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Population density of perch (Perca fluviatilis L.) at egg, larval and adult stages in the dys-oligotrophic Lake Suomunjärvi, Finland

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Between 1974 and 1977 the population density of perch at egg, larval and adult stages in the dys-oligotrophic Lake Suomunjärvi, eastern Finland, was studied quantitatively. In addition, data on fecundity, age, growth, size distribution and biomass were gathered.

The density of eggs deposited on the bottom was calculated from egg clusters sampled quantitatively by a scuba-diver. This gave a mean density of 320,000 eggs/ha at the 0—3 m depth zone, with only low variation between years, sites and depths. Larvae about one week old were sampled quantitatively with the Clarke-Bumpus and CalCoFi net samplers. The results obtained with the latter, which gave much higher densities (mean 6,850 larvae/ha) than the former (2,850/ha), are considered more reliable because of the larger mouth area of the sampler and the higher number of larvae caught.

To estimate the adult population density, a scuba-diver counted the fish directly and the reliability of the method was established by comparing the diver's estimation with that given using a capture-mark-recapture method in a small isolated bay. The mean population density of perch of three years or older was 312 ind./ha. The survival in the total populations of the lake was 8 % from deposited eggs to one week old larvae and 0.05 % from eggs to three year old fish.

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1. Introduction

This paper gives the results of a quantitative study of the egg, larval and adult perch population densities in Lake Suomunjärvi in eastern Finland from 1974 to 1977, in attempt to estimate cohort mortality rates. Most of the previous perch studies have been concerned with age, growth and food, as recently reviewed by Collette et al. (1977) and Thorpe (1977). Only a few papers give absolute population estimates (Toivonen et al. 1964, Williams 1965, Backiel 1971, Holcik 1972, Holcik & Pivnicka 1972, Craig 1974, Lind et al. 1974, Nyberg 1976, LeCren et al. 1977, Craig et al. 1979).

2. Study area

Lake Suomunjärvi, which has an approximate area of 650 ha and a mean depth of 5.7 m and maximum depth of 27 m, is in eastern Finland (Fig. 1). It is divided into southern, central and northern basins by islands and sand banks. The lake is normally ice covered from early November to mid-May. Table 1 represents a summary of the main physico-chemical features. According to experimental gill netting the main species of fish inhabiting the lake are: the cisco (*Coregonus albula,* biomass 30.1 %), the perch (*Perca fluviatilis,* 26.5 %), the whitefish (*Coregonus lavaretus,* 14.1 %), the roach (*Rutilus rutilus,* 12.2 %), the dace (*Leuciscus leuciscus,* 7.5 %) and the pike (*Esox lucius,* 5.3 %).

3. Material and methods

3.1. Population estimation

Egg stage

The number of eggs deposited on the bottom was estimated by a diver collecting along a sunken line in a manner described later under adult estimation — except that the diving was done during daytime. The bottom in the spawning areas was sand, coarse sand or gravel with a few macrophytes and fallen tree branches. The 118 transects in

Table 1. Some physico-chemical and biological features of Lake Suomunjärvi in 1972—1977. The mean, minimum and maximum values are given.

	Epilimnion	Hypolimnion
Cond. $\mu S_{20}°C$	17.3 (16.8 — 17.8)	19.4 (17.7 — 23.3)
pH	6.4 (5.9 — 6.7)	6.0 (5.8 — 6.2)
$KMnO_4$mg/l	32.0 (31.0 — 33.4)	33.3 (30.5 — 36.0)
Tot. N μg/l	306.5 (253.3 —557.7)	376.0 (250.0 — 492.0)
Tot. P μg/l	9.9 (5.0 — 16.3)	15.9 (7.5 — 24.5)
Fe μg/l	327 (202 —469)	1398 (495 —5760)
Mn μg/l	22.0 (16.4 — 28.5)	124.5 (27.3 — 296.0)
Colour mg Pt/l	54.9 (49.0 — 66.0)	77.3 (50.0 — 146.0)
Alkalinity, mval/l	0.06 (0.05— 0.07)	0.05 (0.05— 0.06)
Phytoplanktonic primary production g C_{ass} /m²/year	4.4—18.5	
Production of crustacean zooplankton g/cm²/year (1976)	4.0	

14 different parts of the lake were worked in five depth zones (0—5 m) in the beginning of June in 1974, 1975 and 1977, c. 3—5 days after the estimated maximum spawning period. The diver collected egg clusters in a bag from which they were transferred to a container for volumetric estimation of the egg number in the laboratory. In 20 replicates the deviation from the mean varied between 4.6 and 15.2 % (mean 6.5 %).

Larvae

The number of larvae were estimated using a modified CalCoFi net (Nellen & Schnack 1975) and a modified double mouth Clarke-Bumpus sampler. With the CalCoFi net the samples were taken from an anchored boat with a motor winch using a pulling speed of 2 knots. The mouth area of the sampler was 1 m² and the net bag was cylindrical in front and conical towards the rear. The cylindrical part had a mesh size of 1000 μm and the conical part 333 μm. The lengths of the tows were 100 m each, thus sampling a volume of 100 m³.

The Clarke-Bumpus sampler was towed from a motor boat moving at a speed of 3—4 knots. The mouth area of the sampler was 2 × 0.0167 m² and the mesh size of the net 400 μm. The lengths of the tows were 500 m each and sampling volume 16.7 m³. Both samplers were towed horizontally at the same sites and times in 0—10 m depth zones, and altogether 64 CalCoFi net and 33 Clarke-Bumpus tows were made. Four of the sampling sites (littoral) could be reached to a depth of 4 metres and eight (pelagic) to a depth of 10 metres. The samples were taken about one week after the first observation of hatched larvae. The total length of the larvae caught varied between 5.5 and 7.3 mm.

Adults

The absolute population number in the lake was estimated by direct counting by a scuba diver along transects of known length and width. The reliability of these estimates was established by comparing the diver's estimates for the bay of Lapinlahti (c. 16 ha, max depth c. 10 m) with capture-mark-recapture estimates.

1) The diver method. The diving was performed during the hours of darkness in late August and September. With the aid of a powerful lamp the diver moved along 100 m long weighted ropes laid on the bottom the day before and counted every fish within reach of a 1 m stick. Thus the area investigated was 2 × 100 m. This method has been considered to give reliable population estimates under certain conditions (Sumari 1963, Bagge et al. 1975, Pursiainen 1975). In autumn the perch are found in shallow water and during dark nights they are stationed near the bottom. Under these conditions the escaping distance of the perch is very short and they can actually be touched by the diver. This enables the diver to roughly estimate the length of the fish with scaled stick.

This method was used in nine areas in the middle basin (Fig. 1). Thirty-two transects were worked in 1974 and forty-eight in 1975 at depths of 1—5 m. In 1976 twenty-two transects were dived in two areas in the bay of Lapinlahti, covering depths of 1—10 m.

The 95 % confidence limits for the mean numbers of the scuba diver's counts were calculated for data from different sites (depth zones combined) and (in the bay of Lapinlahti) for depth zone data (sites combined). This was done since the differences in numbers between different depth zones and sites (see results) were not statistically significant. A logarithmic transformation was used. The range of the limits was usually not more than 50 % of the mean.

2) Mark-recapture method. Of 2058 perch caught in traps in the bay of Lapinlahti, 1994 were marked and released and 336 of these were recaptured. The traps, which had a 19.1 mm square mesh (5 mm mesh in 1976) were set during the spawning season in 1 to 6 m of water every 100 m along the shore. The perch were marked by clipping the pelvic fin and each was measured and then released. Marking was carried out for six successive days each year. The population was estimated by the method given by Robson & Regier (1971: 150) using the modification

$$\hat{N}_s = \Sigma (C_t M_t) / (\Sigma R_t + 1)$$

(Ricker 1975) and the 95 % confidence limits by the method given by Ricker (1975: 343). The results of the scuba-diver and mark-recapture are given in Table 4.

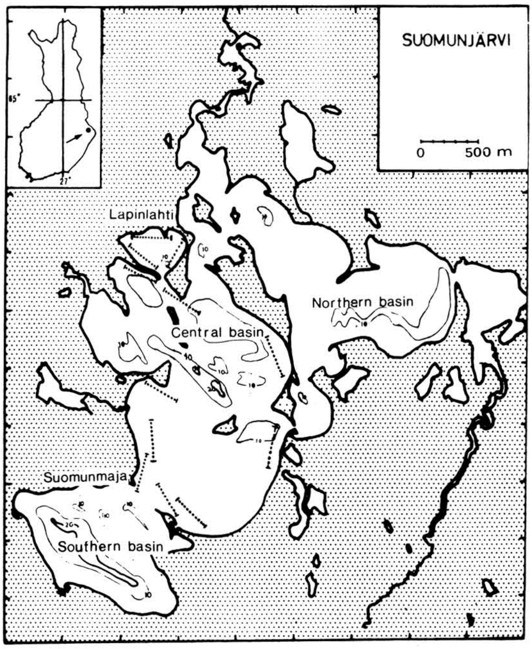

Fig. 1. Lake Suomunjärvi. The dotted lines show the areas used in the diver-counting of perch.

3.2. Fecundity

Some ovaries were preserved prior to spawning in Gilson's Fluid (Bagenal & Braum 1971), and later weighed and subsampled by weighing 200 eggs from each ovary for the calculation of total egg numbers. Before weighing and counting, fragments of ovarian tissue were removed and the eggs were dried on filter paper. The accuracy of replicate subsamples was better than 2 %.

3.3. Age and growth

The age and growth of perch were determined from the scales and checked from the opercular bones. Back-calculations of growth were made using the empirical method of Ricker & Lagler (Tesch 1971). The length of each fish was measured from the anteriormost extremity to the end of the caudal fin (total length) and rounded down to the nearest millimetre. Annuli were formed in June. The date of birth was taken as June 1st.

3.4. Population length and weight distribution

The size distribution of the perch was determined from the fish caught during the mark-recapture experiments and from test fishing during the period 1973—1976 using gill nets of 12, 14, 17, 20, 25, 30, 35, 40, 45, 50 and 65 mm mesh size, 18 m deep vertical gill nets of 8, 10, 12, 14, 16, 18 and 20 mm mesh (Holopainen & Viljanen, 1976), and traps with 19 mm mesh.

Table 2. The number of perch eggs in different depth zones in 1974, 1975 and 1977.

Depth zone (m)	Number of lines	Area (m^2)	Eggs/m^2 $\bar{x}$	95 % CL	Eggs/ whole lake
1974					
0—1	5	500	12.6	1—126	8.61 × 10^6
1—2	6	600	40.6	3—406	22.09 × 10^6
2—3	5	500	21.7	1—277	10.08 × 10^6
0—3	16	1600	26.0	8—70	40.78 × 10^6
1975					
0—1	3	430	36.7	0—2568	25.07 × 10^6
1—2	5	720	30.5	8—98	16.60 × 10^6
2—3	3	430	11.5	0—366	5.34 × 10^6
0—3	11	1580	27.0	9—72	47.01 × 10^6
1977					
0—1	15	1380	61.7	17—216	42.14 × 10^6
1—2	15	1380	64.5	16—238	35.09 × 10^6
2—3	15	1380	2.9	1—4	1.35 × 10^6
3—4	15	1380	0.1	~ 0	0.05 × 10^6
0—4	60	5520	32.3	19—52	78.63 × 10^6

3.5. Biomass and production

The biomass was calculated from the diver's population estimates and the mean weights of perch caught in the gill nets and traps and during the capture-mark-recapture work. Production was estimated using a P/B coefficient of 0.3 based on previous published estimates (Holcik 1972, Holcik & Pivnicka 1972, Lind et al. 1974, Nyberg 1976). This method had to be used as our data did not allow direct production estimates.

4. Results and discussion

4.1. Deposited eggs

The differences between years, sites and depth zones in the densities of eggs on the bottom were not statistically significant except for the low numbers at 2—3 m and 3—4 m in 1977 (Kruskal-Wallis, $P < 0.10$) (Table 2). In 1974 and 1975 no eggs were found deeper than 3 metres, but in 1977 some were also found in the 3—4 depth zone. The small differences between years in density of eggs laid on the bottom agree well with the results of LeCren (1961) and Nyberg (1976).

4.2. Larval population

The mean densities of larvae were 6 850 (CalCoFi net) and 2 850 (Clarke-Bumpus) per ha yielding total populations of 4 440 850 and 1 850 000, respectively. The differences in

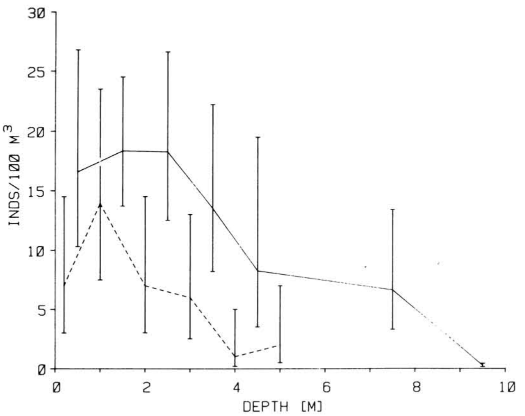

Fig. 2. The catches of perch larvae with CalCoFi net (solid lines) and Clarke-Bumpus (broken line) from different depths in June 1977. The vertical lines refer to 95 % confidence limits.

numbers between different sites and dates with each sampler were not significant. The maximum density was found in the 0—3 m depth zone and it decreased steeply with increasing depth (Fig. 2). The densities of larvae caught with CalCoFi net from the 0—3 m depth zone were higher at the littoral sites (20.5 per 100 m^3) than at the pelagic sites (16.4 per 100 m^3) but the difference was not statistically significant. The higher density of larvae given by the CalCoFi net was considered to be more reliable because of the advantages of the larger mouth of the sampler, the higher number of larvae caught, and better agreement with egg densities. The lower densities given by the Clarke-Bumpus sampler perhaps result from active avoidance of the small-mouthed sampler by the young fish, the disturbing action of the boat ahead of the sampler, or the higher towing speed preventing complete filtration.

4.3. Adult population density

Scuba-diving

The differences in the numbers of perch between depth zones (1—4 m), between different sites and different years (1974—1975) were not statistically significant (Mann-Whitney *U*, $P <$ 0.05) (Table 3). The density was, however, observed to decrease steeply in depth zones over 4 m and perch were only exceptionally observed in depth zones below 6 m. The density estimates were therefore made using the mean values of the whole material and assuming that all the fish were situated in the 0—8 m depth zone. With this assumption, the combination of the results from 1974—1975 (in 1976 diving was performed only in the small bay of Lapinlahti) gave a total population of 202 000 perch aged three years or older (312 ind./ha) for this lake (Table 4).

Mark-recapture

This method is dependent on several underlying assumptions. The clipping of the fin may cause an increased mortality rate, which can result in overestimation of the population size. In our experiment the perch did not, however, show any observable response to the clipping. Secondly, the marked fish should be randomly distributed within the population. This was considered to be achieved due to the small area of the whole bay (diameter c. 500 m), the scattering of the release sites around the bay and the high degree of activity of the spawning fish. One possible error, which would give an underestimation of the population, may result from the differences in perch behaviour caused by trapping and marking. This is reported to lead sometimes to increased vulnerability to retrapping (Stott 1970, Beukema & de Vos 1974, Nyberg 1976). The most serious problem is the representativeness of the sampling. The growth and age analysis reveal that trapping does not give representative samples of perch less than three years old. Moreover, during the spawning time most of the perch were males (89.9 %) but in other seasons the proportion of males was only 35.2 %. When the estimates are corrected so that they concern only perch of three years or older and the number of males is multiplied by the female/male ratio (1.84) of the other seasons, the population estimates for the bay of Lapinlahti are as follows: in 1975 4 250 (4 010—5 150) or 284 ind./ha and in 1976 1 410 (1 140—1 820) or 88 ind./ha (Table 4). The mouth of the bay was open between the autumn of 1975 and spring 1976, which may be one explanation for the difference between the years.

Comparison of the methods.

From the comparison with Lapinlahti made in 1976, the mark-recapture and the scuba-diving methods gave similar results if we assume that all the perch were situated in the 0—8 m depth zone during the diving periods (Table 3). The difference was not statistically significant ($P > 0.05$) and consequently the diving method was here considered to be sufficiently accurate for the estimation of the density of perch in the whole lake.

Table 3. The number of perch per 200 m^2 collected by a diver.

Depth	Central basin 1974			Central basin 1975			Bay Lapinlahti 1976		
(m)	n	mean	range	n	mean	range	n	mean	range
1	6	4.8	1—8	12	8.2	1—27	3	2.7	1—5
2	6	4.5	0—9	12	10.8	2—31	4	1.8	1—3
3	6	6.1	1—21	12	13.6	1—47	4	1.3	1—2
4	6	5.2	0—16	12	6.6	0—16	3	3.3	2—4
5—7							6	0.7	0—1
8—10							4	0.0	—

Table 4. Scuba-diving and mark-recapture results of perch counting in 1974—1976 (means and 95 % confidence limits). S = scuba diving, M = mark-recapture.

	Individuals	Ind./ha
Whole lake		
S 1974	140 600 (90 900—189 800)	217 (140—293)
S 1975	243 500 (206 700—281 200)	376 (319—434)
S 1974—1975	202 200 (169 000—235 500)	312 (261—363)
Bay Lapinlahti		
M 1975	4 520 (4 010—5 150)	284 (252—324)
M 1976	1 410 (1 140—1 820)	88 (72—114)
S 1976	925 (268—1 595)	58 (17—100)

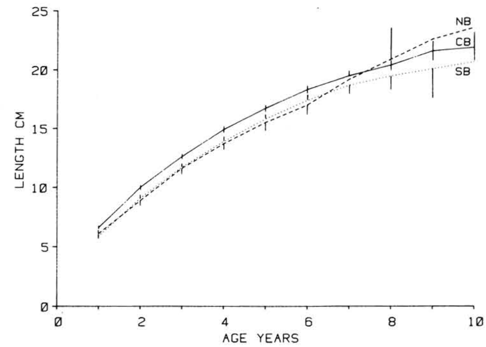

Fig. 3. Growth of perch (total length) in different basins of Lake Suomunjärvi. The vertical lines show the 95 % confidence limits. SB = southern basin, CB = central basin and NB = northern basin.

4.4. Fecundity

Absolute fecundity (total number of eggs in the ovary) was calculated from twenty fish caught in May 1975. The number of eggs was positively correlated with the fish length, and the following regression equation was calculated

$$\log_{10}\text{egg number} = 0.199 + 2.904 \log_{10}\text{length (cm)}$$

($n = 20$, $r = 0.953^{***}$). The fecundity was lower than that obtained by Craig (1974) and Mann (1978), but higher than that obtained by Nyberg (1974). The regression coefficient was, however, similar to those given by these authors.

4.5. Age and growth

Fish length and scale radius showed an allometric relationship of form, $y = ax^b$, where y = total length (cm), x = scale radius (mm × 15) and a and b are constants. These constants were calculated as $a = 0.867$ and $b = 0.701$ ($r = 0.997$; $n = 315$).

In addition, the equation

$$\bar{s}_n = \bar{s}\, s_n / s$$

where s = actual radius of the scale in question, s_n = actual distance to the nth annulus on the scale in question, $\bar{s}$ = average scale radius for a fish of the observed length and $\bar{s}_n$ = adjusted distance to the nth annulus was used to back-calculate lengths at earlier ages. These lengths showed no evidence of Lee's phenomenon. The growth of perch in Lake Suomunjärvi is in fairly good agreement with other published values from Finnish lakes. In the central basin the growth up to the age of six years was significantly faster ($P < 0.01$) than in southern and northern basins (Fig. 3) which did not show any mutual difference in perch growth.

4.6. Population length and weight distribution and sex ratio

The test fishing both with the gill net series and traps gave almost identical size structures for the perch population in the same basin, regardless of the year and season. On the other hand, differences in the mean lengths of perch between different basins were all statistically significant

Table 5. Density, biomass and production estimates of perch populations in selected waters.

	Method	Density (ind./ha)	Biomass (B) (kg/ha)	Production (P) (kg/ha/yr)	P/B	Reference
Gulf of Finland	scuba-diving	260—550				Sumari (1963)
Gulf of Finland	scuba-diving	200—4900				Bagge et al. (1975)
Linnonsalmi strait, Finland	scuba-diving	362—472	9.5			Pursiainen (1975)
Ponds, Finland	poisoning	200—250	2.5—49.5			Toivonen et al. (1964)
River Thames, England	mark-recapture	20—2590				Williams (1965)
Slapton Ley, England	mark-recapture	90—840				Craig (1974)
Klicava reservoir, Czechoslovakia	mark-recapture					Holcik (1972)
	1964	1056	46.1	16.9	0.4	
	1967	163	9.6	2.9	0.3	
	1968	149	6.5	2.2	0.3	
	mark-recapture					Lind et al. (1974)
Lake Kiutajärvi, Finland	age 0	198	0.1	0.2	2.0	
	1	916	8.0	5.5	0.7	
	2	193	10.8	4.4	0.4	
	total	1307	18.9	10.1	0.5	
Lake Vitalampa, Sweden	mark-recapture	470—950	18.6—24.8	7.2—11.9		Nyberg (1976)
Lake Botjärn, Sweden	mark-recapture	1590—2890	27.7—39.7	13.1—26.6		Nyberg (1976)
Windermere, England	CPUE (catch per unit effort)					
	North Basin (1941—1976)	125—3230	11—113			Craig et al. (1979)
	South Basin (1941—1976)	1040—5950	49—260			

(t-test; $P < 0.05$). During the spawning period the catch of small perch was always higher than at other times. At all times vertical gill nets caught more small perch than other fishing equipment. In mark-recapture experiments in the bay of Lapinlahti the difference in size structure between years was statistically significant ($P < 0.01$). During the spawning period most of the perch in all catches were males. The average male:female ratio (three years or older fish) during the spawning period (May-June) was about 10:1 (89.9 and 10.1 %) but in other seasons about 1:2 (35.2 and 64.8 %). The majority of the male perch reached maturity at the age of 2 years or at a length of 9 to 11 cm. The age of maturity of the females was three years and the respective length 11 to 13 cm. In general, the sex ratio of perch is very variable, as summarized by Alm (1946).

4.7. Biomass and production

Using the mean weight (60.5 g) for perch of three years or older given by the test fishing and mark-recapture experiments, their biomass was 12 220 (10 220—14 250) kg or 18.9 (15.8—21.9) kg/ha. If we take 0.3 as the P/B coefficient, we get a corresponding production value: 3 670 (3 070—4 270) kg/year or 5.7 (4.7—6.6) kg/year. These results are of the same size order as those recorded in the literature (Table 5).

4.8. Cohort development

The survival rates between different developmental stages of the perch population have been calculated from our results collected from 1974 to 1977 (Table 6). Several possible errors are included in these calculations because of the crudeness of many estimations and the very fact that we do not follow the same cohort from egg to adult. However year-class strength, mortality rates and fecundity have often been shown to fluctuate very much in successive years (Craig 1974, Viljanen 1975, Nyberg 1976, Le Cren et al. 1977, Craig et al. 1979). In Lake Suomunjärvi, however, relative year-class strengths, which were calculated as described by Kempe (1962), did not suggest marked year-class variations. The year-class strengths from 1963 to 1970 were 107, 98,

Table 6. Cohort development of perch in Lake Suomunjärvi.

	Total number × 10^6	Survival (%)	
Adult (spawning) population (> 3 years)	0.2		
Potential number of eggs (population fecundity)	800		
Eggs deposited on the bottom	60	8	0.05
Larvae (c. 1 week old)	4.5	0.7	
Proportion of 3 year olds in adult population (> 3 years)	0.03		

135, 113, 72, 82, 110 and 106. The potential population fecundity was calculated as the product of the fecundity of an average-sized mature female (17.5 cm, 6 000—7 000 eggs) and the number of mature females in the population. This gave a value 13 times higher than the number of eggs deposited on the bottom. The latter value is here considered to be more reliable and the overestimation of the former to be due to the crudeness of the many assumptions used in its calculation, e.g. the assumption of about 100 % maturity at the age of three years and thereafter yields certain overestimation. The number of larvae seems to be underestimated, because the hatching success of perch eggs is usually reported to be very high (90—100 %, Nyberg 1976). A probable explanation for the low larval densities could be the onset of the highest mortality during the first days after hatching or the existence of the young larvae in the very shallow littoral areas which could not be sampled. Moreover, the time of hatching in perch can be long and some of the eggs might still have been unhatched during sampling. This is unlikely, however, because our preliminary observations suggest a short spawning period in this lake. In our material the survival from deposited eggs to 3 year old fish was 0.05 %. Nyberg (1976) found the survival of the newly-hatched perch fry to one year old to be 0.15—0.01 % and there was no connection between the number of eggs deposited per year and the number of 1 year olds the following year. According to Braum (1967) the survival of whitefish from egg to adult was approximately 0.03 %.

The degree of fluctuation in the numbers of eggs deposited on the bottom was not high between the three years sampled. This suggests a relatively constant perch population and egg production in this lake, unless there is a high degree of fluctuation in larval mortality. In all, the development from deposited egg to 1 year old fish may be the most crucial phase in perch life. Unfortunately this phase is most difficult to follow quantitatively in nature and hence it is a relatively neglected area of research.

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