The fresh-water pearl mussel, *Margaritifera margaritifera* (L.)

On the localization, age, and growth of the individual and on the composition of the population according to an investigation in Pärlälven in Arctic Sweden

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Contents

1. Introduction

Through the Institute of Freshwater Research at Drottningholm the author has had the opportunity in the summer of 1958 to study for the legal authorities the occurrence of the fresh-water pearl mussel, *Margaritifera margaritifera* (L.), in Pärlälven, a river in Arctic Sweden. The material collected in this connexion forms the basis of this paper. A detailed account in Swedish on the investigation and its results having already been presented (HENDELBERG 1959) we shall deal here only with some points of more general interest.

2. The distribution of the fresh-water pearl mussel and the situation of the area of investigation

World distribution

According to the wider conception of the species which is now in common use the fresh-water pearl mussel, *Margaritifera margaritifera* (L.),[1] is holarctic. It occurs in the western as well as in the eastern parts of North Ame-

[1] For a long time the generic name *Margaritana* SCHUMACHER 1817 has been used. For the reasons see, e.g. HENDERSON (1928). According to the "Official Index of Rejected and Invalid Generic Names in Zoology" (HEMMING-NOAKES 1958) this name has, however, to give way to *Margaritifera* SCHUMACHER 1816.

rica, in the north-eastern parts of Asia, and in great parts of central and northern Europe. Within this vast area it is restricted to waters relatively poor in lime (cf., however, BOYCOTT 1925 and 1927) with not too slow current and not too high temperature, i.e. as a rule to forest and mountain regions or in general to regions with crystalline rocks. It is usually not found in the rivers of the plains, yet water courses upon sandy heaths can satisfy the above ecological demands. Thus the fresh-water pearl mussel is found e.g. upon the Lüneburg Heath (Germany) and in south-western Jutland (Denmark). As the result of pearl-fishing and the regulation of the water-courses the fresh-water pearl mussel has become much scarcer, and has disappeared altogether from certain places.

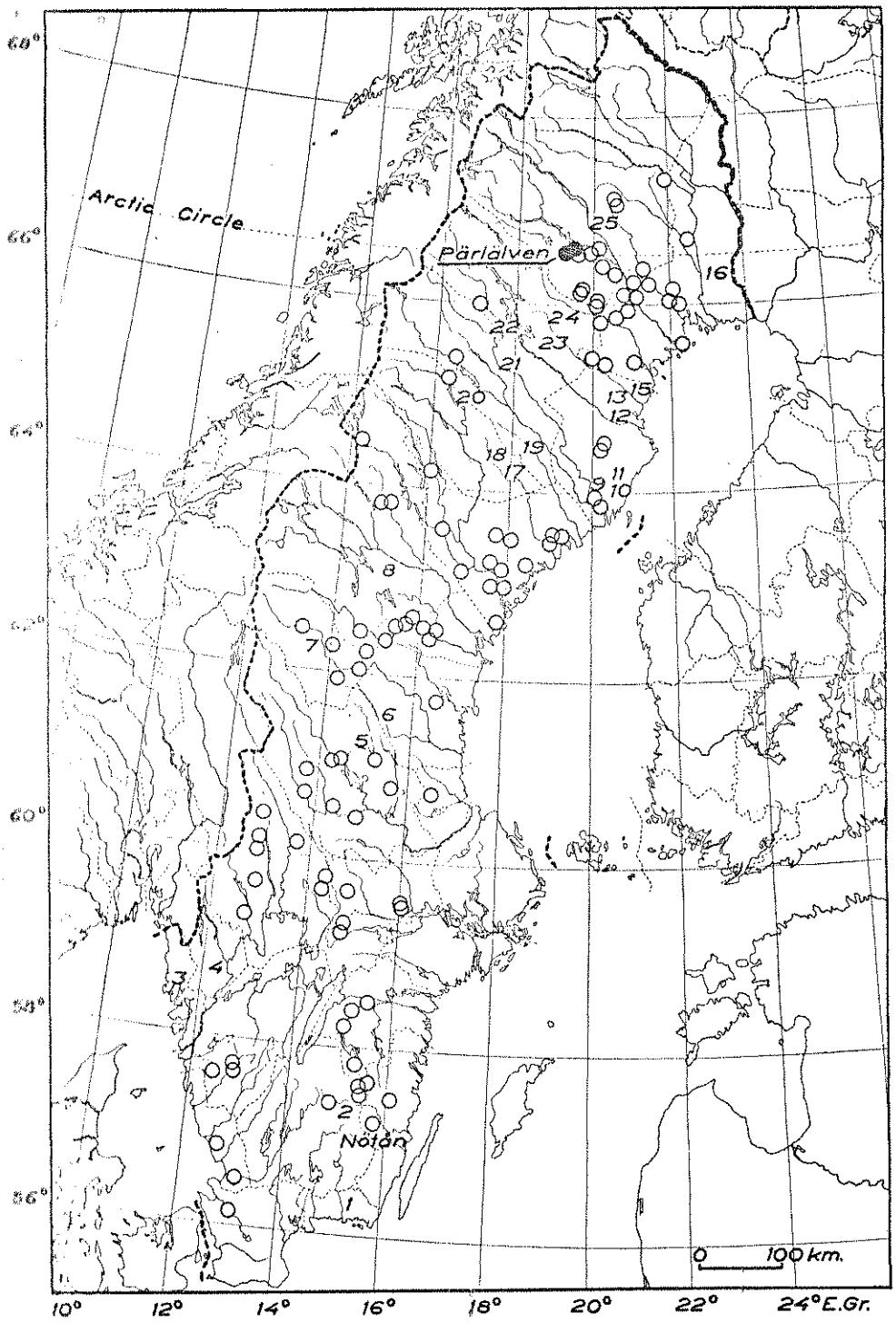
Division into isolated groups

Apart from a larval parasitism upon fishes during some weeks the fresh-water pearl mussel is remarkably stationary. This circumstance in connexion with the fact that the way by water is often long between localities with suitable ecological conditions has led to the result that within its wide area of world distribution the fresh-water pearl mussel has been split into a number of populations which are more or less isolated from each other. In the following a comparision will be made, e.g., with results of investigations upon the Lüneburg Heath, where the populations of the fresh-water pearl mussel can nowadays be considered well separated from the populations examined by the author.

Distribution in Sweden

For the distribution of the fresh-water pearl mussel in Sweden the author has compiled a map, *Fig. 1*, in which circles indicate occurrences of the mussel. Figures indicate less exactly localized ocurrences and, in certain cases, larger regions from which findings have been reported. The markings of the localities are to a great extent based upon sources from the eighteenth century. For this reason the map does not represent the actual conditions, but can nevertheless convey an idea of the natural distribution of the fresh-water pearl mussel in Sweden. A more detailed discussion of the map falls outside the scope of this notice. The author desires nevertheless to point to the close agreement between the distribution of the fresh-water pearl mussel and the extension of areas with soils and rocks poor in lime as given for southern Sweden by HUBENDICK (1947, p. 517).

Fig. 1. The distribution of the fresh-water pearl mussel, Margaritifera margaritifera (L.), in Sweden. The markings of the localities are to a great extent based upon sources from the eighteenth century. Thus the map does not give the actual conditions, but can nevertheless convey an idea of the nautral distribution of the mussel. — Figures indicate less exactly localized occurrences.


68°
66°
64°
62°
60°
58°
56°
Arctic Circle
Pärlalven
Nötån
1
2
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16
17
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25
0 100 km.
10° 12° 14° 16° 18° 20° 22° 24° E.Gr.

Situation of the area of investigation

The river Pärlälven (*Anglice* Pearl River) has a length of 51 km., and is situated (cf. Fig. 1) in the parish of Jokkmokk in the coniferous region immediately below the mountains. It comes from the lake Karats at 415 m. above sea-level, and discharges its waters into the lake Purkijaure 6 kilometres north of the Arctic Circle at the altitude of 272 metres. It is a tributary of the river Lilla Lule Älv, and thus belongs to the drainage system of the river Lule Älv.

3. The localization within the area of investigation

Stock-taking in Pärlälven

From a boat and while wading in the water the bottom of Pärlälven has been examined with a water-glass. Down to a depth of three metres the freshwater pearl mussels which dig themselves down to about three fourths of their length were well visible in the clear water. A scraper that dug into the bottom was used to obtain from greater depths samples that were sifted. This method was used also to find out whether or not there occurred freshwater pearl mussels that escaped detection with the water-glass either by their small size or on account of their being completely buried. In this respect the result was negative. Within regions, where more than some isolated mussels had been encountered, sample areas, to a total number of 30, were very carefully examined. The size of these areas, as a rule 20—100 sq.m., was adapted to the density of the population of the mussels. The number of the mussels, the depth of their occurrence, and the conditions of bottom and current were noted. Furthermore, length, height, and thickness were measured of all specimens that could be collected upon the sample areas. Material was also collected for the determination of age and sex, the analysis of food (found to consist mainly of vegetable detritus), etc. A detailed account of the stock-taking and its results has been given in a previous paper (HENDELBERG 1959). Here we shall deal only with some of the results which are of a more general interest.

The bottoms for the fresh-water pearl mussels

The stock-taking showed only the lower part of Pärlälven, represented in Fig. 2, to contain fresh-water pearl mussels in any greater number. The rapids which occur there, and which are marked with dotted zigzag lines in Fig. 2, are usually rich in boulders, the finer material having been washed away. Upon a considerable part of their bottom the current is so strong that the mussels can not maintain their station. A fair number of specimens

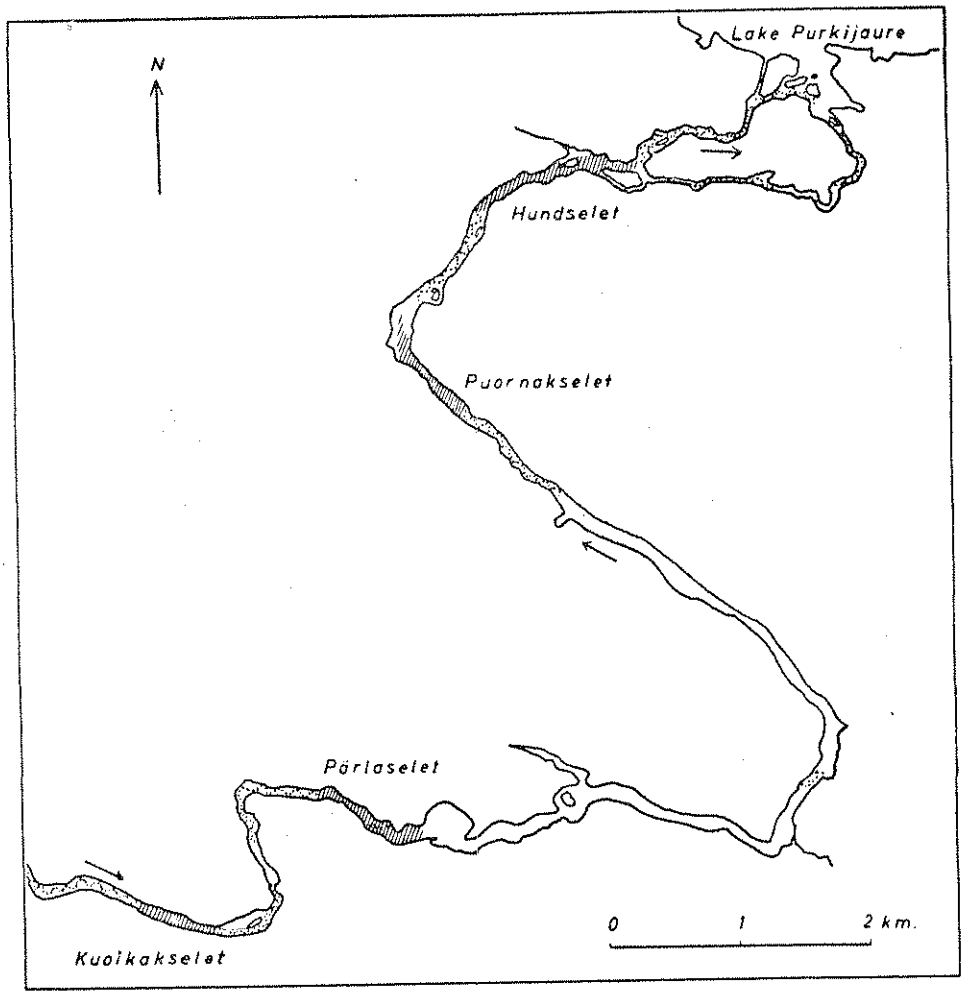

Fig. 2. The lower reaches of Pärlälven with the four regions rich in fresh-water pearl mussels hatched. Dotted zigzag lines mark rapids. Arrows indicate the direction of current.

exist, however, upon suitable bottom behind protecting stones, especially in the marginal parts of the rapids.

The vast majority of the fresh-water pearl mussels is found not in the rapids but within four relatively limited regions, marked by hatching in Fig. 2. The number of individuals in these regions has been calculated to about 2,000 in the uppermost region (Kuoikakselet), to 2,500 in the next (the upper portion of Pärlaselet), to 5,000 in the third (Puornakselet), and, finally, to about 40,000 in the lowermost region (Hundselet). Thus the wealth in mussels increases in downstream direction. There exist in the upper reaches of Pärlälven regions which appear quite suitable for the

fresh-water pearl mussel as far as the conditions of the bottom are concerned, but which are neverhteless free of pearl mussels. We thus find in these regions an upper limit of distribution at the altitude of about 360 m. that is probably climatically conditioned.

The above enumerated regions which are rich in pearl mussels are all situated immediately below greater rapids (see Fig. 2), where the water thus contains a maximum amount of oxygen. Of greater importance for the suitability of these regions for the fresh-water pearl mussels ought to be the conditions of the current and bottom. In these areas the velocity of the current is sufficient almost right across the river to prevent the deposition of sediment. Thus the bottom is as a rule rather stony and solid, and consists of sand, gravel, stones, and often also of larger boulders. In many places the current is so fast that, as in the rapids, the mussels are found only behind bigger blocks. In such places with strong current the author has in some cases observed drifting specimens with the foot streched out. Often, however, the current is weaker, and the mussels are spread over the bottom.

In the parts of Pärlälven, where the flow of the water is relatively quiet (Fig. 2, the greater part of the unmarked portions) sedimentation of silt and plant detritus often takes place. In no case has a single pearl mussel been observed upon the bottoms that had been formed in this way, and that were either bare or covered by "higher" plants. But also within these regions there occur here and there bottoms over which the water flows sufficiently fast to prevent the deposition of fine detrital material. The fresh-water pearl mussels stationed upon these bottoms form, however, only a relatively small percentage of the entire population of the river.

Depth of bottom

The distribution over different depths of bottom of the 153 fresh-water pearl mussels from the sample areas examined (July 14—Aug. 17, 1958) is accounted for in Table I and is represented diagrammatically in Fig. 3.

Table I. The distribution upon different depths of bottom of 153 fresh-water pearl mussels from sample areas in Pärlälven (July 14—Aug. 17. 1958). (Scattered specimens outside the sample areas have been encountered in depths greater than 2.0 metres.)

Depth(m.)	Number	Depth(m.)	Number	Depth(m.)	Number	Depth(m.)	Number
0.0—0.3	0	0.8	15	1.3	15	1.8	1
0.4	1	0.9	7	1.4	13	1.9	3
0.5	9	1.0	15	1.5	22	2.0	1
0.6	16	1.1	9	1.6	5	2.1—	0
0.7	5	1.2	13	1.7	3		

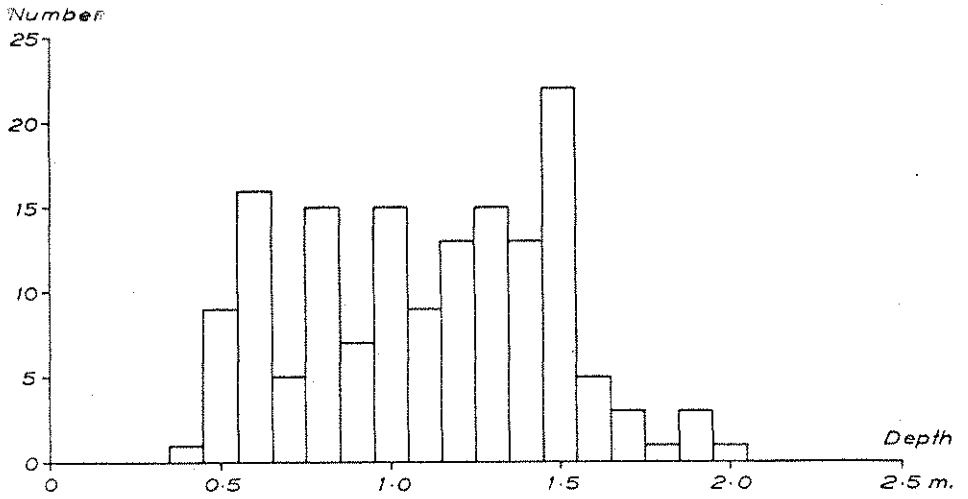

Fig. 3. Diagram for the distribution upon different depths of bottom of 153 fresh-water pearl mussels from sample areas in Pärlälven according to measurements between July 14 and Aug. 17, 1958. (Scattered specimens outside the sample areas have been encountered in depths greater than 2.0 metres.)

The circumstance that more than 90 per cent of the mussels have been encountered at depths from 0.5 to 1.5 metres ought to be connected with the fact that in places, where the river is relatively shallow from one bank to the other, its bottom is fairly hard, and the current fast enough to prevent the sedimentation of silt and detritus. Thus large areas with suitable bottom are found within these depth limits.

The sharp upper limit at the depth of 0.4—0.5 m. can be supposed to be determined by the ice conditions and perhaps also by variations in the depth of the water, since the fresh-water pearl mussel is unable to survive any longer time out of water (cf. BOYCOTT 1921). For the Kola Peninsula the corresponding upper depth limit is given as 0.4 m. (SHADIN 1938), and for Finland as 0.5 m., in extreme cases as 0.3 m. (BRANDER 1957 B).

No distinct lower limit for the distribution in vertical direction could be established. Pearl-fishing is said to have taken place in Pärlälven upon some bottoms at a depth of about 5 metres.

In connexion with the statements about the vertical distribution it has to be pointed out that the fresh-water pearl mussel is capable of shifting its station. (For more detailed information, see e.g. HENDELBERG 1959, pp. 21—22). Once it has reached a suitable spot it probably moves in fairly rare cases only, at all events in the fast current and upon the stony bottom which is the rule in Pärlälven.

Is the present localization of the fresh-water pearl mussels in Pärlälven natural?

Old reports about the population density of the fresh-water pearl mussel in Pärlälven show that the population is now much thinner, probably mainly in consequence of the pearl-fishing which has been very intensive at times (cf. S. EKMAN 1910). This can have caused a shifting of the distribution of the mussels upon different regions. It is, however, not possible that an exclusive localization to bottoms of a certain type, viz. the bottoms, where no fine sedimentary material is deposited, should be due to pearl-fishing, but must be the result of natural conditions.

An important factor of localization

As it can be seen from the foregoing, the sedimentation of silt and plant detritus is an important factor for localization. The occurrence of such fine sedimentary material prevents the occurrence of the fresh-water pearl mussel. This rule seems to apply without exception. Good examples for it are found within the above mentioned regions rich in pearl mussels. Where in these regions sedimentation takes place in certain spots, e.g. in back waters, the mussels are missing. The fresh-water pearl mussel has on the other hand been encountered in small discharging branches of the river, where the current was very weak, but where for other reasons no sedimentation took place. The descriptions derived from other localities for the fresh-water pearl mussel corroborate the observations made by the author. See for instance for Swedish localities FISCHERSTRÖM (1759, p. 143), TH. EKMAN (1905, p. 5), S. EKMAN (1910, p. 409), SUNDLER (1923, p. 45), and VALLIN (1942, p. 656). No stress has, however, been laid upon the rôle of the sedimentation. It is of course possible that the sedimentation makes the bottom unsuitable by simply depriving the mussels of a secure anchoring ground. The possibility can, however, not be excluded that it acts upon the fresh-water pearl mussels in other respects.

4. Methods for the determination of age

What age can a fresh-water pearl mussel attain?

The idea about the great age reached by the fresh-water pearl mussel is an old one. In the 1740s it was believed to be able of attaining a very great age (MALMER 1742). Two decades later it was said to be able of reaching the age of one hundered years or more (GIESSLER 1762). No information is, however, supplied in support of these statements.

Determination of age on the basis of the lines of growth of the shell

At the beginning of the twentieth century TH. EKMAN (1905) studied the age of fresh-water pearl mussels from Härjedalen in Sweden. The periostracum was removed by boiling in sodium lye, whereupon the lines of growth became clearly visible. EKMAN had good reasons to interprete these rings as annual features, and could thus determine the age of the oldest specimens as about 100 years.

As the result of an investigation in Bavaria ALTNÖDER (1926) proved the lines of growth really to be annual features. On fresh-water pearl mussels that had been marked he could establish a longitudinal growth of 0.72 mm. from Sept. 1923 to June 1924 (average 0.08 mm. per month) and 0.91 mm from June 1924 to Sept. 1924 (average 0.30 mm. per month), and that in the course of one year a new line of growth had been formed.

It is not quite easy to see the lines of growth of the shell, especially those which have been formed by the mussel at a greater age, when the longitudinal growth is very feeble. Thus EKMAN was unable by his method to state the age of the oldest specimens more closely than at "80—100 (or more) years" (1905, p. 8, author's translation). On specimens, where the periostracum had not been removed, the zone which has been formed during the winter is evident as a dark raised swelling. On such untreated specimens an age of up to about 15 years can be determined with a fair precision. According to the investigations of the author EKMAN's method has permitted at least in certain cases to determine exactly the age of individuals of up to 30—40 years.

WELLMANN's *method for the determination of age*

By counting the annual layers in the ligament WELLMANN (1938) devised a new method for the determination of age of the pearl mussel. The layers were counted in the median plane after the ligament had been cut through with a saw. Glycerine was used in order to prevent drying and the cracking resulting from it. In the ligament the annual layers, also the latest in old specimens, are very well visible. However, in old mussels the anterior portion of the ligament is partly destroyed by corrosion or rather a combination of chemical action and wear upon the bottom. From his experience WELLMANN believed himself able to estimate the number of annual layers that had been destroyed in this way. "Bei einiger Erfahrung ist es jedoch möglich, einigermassen abzuschätzen, wieviel Jahreslamellen zerstört worden sind" (WELLMANN 1938 p. 548). But no information is supplied about what part of the given age is based upon estimation. On account of the possible errors involved in this estimation WELLMANN has excluded from his results values obtained from specimens with strongly corroded umbo.

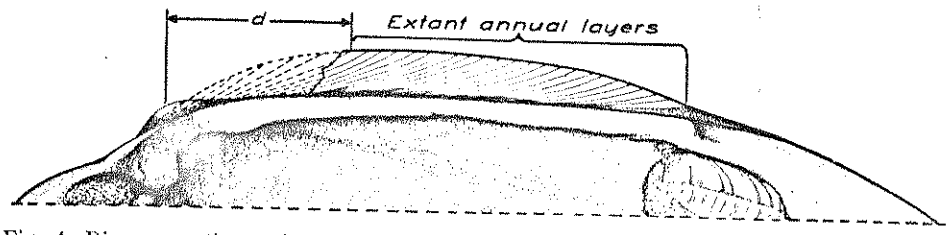

Fig. 4. Diagrammatic section through the ligament of a fresh-water pearl mussel. Step one in the determination of the age (see the text) gives in this case 23 years. In step two the distance d is measured, whereupon the number of years corresponding to this distance is read off in the diagram in Fig. 5.

Method for the determination of age applied in the investigation in Pärlälven

As mentioned above the previously utilized methods for the determination of age of the fresh-water pearl mussel had some defects, TH. EKMAN's by supplying very unreliable results for specimens of greater age, WELLMANN's by the fact that the influence of corrosion of the umbo had not been worked out.

In determining the age of fresh-water pearl mussels from Pärlälven the author has, like WELLMANN, based himself upon the annual layers in the ligament. The influence of corrosion of the umbo could be calculated after a study of the growth of the ligament. The method elaborated for determination of age can be divided into three steps:

1) The number of extant annual layers in the ligament (see Fig. 4) is counted.

2) The distance from the umbo to the point where the anteriormost extant limit between two annual layers reaches the upper margin of the ligament (the distance d in Fig. 4) is measured, and the corresponding number of years is read off on a diagram about the growth of the ligament (Fig. 5).

3) The age of the fresh-water pearl mussels is obtained by the addition of the values derived from the first and the second step.

With this method the author believes himself able fairly exactly to calculate the age also of old specimens. Errors can admittedly occur with regard to the minor portion of the age as calculated according to step two. These ought, however, only in exceptional cases to surpass 3 per cent of the total age of the mussel (see below).

The anual layers are counted in a sagittal section through the ligament. The cutting-through of it when once dried has proved difficult. A simple method which has been followed with most of the examined objects consisted in carefully forcing the dry valves apart. With a $\times 20$ magnification it is very easy to count the annual layers in the ligament, especially along

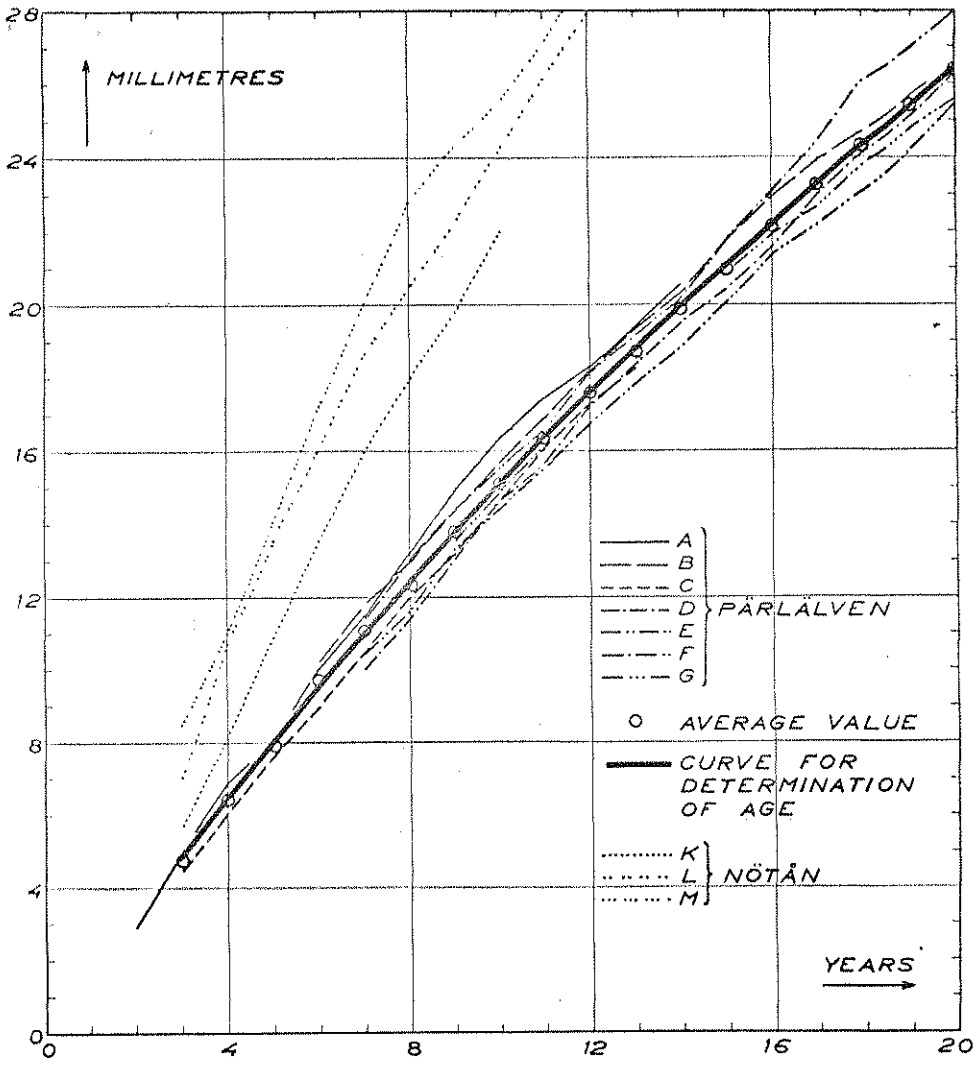

Fig. 5. Diagram for the growth of the ligament.

its upper border, where they are fairly thick (see Fig. 4). Like WELLMANN the author has checked that the number of the layers in the ligament actually coincides with the number of annual lines in the shell (see below).

In the second step of the determination of age the number of annual layers is calculated that have been removed from the ligament by corrosion of the umbo. For this purpose a diagram (Fig. 5) is used which has been constructed in the following way.

For seven out of the 28 specimens kept from the collection in Pärlälven the age could be determined with the help of the lines of growth of the

shell. In the two youngest specimens (A and C), 14 and 13 year old, respectively, the lines of growth could be counted directly upon the untreated shells. The remaining five were according to TH. EKMAN's method boiled in sodium lye until the periostracum had been loosened. The lines of growth of the shell were then counted under 20 times magnification. A control was obtained by studying upon surfaces of fractures the periostracum lamellae mentioned by WELLMANN (1938 p. 548) which at the border of the annual rings continue into the prisma layer. Of the specimens that have been examined in this way two (B and D) were found to be 33 years, two (E and G) 34 years, and one (F) 37 years old. Once the age of the mussel was known, the annual layers could be numbered by counting backwards, i.e. beginning from the latest layer. The distance from umbo to the hindmost point of each annual layer was measured, and entered into the diagram (Fig. 5) against the corresponding number of years. For every year the mean value of these lengths was calculated. In the diagram these mean values have been denoted with circles. The curve obtained upon the basis of these values has then been used in step two of the determination of the age. The measuring of distance d (see Fig. 4) thus always starts from the umbo. This, like the oldest part of the ligament, is often corroded, but in this case its position can easily be determined with the help of the convexity of the shell and of the umbocentrically situated lines of growth.

In the calculation of the age by means of the lines of growth of the shell the line corresponding to a length of roughly 6—7 mm. (see Table III) has been assumed as formed at the end of the year after the year witnessing the glochidium stage. At this time the mussel has been considered to be one year old, as the age has been indicated according to the practice of TH. EKMAN and WELLMANN. For the sake of comparison it can be mentioned that TH. EKMAN (1905, p. 7) has found the corresponding length in freshwater pearl mussels from Härjedalen to be about 6 mm., and that WELLMANN (1938, p. 550) has found this length in specimens from the Lüneburg Heath to be about 7.5 mm. The diagram in Fig. 5 also counts the year in which the mussel is assumed to have passed its glochidium stage. In the statements of the age according to the above-mentioned practice one year had consequently to be deducted from the value read from Fig. 5.

The magnitude of the error which can arise from step two has been calculated in the following way. An examination by TH. EKMAN (1905) based upon the growth lines of the shell shows that, at least up to the age of 15 years, the variations of age amount for a given length to no more than about 20 per cent. Provided that this were of universal application and that the diagram in Fig. 5 were based upon a sufficiently great number of observations, it would be possible to determine the part of the age obtained by step two with an error of ± 10 %, whereas we now have to calculate with up to ± 20 %. The number of years obtained in step two represents only

fraction of the entire age of the mussel, as a rule less than 15 On this account the error in the determination of age by the method the author would only exceptionally amount to more than 20 % i.e. 3 %. If the diagram for step two were based upon a sufficiently aber of mussels, this figure could be brought close to 1.5 % (10 % or to a still lower figure, since in the actual case the corrosion abo is relatively smaller.

above we have dealt with the reliability of the method for the ation of age used by the author in the examination of fresh-water ssels coming from the same region as those which have formed the the diagram in Fig. 5. Populations from different localities can ntially different rates of growth. In illustration of this fact have ered into Fig. 5 the values obtained for three fresh-water pearl from one of the southernmost localities in Sweden, viz. Nötån in (see Fig. 1). The length of the ligament of these mussels as well total length were considerably greater than the corresponding ns in mussels of the same age from Pärlälven. Some additional s obtained from Nötån likewise show roughly the same strong s the three accounted for in Fig. 5. For obtaining the most correct ssible in the determination of age of a number of fresh-water pearl from a given population it is thus necessary to establish a diagram as to that in Fig. 5 upon the basis of young mussels from that very

1. Growth of the ligament in seven fresh-water pearl mussels from n (A—G) and in three from Nötån (K—M) according to values for the distance d (see Fig. 4), expressed in millimeters, after the corresponding year.

	A	B	C	D	E	F	G	K	L	M
...	2.9	—	—	—	—	—	—	—	—	—
...	5.1	—	4.5	—	—	—	—	5.7	7.1	8.5
...	6.9	—	6.1	—	—	—	—	8.2	10.8	11.0
...	8.1	—	7.7	—	—	—	—	10.9	13.6	14.1
...	10.0	10.2	9.0	—	—	—	—	13.6	16.1	17.2
...	11.5	11.8	10.5	10.0	10.5	11.4	—	16.0	18.7	20.0
...	13.2	13.0	12.0	11.4	11.7	13.1	12.2	18.0	20.6	22.8
...	15.0	14.4	13.2	13.1	13.3	14.6	13.6	19.8	22.2	24.3
...	16.4	15.7	14.7	14.7	14.5	15.6	14.8	22.0	24.2	25.5
...	17.5	16.9	16.2	15.7	15.6	16.6	16.2	—	26.2	27.1
...	18.4	18.2	17.3	17.2	16.8	18.2	17.4	—	27.9	28.9
...	19.5	19.5	18.3	18.3	17.9	19.2	18.9	—	29.1	30.2
...	20.6	20.3	—	19.5	18.9	20.1	20.0	—	30.2	31.4
...	—	21.8	—	20.4	20.1	21.8	20.9	—	31.5	32.7
...	—	22.9	—	21.6	21.4	23.0	21.9	—	—	—
...	—	23.9	—	23.0	22.2	24.4	22.7	—	—	—
...	—	24.7	—	24.2	23.1	26.1	23.8	—	—	—
...	—	25.7	—	25.2	24.2	27.0	24.8	—	—	—
...	—	26.5	—	26.3	25.4	28.0	25.6	—	—	—

Table III. The total length at different ages according to the annual lines growth of the shell in seven fresh-water pearl mussels from Pärlälven (A and in three from Nötån (K—M), in millimetres.

Annual line	A	B	C	D	E	F	G	K	L
1	6.0	—	—	6.5	7.0	—	—	13.0	—
2	11.5	—	12.0	14.5	14.0	—	—	21.5	19.0
3	17.0	16.0	18.0	18.0	20.0	20.5	19.0	29.0	28.0
4	24.5	21.0	24.0	22.0	23.0	26.5	24.5	38.0	37.5
5	29.5	26.0	29.0	25.5	27.0	29.5	28.0	45.5	42.5
6	33.5	31.0	33.0	29.5	33.0	34.5	34.0	52.5	52.0
7	40.5	36.5	39.0	34.0	36.5	40.0	38.5	56.0	58.5
8	44.0	40.5	42.5	39.0	42.0	45.0	43.5	60.0	66.0
9	49.5	45.0	46.0	43.0	44.0	49.5	47.5	67.5	70.5
10	53.0	49.5	50.5	48.5	49.0	53.0	50.5	—	73.5

locality. For checking the applicability of the diagram to a mussel that to be examined the length corresponding to, e.g., the tenth line of grow of the shell can be measured or, if the corrosion of the umbo is great, t density of the lines of growth of the shell is determined, for instance counting the zones of growth between two and five centimetres behind umbo, and comparison can be made with the mussels upon which diagram for the growth of the ligament has been based.

The figures which have formed the base of Fig. 5 are given in Table

5. The growth of the individual and the composition of the population

Results of the determination of age

The age of 28 fresh-water pearl mussels collected in Pärlälven has b examined according to the method accounted for above. The results be seen in Table IV in which the mussels have been arranged accord to the calculated age. In addition to the age the table contains the sex, wh ever this has been determined (see below), together with length and we of shell.

The mussels had been obtained from the following localities (see Fig Kuoikakselet (Nos. 117, 120, 122, and 124), Pärlaselet (Nos. 7 and Puornakselet (Nos. 27—43), Hundselet (Nos. 67, 110, and 111), and charging branches of the river (Nos. 49 and 50). Thus the majority, 17, c from Puornakselet, where upon three sample areas all the specimens been collected. The remaining 11 were taken at random.

The specimen that proved to be the oldest one in the investigatio Pärlälven had a ligament with 108 annual layers. The ligament was dest ed to a point 12 mm. behind the umbo, corresponding according to the

Results of the determination of age of 28 fresh-water pearl mussels (alven. The letters after the number of the mussels indicate the specimens forming the base of the diagram in Fig. 5.

	Sex	Length (mm.)	Weight of shell (g.)	Distance (mm.)	Years corresp. to distance d	Age (years)
	♂	63	7.25	4.5	*3*	13
	—	70	9.00	2.9	*2*	14
	—	99	29.51	11.0	7	30
	♂♀	93	30.13	11.0	7	31
	♂♀	100	31.82	10.0	*7*	33
	♂♀	101	32.25	10.2	*6*	33
	♂♀	94	30.92	10.5	7	34
	—	98	28.32	12.2	*8*	34
	♂	105	39.34	8.5	5	34
	♂	74	12.89	12.5	(8)	(36)
	—	106	42.58	11.4	7	37
	♂	100	35.65	12.0	8	40
	♂♀	101	38.35	11.5	7	42
	♂♀	112	43.54	9.5	6	42
	♂♀	108	57.29	11.0	7	48
	♂♀	110	49.16	8.5	5	50
	♂♀	123	66.31	11.5	7	51
	♂♀	101	50.96	12.0	8	52
	♂♀	113	55.79	9.0	6	52
	♂	76	15.67	11.0	(9)	(55)
	—	136	105.9	20.0	14	71
	—	124	86.80	22.0	16	80
	♂	123	85.87	25.0	19	83
	♂	116	72.40	21.0	15	88
	♂	123	86.71	17.0	11	90
	♂	125	93.00	25.5	19	91
	—	134	129.0	27.0	21	105
	—	145	130.7	12.0	8	116

Fig. 5, i.e. on comparison with yong mussels, to a period of 8 years. e age of the mussel is 108+8=116 years. According to the above s the possible error is at most 20 per cent of 8 years, i.e. less than at of the whole age.

of the mussels (Nos. 38 and 29), according to Table IV 36 and 55 l, respectively, are of exceptionally small size, real dwarfs. Already glance reveals that they are not young specimens, both exhibiting eriostracum and heavy corrosion of the umbo. These mussels are somewhat older than stated here, the part of age obtained accordp two (see above) of the age determination being too low since cimens evidently have been stunted right from the beginning.

age determination it has been noted that secondary, feeble layers of winter type in the summer layers of the ligament (cf. WELL-38, p. 546) occur only to a small extent in the specimens from . They are, however, well marked in the specimens obtained from southern Sweden.

Length — age ratio

Already the preceding chapter ought to have made it clear that it is not possible to base a determination of age upon the total length of the fresh-water pearl mussel except perhaps, when very young individuals are concerned. This is due to the fact that the individual variation in length between specimens of the same age and from the same locality is great in relation to the longitudinal growth during the later life of the mussel. Compare, e.g., WELLMANN 1938, Fig. 10 (p. 551). According to this illustration the longitudinal variation is greater for specimens of about 30 years than the difference in average length between specimens of 25 and 60 years, respectively. It can nevertheless be of interest to study information about the average length at a certain age in populations from different regions.

On fresh-water pearl mussels from Pärlälven the first line of growth of the shell has been found to correspond to a length of 0.6—0.7 cm. and the tenth to about 5.0 cm. (7 specimens between 4.8 and 5.3 cm.). According to TH. EKMAN (1905), who based his investigations in Härjedalen (Sweden) upon the lines of growth of the shell, the mussels should have been 0.5—0.7 cm. long at the age of one year and about 4.6 cm. at the age of 10 years (11 specimens between 4.25 and 4.9 cm). (This difference between the populations from Pärlälven and Ljusnan in Härjedalen is perhaps not a real one, but may possibly depend on EKMAN's discerning a line of growth between the two lines which by the author have been interpreted as the first and the second — compare Table III with the list given by TH. EKMAN (1905) on page 7.) According to German investigations (ALTNÖDER 1926, WELLMANN 1938, BOETTGER 1954) the average length of specimens of ten years is about 6 centimetres. A considerably stronger growth has been observed for 5 specimens obtained from Nötån (see Fig. 1) in southern Sweden. These had already with their sixth line of growth attained lengths between 5 and 6 centimetres (cf. Table III). It is, however, not known to the author, whether or not these specimens are representative for the population in question.

For old specimens the length — age ratio varies strongly, and the given average values are few and as a rule uncertain. However, it can be mentioned that the German investigations have shown the age of 40 years to correspond to a length of about 10 cm, which is about the same as the value obtained in Pärlälven; see Table IV.

Relation between weight of shell and age

While the longitudinal growth slows down with increasing age, the increase in the weight of the shell takes place at a roughly uniform rate throughout the major part of the life of the fresh-water pearl mussel. This has been demonstrated by WELLMANN (1938) in the course of his investi-

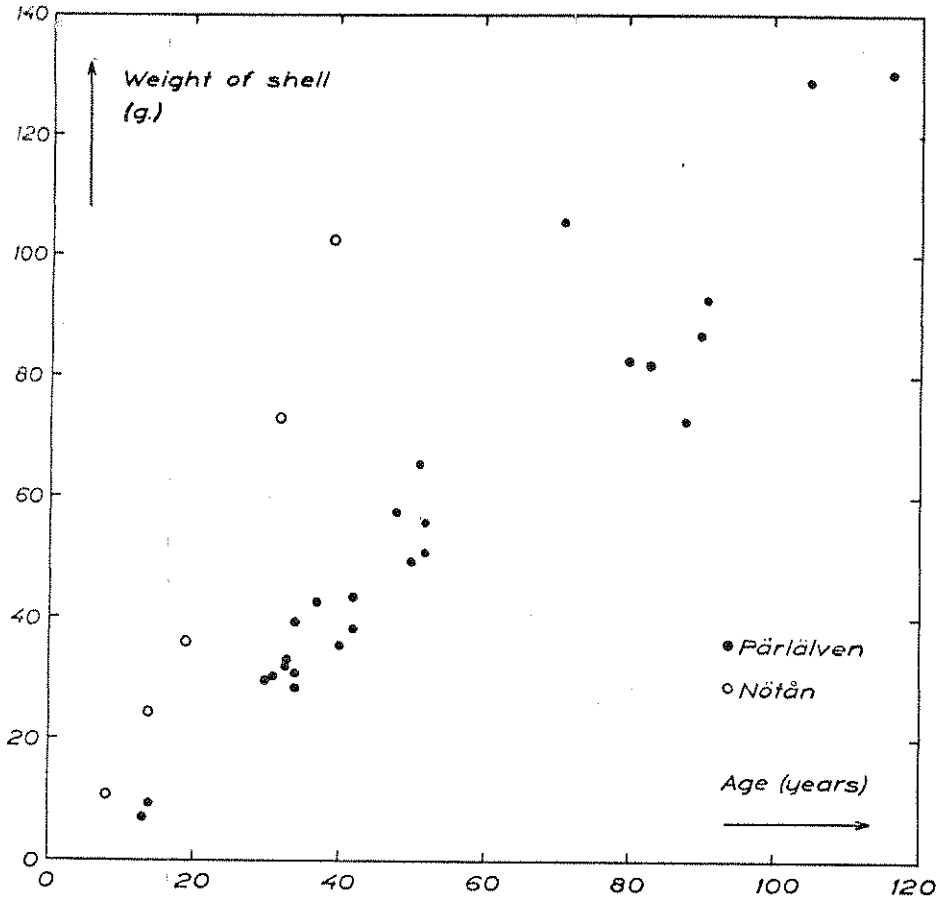

Fig. 6. Diagram representing the relation between age and weight of shell for 26 fresh-water pearl mussels from Pärlälven. For the sake of comparison the five specimens obtained from Nötån in southern Sweden (see the text) have been entered into the diagram.

gations upon the Lüneburg Heath, and has been corroborated by the investigations in Pärlälven; see Fig. 6 which is based upon the figures in Table IV. (For different reasons, amongst others the uncertain determination of the age, the two stunted shells have not been included into the illustration.)

For the majority of the specimens from Pärlälven the average annual increase falls between 0.85 and 1.4 g. The shells of the two oldest (116 and 105 years) specimens examined weighed 130.7 and 129.0 g., respectively, corresponding to an average annual increase of 1.1(3) and 1.2(3) g., respectively.

For the comparison with populations from other localities it can be mentioned that WELLMANN found the mean value of the average annual growth in the population on the Lüneburg Heath to about 1.2 g. A much stronger

growth of the shell, the average increase amounting to about 2 g. *per an* is exhibited by the specimens obtained from Nötån in southern Swe For three of these five specimens the lines of growth of the shell perm a determination of the age as 9, 14, and 19 years, respectively. The co ponding weight of the shell was 9.39, 24.17, and 36.12 g. The remai two weighed 73.23 and 103.4 g., respectively. Their ligament containe and 33 annual layers, respectively, and the distance d (see Fig. 4) 17 mm. in either of them. This permits, according to the average values K, L and M in Fig. 5, the calculation of their age at about 32 and 39 y respectively, which figures can be given with an exactitude of about years. In spite of the small number of specimens and in spite of the that we can not tell, whether or not they are representative for the reg where they have been collected, the great difference between their gro and the growth of the specimens from Pärlälven has nevertheless indu me to set them out in Fig. 6.

Length — height ratio

Length and height have been measured on 112 fresh-water pearl mus from Pärlälven. (For the definition of these dimensions see, e.g., EA 1948, Fig. 1.) The measurements show that during the growth of the mus the length increases relatively more than the height, and that at a giv length there occur great individual variations in the length — height ra see Fig. 7 and compare WELLMANN 1938 pp. 556—561. In this connexi the influence of the environment upon the shape of the shell is of intere According to several authors the shell becomes relatively lower, i.e. mo elongated, if the animals are stationed in a faster current (cf. ALTNÖD 1926). Others, e.g. WELLMANN, have not found any significant differen between different localities with different speed of current in one and t same brook. A distinct difference was, however, observed between two di ferent brooks, viz. Lachte and Lutter, in spite of the fact that they join their lower courses, and that the chemical composition of the water is pret much the same. The question about the cause of the difference in the lengt height ratio has therefore to be left open for the time being, since neith the author has found any pronounced tendencies in any given direction It might, however, be mentioned that pearl fishers along the Pärlälven appl the term "rapid shells" to elongated shells with a concave ventral margi

Determination and distribution of sexes

For all 17 specimens from three sample areas in Puornakselet the ag has been determined (see above). For them and, in addition, three othe specimens also the sex has been determined. According to former inform

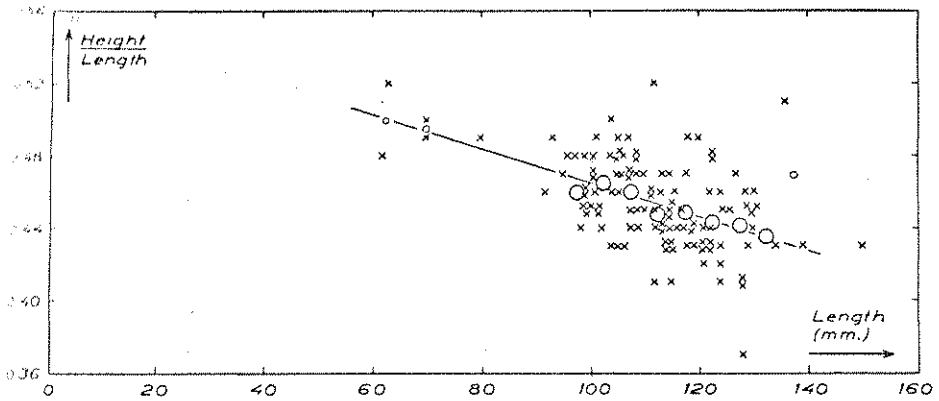

Fig. 7. Growth diagram based upon the measurements of height and length taken from 112 fresh-water pearl mussels from Pärlälven. Within each interval of 5 mm. of length the average value of the height—length ratio has been marked with a small circle for 2—4 mussels, and with a large circle for greater numbers.

tion the sexes do not differ in the morphology of the shell, at least not to such an extent that the differences could serve for the determination of the sex. For this reason eosin-haematoxylin-stained sections through the gonads were examined under the microscope. Of the 20 specimens examined 9 proved to be females, and 11 males. Thus no hermaphrodites were found, compare WELLMANN (1938, p. 544) who found one out of eighty examined specimens to be a hermaphrodite.

From the material examined by the author it has not been possible to establish any significant difference between the growth of the shell of females and males, cf. Table IV.

Composition of the population of the fresh-water pearl mussel in Pärlälven

Since it is not possible to determine the age of the fresh-water pearl mussels or at least of the older specimens by an examination of the living specimen, the author has used the length of the mussels as a base for a rough analysis of the composition of the population in Pärlälven as it can be deduced from the 112 specimens from the stock-taking areas that had their length measured. On account of the fact that conclusions about possibly existing differences between the populations upon different localities would be based upon an insufficient number of specimens, the author has accounted for the whole material of the investigation in one single table, Table V. This table has been represented in the shape of a diagram in Fig. 8. It can be seen that 10 specimens are shorter than 96 mm., the length which

Table V. The distribution of length in 112 fresh-water pearl mussels from Pärlälven.

Length (mm.)	Number	Length (mm.)	Number	Length (mm.)	Number
—60	0	91— 95	3	126—130	6
61—65	2	96—100	9	131—135	6
66—70	2	101—105	16	136—140	2
71—75	1	106—110	16	141—145	1
76—80	2	111—115	18	146—150	1
81—85	0	116—120	13	151—	0
86—90	0	121—125	14		

according to the foregoing r o u g h l y corresponds to the age of 30 years. Among these exist the two stunted specimens which have been accounted for above. (As their age, at least 36 and 55 years, respectively, is much greather than what could be deduced from their lengths they have not been included in the diagram in Fig. 8.) Thus only about 7 per cent of the sample should be younger than 25—30 years.

According to MÜLLER (1957) no specimens shorter than 2 cm should have been observed. It has, however, been reported that 28 specimens no longer than 15 mm. have been found upon the sandy bottom of the river Ibesibetu in Japan (KOBA 1933), and 4 specimens shorter than 20 mm., the shortest 9.5 mm. long, are said to have been encountered in River Conway upon the British Isles (JACKSON 1925). Since it thus is possible to discover even specimens of this small size, and since TH. EKMAN (1905, p. 6) has found that also the small specimens occur upon the same localities as the adults, and that they very often, perhaps always, live just as visible, the observed conditions m i g h t be indicative of a rather feeble rejuvenescence of the popu-

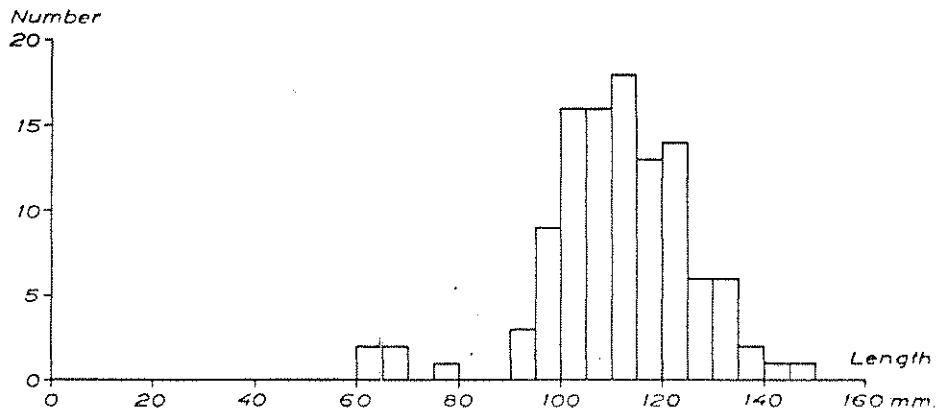

Fig. 8. The distribution in length in 110 fresh-water pearl mussels from Pärlälven. (From this diagram the two stunted specimens mentioned in the text have been excluded.)

in Pärlälven. In this case this can be supposed to depend to a large upon the thinning-out of the population resulting from pearl-fishing, on of course derive in part also from other causes like a decrease in number of fishes suitable for the parasitism of the glochidia or the of the floating of timber (cf. LUNDGREN 1935).

6. Summary

1) The fresh-water pearl mussel, *Margaritifera margaritifera* (L.), is hol- and separated nowadays into a number of more or less isolated rrences. Owing to pearl-fishing and the regulation of the watercourses s become much scarcer, and has entirely disappeared from many pla- (p. 149, 150).

2) A map about the natural distribution of the fresh-water pearl mussel Sweden has been compiled by the author (p. 150 and Fig. 1).

3) Attention is called to the close agreement between this distribution the extension of soils and rocks poor in lime (p. 150).

4) At the altitude of about 360 m. there has been established in Pärlälven probably climatically conditioned upper limit of distribution (p. 154).

5) The bottoms for the fresh-water pearl mussel in Pärlälven are describ- The importance of the sedimentation for the localization is pointed out. places, where sedimentation of fine detrital material occurs, no specimens ve been encountered (p. 152; 156).

6) The distribution in Pärlälven of the fresh-water pearl mussel upon fferent depths is accounted for. More than 90 per cent of the mussels have en encountered between the depths of 0.5 and 1.5 metres (p. 154).

7) An account is given of the method that has been used for the deter- nation of age of the fresh-water pearl mussels in Pärlälven. The method based upon the existence of annual layers in the ligament. Since the author s constructed a diagram of the ligament growth (Fig. 5) which has made possible to calculate the number of annual layers destroyed by corrosion the umbonal region, this method has been made very certain, the error lso for old specimens being below 3 per cent of the total age (p. 158).

8) The results of the determination of age are accounted for. The age the oldest specimen has been calculated to 110 (±2) years (p. 162).

9) While the longitudinal growth slows down with increasing age, the ncrease of the weight of the shell is roughly uniform during the greater part of the life of the fresh-water pearl mussel. In Pärlälven the mean value the annual increase is about 1.2 g. Comparisons are made with specimens btained from a river in southern Sweden. (P. 164).

10) The length-height ratio which decreases with the increasing age of the fresh-water pearl mussel, and which by some authors is believed to de-

pend upon the strength of the current has been determined for 112 specimens from Pärlälven. The result is accounted for in Fig. 7. (P. 166.)

11) In 20 specimens from Pärlälven the gonads have been microscopically examined. Of these nine proved to be females, eleven males (p. 166).

12) The composition of the population of the fresh-water pearl mussel in Pärlälven is accounted for. According to the length only eight of the 112 encountered specimens (7 per cent) were younger than about 30 years. This fact might point to a relatively feeble rejuvenescence of the population. (P. 167)

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... which were of importance almost exclusively for the knowledge about the distri- ... of the fresh-water pearl mussel, e.g. a great number of the papers that had been ... the elaboration of the map over the distribution in Sweden, have not been included ... above list.