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Distribution, population dynamics and production of Mysis relicta (Lovén) in southern Finland

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In Pääjärvi, an oligotrophic lake in southern Finland, *Mysis relicta* (Lovén) has a life span of 1 or 2 years. Young liberated in late April and early May attain maturity during the first summer and autumn and start breeding in early December, whilst those liberated in late May and June remain immature till the next spring and then breed earlier than the offspring of the former group. The latter group start to release their young in late April, offspring of the former group not until May—June. Thus the two groups show a regular alternation of early and late breeding.

Most of the population lives within the 20 m isobath. A small proportion migrate to shallower parts after the autumn circulation. During the summer the mysids are almost totally pelagic, but in the autumn they shift to a benthic life.

The population reaches its maximum size (about 300—400 million individuals) in early July. In winter there are only 20—40 million mysids in the lake.

Biomass (B) is maximal in September—October and minimal in spring at the time when the embryos are liberated. Great annual variation was observed, 200—600 kg ash-free dry weight (AFDW).

The growth of *M. relicta* seems to fit the logistic model. It ceases during the winter and begins again in May. The mysids attain a mean weight of about 4.0 mg (AFDW) in the first year and 8.0 mg in the second.

Annual production (P) varies from about 500 kg to 800 kg (AFDW). The P/B ratio varies between 3.0 and 3.8, depending on the year and the method of calculating production.

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1. Introduction

Mysis relicta Lovén, the only freshwater species of this genus, is generally accepted to have originated from the marine *M. oculata* (RICKER 1959) during the last glaciation. *M. relicta* is common in the deeper and therefore cold oligotrophic lakes of Scandinavia, but is also found in Britain, Germany and North America TATTERSALL & TATTERSALL 1951, SEGERSTRÅLE 1956, 1957, 1966, HOLMQUIST 1959). SAYRE & STOUT (1965) reported it from some eutrophic lakes in USA, and in Finland I have observed it even in slightly polluted waters.

During the last 20 years *M. relicta* has been successfully introduced into several lakes and reservoirs to improve the food supply of fish (e.g. SPARROW *et al.* 1964, SCHUMACHER 1966, STRINGER 1967, GOSHO 1975). In Scandinavia this possibility has been studied by FÜRST (1972a, 1972c) and GRIMÅS *et al.* (1972).

The papers published in Finland deal mainly with the distribution of this species, although they include some ecological information (VALLE 1927, 1930, SEGERSTRÅLE 1956, SÄRKKÄ 1976).

There has been practically no quantitative work on *M. relicta*. The present study forms part of an ecological investigation of three large crustaceans occurring in Pääjärvi.

2. Study area

The mesohumic and oligotrophic Pääjärvi (61° 04'N 25° 05'E) is one of the deepest lakes in Finland (max. 87 m), with an area of 13.5

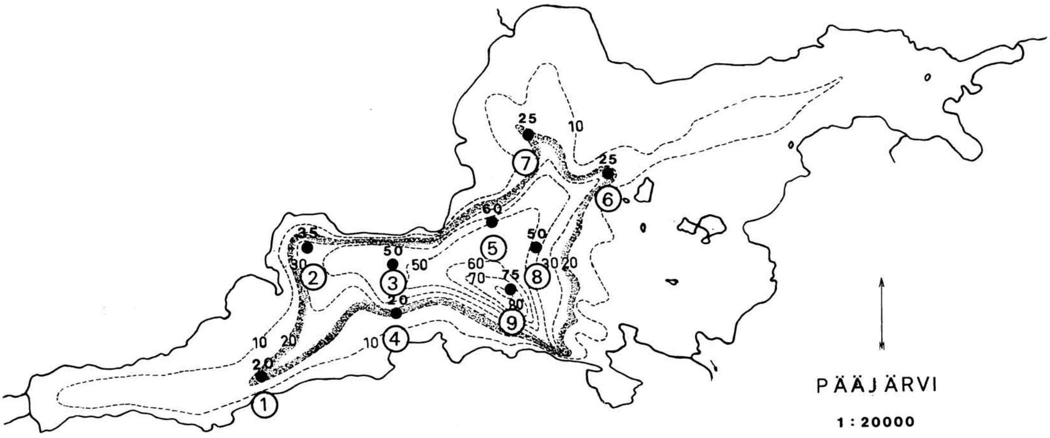

Fig. 1. Pääjärvi. Black circles mark the sampling sites. The depths are given above the circles and the numbers of the stations below. The shaded belt inside the 20 m isobath limits the area where *Mysis relicta* normally lives in the lake.

km² and a volume of c. 206 million m³. The lake is normally ice-covered from mid-December to early May. Fig. 1 shows the study area and Fig. 3 the annual temperature curves. Details of the features of the lake have been published by NISSINEN (1961), GRANBERG (1970), RUUHIJÄRVI (1974), ILMAVIRTA & KOTIMAA (1974) and ELOMAA (1976, 1977).

The sites of the sampling stations are seen in Fig. 1. The depths of the stations are as follows:

Station	Depth	Station	Depth
1,4	20 m	3,8	50 m
6,7	25	5	60
2	35	9	75

3. Material and methods

A. Material

The material was collected in 1973, 1974, 1975 and 1976. The vertical and horizontal distribution of *M. relicta* was surveyed and the sampling methods developed in 1973. The material of this study comprises c. 15 000 individuals, 12 000 of them collected during the quantitative study begun in 1974. The remaining samples were taken in 1973 and 1974 to study the vertical and horizontal distribution and to estimate growth before the quantitative study was begun.

B. Sampling procedure

Benthic sledges of different kinds were tried (e.g. REYNOLDS & DEGRAEVE 1972), and also the Clarke-Bumpus sampler (BEETON 1960) and vertical net hauls (e.g. CARPENTER *et al.* 1973) used earlier for sampling *Mysis relicta*. In summer the *Mysis* population is almost entirely pelagic, so the benthic sledge can be used only for qualitative sampling. In winter, when the population is benthic, the ice cover hampers sampling with the sledge. The Clarke-Bumpus sampler was very useful in summer, but similarly could not be used in winter. Even in summer it could not be used below 50 m because the bottom morphology prevented long hauls. Therefore the Clarke-Bumpus sampler was used only for preliminary observations on the vertical distribution of mysids and for brief comparisons with the routine sampler. The Clarke-Bumpus sampler used was a modified version of the original one equipped with a pair of nets and with an electronic current meter. The sampling depth was checked from the boat with an echo sounder.

Quantitative samples were taken with a simple net 0.5 m² in diameter. The mesh was usually 0.5 mm; in spring, when some of the mysids were small, it was 0.1 mm. No conical part was placed in the front of the net. The net was lowered to the bottom and allowed to stay there for a few minutes to let the animals redistribute normally. It was then pulled to the surface at a speed of about 0.5 m/s. When the net reached the surface the pressure wave caused was not, apparently, very strong. It was impossible, however, to estimate the number of mysids escaping from the sampler.

C. Sample design

In February and March 1974, 120 random samples were taken below the 5 m isobath level to study the horizontal distribution of the mysids. Since only about 1.5 % of the population lived above the 20 m isobath during this period, the sampling stations were located within this contour line. The shallower parts of the lake were also surveyed a few times. The study area sampled at random was divided into the following strata:

Strata	Area km^2	No. of samples per period
20—25	0.70	2—6
25—35	0.75	1—3
35—50	0.48	2—6
50—60	0.20	1—2
60—87	0.05	6—9

The size of the mysid population during each sampling period was calculated by the standard methods for stratified random sampling (ELLIOT 1971, SNEDECOR & COCHRAN 1972). The following formulae were used to calculate the population size and the sampling error:

$$\bar{x} = \frac{n_1\bar{x}_1 + n_2\bar{x}_2 + \ldots n_k\bar{x}_k}{n},$$

where $\bar{x}$ is the mean number of animals per m^2 in the study area, $\bar{x}_1$, $\bar{x}_2$, ...$\bar{x}_k$ are the arithmetic means for the areas of the different strata and n_1, n_2, ...n_k the relative weights attached to each stratum.

$$s\ (\bar{y}_{st}) = \sqrt{(1/n\ n_1 s_1^2 + n_2 s_2^2 + \ldots n_k s_k^2)},$$

where s_1^2, s_2^2, ...s_k^2 are the variances of the different strata and $s\ (\bar{y}_{st})$ the standard error of the mean. If only one sample was taken per stratum, then the variance was obtained from Taylor's power law fitted to the variance-to-mean ratio of the whole study.

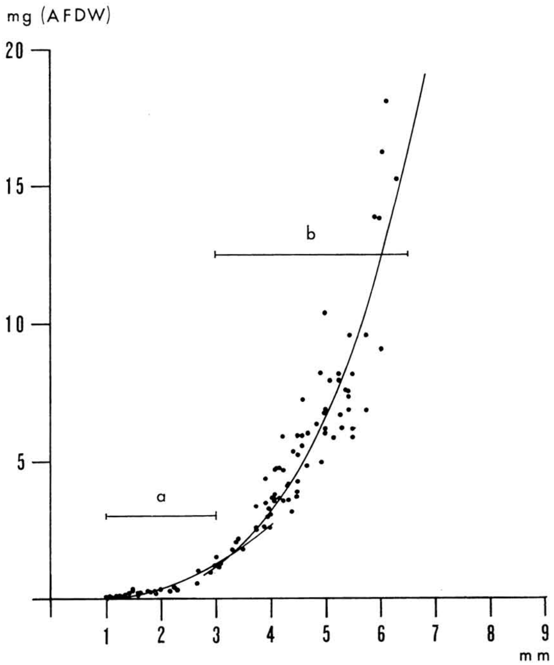

Fig. 2. Relation of length of carapace (from rostrum to caudal groove) to ash-free dry weight (AFDW) in *Mysis relicta*. The power function *a* (see text) was used to determine the weights at carapace lengths below 3 mm and the function *b* above 3 mm.

D. Determination of biomass

The mysids were taken to the laboratory alive and studied immediately under a stereomicroscope. Body length, the dimension used by most authors, was difficult to measure, because the mysids flexed their tails. Instead, the length was measured from the tip of the rostrum to the groove in the caudal edge of the carapace. For the dry weight the animals, when measured, were placed in small tared cups (about 5 mg) of thin aluminium foil and dried at 60 °C for 12 h. The ash-free dry weight (AFDW) was obtained by ignition of the samples in a muffle oven at 505 °C for 4—5 h. A Cahn Automatic Electrobalance (accurate to within 0.001 mg) was used.

Two power functions were fitted to the length-weight data. The first function was fitted to the animals with a carapace <3 mm (*a* in Fig. 2), the second to those with a carapace > 3 mm (*b* in Fig. 2). The power functions are characterized in the following tabulation:

$$y = ax^b$$

	a	*b*	*r*	n
< 3 mm	0.0532	2.8357	0.9614	40
> 3 mm	0.0265	3.4207	0.9620	74

The fit does not seem to be good for animals weighing more than 10 mg (AFDW), but this does not affect the results, because the number of such animals was always negligible.

The sexes were separated after the fifth pleopods of the males were distinguishable. By then the mysids had attained weights of 1.8—2.0 mg (AFDW) and carapace lengths of 3—4 mm (Fig. 11). Animals in the same size class without fifth pleopods were classified as females.

During the breeding season the brood pouches of some females were opened, the embryos and the females weighed, and the embryos counted to estimate fecundity.

4. Results

A. Life cycle

In Pääjärvi *Mysis relicta* is a strict winter breeder. JUDAY & BIRGE (1927) observed egg-bearing females during July-August, but they were more common in October. FÜRST (1972a) has described summer breeding in some Swedish lakes.

The first sperm-carrying males were seen in late September. Copulation probably starts in

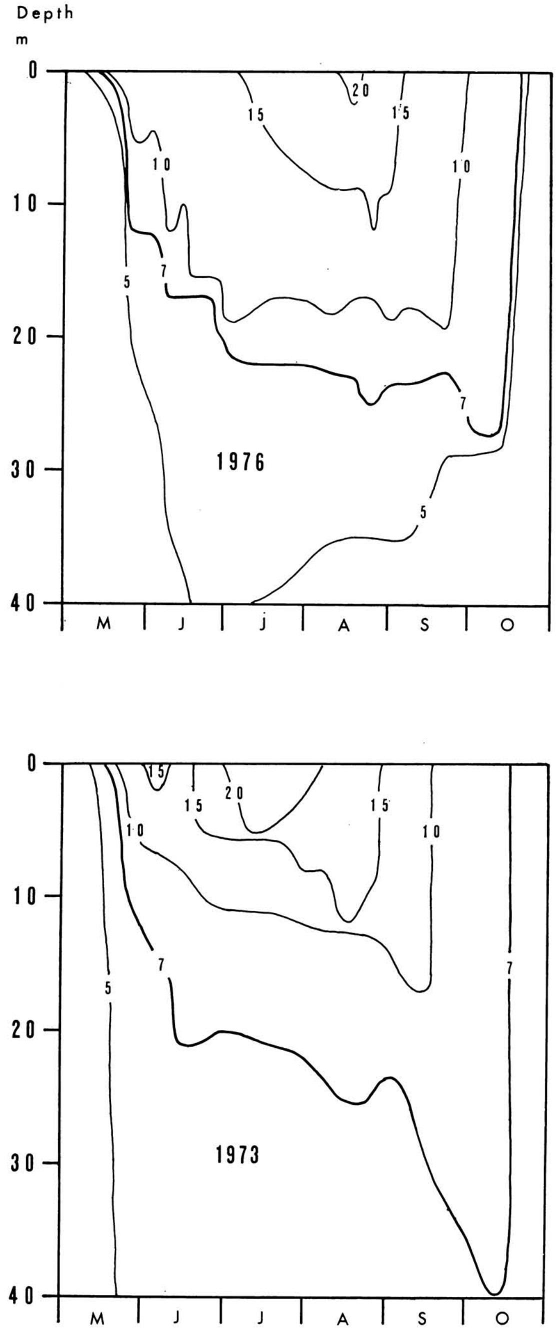

Fig. 3. The isotherms (°C) of the water column at the 75 m station (No. 9) in Pääjärvi in 1973 and 1976.

early October and continues till the end of the year. The mature males die after copulation (Figs. 7, 8). The first ovigerous females are normally found in late October (Fig. 7); only one egg-bearing female was found at the end of September and all mature females have eggs by the end of February (Figs. 7, 8). The first embryos are released in late April and the last in late June. The females die soon after they have liberated the young (see Fig. 8). Only exceptionally were large females found in summer (a few individuals weighed 15—18 mg AFDW); they were probably too old to breed. Some females have been reported to breed twice (LASENBY 1971, FÜRST 1972a), but this cannot be a common phenomenon in Pääjärvi, because adult females almost all die in the spring.

The young released in April and early May reach maturity during the summer and most of them breed at the end of the year, whereas those liberated in late May and June spend their first winter immature. The young probably have to reach 2.5 mg (AFDW) in late September in order to breed the first autumn. Those that remain immature through the first winter grow rapidly during the following summer and mature in early autumn (Fig. 11). Their young are liberated in early spring and mature the same year.

Females that breed in their first year reach the age of 13—14 months and males 8—10 months. Females that breed in their second year have a life span of about 22 months and males 16—18 months (see Fig. 6 and Sect. G, p. 255).

B. Distribution in Pääjärvi

The vertical and horizontal distribution of *Mysis relicta* is affected by temperature, light intensity and transparency of the water (BEETON 1960). Most of the lakes where the species has been studied are much more transparent than the humic Pääjärvi, where the euphotic zone is only 4 m and where no light is visible below 8 m. In Lake Michigan, for instance, light is still visible at 84 m (ROBERTSON *et al.* 1968). There the mysids are abundant at 262 m depth and they were abundant on the bottom at 144 m on 26 and 28 June. Only a few were seen on the bottom at 42 and 84 m and none in the pelagic region at the same depths. In Pääjärvi they were mainly pelagic at the same time (on 15 June 1973 maximum at 15 m; Fig. 4). In other lakes studied *M. relicta* seems to be almost benthic during the day (e.g. BEETON 1960, FÜRST 1972a).

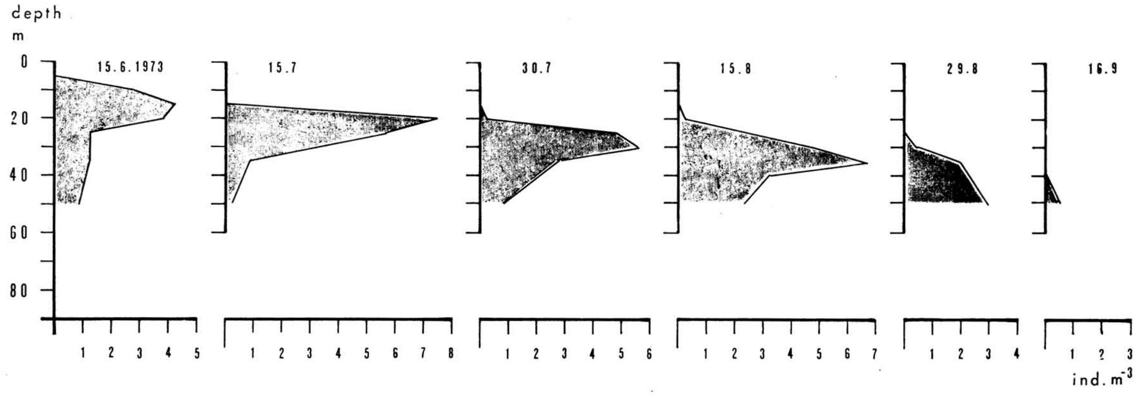

Fig. 4. The vertical distribution of *Mysis relicta* above the depth of 50 m during summer 1973 near station 9.

M. relicta tolerates a wide range of temperatures. According to PENNAK (1953), the maximum temperature tolerated by this species for long periods is 14 °C, but it has also been observed at higher values (18—22 °C, RICKER 1959; 18 °C, HOLMQUIST 1959; 22 °C, DEGRAEVE & REYNOLDS 1975).

The tolerance of high temperatures is connected with vertical migrations (JUDAY & BIRGE 1927, VALLE 1927, BEETON 1960, TERAGUCHI *et al.* 1975). In summer 1973 I studied diurnal migrations only qualitatively. The layer of maximum density was about 10 m higher at night than during the day, and then some animals were even captured at the surface. A quantitative study by Grönholm (verbal comm.) confirmed these observations.

The temporary tolerance of high temperatures enables this species to avail itself of the rich food supply at higher water levels, however, the time the mysids spend in the epilimnion is limited to the dark period of the night, which is relatively short at the latitude of Pääjärvi.

The vertical distribution of *M. relicta* in Pääjärvi seems to be determined at least partly by temperature, because the mysids always remain below a certain limit for most of the day (see Fig. 4). In 1973 peak density was just below 15 m in June and at 35 m in August; no studies were made with the Clarke-Bumpus sampler after this date. In summer 1976 peak density was observed at 20 m till mid-September. The vertical distribution of the mysids seemed to parallel the changes in the 7 °C isotherm (Fig. 3). In 1973 the 7 °C isotherm extended deeper than in 1976 and reached 40 m in October. In 1976 the lake water was colder and accordingly the mysids stayed much longer at 20 m.

That 7 °C is the limiting temperature for *M. relicta* is also supported by a respiration experiment (RANTA & HAKALA, in press) during which strong wind caused the temperature to rise from 6.8 °C to 7.4 °C. Mortality then rose to 60 %, compared with less than 20 % when the temperature was below 7 °C.

The layer of maximum density below the epilimnion was only a few metres and composed mainly of young animals. Since the older animals were mostly found in deeper water, it may be that young mysids are less sensitive to higher temperatures.

The horizontal distribution of mysids is also determined by the 7 °C isotherm. In summer they were not found on the bottom above the 20 m bathymetric contour, and at 20—25 m they were quite rare (2—20 individuals/m^2) for most of the year. But during a short period in June this stratum contained 100—150 individuals/m^2, practically all of them just liberated. Thus the one-year-old females probably release their young in the shallower parts of the lake.

At 35 m the numbers are higher and the maximum was observed at 75—87 m. The greatest numbers (about 250 ind./m^2) were observed in autumn just after the overturn, probably owing to horizontal migration caused by the descending thermocline. After the circulation some mysids migrated to the shallower parts of the lake. Although in February specimens were occasionally found even at 8 m, only about 1.5 % of the population ever ventured above the 20 m contour.

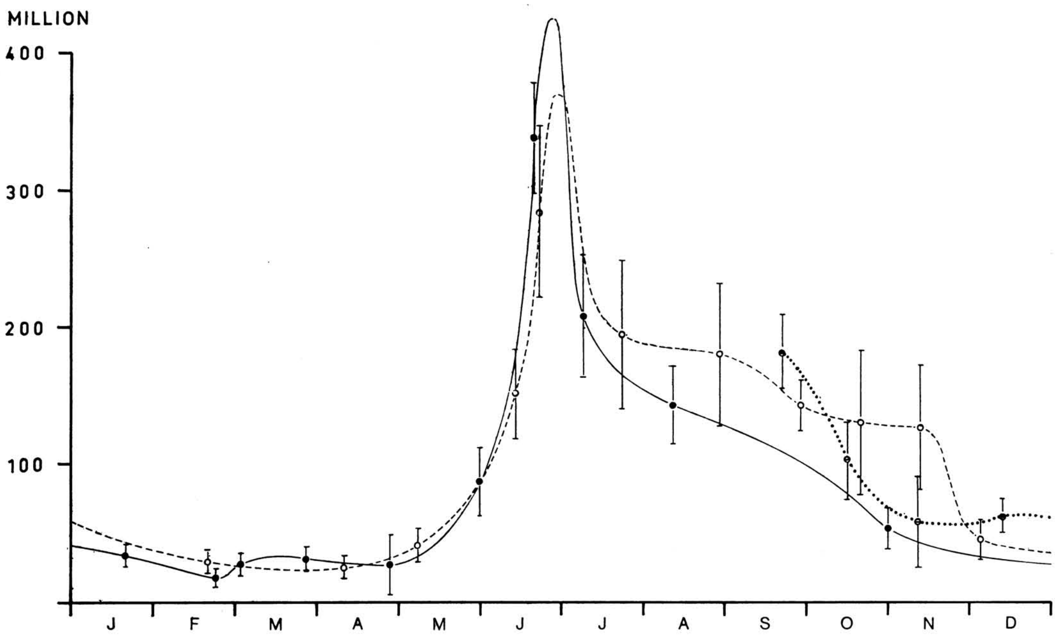

Fig. 5. The annual variation in the size of the *Mysis relicta* population in Pääjärvi in 1974 (dotted line), 1975 (dashed line) and 1976 (solid line).

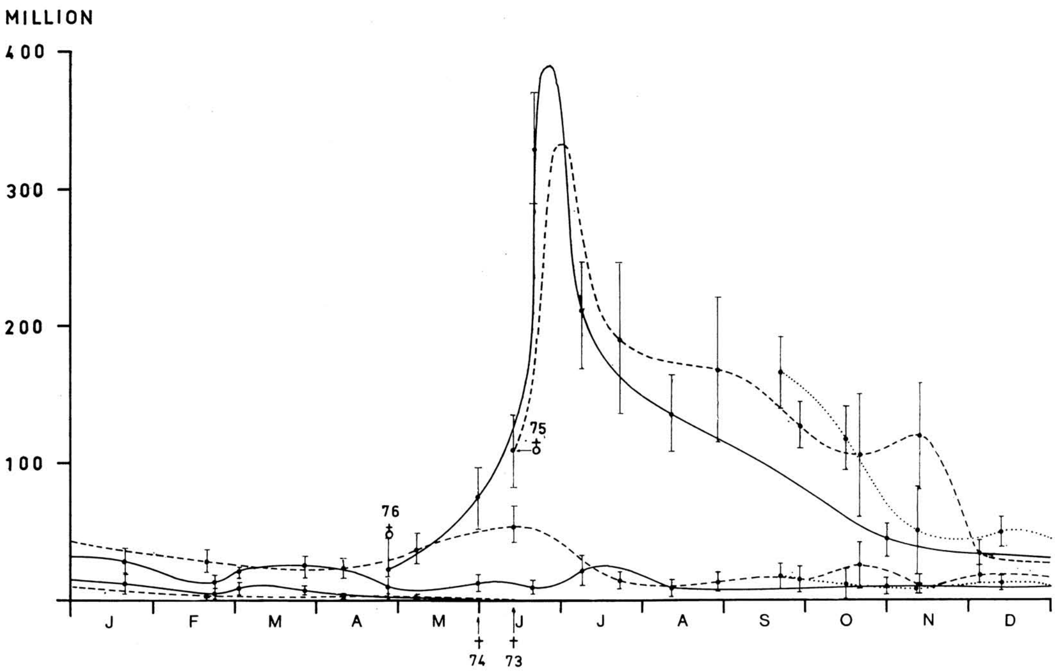

Fig. 6. The annual variations in the two cohorts of the *Mysis relicta* population in Pääjärvi in 1974 (dotted lines), 1975 (dashed line) and 1976 (solid lines). The lower curves represent the second cohorts of each year. The appearance of the new cohorts are marked on the figures as well as the disappearance of the old cohorts. Quantitative studies were started in September 1974.

C. Annual variation in population size

Fig. 5 shows the variations in the size of the population during the study years. The maximum population size was observed at the end of June (282 million individuals in 1975 and 337 million in 1976). The actual values may have been a little higher, because the maxima were perhaps not sampled. The maximum is followed by a rapid decrease in July, when heavy predation reduces the younger generation. At the end of July 1975 there were 194 million individuals and in 1976 about 140 million. From August to October mortality is relatively low. However, there is a great annual fluctuation in the population size, probably caused by availability of food.

The population is at a minimum in winter just after the last of the males have copulated and died. At this time of year there were 29 million mysids in 1974, 38 million in 1975 and about 18 million in 1976.

The annual variation in population size depends largely on the size of the first cohort (Fig. 6). The second cohort contributes only 10—15 % in winter, 14 % in October—November and about 8 % during the maximum.

Mature males are practically absent from March to May (Fig. 7). In June the overwintered males start to mature, in August the number of mature males increases rapidly, and in September many of the first-cohort males mature. The maximum of mature males was observed in late October (73 million in 1974 and 77 million in 1975). The smaller maximum in 1976 is partly explained by the scarcity of food due to the low temperature in late summer, but probably the maximum was not observed because the intervals between the samples were long. Ovigerous females first appear in late October (Fig. 7), and reach a maximum in February—March. After liberation of the first embryos in April their numbers decrease, and by late June there are none.

The great annual variation in the numbers of ovigerous females is reflected in the population maxima of the following summers (Figs. 5, 6). During the breeding season of 1974—1975 there were about 20 million ovigerous females and during 1975—1976 about 37 million.

In late January the majority of mature females were ovigerous (Fig. 8). Only about 7—10 % of the mature females failed to breed.

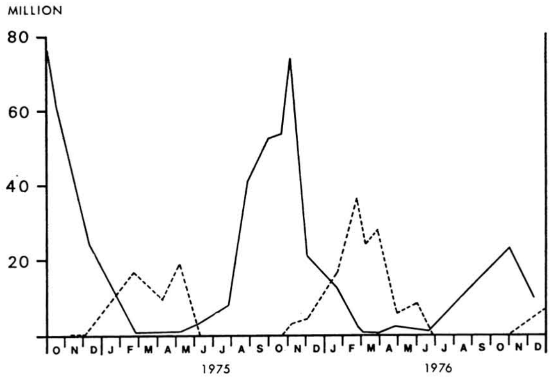

Fig. 7. The annual variations in the numbers of adult males (solid line) and ovigerous females (dashed line).

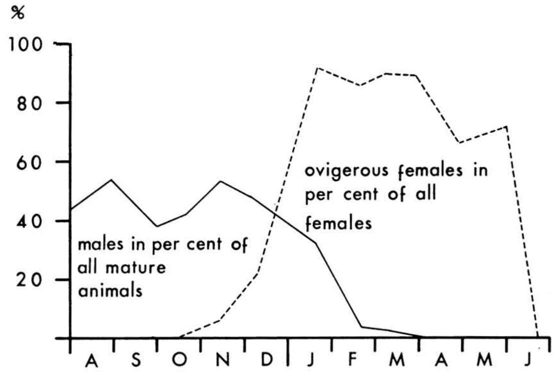

Fig. 8. The variations in the percentages of mature males (solid line) and ovigerous females (dashed line) during the breeding seasons 1975—1976.

After the onset of the breeding season the sex ratio of mature males and females was about 50 : 50 (Fig. 8), but in October there were only about 40 % of mature males. In mid-November the number rose again to 50 %. The temporary drop is significant and is explained by the death of the second-cohort males after copulation. The maturation of the first-cohort males in November restored the balanced sex ratio.

D. Annual variation in the biomass

Total biomasses in the lake (Fig. 9) were estimated from the mean weights of the cohorts. In the beginning of each year the total biomass was about 200 kg (AFDW), but after this it

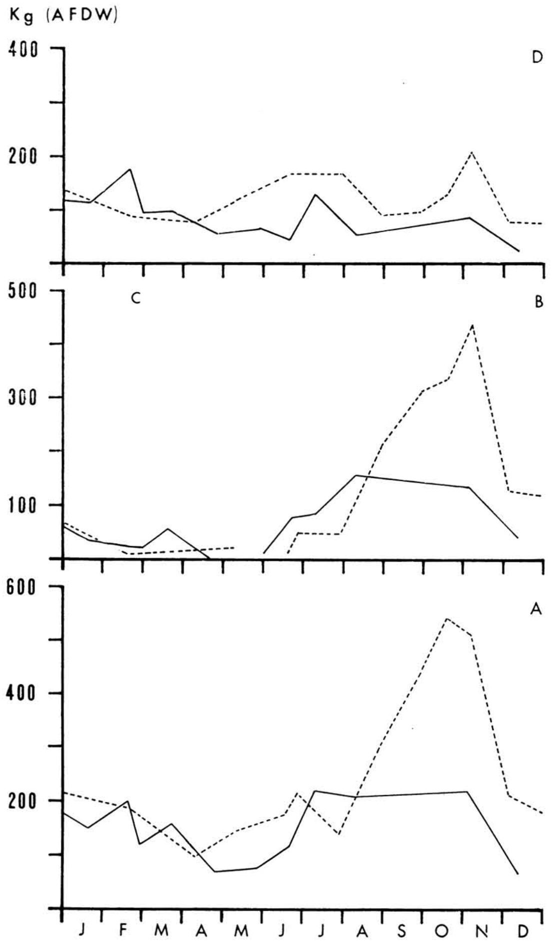

Fig. 9. The annual variations in the biomass of *Mysis relicta* in Pääjärvi during 1975 and 1976. Dotted line 1975 and solid line 1976. (A) Variations in the total biomass, (B) in the biomass of cohort I, (C) in the biomass of the 2-year-old generation and (D) in cohort II.

fell to 90—100 kg owing to the mortality of the copulated males and the older females liberating the embryos in April. The young make good this loss during May and June, but the total biomass does not increase until August because the mortality of the young is heavy in July. The rapid growth of the biomass in August is due mainly to the growth of the first-cohort individuals. The maximum biomasses were observed in October, 530 kg in 1975, 210 kg in 1976. The latter value may be too low, however, because of the long sampling interval.

The variation in the biomass of the second cohort is fairly large because this cohort is poorly represented in the samples. The biomass of this cohort seems to be around 100 kg. The growth of the animals of this cohort rapidly compensates for the decrease in biomass caused by death of the old females in the spring. A slight decrease in late autumn is caused by the death of the males after copulation.

The mean total biomass was 261.5 kg in 1975 and 145.1 kg in 1976.

E. Growth and growth rate

Growth in *Mysis relicta* has usually been expressed as increase in body length (e.g. Tattersall & Tattersall 1951, Fürst 1972b, Reynolds & DeGraeve 1972, Lasenby & Langford 1972). Lasenby & Langford (1972) also gave the length/weight relation, but there is no other information about weight. Therefore it is impossible to compare my data on growth with those from other lakes.

Fig. 10 shows the growth of *M. relicta* in Pääjärvi. The data of the 1974, 1975 and 1976 generations were fitted to the logistic model with the *k* trial and error method. To illustrate the cessation of growth the curves for the different growth periods are linked, although the mean weight of each cohort actually drops during the winter.

In December—January the mean weight of the embryos was 0.102 mg (AFDW). During embryonic development they lost weight, and at the end of the breeding season they weighed 0.082 mg. Lasenby & Langford (1972) reported the weight of the eggs of this mysid as 0.12 mg (dry weight) in an arctic lake and 0.20 mg in a temperate lake. If the ash content (about 10 %) is subtracted from the dry weight, the former value agrees well with the ash-free dry weights of the mysids in the early embryonic stage in Pääjärvi.

In Pääjärvi *M. relicta* grows in two phases. During the first summer it reaches a mean weight of 3—4 mg, depending on the conditions. No growth was observed while the lake was ice-covered. The second growth period starts in May and the final mean weight (8 mg) is reached in October-November. The occurrence of 15—18 mg females in late summer was mentioned before.

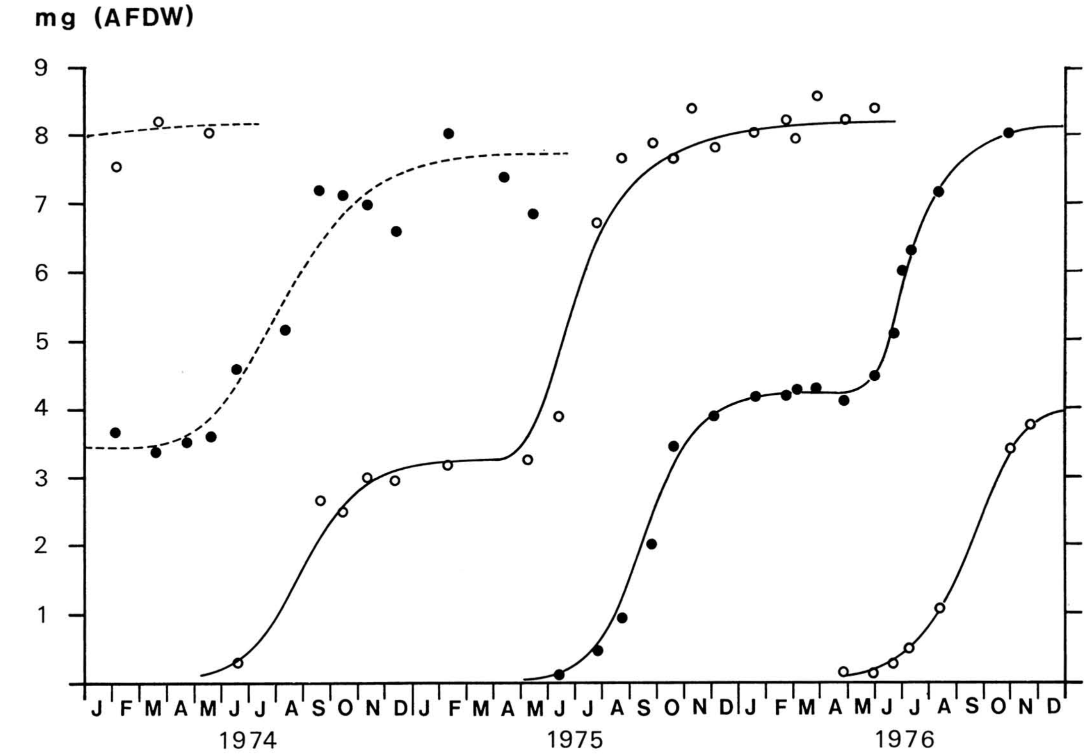

Fig. 10. The growth of *Mysis relicta* generations during the study years. The growth curves of cohort II of 1974 and cohort II of 1973 (dashed lines) are fitted by eye because the data are insufficient.

The cessation of growth in winter was not so evident in the other populations studied. According to REYNOLDS & DEGRAEVE (1972), the mysids of Lake Michigan grow 1 mm per month in December–July and 1.7 mm in January–April. TATTERSALL & TATTERSALL (1951) found an average monthly growth rate of 1 mm, the rate increasing in summer and decreasing in winter. In Stony and Char Lakes in Canada growth did not seem to cease in winter either (LASENBY & LANGFORD 1972). In Lakes Torrön and Vättern in Sweden (FÜRST 1972b) growth evidently ceased in winter in almost the same way as in Pääjärvi.

The growth rate was fitted to the logistic model

$$y = \frac{k}{1 + e^{a + bx}}$$

The embryos had a mean weight of 0.082 mg in the middle of April and after this date the measured mean weights of the cohorts were used. k, a, b then had the following values:

Cohort		k	a	b	r
1974	I	3.1930	6.8595	—0.0335	0.9775
	II	8.1500	6.7311	—0.0181	0.9340
1975	I	4.1850	5.1428	—0.0376	0.9930
	II	8.1265	10.2761	—0.0266	0.9975
1976	I	3.9200	4.2427	—0.0282	0.9946

Comparisons of the growth of the sexes is difficult, because the length-weight relation was fitted to the whole population. The differences in the growth rates would obviously have been greater if the sexes had been considered separately. The mortality of mature males and females at different times of year affected the mean weights of both sexes. For example, the males of the 1975 cohort attained a mean weight of 4.169 mg at the end of the year, but in February the value was only 3.254 mg owing to the death of the males after copulation.

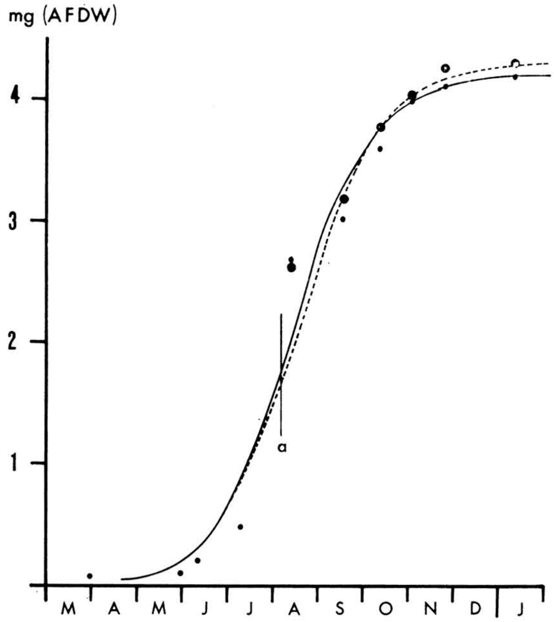

Fig. 11. The growth of *Mysis relicta* (cohort I) females and males in 1975 (broken line and large circles females, solid line and small circles males). (a) The date after which the sexes were distinguished.

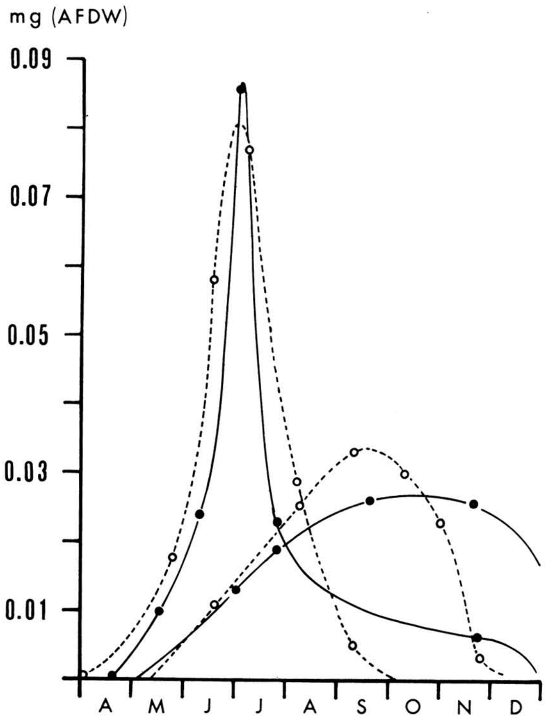

Fig. 12. The daily growth increments of the two cohorts of *Mysis relicta* during 1975 (dashed lines) and 1976 (solid lines). The higher curves (left) cohort II (overwintered) and the lower curves cohort I (newborn).

During the same period the number of females was relatively constant. At the end of the year they weighed 4.279 mg and in late April the value was still 4.080 mg, although some of the largest females had already died.

For these reasons practically no differences were observed in the growth of the sexes during the first growth period (Fig. 11). After the second summer, however, the difference was evident, the females of the 1975 cohort reaching a mean final weight of 8.226 mg and the males 7.478 mg.

The daily growth increment curves (Fig. 12) show that the second cohort reaches its maximum growth rate much earlier than the first cohort. The second cohort also has a much shorter period of rapid growth, its daily growth increments being maximal (0.08—0.09 mg) in June—July. In August the first cohort has a higher growth rate than the second and its daily increments are maximal in September—October (0.030—0.033 mg).

If the absolute daily increments are compared, the relatively small growth increments of the first cohort are due, of course, to the smaller body weight, but the slow growth rate, especially in the summer, may be caused by strong competition for food. Environmental factors prevent the population from using the most productive water layers (Ilmavirta & Kotimaa 1974, Latja 1974) for most of the day during periods of high population density.

The second cohort starts feeding immediately when primary production starts in spring. Owing to the relatively small number of animals in this cohort, competition for food is probably small. The older mysids feed in the whole pelagic region below 20 m, but seem to avoid the layer where the young reach maximum density. They also migrate to the upper water layers at night.

I did not study the food of *M. relicta*, and quantitative information on the subject seems to be meagre. According to most authors, the species feeds on detritus (e.g. Tattersall & Tattersall 1951, Holmquist 1959, Beeton 1960, Lasenby & Langford 1973). These authors also found that the mysids feed on phytoplankton and algae of the periphyton and on many species of zooplankton.

The vertical distribution of *M. relicta* in Pääjärvi indicates that the bottom detritus plays a negligible role. Only a fraction of the population is in contact with the bottom in summer, and so the tripton is the only source of detritus food, if this is consumed as food in summer at all. Small mysids are supposed to feed on the smaller algae, protozoa and larvae of zooplankton and shift to larger food particles as they grow. The larger second-cohort mysids feed on larger species of zooplankton and on their young (SAYRE & STOUT 1965). The rapid growth of the second cohort in early summer may partly reflect the higher energy value of the food.

The varying environmental conditions in the lake during the late summer are reflected in the growth rates of both cohorts. In autumn 1975 their growth stopped even before food supplies ran out, but in 1976 they continued growth to almost the end of the year. Scarcity of food earlier in the summer and autumn may have prevented the animals from attaining the optimal size for breeding at the normal time and so the energy was directed towards growth.

Slowing down of growth in the second cohort may perhaps be caused by food competition when the more numerous first cohort, subsisting on the same food items, descends towards the bottom.

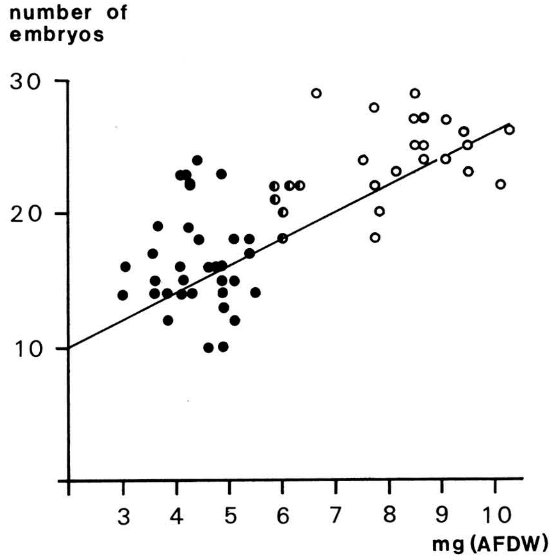

Fig. 13. The fecundity of *Mysis relicta* in Pääjärvi. The numbers of embryos per female are plotted against the weights of the females (closed circles cohort I, open circles cohort II females). The regression (a = 5.985, b = 2.009) is significant at the 0.001 level.

F. Fecundity

TATTERSALL & TATTERSALL (1951) reported that in Britain mysid females, according to their size, produce 10—40 eggs per brood. In Sweden HOLMQUIST (1959) observed that mysid females carry 40—45 eggs. FÜRST (1972b) found a linear relation between body size and number of embryos in the brood pouch. *M. relicta* in Pääjärvi showed the same relation (Fig. 13).

The maximum number of embryos per brood was 29. In January, before egg-laying was completed, the mean number was 15.6, in early February it was 18.5 and in early March 18.5. This is thought to be the definitive mean number for the whole population. In the first-

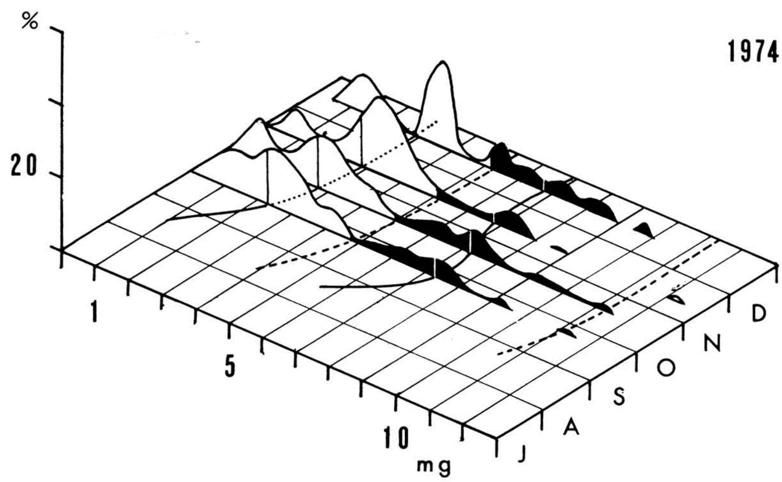

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Fig. 14. The weight frequency distribution of the *Mysis relicta* population in autumn 1974 in Pääjärvi. The cohorts are separated by dashed lines (cohort II shown with black) and the mean weights of the cohorts are shown by solid or dotted lines.

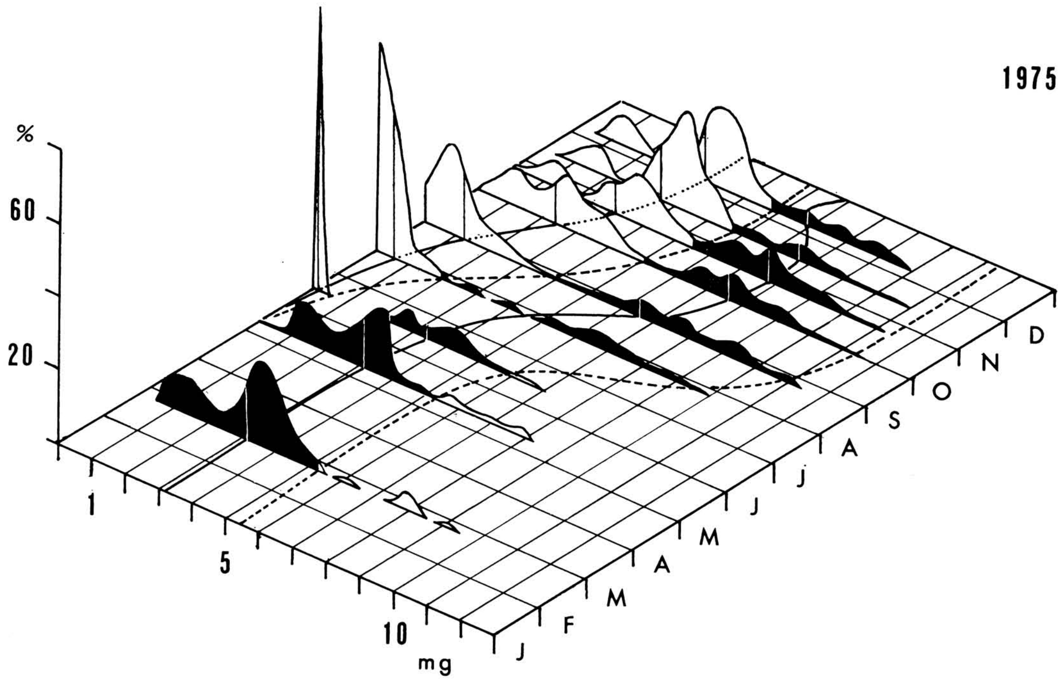

Fig. 15. The weight frequency distribution of *Mysis relicta* in 1975.

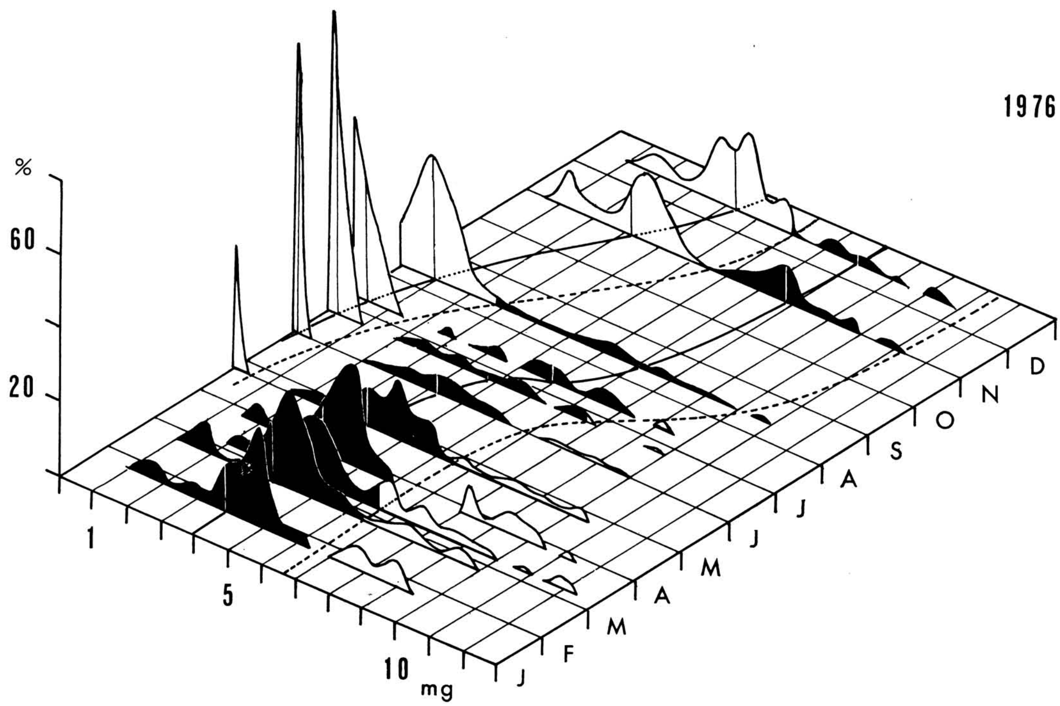

Fig. 16. The weight frequency distribution of *Mysis relicta* in 1976.

cohort females the mean was 16.4, in the second-cohort females 22.9.

The fecundity of *M. relicta* in Pääjärvi seems to be practically the same as in Lakes Vättern and Yxningen in Sweden (Fürst 1972b). In Stony and Char Lakes in Canada the mean number of embryos (12) was much lower (Lasenby 1971). If the number of ovigerous females in the whole lake is 20 to 40 million, then these will produce 340—740 million embryos a year. This approximation is not far from the maximum number of individuals observed (Figs. 5, 6). The difference between the expected and observed maxima is explained by the relatively long period (about 2 months) over which the embryos are released. During this time mortality among the young generation is evidently high.

G. Cohort discrimination

The weight frequency distributions of the *Mysis relicta* population are presented in Figs. 14, 15 and 16. During their first summer the younger generation (just born I cohort) seems to be a homogeneous group, but in September it can be split into two separate size groups. Towards the end of the year these (sub)cohorts become distinct, and only the heavier subcohort breeds in winter. During the next summer the lighter subcohort is split into many weight groups. This is due to the different growth rates of males and females. In Figs. 14, 15 and 16, however, it is impossible to discern any logical pattern, because the number of individuals in the samples was very small at this time of year and the sampling error is correspondingly high.

The splitting of the first cohort shows that the embryos were liberated in two phases, the first group in April and early May and the second group in late May and June. The liberation period may be continuous, but is characterized by these two maxima. In spring and summer these size groups could not be distinguished with the aid of the length-weight relation used. A method based on the weights would have made it possible to distinguish the two subcohorts earlier.

The two weight groups in the younger generation indicate that it actually consists of two subcohorts, the heavier being offspring of the mysids breeding in the second year and the lighter of the mysids breeding in the first year. These two cohorts probably interbreed to some extent. The two subcohorts within the generation are treated as a single cohort for practical reasons (in summer it is impossible to distinguish them from each other, which complicates calculations of such variables as growth and production).

In autumn cohort discrimination is subjective, because the proportion of second-cohort individuals is relatively small. Death of the males after copulation also changes the weight frequency distribution considerably. In early winter after growth ceased the limit between the cohorts was estimated to lie at about 5.5—6.0 mg (AFDW).

H. Production

No previous information is available about the production of *Mysis relicta*. Three methods were used to estimate the production of the mysid population in Pääjärvi, viz. Allen's method (Fig. 17), the normal elimination method (both described by Winberg 1971), and the LeBlond-Parsons (1977) method. The equation used was $P = (1 + m/g)\ \Delta B$, where P is cohort production, m is mortality and g the observed growth rate of the biomass. ΔB is the observed change in the biomass. The total mysid production (kg AFDW/year) in the lake, as calculated by these three methods, is shown below:

Cohort	Allen's method		Elimination method		LeBlond & Parsons	
	1975	1976	1975	1976	1975	1976
I	654.0	480.0	435.7	264.8	469.3	506.5
II	161.0	70.0	229.3	118.1	202.6	37.9
III	14.0	4.0	146.6	65.5	104.9	2.1
Total prod.	829.0	554.0	811.6	448.4	776.8	546.5

The production per m^2 can be obtained by dividing the values above by 1.35×10^7 or, if values are wanted for the area where the mysids actually live, by 2.88×10^6.

A considerable amount of production is connected with moulting, which, according to Holmquist (1959), occurs at intervals of 17—30 days during the growing seasons. If this approximation is accepted, then the mysids of

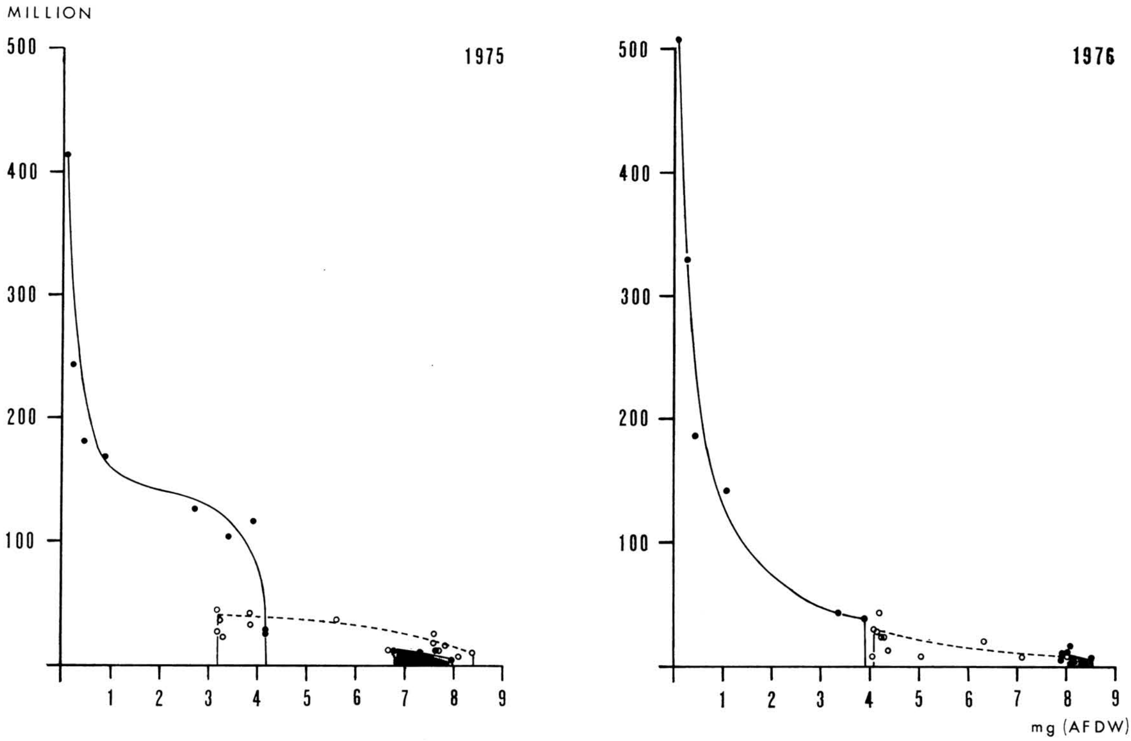

Fig. 17. Production of *Mysis relicta* in Pääjärvi in 1975 and 1976 according to Allen's method. The mean weights of the population are plotted against the corresponding numbers of individuals in the lake. The solid line (left in the figures) is the production of cohort I and the dashed line the production of cohort II. The small shaded area is the production of the two-year-old generation, which dies by June.

Pääjärvi moult about 16—28 times during their 2-year life span. The skins cast at moulting were found to weigh 5—10 % of the AFDW of the animals. Moulting is thus a very important part of production and of the energy budget.

The *P*/*B* coefficients were, according to Allen's method, 3.0 in 1975 and 3.8 in 1976 and according to the LeBlond-Parsons method, 3.2 in 1975 and 3.7 in 1976.

5. Discussion

Quantitative sampling of large Crustaceans is made difficult by the relatively low population densities, for the sample unit should be large enough to give sufficient data about all the elements of the population and production. If the number of samples is kept small because of the labour involved, the estimates will be inaccurate. This increases the unexplained variation in the numbers of the smaller groups (e.g. ovigerous females). The annual vertical and horizontal migrations also reduce the sampling accuracy, because the sampler is less efficient in the pelagic region than at the bottom.

Stratified random sampling is perhaps the best way of sampling a free-swimming and migrating species of this kind, but there should be flexibility in weighting the strata according to the migrations and changes in the abundance of the animals.

The efficiency of the sampler could not be checked in this study, but the two simultaneous estimates of population size obtained with the improved Clarke-Bumpus sampler in June 1976 gave closely comparable results (Grönholm, personal comm.).

Comparison of the scanty published ecological data on *Mysis relicta* with those for Pääjärvi shows that in this lake the species has a life span intermediate between those in an arctic and in a temperate lake. In arctic lakes at the northern limit of its range the species may survive for at least 2 years, but in temperate lakes it lives only 1 year (LASENBY & LANGFORD 1972). In Pääjärvi this species has a life span of 1 or 2 years. The alternation of early and late breeding shows that these groups are not genetically isolated. The summer breeding reported by FÜRST (1972b) is probably an adaptation to more temperate lakes or better food conditions.

The flexibility of the life cycle will be advantageous if environmental conditions vary greatly from year to year. The two generations prevent any major fluctuations in the size of the population, because one or other group is always better adapted to tolerate a given environmental stress. However, the mysids of Pääjärvi seem to be very sensitive to changes in environmental conditions. The variations in population size, biomass and production indicate that the mysids use the available resources effectively and that changes in available food are rapidly reflected in population size and in growth.

The diurnal vertical migrations of *M. relicta* can be interpreted as an adaptation for avoiding predation by fish. The more transparent the lake the longer the migrations, but in shallow transparent lakes the species is forced to adopt a totally benthic life (LASENBY 1971). In Pääjärvi, where the transparency is low, the young mysids spend less energy in migrations than in less humic, transparent lakes.

Detritus is probably not a very important source of food for the mysids in Pääjärvi. This is indicated by the cessation of growth in winter, the only time of year when the species lives near the bottom.

The relatively high density of *M. relicta* in Pääjärvi shows that this species is highly adapted to life in deep temperate humic lakes. Its vertical distribution is mainly determined by temperature. Because of the low light intensity the mysids are not forced to hide near the bottom, so they are able to stay close to the productive layers for most of the day. This and the evidently low predation are perhaps the main reasons for the relatively high population densities in Pääjärvi.

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References

BEETON, A. M. 1960: The vertical migrations of Mysis relicta in Lakes Huron and Michigan. — J. Fisheries Res. Board Can. 17:517—539.

CARPENTER, G. F., MANSEY, E. L. & WATSON, N. H. F. 1974: Abundance and life history of Mysis relicta in St. Lawrence Great Lakes. — J. Fisheries Res. Board Can. 31:319—325.

DE GRAEVE, G. M. & REYNOLDS, J. B. 1975: Feeding behavior and temperature and light tolerance of Mysis relicta in the laboratory. — Trans. Amer. Fisheries Soc. 104(2):394—397.

ELLIOT, J. M. 1971: Some methods for the statistical analysis of samples of benthic invertebrates. — Freshwater Biol. Assoc. U. K., Scient. Publ. 25: 1—144.

ELOMAA, E. 1976: Pääjärvi, representative basin in Finland: comparative studies of climatological condition over the lake and the surrounding land areas in 1969—1970. — Fennia 146: 1—40.

—»— 1977: Pääjärvi, representative basin in Finland: heat balance of a lake. — Fennia 149:1—33.

FÜRST, M. 1972a: On the biology and introductions of the opossum shrimp Mysis relicta Lovén. — Acta Univ. Upsaliensis 207:1—7.

FÜRST, M. 1972b: Livscykler, tillväxt och reproduction hos Mysis relicta Lovén. — Information från Sötvattens-Laboratoriet Drottningholm 11:1—41.

—»— 1972c: Experiments on the transplantation of new fishfood organisms into Swedish impounded lakes: the feeding habits of brown trout and char in Lake Blåsjön. — Verh. Internat. Ver. Limnol. 18:1114—1121.

GOSHO, M. E. 1975: The introduction of Mysis relicta into freshwater lakes (a literature survey). — Univ. Washington, College of Fisheries, Fisheries Research Institute, Circular 75—2:1—66.

GRANBERG, K. 1970: Seasonal fluctuations in numbers and biomass of the plankton of Lake Pääjärvi, southern Finland. — Ann. Zool. Fennici 7: 1—24.

GRIMÅS, U., NILSON, N. A. & WENDT, C. 1972: Lake Vättern: effects of exploitation, eutrophication, and introductions of the salmonid community. — J. Fisheries Res. Board Can. 29:807—817.

HOLMQUIST, C. 1959: Problems on marine-glacial relicts on account og investifations on the genus Mysis. — 270 pp. Lund, Sweden.

ILMAVIRTA, K. & KOTIMAA, A.-L. 1974: Spatial and seasonal variations in phytoplanktonic primary production and biomass in the oligotrophic lake Pääjärvi, southern Finland. — Ann. Bot. Fennici 11:112—120.

JUDAY, C. & BIRGE, E. A. 1927: Pontoporeia and Mysis relicta in Wisconsin lakes. — Ecology 8: 445—452.

LASENBY, D. 1971: The ecology of Mysis relicta in an arctic and a temperate lake. — Ph.D. Thesis, Univ. Toronto, Toronto, Ontario. 119 pp.

LASENBY, D. & LANGFORD, R. R. 1972: Growth, life history, and respiration of Mysis relicta in an arctic and a temperate lake. — J. Fisheries Res. Board Can. 29:1701—1708.

LASENBY, D. & LANGFORD, R. R. 1973: Feeding and assimilation of Mysis relicta. — Limnol. Oceanogr. 18:280—285.

LATJA, R. 1974: Pääjärven eläinplankton. (Summary: Zooplankton). — Luonnon Tutkija 78:153—156.

LEBLOND, P. H. & PARSONS, T. R. 1977: A simplified expression for calculating cohort production. — Limnol. Oceanogr. 22:156—157.

NISSINEN, I. 1961: Pääjärven profundaalin pohjaeläimistöstä. — Manuscript, Inst. Limnol. University of Helsinki.

PENNAK, R. W. 1953: Fresh-water Invertebrates of the United States. — Ronald Press Co. 796 pp.

RANTA, E. & HAKALA, I. 1978: Respiration of Mysis relicta (Crustacea, Malacostraca). — In press.

REYNOLDS, J. B. & DEGRAEVE, G. M. 1972: Seasonal population characteristics of the opossum shrimp, Mysis relicta, in southeastern Lake Michigan, 1970—71. — Proc. 15th Conf. Great Lakes Res. 117:1—131.

RICKER, K. E. 1959: The origin of two glacial relict crustaceans in North America as related to Pleistocene glaciation. — Can. J. Zool. 37: 817—893.

ROBERTSON, A., POWERS, C. F. & ANDERSON, R. F. 1968: Direct observations on Mysis relicta from a submarine. — Limnol. Oceanogr. 13:700—702.

RUUHIJÄRVI, R. 1974: A general description of the oligotrophic lake Pääjärvi, southern Finland, and the ecological studies on it. — Ann. Bot. Fennici 11:95—104.

SÄRKKÄ, J. 1976: Records of relict Crustaceans in lakes drained by the river Kyminjoki, Finland. — Ann. Zool. Fennici 13: 44—47.

SAYRE, R. C. & STOUT, W. H. 1965: Opossum shrimp collection. — Habitat Improvement Project, Oregon State Game Commission, 16:1—15.

SEGERSTRÅLE, S. G. 1956: The distribution of glacial relicts in Finland and adjacent Russian areas. — Soc. Sci. Fennica, Comment. Biol. 15(18): 1—35.

—»— 1957: On the migration of glacial relicts of northern Europe, with remarks on their prehistory. — Soc. Sci. Fennica, Comment. Biol. 16(16): 1—117.

—»— 1966: Adaptational problems involved in the history of glacial relicts of Eurasia and North America. — Rev. Roum. Biol.-Zool. 11:59—66.

SCHUMACHER, R. E. 1966: Successful introduction of Mysis relicta (Lovén) into a Minnesota lake. — Trans. Amer. Fisheries Soc. 95:216—219.

SNEDECOR, G. W. & COCHRAN, W. G. 1972: Statistical methods. — 593 pp. Iowa State University Press, Ames, Iowa, U.S.A.

SPARROW, R. A. H., LARKIN, P. A. & RUTHERGLEN, R. A. 1964: Successful introduction of Mysis relicta Lovén into Kootenay Lake, British Columbia. — J. Fisheries Res. Board Can. 21: 1325—1327.

STRINGER, G. E. 1967: Introduction of Mysis relicta Lovén into Kalamalka and Pinaus lakes, British Columbia. — J. Fisheries Res. Board Can. 24: 463—465.

TATTERSAL,L W. M. & TATTERSALL, O. S. 1951: The British Mysidacea. — 460 pp. Bartholomew Press, London.

TERAGUCHI, M., HASLER, A. D. & BEETON, A. M. 1975: Seasonal changes in the response of Mysis relicta Lovén to illumination. — Verh. Internat. Verein. Limnol. 19F: 2089—3000.

VALLE, K. J. 1927: Ökologisch-limnologische Untersuchungen über die Boden und Tiefenfauna in einigen Seen nördlich vom Ladoga-See. I. — Acta Zool. Fennica 2:1—177.

—»— 1930: Über das Auftreten von Mysis relicta und Corethra plumicornis während des Sommers in einigen Seen von Südost-Finnland. — Arch. Hydrobiol. 21:483—492.

WINBERG, G. G. 1971: Methods for the estimation of production of aquatic animals. — 175 pp. Academic Press, London and New York.

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