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# The biology of *Phoxinus phoxinus* (L.) and other littoral zone fishes in Lake Konnevesi, central Finland

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In May and June 1983 1017 fish were obtained from electrofishing surveys at 18 littoral sites in the southern basin of the oligotrophic Lake Konnevesi. *Phoxinus phoxinus*, the minnow, was the numerically dominant species, forming 60 % of the catch.

The minnows reached 50.9 mm fork-length by their second birthday, which was the age of first maturity. The sexes did not differ significantly either in length or numbers in the first three age-classes. Few males survived to their fourth birthday and the oldest fish, aged five years, was a female.

In prespawning females the number and diameter of ripe eggs was positively correlated with body size. Some females still contained ripe eggs on 15 July, 50 days after the first spent females had been captured. Analysis of the changes in egg numbers in the gonads over this period indicates that each female ripens and sheds several batches of eggs over the spawning season.

*Nemacheilus barbatulus* formed 28 % of the catch and was the most evenly and widely distributed fish in the littoral zone, occurring at all 18 sites, whereas the minnow was common at the sites with the largest rocks. Eight other species, of which *Cottus gobio, Perca fluviatilis, Lota lota* and *Gymnocephalus cernua* were the most abundant, formed the remaining 12 % of the catch.

Zippin population estimates gave a total fish density of 1.75/m$^2$, while the total biomass was 4.78 g/m$^2$. The main contributors to biomass were *N. barbatulus* 51 %, *P. phoxinus* 31 % and juvenile *L. lota* 13 %. The annual production of *N. barbatulus* was 1.43 g/m$^2$ and that of *P. phoxinus* 0.96 g/m$^2$.

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## 1. Introduction

Studies on the freshwater fishes of Finnish lakes have concentrated on species of commercial value. Much less is known about the smaller species which dominate the littoral zones of these waters. However, Sauvonsaari (1971) and Mills & Eloranta (in press) have investigated the age, growth and reproduction of the stone loach *Nemacheilus barbatulus* (L.) in lakes Päijänne, Pälkänevesi and Konnevesi and Myllylä et al. (1983) describe some aspects of the biology of the minnow *Phoxinus phoxinus* (L.) in Eastern Lapland.

Our paper examines the age, growth and reproduction of *P. phoxinus* in the southern basin of Lake Konnevesi and, by means of electrofishing surveys, we have assessed the numbers and biomass of other, less abundant, species including the bullhead *Cottus gobio* L. and juvenile specimens of burbot *Lota lota* (L.). Konnevesi is a large oligotrophic lake (area 188 km$^2$, electrolytic conductivity 4.4 mS/m) situated in central Finland, 60 km north-east of Jyväskylä. Tuunainen (1972) describes the physical and chemical characteristics of the lake. Toivonen (1972) lists the fish species present in the lake and gives the results of gill net surveys. In southern Konnevesi vendace, perch, burbot and whitefish formed 87.8 % of the catch by weight.

## 2. Materials and methods

### 2.1. Sites and sampling

On 18-20 May, 26 May, 2-3 June and 10 June 1983, samples of fish were obtained by D.C. electrofishing at a total of 18 littoral sites in Etelä-Konnevesi, between the Siikakoski rapids in the West and the Mäkäräniemi peninsula in the East. We fished the band of rocks along the shore line. This was generally between two and five metres wide with a water depth of one metre or less. Over the 18 sites the average rock diameter varied from about 10 cm to over 50 cm. Seven sites of known area were fished quantitatively (2 on 19 May, 5 on 2-3 June) using three successive electrofishings. Stop nets (8 mm mesh) were placed along the boundary between the rocky littoral zone and the deeper sandy areas to prevent the larger fish escaping.

Additional samples of *P. phoxinus* were obtained by electrofishing similar littoral areas on 23 June, 15 July, 24 August, 28 September and 10 October. The last two samples were accidentally mixed but, because they were taken only two weeks apart, they were treated as one combined sample from the mean date of 4 October. Thus, samples of *P. phoxinus* were obtained on eight separate dates. The fork lengths, weights and gonad weights of the fish examined from catches between 18 May and 10 June were determined from fresh specimens. The later samples of *P. phoxinus* were preserved in 4 % formalin solution before being weighed and measured. Regressions of lengths and of weights before and after preservation showed that in a sample of 20 fish (fresh lengths 22.5 to 74.5 mm) preservation resulted in a reduction in length of 2.1 % and an increase in weight of 4.8 %. The measurements for the preserved specimens were adjusted accordingly.

The gonads of 74 randomly selected females were preserved in Gilson's fluid (Bagenal & Braum 1968). In gonads where there was a clearly distinct peak of large eggs the number and size distribution of the eggs was determined. All eggs 0.2 mm or more in diameter were counted in 53 of these gonads (between six and nine from each of the eight samples) and the diameters of subsamples of 200 eggs from each gonad were measured to determine the size-frequency distribution.

### 2.2. Ageing

Otoliths were used to age four of the species. Rings on these bones followed the patterns described by Eloranta (1983) for *Lota lota*, Kännö (1969) and Smyly (1955) for *Nemacheilus barbatulus* and Smyly (1957) for *Cottus gobio*. Myllylä et al. (1983) aged *P. phoxinus* using otoliths and Frost (1943) also mentions their use in ageing this species, but most previous workers have aged *P. phoxinus* using the patterns of circuli on the scales. Parts of the scale where the circuli lie close together are assumed to represent the interruption in growth that occurs during winter and which is termed the annulus. This is difficult in the minnow as the number of circuli is low and the nature of such annuli is often far from clear. Neither Myllylä et al. (1983) nor Frost (1943) give details of how they interpreted the rings on the otoliths and Beamish & McFarlane (1983) comment that the requirement to validate ageing techniques is often forgotten. In this study the use of minnow otoliths was validated by comparing the number of rings present and the fork lengths of the fish with the length-frequency distribution of the 612 minnows caught between 18 May and 10 June (Fig. 1). Viewed with reflected light, no narrow, dark hyaline bands were visible between the centre and the outer edge of the otoliths of individuals from the first length-frequency peak (19-38 mm fork length) (Fig. 1), indicating that individuals from this group of fish were one year old and were about to commence laying down the second opaque (growth) zone on their otoliths. All the fish between 38 and 53 mm fork length had one dark winter band between the centre and the edge of their otoliths. The change from one dark band to two dark bands at a fork length of between 53 and 56 mm coincided with the interface between the second and third length-frequency peaks (Fig. 1, Table 1). There was a larger area of overlap in the lengths of fish whose otoliths displayed three or four rings and no distinct peaks were visible in the length-frequency distribution. However, the general correspondence between length frequency and ring number provides a sound basis for age determination. As an additional check, a sample of otoliths from 20 minnows was aged independently by the second author; we agreed in 19 cases, in the 20th we differed by one year.

Scales were taken for ageing from pike, *Esox lucius* L., perch *Perca fluviatilis* L. and ruff, *Gymnocephalus cernua* (L.). Annuli had just formed on the outer edge of some of the scales, particularly those from fish caught in June.

### 2.3. Condition

An index of condition ($CI$) was calculated for male and female *P. phoxinus* using the general formula:

$$CI = 10^5\, W / L^3$$

where $W$ = wet weight (g) and $L$ = fork length (mm). This general index was used to calculate two measures of the relative fatness of the fish and one of gonad development. Total fish weight was used to determine total condition, total weight minus gonad weight to give somatic condition, and gonad weight alone to give the gonadosomatic index (GSI). The GSI has been calculated more commonly as a proportion of the gonad weight to the total or somatic weight but it is more appropriate to use an index which is independent of weight because of the large fluctuations that occur (giving rise to the observed changes in condition).

### 2.4. Population estimates

The seven sites fished quantitatively averaged 46.5 m$^2$ (range 30.8-66.6 m$^2$), giving a total of 325.5 m$^2$. Only *N. barbatulus* was present in sufficient numbers to allow separate density estimates for each site to be made. Hence, catches from the first, second and third electrofishings across all seven sites were combined to calculate population densities. The numbers of each species were then estimated using the Zippin triple-catch removal method (Zippin 1956, Mann & Penczak 1984) and for each species the applicability of the model was proven using the goodness-of-fit statistic $T$ (Seber 1973). Because of differences in fishing efficiency between mature and immature *P. phoxinus*, separate determinations were made for each group.

The biomass or standing crop of each species was deter-

Table 1. The relationship between fork length of *Phoxinus phoxinus* from Lake Konnevesi and the number of narrow dark bands visible on the otoliths.

| Fork length (mm) | Dark bands: 0 | 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| 29-30 | 1 | | | | |
| 31-32 | 2 | | | | |
| 33-34 | 2 | | | | |
| 35-36 | | | | | |
| 37-38 | 1 | | | | |
| 39-40 | | | | | |
| 41-42 | | 2 | | | |
| 43-44 | | 2 | | | |
| 45-46 | | 2 | | | |
| 47-48 | | 2 | | | |
| 49-50 | | 10 | | | |
| 51-52 | | 4 | | | |
| 53-54 | | 4 | 1 | | |
| 55-56 | | 2 | 3 | | |
| 57-58 | | | 4 | | |
| 59-60 | | | 6 | | |
| 61-62 | | | 7 | | |
| 63-64 | | | 3 | 1 | |
| 65-66 | | | 3 | 4 | |
| 67-68 | | | 1 | 5 | |
| 69-70 | | | 1 | 4 | |
| 71-72 | | | | 1 | |
| 73-74 | | | | 2 | |
| 75-76 | | | | 1 | |
| 77-78 | | | | | 1 |

Table 2. Mean fork length (mm, *n* within parentheses) and age-group in *Phoxinus phoxinus* from Lake Konnevesi, 18 May to 10 June 1983. The age was estimated in two different ways.

| Aging method | Age (years) 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| Estimation from length distrib. | 27.9 (219) | 50.9 (130) | 60.4 (213) | 66.7 (49) | 78.0 (1) |
| From otoliths | | | | | |
| males | | 49.2 (16) | 60.4 (14) | 65.0 (1) | |
| females | | 50.0 (10) | 61.1 (15) | 68.8 (17) | 78.0 (1) |

mined from the product of the Zippin population estimates and the mean wet weights for each species.

### 2.5. Production of *P. phoxinus* and *N. barbatulus*

The production of *P. phoxinus* and *N. barbatulus* at the sites fished quantitatively was estimated using Allen's (1951) graphical method in which, for each year, the number of survivors of each year-class is plotted against their mean weight. The area under this curve represents the annual production. The numbers of mature and immature *P. phoxinus* and *N. barbatulus* were obtained from the Zippin population estimates (Table 5). As both species were spawning at the time of sampling they were considered to have just reached their birth dates. The proportions of *P. phoxinus* and *N. barbatulus* of each age (Table 6) were estimated from the aged otoliths taken from the 18 May - 10 June 1983 samples, adjusted according to the length frequencies of all the fish caught. The mean weight of each age-group of fish was determined from the mean weights of aged sub-samples rather than from logarithmic length-weight regressions. This was because in each species the geometric means derived from such regressions were between five and ten percent lower than the arithmetic means. Since the aged four-year-old minnows were not a random sample, a subset of 11 fish which had a mean length similar to that estimated from the frequency distribution (Table 2) were used for the weight determination. In order to include egg weight in the production estimates, spent female *N. barbatulus* were not included in the mean weight determinations.

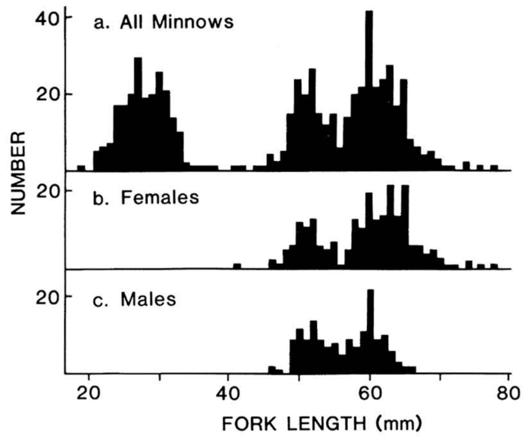


Fig. 1. Length-frequency distribution of *Phoxinus phoxinus* caught in the littoral zone of Etelä-Konnevesi between 18 May and 10 June 1983.

## 3. Results

### 3.1. Age, length and sex ratios in *P. phoxinus*

The 219 one-year-old minnows from the first peak in the length-frequency distribution had a mean length of 27.9 mm and were all immature. The mean lengths of the older fish aged from otoliths (Table 2) were compared with the lengths derived from the ratio of otolith ages for 2 mm length classes (Table 1) and the numbers from the size-frequency distribution (Fig. 1a). The agreement was generally good but the 2 mm discrepancy for four-year-old fish reflects our selection of a higher proportion of otoliths from the largest specimens and the lower estimate of 66.7 mm mean length (Table 2) will be the more accurate.

The differences in length between the male and female minnows aged from their otoliths were not significant ($\chi^2$ tests $P>0.10$) for either two- or three-year-old fish. The largest and oldest minnow caught was a 78 mm five-year-old female.

Apart from the first age-group, it was possible to determine the sex of all the fish caught between 18 May and 10 June. These comprised 233 females and 159 males. Ten fish, five of each sex, showed only slight gonad development and were classed as immature. They were all small two-year-old fish (mean ♀ size 47.2 mm, mean ♂ size 46.4 mm). The overall numbers of the mature minnows deviated significantly from a 1:1 sex ratio ($\chi^2 = 14.7$, $P<0.01$).

The two peaks in length-frequency in mature *P. phoxinus* occur on either side of the 56 mm length-class (Fig. 1a). The peak below this length, principally of two-year-old fish, contained an even sex ratio (68 females: 73 males) (Fig. 1b, c). The larger peak was composed of both three- and four-year-old fish, but between 56 and 63 mm length, where most fish are three years old, there was also an even sex ratio (77 females: 73 males) (Fig. 1b, c). Similarly, there were no significant differences in the numbers of male and female two- and three-year-old fish aged from otoliths (Table 2) ($\chi^2$ tests $P<0.10$). Thus, the difference in sex ratios was confined to the larger, four-year-old fish. The largest male minnow was 66 mm long but 24 females exceeded this length and, of the 19 aged four-year-old fish, 18 were female, as was the sole five-year-old fish (Table 2).

The number of minnows in each age-class declined, with the exception of three-year-old fish. Possibly in this case the diminishing effects of mortality were offset by fluctuations in year-class strength.

### 3.2. Condition

Female *P. phoxinus*. The total condition and GSI of female fish remained stable throughout May and June (Fig. 2a, Fig. 3a). In the first sample of fish, collected 18–20 May, there were significant product moment correlations ($r$) between the indices of condition and fork-length ($P<0.01$). Linear regressions of the form $CI = a \times bL$, where $a$ and $b$ are constants, were fitted to the data. Only 9.3 % of the variation ($r^2$) in somatic condition was accoun-

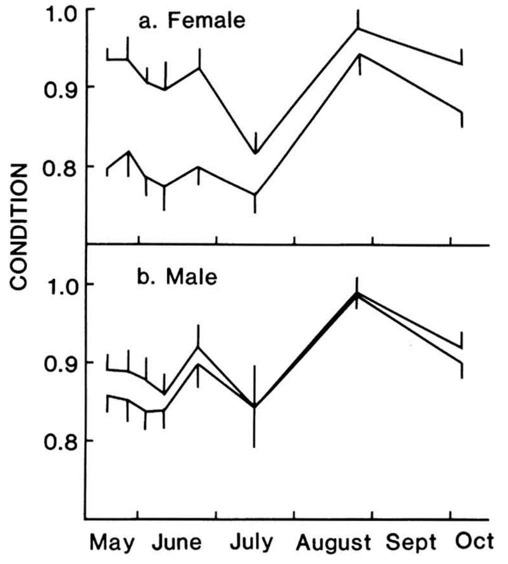


Fig. 2. Changes in condition in *Phoxinus phoxinus*. Upper lines — total condition. Lower lines — somatic condition. Vertical lines denote + or − 95 % confidence intervals.

ted for by this relationship ($a = 0.639$, $b = 0.0027$, $n = 105$) but for GSI and length the regression accounted for 52.7 % of the variation. The mean GSI values for each age group of mature females predicted by this regression ($a = -0.122$, $b = 0.0043$, $n = 105$) were: II group, 0.097, III group, 0.138, IV group, 0.165. There were no further significant relationships between these variables in the remaining May and June samples.

Between 3 June and 15 July there was a sharp drop in total condition principally because of a fall in GSI (Fig. 3a). This decline in GSI continued until late August, at which time both somatic and total condition were increasing (Fig. 2a). Total condition shows little change between October and May but somatic condition drops as resources are transferred from somatic tissues to the gonads (Fig. 2a, 3a). The July, August and October samples all showed significant positive correlations between total and somatic condition and length ($P<0.05$) but the level of individual variation was high and regressions between the variables explained only a small proportion of the total variance (range 27.9–36.8 %). The August and October samples (but not the July sample) showed significant relationships

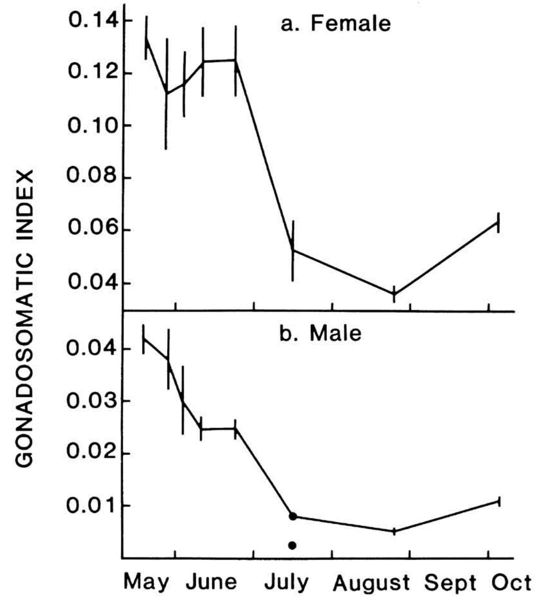


Fig. 3. Changes in gonadosomatic index in *Phoxinus phoxinus*. Vertical lines denote 95 % confidence intervals. Solid circles — see text.

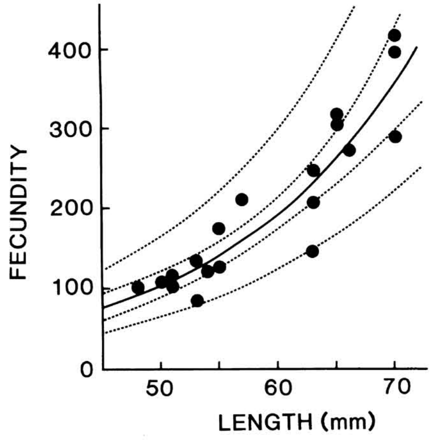


Fig. 4. The relationship between the fork-length of prespawning female *Phoxinus phoxinus* and fecundity (=the number of ripe eggs in the gonads). The curve represents the fit of an exponential model (Eq. 1). The dashed lines denote the 95 % confidence intervals for the curve (inner pair) and for new individuals (outer pair).

($P<0.01$) between GSI and length ($r^2$ values 49.4 and 40.2).

Male *P. phoxinus*. Male somatic condition remained stable from May to July, apart from a sudden jump on 23 June (Fig. 2b). During this period the decline in GSI (Fig. 3b) caused the gap between somatic and total condition to narrow but the general seasonal pattern was similar to that for female *P. phoxinus* (Fig. 2a, b).

The 15 July sample contained few male fish and Fig. 3b shows the GSI values for both the one II group specimen and the six I group fish (lower value) which would not spawn for the first time until the following year. By October, the mean GSI had risen to 0.0112 (1.23 % of body weight) compared to a mean of 0.0418 (4.65 % of total body weight) in the 18–20 May samples indicating considerable gonad development during the winter. As in the female *P. phoxinus*, there was a positive correlation between the indices of condition with length ($P<0.01$) in the 18–20 May samples, indicating that the larger fish were fatter and had relatively larger gonads than smaller individuals, though the variability was high. With the exception of the August sample, there were no other significant correlations between length and the indices of condition and GSI.

### 3.3. Reproduction and fecundity

The fecundity of fish species which spawn one batch of eggs each year can be simply determined by counting the number of ripe eggs present in the gonads prior to the commencement of spawning. Assessed on this basis, the minnows caught in Konnevesi between 18 and 20 May 1983 spawned 97.3 eggs/g total weight (±9.2, 95 % confidence intervals). An exponential relationship of the form:

$$\ln F = 1.47 + 0.0628\,L,\ r = 0.92 \qquad \text{(Eq. 1)}$$

accounted for 84.2 % of the variation between fork length ($L$) and the number of ripe eggs ($F$) (Fig. 4).

However, two considerations indicated that in this population the female *P. phoxinus* were fractional spawners. Firstly, the spawning season was prolonged; some females still contained ripe eggs on 15 July, 50 days after the first spent females were captured. Secondly the size-frequencies of the eggs from the gonads of ripe females showed that in addition to large ripe eggs and small oocytes, generally 0.30 mm or less in diameter and containing limited numbers of yolk droplets, there was a group or groups of intermediate-sized vitellogenic oocytes (Fig. 5). The number of oocytes in this intermediate size-range tended to de-

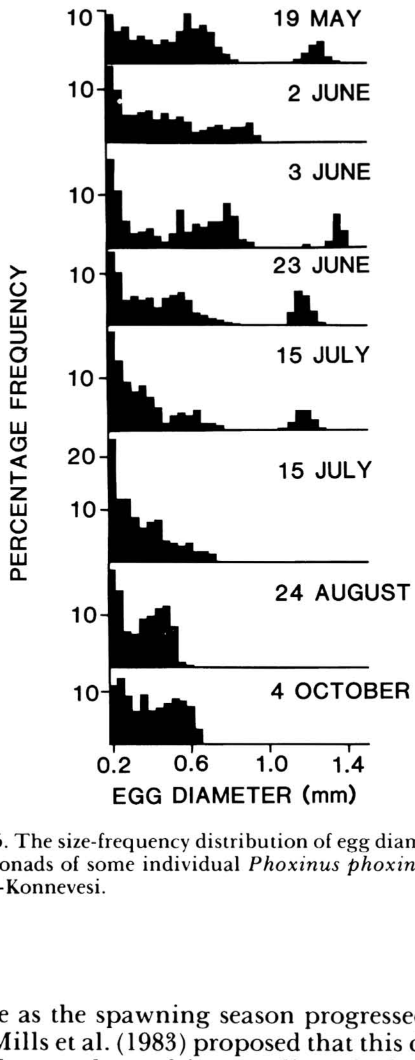

Fig. 5. The size-frequency distribution of egg diameters in the gonads of some individual *Phoxinus phoxinus* from Etelä-Konnevesi.

cline as the spawning season progressed (Fig. 5). Mills et al. (1983) proposed that this decline in the numbers of intermediate-sized oocytes could be used to provide an estimate of fecundity in fractional-spawning *N. barbatulus* in an English stream. This approach gives a minimum estimate, as any replenishment of the stock of vitellogenic oocytes during the spawning season will not be included.

Absolute fecundities are often standardized to allow comparisons to be made between fish of different lengths. Usually the absolute (total) fecundity is divided by either total or somatic wet weight to give relative fecundity (Mills et al. 1983). However, because of fluctuations in condition it was decided that a more stable index of fecundity would be provided by the relationship:

$$S = 10^5 F / L^3 \qquad \text{(Eq. 2)}$$

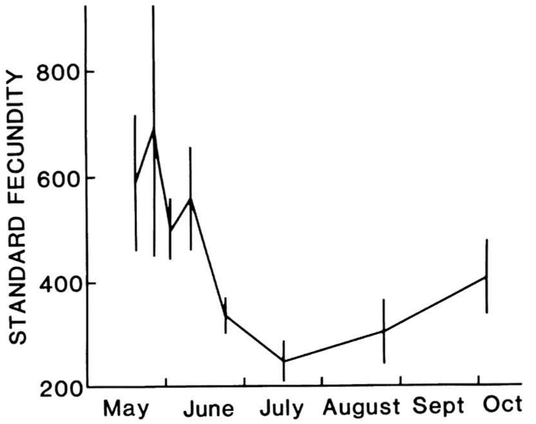

Fig. 6. The annual cycle of standard fecundity in *Phoxinus phoxinus* from Etelä-Konnevesi.

where $S$ = standard fecundity, $F$ = absolute number of eggs >0.3 mm, $L$ = length (mm). Standard fecundity was greatest in May when spawning was just beginning and it then fell to a minimum value in July, recovering in August and October (Fig. 6). The difference between the mean values in May and in July can be used to calculate a minimum estimate of annual fecundity. However, corrections can be made to improve the accuracy of this estimate. In equation 2 any increase in $L$ will depress the standard fecundity. Consequently, values determined once the growth season has commenced will slightly overestimate the number of eggs spawned simply because the stock of oocytes >0.3 mm will now be contained in a longer fish.

Whilst the precise growing season of *P. phoxinus* in Konnevesi is not known, most growth probably occurs between June and September (120 days), when the water temperature is over 10° C (Tuunainen 1972). The length of an individual fish in May, before growth and spawning have commenced, can be estimated from the length of fish caught at any time during the growth period. To do this the instantaneous rate of length increase ($GL$) for the year class to which the individual belongs must be substituted into the following equation:

$$\ln L_o = \ln L_x - (GL \cdot x / \Delta t)$$

where $GL$ = instantaneous growth rate, $\Delta t$ = length of growth season, $x$ = days of growth season elapsed, $L_x$ = length at day $x$ (mm), $L_o$ = overwintering length (mm).

Table 3. Estimated egg production by *Phoxinus phoxinus* from Lake Konnevesi.

| | Age (years) | | |
|---|---|---|---|
| | 2 | 3 | 4 |
| Mean fish length (mm) | 50.9 | 60.4 | 66.7 |
| Number of ripe eggs in prespawning fish (Eq. 1) | 106 | 193 | 287 |
| Number of eggs over 0.3 mm diameter determined from standard fecundity (Eq. 2) | | | |
| May | 834 | 1394 | 1877 |
| June[1] | 340 | 569 | 768 |
| Egg production over spawning season May - June | 494 | 825 | 1109 |

[1] Corrected values of standard fecundity.

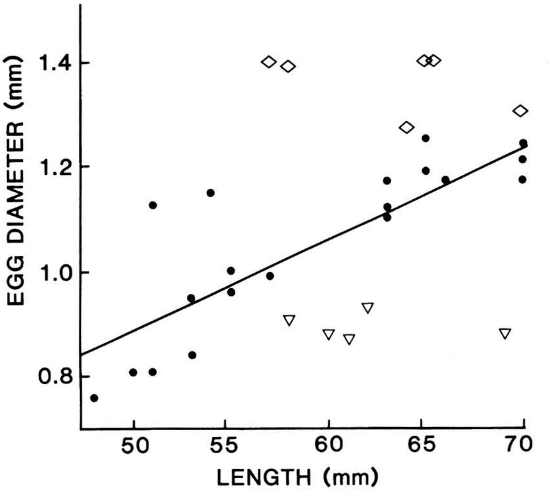


Fig. 7. The relationship between fork-length and the mean diameter of the largest group of eggs in *Phoxinus phoxinus*. Line-fit of a linear regression to the data from 18-20 May 1983 (circles). Triangles — 2 June, diamonds — 3 June.

For example, for a 62 mm III group minnow caught in the 15 July sample:

$$\ln L_o = 62.0 - 0.0988\,(45/120),$$

giving an estimated prespawning length of 59.7 mm.

A second correction is needed because three of the nine gonads examined from the 15 July samples contained any ripe eggs. As no fish in subsequent samples contained any ripe eggs, it was assumed that these ripe eggs would soon have been spawned. Only the remainder of the >0.3 mm eggs represented part of the spawning stock for the following year.

In May the mean standard fecundity was 632.6 (±112, 95 % confidence interval). The uncorrected July value was 247.4, increasing to 278.4 after correction for growth but reducing to 258.7 (±36, 95 % confidence intervals) after correction for the presence of ripe eggs. Substraction of this corrected S from the initial May figure gives a reduction of 373.9 in S over the spawning season. Substitution of this value into equation 2 enables the number of eggs spawned by a minnow of a given length to be determined (Table 3). These estimates are approximately four times greater than the numbers of ripe eggs found in prespawning females (Table 3). This suggests that the fish spawned at least four successive batches of eggs. As the first spent fish were caught on 26 May and some females still contained ripe eggs on 15 July, these batches were spawned over a period of approximately 50 days.

There was a significant ($P<0.01$) positive linear relationship between length ($L$) and the mean diameters of ripening eggs ($D$) in the 18-20 May samples (Fig. 7):

$$D = 0.0428 + 0.0170\,L, \; r = 0.82, \; N = 19.$$

This could indicate either that larger fish lay larger eggs or that the eggs in the larger fish are at a more advanced stage of development and will be spawned before those from smaller females. There were no significant correlations between egg diameter and length in the subsequent samples ($P>0.10$). The largest eggs (1.4 mm diameter) (Fig. 7) were found in a sample of *P. phoxinus* from 3 June in which the females freely released eggs from the oviduct following gentle pressure on the abdomen. Fish caught at another site the previous day (2 June) contained smaller eggs (0.87-0.93 mm diameter) which were presumably some days away from being released (Fig. 7).

### 3.4. Species composition and distribution of fish in the littoral zone

*Phoxinus phoxinus* was the numerically dominant species from the 18 littoral zone sites

Table 4. Species composition and distribution on 18 littoral zone sites in Etelä-Konnevesi.

| | Frequency Number | % | Occurrence Sites | % |
|---|---|---|---|---|
| *Phoxinus phoxinus* | 612 | 60.1 | 14 | 77.8 |
| *Nemacheilus barbatulus* | 281 | 27.6 | 18 | 100 |
| *Cottus gobio* | 38 | 3.7 | 13 | 72.2 |
| *Perca fluviatilis* | 27 | 2.7 | 6 | 33.3 |
| *Lota lota* | 26 | 2.6 | 16 | 88.9 |
| *Gymnocephalus cernua* | 19 | 1.9 | 8 | 44.4 |
| *Pungitius pungitius* | 7 | 0.7 | 6 | 33.3 |
| *Esox lucius* | 3 | 0.3 | 2 | 11.1 |
| *Rutilus rutilus* | 3 | 0.3 | 2 | 11.1 |
| *Lampetra* sp. | 1 | 0.1 | 1 | 5.6 |

fished between 18 May and 10 June 1983, forming 612 out of the 1017 fish caught (Table 4). The distribution of this shoaling species was uneven with 293 of these minnows caught on only three of the sites. At each of these sites the substrate included a high proportion of rocks larger than 30 cm diameter. No minnows were caught at four sites and at three of these the substrate consisted of small stones approximately 10 cm in diameter. The small immature minnows generally formed separate shoals from the adult fish.

*Nemacheilus barbatulus* formed 27.6 % of the catch and was very evenly distributed (Table 4). However, most of these were adults and only 18.9 % of those caught were juveniles aged one or two years. Sauvonsaari (1971) reported a similar phenomenon in his study on the species in other Finnish lakes. Mills & Eloranta (in press) give a detailed description of the age, growth and reproduction of *N. barbatulus* in Lake Konnevesi.

After *P. phoxinus* and *N. barbatulus* the most abundant species was the bullhead, *Cottus gobio*, which formed 3.7 % of the catch and was present at most sites (Table 4). Only immature or spent specimens were caught. Three age-groups were present, with mean lengths of 36.6 (7 fish aged), 56.3 (12) and 62.6 (7) mm. The burbot, *Lota lota*, though quite scarce (26 individuals) was found at all except two of the sites, with 11 sites containing a single individual. No sexual development was observed in any of these fish and there were three year-classes with mean lengths of 94 (3), 150 (9) and 207 (2) mm. Most of the specimens of *Gymnocephalus cernua* were also immature fish, probably one or two years old, though their scales could not be aged satisfactorily. A few larger fish (lengths 95–104 mm) did have developing gonads. Five age-groups of perch, *Perca fluviatilis* were captured with mean lengths of 52.9 (16 fish), 74.7 (3), 103.5 (4), 128.3 (3) and 140 (1) mm. None contained gonads weighing over 0.05 g. The three pike were 130, 155 and 176 mm long and all were approaching their second birthday.

### 3.5. Population density and biomass in the littoral zone

Fishing efficiency was lowest for the small benthic species *N. barbatulus* and *C. gobio* (Table 5). The latter species in particular showed a low attraction to the fishing gear and specimens were often difficult to locate and remove from amongst large rocks. Whilst the numbers caught in each age-group of *P. phoxinus* do not indicate the type of serious undersampling of the immature specimens that occurred in *N. barbatulus*, fishing efficiency for the juveniles was not as high as that for the adult fish (Table 5). Consequently, separate population and biomass estimates were made for the two groups. This was not possible in *N. barbatulus* due to the very small numbers of juveniles captured.

Goodness-of-fit tests showed that the Zippin triple-catch model was appropriate for the estimation of population densities (Mann & Penczak 1984) for the five most numerous species in the quantitative samples. The confidence intervals for the Zippin estimates (Table 5) were small relative to population size (except for *C. gobio*). The estimated density of *P. phoxinus* was 1.22 individuals/$m^2$ and that of *N. barbatulus* 0.40/$m^2$ out of a total fish density of 1.75/$m^2$. Immature *P. phoxinus* made only a minor contribution to biomass and the total contribution of all *P. phoxinus* was only 31.1 % of the total standing crop of 4.78 g/$m^2$, whereas *N. barbatulus* contributed 50.9 %. *L. lota* made the only other sizable contribution to the biomass (12.7 %) (Table 5).

### 3.6. Production of *Phoxinus phoxinus* and *Nemacheilus barbatulus*

Production estimates for both these species are approximately one gram per square meter (Table 6a, b). Peak production in *P. phoxinus* occurred during the second year of life but in

Table 5. Zippin population estimates from quantitative electrofishings (mean ±95% conf. interval), fish densities ($N/m^2$), mean weights ($\bar{W}$) and biomass estimates ($\bar{B}$) for the littoral zone of Etelä-Konnevesi.

| | Numbers of fish caught | Fishing efficiency (p) | Zippin population estimate | $N/m^2$ | $\bar{W}$ (g) | $\bar{B}$ ($g/m^2$) | Percentage of total biomass |
|---|---|---|---|---|---|---|---|
| Immature *P. phoxinus* | 132 | 0.53 | 147.3±14.7 | 0.453 | 0.153 | 0.069 | 1.4 |
| Adult *P. phoxinus* | 244 | 0.72 | 249.5±4.7 | 0.767 | 1.851 | 1.420 | 29.7 |
| *N. barbatulus* | 109 | 0.45 | 130.7±21.8 | 0.402 | 6.051 | 2.434 | 50.9 |
| *C. gobio* | 13 | 0.38 | 17.1±11.7 | 0.053 | 1.264 | 0.067 | 1.4 |
| *L. lota* | 11 | 0.61 | 11.7±2.6 | 0.036 | 16.917 | 0.609 | 12.7 |
| *G. cernua* | 10 | 0.65 | 10.4±1.3 | 0.032 | 4.76 | 0.152 | 3.2 |
| Others | 6 | - | - | 0.018[1] | 1.73 | 0.031 | 0.7 |
| Total | | | | 1.745 | 4.781 | | |

[1] Minimum estimate based on number caught.

Table 6. The densities $N/m^2$, mean wet weights $\bar{W}$, biomass $\bar{B}$ and annual production P of each age-group of *Phoxinus phoxinus* and *Nemacheilus barbatulus* in the littoral zone of Etelä-Konnevesi.

| | | Age (years) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | Totals | $P/\bar{B}$ |
| *Phoxinus phoxinus* | $N/m^2$ | 0.453 | 0.253 | 0.416 | 0.096 | 0.002 | | 1.220 | |
| | $\bar{W}$ | 0.16 | 1.16 | 2.04 | 2.85 | 4.91 | | | |
| | $\bar{B}$ | 0.069 | 0.293 | 0.847 | 0.274 | 0.012 | | 1.495 | |
| | P | 0.353 | 0.284 | 0.218 | 0.101 | | | 0.956 | 0.639 |
| *Nemacheilus barbatulus* | $N/m^2$ | 0.033 | 0.043 | 0.113 | 0.129 | 0.079 | 0.006 | 0.402 | |
| | $\bar{W}$ | 0.51 | 1.85 | 4.80 | 6.72 | 10.74 | 14.63 | | |
| | $\bar{B}$ | 0.017 | 0.079 | 0.541 | 0.867 | 0.848 | 0.089 | 2.441 | |
| | P | 0.051 | 0.229 | 0.232 | 0.403 | 0.133 | | 1.048 | 0.429 |
| *N. barbatulus* (numbers in each year class estimated from Eq. 3) | $N/m^2$ | 0.212 | 0.175 | 0.137 | 0.100 | 0.063 | 0.025 | 0.712 | |
| | $\bar{W}$ | 0.51 | 1.85 | 4.80 | 6.72 | 10.74 | 14.63 | | |
| | $\bar{B}$ | 0.108 | 0.323 | 0.658 | 0.672 | 0.677 | 0.366 | 2.804 | |
| | P | 0.261 | 0.461 | 0.224 | 0.320 | 0.168 | | 1.434 | 0.511 |

*N. barbatulus* it did not occur until the fourth year of life. This difference is partly attributable to the serious under-representation of one- and two-year-old *N. barbatulus* in our catches which will depress the estimates of density, biomass and production. Consequently, we fitted a linear regression to the densities of loach (Table 6b) in the older age groups (3 to 6 years old) times the area fished ($325.5/m^2$).

$$N = 81.0 - 12.1T, r = 0.88, \qquad \text{(Eq. 3)}$$

where $N$ is the number of loach in each year-class ($T$). The inclusion of these estimated numbers of juvenile loach (Table 6c) results in a small increase in biomass but a larger increase in annual production from 1.05 to 1.43 g per square metre. The production to biomass ratio is also increased, bringing it closer to the value calculated for *P. phoxinus* (Table 6).

## 4. Discussion

### 4.1. Age and growth of *P. phoxinus*

The mean fork lengths of minnows as measured either in their third winter of life or at their nominal third birthday include: Ulkokrunni Island, Bothnian Bay 54 mm; Papulampi, a small lake in Eastern Lapland 58 mm (Myllylä et al. 1983); Lake Konnevesi, central Finland 60.4 mm (this paper); an unproductive stream, Southern England 63 mm (Mann 1971); a small upland lake, Wales 65 mm (Wootton & Mills 1979); Lake Windermere, Northern England 68.8 mm (Frost 1943); a productive stream, Southern England 71 mm (Mann 1971); the River Tees, Northern England 78 mm (Crisp et al. 1974). Thus, whilst the Konnevesi population grows faster than the populations in the northern part of Finland it grows more slowly than those in other parts of Europe.

The life-span of *P. phoxinus* varies from populations in southern English streams (Mann 1971) and in northern England (Frost 1943), where few fish survive to their third birthday, to many populations which contain four- and sometimes five-year-old individuals, including the Maszarka Stream in Poland (Starmach 1963), German streams (Tack 1940) and the River Sirhowy in Wales (Williams & Harcup 1974). The maximum size reached by individuals in the short-lived populations is usually around 80 mm fork length, whilst fish can reach 120 mm or more in some of the longer-lived ones. The Finnish populations are all long-lived but in Konnevesi, and especially in the Bothnian Bay, the maximum size is also small (78 and 66 mm fork length respectively). Despite their slow growth rate, fish at Papulampi (Lapland) did reach 105 mm because they were exceptionally long-lived, with the maximum of 11 years being approximately double that of the other populations. While there are exceptions, *P. phoxinus* populations do tend to display a relationship between slow growth and a long life-span and conversely fast growth and a short life-span. This relationship is found between populations of several widely-distributed freshwater species, including *N. barbatulus* and *C. gobio* (Mann et al. 1984) and *Lota lota* (Eloranta 1982).

#### 4.2. Reproduction and fecundity in *P. phoxinus*

There is also a relationship between growth rate and age at sexual maturity. About 98 % of female, and 90 % of male, fish in the River Tees were sexually mature in their second year (Crisp et al. 1974) and in Windermere a few fish of this age were mature (Frost 1943). However, in the slow growing populations in Wales (Wootton & Mills 1979) fish began to spawn at the start of their third year of life and in Konnevesi, whilst most fish were mature at this age, 8 % did not mature until the start of their fourth year. In both these habitats the spawning season is restricted to less than two months compared to a two- to three-month season, commencing in May, in most habitats (Frost 1943; Papadopol & Weinberger 1975; Soin et al. 1981).

Where the sex ratio of *P. phoxinus* has been investigated, there is agreement that females predominate amongst the oldest age- or size-classes (Frost 1943; Podubský & Štědronský 1956; Myllylä et al. 1983; this study).

The literature contains several estimates of the fecundity of *P. phoxinus* where the numbers of ripe or large eggs in samples of prespawning females have been used to generate logarithmic regressions of fecundity on length. If these relationships are used to calculate the mean prespawning complement of large eggs in a 65 mm (fork length) female, fish from the River Tees are most fecund, with 488 eggs (Crisp et al. 1974) followed by 448 in the Seacourt stream, lowland England (Pitcher & McDonald 1973); 400 in the River Sirhowy, South Wales and 258 in Lake Konnevesi. Wootton & Mills (1979) found an even lower fecundity in the slow-growing population of a small upland lake but their estimate of 240 eggs "in the size class that was clearly separate from the other classes" is based on weekly samples over an extended period and probably includes fish which have recently spawned. Their relationship between length and fecundity accounted for only 30 % of the variance, against 84.2 % for the present study and 74.3 % in that of Williams & Harcup (1974). Little comparative information is available on egg size, though Soin et al. (1981) give 1.13 mm, Bullough (1940) 1.2 mm and Frost (1943) 1.4 mm as the diameter before water absorption, compared to a maximum of 1.4 mm in Lake Konnevesi.

Frost (1943) suggested that the Windermere minnow population produces only a single batch of eggs annually, though histological studies on prespawning Windermere fish do indicate three distinct size-classes of eggs (Bullough 1940), a common feature of fractional spawning species (Mackay & Mann 1969, Mills et al. 1983). Soin et al. (1981), Podubský & Štědronský (1956) and Papadopol & Weinberger (1975) all comment on this size distribution of eggs and suggest that spawning is done by degrees. Only Papadopol & Weinberger (1975) attempt to estimate total egg production over the spawning season. They divided the oocytes into four groups: 1) yellow 0.9–1.2 mm; 2) yellowish-white 0.4–0.7 mm; 3) semi-transparent 0.1–0.3 mm; 4) minute $>$0.1 mm. They assumed all eggs in groups

1-3 were shed and as group 1 comprised 25% of this total they suggested that at least four successive spawnings occurred. They give fecundities for various size ranges with fish of 57.5-62.4 mm standard length (approximately 60-65 mm fork length) from the Berga River in Roumania, containing 686 ripening eggs, higher than any other estimate, and a total complement of 2704 oocytes >0.1 mm diameter. No information is given of the size distribution of oocytes in the gonads during and after the spawning period and consequently it is difficult to assess the accuracy of the estimate. However, it is markedly greater than the estimated 1027 eggs spawned by a 65 mm Konnevesi female.

Absolute fecundity is lowest in *P. phoxinus* in the oligotrophic Welsh (Wootton & Mills 1979) and Finnish (this study) lakes. Some species, such as *N. barbatulus* and *C. gobio*, which are fractional spawners in productive habitats, not only have lower absolute fecundities in less productive habitats and towards the northern limits of their distribution, but also produce only a single main batch of eggs annually (Mann et al. 1984; Mills & Eloranta in press). Whilst this is clearly not true of the Konnevesi population of *P. phoxinus*, the distribution of this species extends further north than either *N. barbatulus* or *C. gobio* and we would suggest that populations such as the one in Papulampi and the one known to exist in the River Teno may only spawn a single group of eggs annually.

### 4.3. The littoral zone fish community

Sauvonsaari (1971) found up to 1.5 or 2.0 specimens of *N. barbatulus* per square metre in Lake Päijänne at depths of under one metre and amongst stones five to fifteen centimetres in diameter. Allowing for under-sampling of smaller specimens Sauvonsaari suggested that total density might be as much as four to five fish per square metre in Päijänne but in Lake Pälkänevesi it reached a maximum of only 0.3 loach per square metre. Our overall estimate of 0.40 fish per square metre or 0.71, allowing for size bias in sampling is closer to the latter estimate but includes sites with a variety of substrate sizes.

Sauvonsaari (1971) found that *C. gobio* followed *N. barbatulus* in abundance, often occurring under the same stone. Less common species were *P. phoxinus, P. pungitius* and *L. lota* with small numbers of *G. cernua, P. fluviatilis, E. lucius* and *C. poecilopus*. In Konnevesi the order of abundance is reversed, with *P. phoxinus* followed by *N. barbatulus* and then *C. gobio*. Eloranta (1983), however, found that *C. gobio* was by far the most abundant species in the rapids leading from Konnevesi, with only small numbers of *N. barbatulus* and no *P. phoxinus*. The factors controlling competitive advantage between the three species could be related to flow, habitat structure or food availability and obviously require further, more detailed examination.

In terms of biomass the order of importance in Konnevesi changes from *P. phoxinus, N. barbatulus, C. gobio* (Table 4) to *N. barbatulus, P. phoxinus, L. lota* (Table 5). Both Sauvonsaari (1971) and Eloranta (1983) found very few mature specimens of *L. lota* in littoral areas. This was also true of *P. fluviatilis, R. rutilus* and *E. lucius*. Of the less common littoral zone species we only caught adult specimens of *P. pungitius* and possibly *G. cernua*.

In conclusion, the littoral zone of Etelä-Konnevesi is dominated, in terms of numbers, biomass and production by *P. phoxinus* and *N. barbatulus* (Tables 4, 5, 6), two small non-commercial species. However, it does contain juveniles of commercial species, particularly of *L. lota* and *P. fluviatilis*.

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