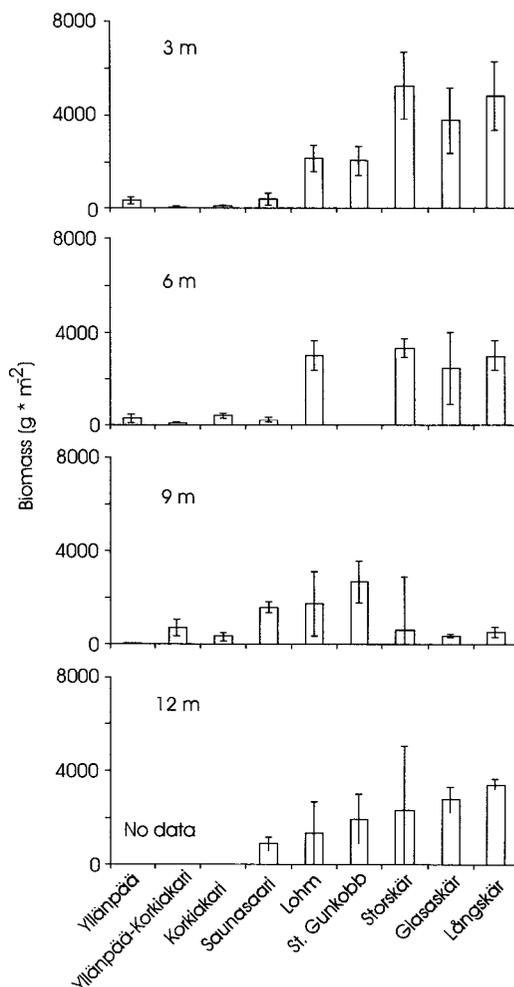


Fig. 3. Biomass of common mussels in the Archipelago Sea, northern Baltic Sea in 1996.

Korkiakari, and Korkiakari) was characterised by a very low abundance of mussels in comparison with the middle and outer parts of the archipelago. Two-way ANOVA revealed significant differences in abundance among the archipelago zones and an interaction between the zones and depths (Table 1A). As a posterior test, the HSD-test clarified differences among certain archipelago zones e.g. the mean difference in *Mytilus* abundance between the inner and middle archipelago zones (-0.9326 , $SD = 0.104$, $p < 0.000$), and between middle and outer archipelago (-0.3360 , $SD = 0.094$, $p < 0.002$).

With regard to the vertical distribution of

Mytilus, abundance was often higher near the surface (3 and 6 meters) than deeper (Table 1B). Maximal biomass 3800–5400 g m⁻² was also found at a depth of 3 m in the outermost localities (Fig. 3). *Mytilus* biomasses differed significantly among the archipelago zones e.g. Kruskal Wallis test among the archipelago zones ($H = 37.985$, $df = 2$, $p < 0.000$), while among depths no significant difference ($H = 5.771$, $df = 3$, $p < 0.123$), was observed.

Size and age distributions

The size distribution in the studied settlements was fairly variable (Fig. 4). For the most part,

the populations in the innermost and middle archipelago (the islands of Korkiakari and Saunasaari respectively) consisted of small individuals in the 4–6 mm size range. In the outermost locations (St. Gunkobb and Långskär) the modal size of the mussels was about twice that, i.e. 8–12 mm in length (Fig. 4). The largest individual, measured at 38 mm, was found at Saunasaari.

In the material collected in July 1996 juvenile mussels were returned with shell lengths of only ca. 0.9 mm (range 0.6–1.0 mm) (Fig. 5) with shell structures which could be considered as annual rings. The summer of 1996 was abnormally cold (Antsulevich *et al.* 1999) and spat of this year was not expected to

Table 1. Two way ANOVA on differences in *Mytilus* abundance between archipelago zones (SW-Finland in 1996) and depths, and contrasts between depths.

A: Tests of Between-Subject Effect.

Source	df	Mean Square	<i>F</i>	<i>p</i> <	Observed Power
DEPTH	3	0.222	1.383	0.253	0.356
ZONE	2	11.761	73.368	0.000	1.000
DEPTH × ZONE	5	0.666	4.154	0.002	0.947
Error	86	0.160			

R Squared = 0.674

B: Contrasts between depths in *Mytilus* abundance in different archipelago zones. GLM abundance by zone and depth, $df = 1$.

	MS	<i>F</i>	<i>p</i> <
Inner archipelago			
3 m vs 6 m	0.593	3.698	0.058
3 m vs 9 m	0.347	2.163	0.145
6 m vs 9 m	1.724 ⁻⁰²	0.108	0.744
Middle archipelago			
3 m vs 6 m	1.879	11.723	0.001
3 m vs 9 m	0.387	2.412	0.124
3 m vs 12 m	0.922	5.752	0.019
6 m vs 9 m	0.561	3.5	0.065
6 m vs 12 m	0.169	1.052	0.308
9 m vs 12 m	0.155	0.714	0.4
Outer archipelago			
3 m vs 6 m	9.209 ⁻⁰²	0.574	0.451
3 m vs 9 m	1.189	7.42	0.008
3 m vs 12 m	0.515	3.214	0.077
6 m vs 9 m	0.62	3.865	0.053
6 m vs 12 m	0.172	1.0712	0.304
9 m vs 12 m	0.139	0.867	0.354

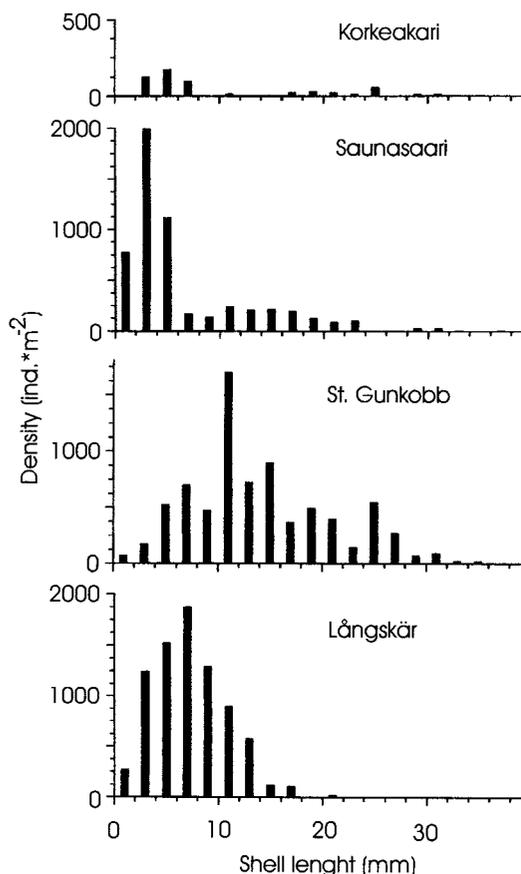


Fig. 4. The size distribution of the common mussel populations in different parts of the Archipelago Sea, northern Baltic Sea in 1996.

occur before the third week of August. Subsequently, all juveniles from the generation produced in 1995 were studied more closely. During their first winter, when growth is suspended, the shell length of this cohort varied from 0.6 to 4.8 mm. For further verification, spat which had settled on an artificial reef at the Island of Seili, in July 1993 only two to three weeks prior to sampling, were investigated. These specimens had a shell length of 0.7–1.2 mm, and had no shell structures resembling the growth marks in juveniles collected in 1996. Thus, the marks on the shells from 1996, corresponding to the length around 0.9 mm, were indeed the first annual rings of late settled and slowly growing mussels born in 1995. Following late settlement the

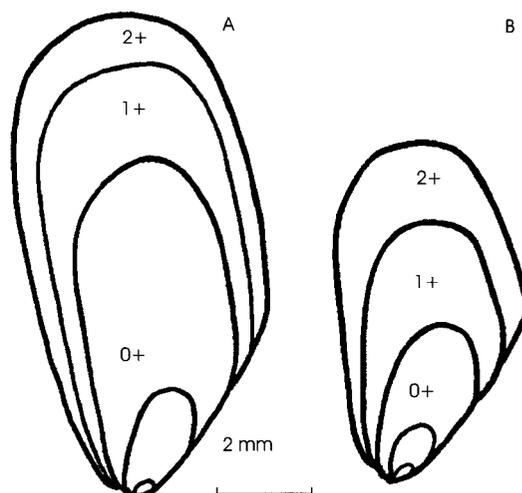


Fig. 5. Left shell valves of *Mytilus edulis*. — **A:** active growing mussel; — **B:** slow growing (dwarfed) mussel from the same habitat (the Island of St. Gunkobb, SW Finland), northern Baltic Sea in 1996.

subsequent annual growth for these individuals was poor. They remained exceptionally small with the result that 5–6 year old “dwarfed” individuals may be of the same size as a two-year-old normally growing individual (Fig. 5). In the Archipelago Sea, dwarf mussels were found at every locality except at the Island of Korkeakari. They were very common in the outermost archipelago areas, where they often formed up to 20% of individuals in mussel settlements.

The age structure in the studied populations showed a general seawards decrease of length-at-age (Table 2), with studied populations generally displaying a very uneven age structure. This was shown by differences in the abundance of age groups within the habitats, in the maximal life duration among the habitats, and by the variability of modal sizes of individuals within the cohorts (Table 2). Furthermore, the largest abundance of mussels at two stations (St. Gunkobb and Långskär) was not formed by the first generation (Table 2). Neither do the abundances of age classes from 3 to 7 years decrease evenly with the age. Finally, at the island of Korkeakari, the cohort 1+, which should be one of the most numerous, was not found at all (Table 2).

Growth

The mussel growth rates and parameters of the von Bertalanffy equations for various locations showed a similar decrease towards the outer archipelago that was found in the age structures (Table 3), and interestingly, also a decrease of the mussel growth rate from the middle towards the inner archipelago. Corresponding growth curves (Fig. 6) corroborate the decreasing growth rate from the middle part of the archipelago towards the outer and inner margins.

The analysis of residual dispersions demon-

strated that the compared growth curves were heterogeneous (Fig. 7 and Table 4). The average growth rates of mussels at the islands of Saunasaari and Lohm were higher than in other areas, while the mussels at Långskär (the outermost site) had the slowest growth rate. When the mussel populations were classified by the average growth rate, those of the islands of Saunasaari and Långskär were grouped separately from the others, as indicated by the F/F_{cr} ratio (Fig. 7A). The same analysis was repeated with only the oldest mussels (age 4 years and older), which resulted in even more pronounced differences (Fig. 7B).

Table 2. Age structure of *M. edulis* populations in different sites at depth of 9 m (Archipelago Sea; Northern Baltic Sea) in summer 1996. L = average shell length (mm), ind. = individuals, – = no data.

Site	Korkiakari		Saunasaari		St. Gunkobb		Långskär	
	L	ind. m^{-2}	L	ind. m^{-2}	L	ind. m^{-2}	L	ind. m^{-2}
0+	4.2	433	4.2	3820	3.2	1075	2.0	1116
1+	–	–	11.6	640	5.6	1275	5.8	5033
2+	13.8	50	17.5	390	9.7	1650	8.8	1320
3+	18.3	43	22.0	260	13.2	1550	12.2	217
4+	23.2	50	23.9	10	15.2	1350	14.6	118
5+	22.8	25	28.7	70	22.2	1350	20.5	8
6+	20.0	8	31.1	20	28.0	225	21.1	18
7+	29.7	25	–	–	29.0	100	–	–
8+	31.0	15	–	–	–	–	–	–
Total:	649		5210		8575		7830	

Table 3. Reconstruction of linear shell growth of common mussel in different populations (Archipelago Sea) in summer 1996. L = average shell length in winter, (mm); n = number of specimens studied; k , L_{∞} and t_0 = parameters of von Bertalanffy model (Eq. 1), – = no data.

Site	Korkiakari		Saunasaari		Lohm		St. Gunkobb		Långskär	
	L	n	L	n	L	n	L	n	L	n
0+	2.0	52	1.8	107	1.4	57	1.8	28	1.3	53
1+	–	–	6.8	22	6.0	21	4.8	15	4.0	148
2+	5.8	6	13.5	27	9.3	19	8.8	10	6.8	67
3+	10.2	5	16.9	13	13.2	9	13.0	23	10.6	12
4+	14.8	6	21.2	1	18.1	3	17.0	18	12.2	9
5+	18.5	3	25.5	7	22.9	4	21.6	18	18.2	1
6+	21.6	1	27.7	2	26.8	3	25.7	9	20.0	2
7+	24.2	3	–	–	31.9	2	28.3	4	–	–
8+	29.5	2	–	–	33.5	1	–	–	–	–
k	0.0860		0.1296		0.0132		0.0017		0.0035	
L_{∞}	58.72		50.53		335.30		2350.00		933.80	
t_0	0.6831		0.7588		0.7406		0.6857		0.7579	

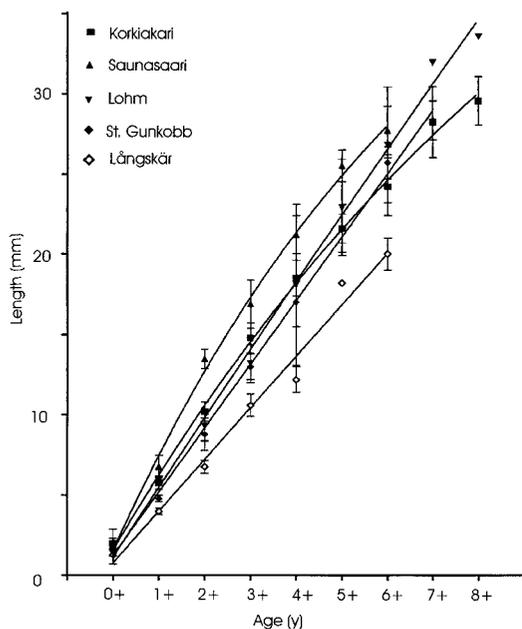


Fig. 6. *Mytilus edulis* linear growth reconstruction in the archipelago of SW Finland, northern Baltic Sea in 1996. Vertical lines indicate standard deviation.

Discussion

Abundance and biomass

Both abundances and biomasses of *Mytilus* showed a clear seawards increase from the inner study area towards the outer archipelago, although among depths no general differences were

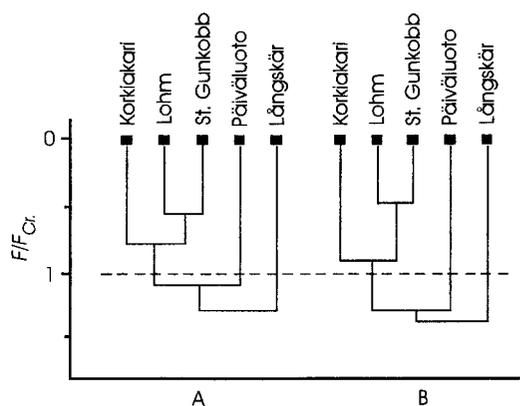


Fig. 7. Classification of the populations of common mussels (SW Finland, northern Baltic Sea) by average growth rate. — **A:** based on marks of winter period of growth suspension; — **B:** the same based only on mussels older than four years. F/F_{cr} = a measure of distance according to Maximovich (1989). Dotted line = the level of significant difference.

recorded (Figs. 2–3 and Table 2). Generally, the abundance in studied habitats ranged from 3000 to 26000 ind. m^{-2} . Kautsky (1982b) reported the abundance of 17000 to 28000 ind. m^{-2} (from a depth of 4 m) in the Swedish Baltic Sea coast, an area he described as “relatively unpolluted archipelago near the Askö laboratory about 70 km south of Stockholm” (Kautsky 1982b: p. 118). This is almost identical to the results of the present work from a depth of 3 m in the outer part of archipelago (17500 to 26000 ind. m^{-2}).

Table 4. Comparison of growth curves of common mussel from various locations in the Archipelago Sea, northern Baltic in 1996.

A: Analysis of residual dispersion of growth curves on Fig. 7. F_{cr} = critical value of the F -distribution $\alpha < 0.05$, S^2 = residual dispersion.

Source of variation	df	Sum of squares	S^2	F -ratio	F_{cr}
On single equations	25	108.53	4.37	–	–
On common equation	37	421.29	11.39	2.62	1.88

B: Two by two growth curves comparison. Measure of distance = ratio F/F_{cr} .

Korkiakari	Storskär	Saunasaari	St. Gunkobb	Storskär
0.57				Saunasaari
0.55	1.41			St. Gunkobb
0.44	0.30	2.22		Långskär
0.57	0.48	5.65	0.48	

High variability of the abundance and biomass values, which has been described above, is fairly typical for blue mussels (Seegersträhle 1961, Seed 1969, Rasmussen 1973, 1977, Samtleben 1977, Kautsky 1982b, Golikov *et al.* 1988). The difference in vertical distribution was due to the variable distribution of juveniles (Antsulevich *et al.* 1999), and similar observations were made at the Swedish coast of the Baltic Sea (Kautsky 1982b). Because bigger mussels usually occupy deeper sites, the vertical differences in the biomass is less pronounced than differences in abundance.

Size and age distributions

In general, the mussels of the Archipelago Sea are rather small; maximal size is under 40 mm, with a large part of the population being smaller than 20 mm in length. However, such a size structure is normal and even typical for the eastern and central Baltic Sea areas (Kautsky 1982b, Öst and Kilpi 1997). A peculiar character of the size structure of mussel populations in the Archipelago Sea is a decrease of the modal size in the outermost settlements towards the open sea. A similar situation was described from Kandalaksha Bay (the White Sea), where the mussels from the outer part of the archipelago were considerably smaller and slower growing (Golikov *et al.* 1988) than those in the nearshore sites. In both cases, such results can probably be explained by relatively poor feeding conditions (lower abundance of phytoplankton and concentration of detritus) in the open sea habitats in comparison with more inshore areas.

The maximal age of mussels collected in the Archipelago Sea was 9 years with the majority of the populations being under the age of 4–6 years (Table 2). Quite similar age structures were described for blue mussel populations in other areas (Seed 1969, Samtleben 1977, Kautsky, 1982b, Golikov *et al.* 1988), including the *Mytilus trossulus* population from the East Siberian Sea (Gagaev *et al.* 1994).

There was no continuous pattern found in the reproduction and subsequent recruitment of studied populations characterised by a very irregular

number of the 0+ age group (Table 2). Many natural interrelations within a mussel population may be responsible for this. For example, differences in settlement could be caused by biochemical repellence of the juveniles by adult individuals (Seed 1969, Morse 1990), different depth and biotope preferences between adults and juveniles (Kautsky 1982b, Antsulevich *et al.* 1999), ecological succession and cyclic re-occurrence of the mussel beds (Lukanin *et al.* 1986), selective predators (Öst and Kilpi 1998), and even active or passive (with kelps or detached algae) migration of the mussels (Antsulevich *et al.* 1999).

Growth

Growth rate is one of the most important indicators of living conditions for mussels.

Differences in the growth rate of blue mussels and other bivalves from different depths were demonstrated in neighbouring areas of the northern Baltic (Seegersträhle 1960, Kautsky 1982b, Littorin and Gilek 1999); they result from the vertical gradients of environmental factors. Comparable horizontal differences in growth rates were found among the Archipelago zones, these corresponded well to known environmental gradients, e.g. nutrients, chlorophyll, salinity and temperature (e.g. Hänninen *et al.* 2000). In this way, the average growth curve, which “accumulates” changes in the individual growth from many individuals and several (7–9) past years, reflects the quality of certain habitat. The best conditions for mussels are met in the middle archipelago areas while optimal growth conditions deteriorate from the middle archipelago in both seaward and landward directions. However, the reasons for such worsening are probably quite different. The inner archipelago may be impacted by industry in the City of Turku as well as freshwater runoff from the Aura river. The influence of freshwater creates osmotic stress for the mussels. For *Mytilus edulis*, freshwater is known to suppress the activity of cilia or filtering activity, while oxygen consumption of the gill tissue may increase (*see* discussion by Seegersträhle 1960). Lower temperatures and

low chlorophyll contents of the water (Kirkkala 1998) probably also control the growth rate of mussels in the outermost areas of the archipelago.

The dwarfing phenomenon was described for the Baltic and the White Sea populations by Kautsky (1982a) and Golikov *et al.* (1988), respectively. In the present work, dwarf individuals were found in the entire study area but they were more common in the outer archipelago, at the islands of St. Gunkobb and Långskär. Analysing the age structure of the blue mussel populations at the Swedish coast, Kautsky (1982b) noted that “most settled mussels form a pool of completely suppressed non-growing individuals”. In Kandalaksha Bay of the White Sea the whole population consisted of only dwarf mussels at a depth of 15 m (Golikov *et al.* 1988). Kautsky (1982b) proposed that dwarfed mussels create an additional reserve of fertile young individuals. The authors of the present work have another opinion. No signs of a later, compensatory growth were found in slow-growing mussels in the Archipelago Sea. Considering quantitative population effects, such mussels are a burden rather than a reserve; they compete for food and space but do not contribute to the population growth. Therefore, dwarf mussels are not only temporarily slow-growing i.e. they are late not only for the start of the growing season, but remain small and slow growing for the rest of their life cycle. Moreover, according to our results all big mussels in populations are initially the most actively growing individuals.

Generally, the genetic separation of *M. edulis* from *M. trossulus* could make it difficult for comparisons to be made between populations from the Baltic (i.e. *trossulus*) and e.g. White Sea, thus the discussions must be treated with this caution.

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References

- Allen R.L. 1976. Method for comparison of fish growth curves. *N.Z.J. Mar. Freshwater Res.* 10: 687–692.
- Antsulevich A., Laihonon P. & Vuorinen I. 2000. Employment of artificial reefs for environmental maintenance in the Gulf of Finland. In: Jensen A.C., Collins K.J. & Lockwood A.P.M. (eds.), *Artificial reefs in European seas*, Kluwer Acad. Publ. Dordrecht, Boston, London, pp. 319–330.
- Antsulevich A.E., Maximovich N.V. & Vuorinen I. 1999. Population structure, growth and reproduction of the common mussel (*Mytilus edulis* L.) off the Island of Seili (Archipelago Sea, SW Finland). *Boreal Env. Res.* 4: 367–375.
- Bagge P., Jumppanen K., Leppäkoski E. & Tulkki P. 1965. Bottom fauna of the Finnish south-western archipelago. III. The Lohm area. *Ann. Zool. Fennici* 2: 38–52.
- Bulnheim H.-P., Gosling E. 1988. Population structure of mussels from the Baltic Sea. *Helgoländer Meeresuntersuchungen* 42: 113–129.
- Gagaev S.Yu., Golikov A.N., Sirenko B.I. & Maximovich N.V. [Гагаев С.Ю., Голиков А.Н., Сиренко Б.И. & Максимович Н.В.] 1994. Ecology and distribution of the mussels *Mytilus trossulus septentrionalis* Clessin, 1989 in the Chauna bay of the East Siberian Sea. *Exploration of the fauna of the Seas* 47(55): 254–263. [In Russian with English summary].
- Golikov A.N., Maximovich N.V. & Sirenko B.I. [Голиков А.Н., Максимович Н.В. & Сиренко Б.И.] 1988. On distribution, growth and production of *Mytilus edulis* L. with reference to settlements off the Sonostrov Island (the White Sea). *Exploration of the fauna of the Seas* 39(47): 97–108. [In Russian with English summary].
- Granö O., Roto M. & Laurila L. 1999. Environment and land use in the shore zone of the coast of Finland. *Turun yliopiston maantieteen laitoksen julkaisu* [Publications of the Geographical Institute of the University of Turku] 160. 76 pp.
- Gosling E.M. 1992. Systematics and geographic distribution of *Mytilus*. In: Gosling E.M. (ed.), *The mussell Mytilus: ecology, physiology, genetics and culture*, Elsevier Science publishers, Amsterdam, pp. 1–20.
- Haapala J. & Alenius P. 1994. Temperature and salinity statistics for the Northern Baltic Sea 1961–1990. *Finnish Marine Res.* 262: 51–121.
- Helminen H., Juntura E., Koponen J., Laihonon P. & Ylinen H. 1998. Assessing of long distance background nutrient loading to the Archipelago Sea, northern Baltic with a hydrodynamic model. *Environmental Modelling & Software* 13: 511–518.
- Hänninen J., Vuorinen I., Helminen H., Kirkkala T. & Lehtilä K. 2000. Trends and gradients in nutrient concentrations and loading in the Archipelago Sea, Northern Baltic. *Estuarine, Coastal and Shelf Science* 50: 153–171.

- Häyrén E. 1900. Längs-zonerna i Ekenäs skärgård. *Geografiska Föreningens tidskrift* 12: 222–234.
- Jaatinen S. 1960. Geografiska regioner. *Atlas över Skärgårdsfinland utg. av Nordenskiöld-Samfund i Finland*. Map 15. Helsinki.
- 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.
- Kautsky N. 1982a. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. *Mar. Biol.* 68: 143–160.
- Kautsky N. 1982b. Growth and size structure in a Baltic *Mytilus edulis* population. *Mar. Biol.* 68: 117–133.
- Kirkkala T. 1998. Miten voit saaristomeri? *Ympäristön tila Lounais-Suomessa* 1: 1–70.
- Laihonen P., Hänninen J., Chojnacki J. & Vuorinen I. 1996. Some prospects of nutrient removal with artificial reefs. In: Jensen A.C. (ed.), *European artificial reef research. Proceedings of the 1st EARRN Conference, Ancona, Italy, March 1996*, pp. 85–96.
- Littorin B. & Gilek M. 1999. Vertical patterns in biomass, size structure, growth and recruitment of *Mytilus edulis* in an archipelago area in the Northern Baltic Sea Proper. *Ophelia* 50: 93–112.
- Lukanin V.V., Naumov A.D. & Fedyakov V.V. [Луканин В.В., Наумов А.Д. & Федяков В.В.] 1986. [Dynamics of the size structure of the White Sea blue mussels settlements]. In: Lukanin V.V. & Fedyakov V.V. [Луканин В.В. & Федяков В.В.] (eds.), *Ecological investigations on benthic organisms of the White Sea*, ZIN AN SSSR, Leningrad. pp. 50–63. [In Russian].
- Maximovich N.V. [Максимович Н.В.] 1989. Statistical comparison of growth curves. *Vestnik Leningr. Univ.* 3(4): 18–25. [In Russian with English summary].
- McDonald J.H., Seed R. & Koehn R.K. 1991. Allozymes and morphometric character of three species of *Mytilus*. *Mar. Biol.* 111: 323–333.
- Morse D.E. 1990. Recent progress in larval settlement and metamorphosis: closing the gaps between molecular biology and ecology. *Bull. Mar. Sci.* 46 2: 465–483.
- Öst M. 1995. *Ejders (Somateria mollissima) val av blåmusslor (Mytilus edulis) i Norra Östersjön — är små musslor bättre än stora?* M.Sc. thesis, University of Helsinki. 51 pp.
- Öst M. & Kilpi M. 1997. A recent change in size distribution of blue mussels (*Mytilus edulis*) in the western part of the Gulf of Finland. *Ann. Zool. Fennici* 34: 31–36.
- Öst M. & Kilpi M. 1998. Blue mussels *Mytilus edulis* in the Baltic: good news for foraging eiders *Somateria mollissima*. *Wildlife Biology* 4: 81–89.
- Petersen G.H. 1977. The density, biomass and origin of the Bivalves of the central North Sea. *Medd. Danm. Fisk-og Havunders.* N.S. 7: 221–273.
- Rasmussen E. 1973. Systematics and ecology of the Ise-Fjord marine fauna (Denmark). *Ophelia* 11: 1–507.
- Samtleben C. 1977. Klappenwachstum und Entwicklung von Grössenverteilungen in Populationen von *Mytilus edulis* L. *Meyniana* 29: 51–69.
- Seed R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. 1. Breeding and settlement. *Oecologia* 3: 277–316.
- Seed R. 1976. Ecology. In: Bayne B. (ed.), *Marine mussels*. Cambridge Univ. Press, pp. 13–65.
- Seed R. 1992. Systematics, evolution and distribution of mussels belonging to the genus *Mytilus*: an overview. *Am. Malac. Bull.* 9: 123–137.
- Seed R. & Suchanek T.H. 1992. Population and community ecology of *Mytilus*. In: Gosling E. (ed.), *The mussel Mytilus: ecology, physiology, genetics and culture*, Elsevier, pp. 87–169.
- Segersträhle S.G. 1960. Investigations on Baltic populations of the bivalve *Macoma baltica* (L.). *Soc. Sci. Fenn. Comment. Biol.* XXIII 2: 1–72.
- Segersträhle S.G. 1961. Fluctuation in the abundance of benthic animals in the Baltic area. *Soc. Sci. Fenn. Comment. Biol.* XXIII 9: 3–19.
- Seinä A. & Peltola J. 1991. Duration of the ice seasons and statistics of fast ice thickness along the Finnish coast. 1961–1990. *Finnish Marine Res.* 258: 46.
- 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.
- Vahteri P., Mäkinen A., Salovius S. & Vuorinen I. 2000. Drifting algal mats conquering the sea floor of the Archipelago Sea, in the SW Finland. *AMBIO* 6: 338–337.
- Varvio S.-L., Koehn R.K. & Väinölä R. 1988. Evolutionary genetics of the *Mytilus edulis* complex in the North Atlantic region. *Mar. Biol.* 98: 51–60.
- Väinölä R. & Hvilsum M.M. 1991. Genetic divergence and a hybrid zone between Baltic and North Sea *Mytilus* population (Mytilidae, Mollusca). *Biol. J. Linn. Soc.* 43: 127–143.
- von Bertalanffy L. 1938. A quantitative theory of organic growth. *Human Biol. Baltimore* 10: 181–213.
- von Numers M. & van der Maarel E. 1998. Plant distribution patterns and ecological gradients in the Southwest Finnish Archipelago. *Global Ecology and Biogeography Letters* 7: 421–440.