YEAR GLASS STRENGTHS OF PERGH AND PIKE IN WINDERMERE

Charlotte Kipling

A year class consists of all the fish hatched in any particular year, and year class strengths are a measure of their abundance at some particular age. In the present work the strengths of all year classes have been estimated at the age of three years and are referred back to the appropriate year of hatch.

There have been big variations in year class strengths in Windermere during the past thirty years (Le Cren 1955, Kipling \& Frost 1970); the strongest pike (Esox lucius L.) year class was about seven times as abundant as the weakest, and the strongest perch (Perca fuviatilis L.) year class at least 400 times as abundant as the weakest. I have attempted to identify some of the factors associated with these variations.

The data have been obtained from the fisheries and sampling carried out by the FBA since 194I (Worthington 1950, Bagenal 1970).

The fishery for perch was operated from I94I to I964, using traps made of wire mesh, in May and June, which is the spawning season. Almost all the perch caught have been between 100 and $200 \mathrm{~mm}(4-8 \mathrm{in})$ in length, and have rarely exceeded 300 mm ( I 2 in ). In the north basin from 194 r to 1947 a weight of nearly 50 Mg (tons) of perch was removed. The fishery was not continued after 1947, but in all subsequent years up to the present samples have been taken in order to monitor the population. In the south basin the fishery continued from I941 to 1964 , but after 1947 was on a reduced scale. Nearly 70 Mg (tons) weight of perch was removed from the south basin, most of it in the first few years of the fishery. Samples have also been taken in the south basin to monitor the population.

The fishery for pike has been operated in every year from I944 to the present, using gill nets with a mesh of $64 \mathrm{~mm}\left(2 \frac{1}{2} \mathrm{in}\right)$ bar. The nets catch pike of lengths from 550 mm ( 22 in ) to over I metre ( 39 in ). They are set during the autumn and winter, and all the shallow areas of the lake are fished during the season. In the first year of the fishery about $75^{\circ}$ pike, weighing about 3 Mg (tons), were removed, and in each subsequent year about 300 pike (about I Mg (ton) weight) have been removed.

Thus the fisheries for perch and pike have differed considerably. The perch population in the north basin was reduced drastically from I94I to 1947 when the fishery then ceased; in the south basin the population was reduced from I94I to 1947 and a much less intensive fishery continued until I964. The pike fishery has continued every year since 1944, removing from both basins each year about one third of those pike large enough to be caught in the gill nets. The effects of these fisheries on the fish populations of the lake have been decisive and long lasting.

The ages of the fish, or a sample of them, were found from opercular bones, and, with the age of the fish and the date of capture known, each fish could be allocated to a year class.

In this brief report there is no space to discuss the interesting changes in population numbers, biomass and growth which have been observed in both the perch and pike populations, and mention will be made of these changes only when they are relevant to year class strengths. It is also not possible to discuss the methods used in estimating year class strengths or the errors involved. The methods have included catch per unit effort, virtual population, tagging experiments and simple mathematical models.

How important can one particular year class be to the whole population?
At any time there are in the lake perch and pike of all ages from under one year to about twenty years; both species have similar life spans. However, comparatively few survive beyond eight years, and most are sexually mature at an age of either two or three years, so the bulk of the


Fig. x. Age distributions of male perch caught in the north basin of Windermere in r943, 1953, 1963 and r966, expressed as percentage of the male catch.
adult population is contained in only a few age groups. Figure $I$ shows the age distributions of male perch caught in the north basin in four different ycars. In 1943 the two-year-olds were the most abundant age group, and in 1953 the catch was dominated by the 1949 year class, then aged four years. In 1963 the four-year-old I959 year class formed $70 \%$ of the catch and no two-year-old fish were caught; in 1966 the same 1959 year class continued to dominate the catch at age seven, with very few younger fish, and the 1957 and 1955 year classes were still in evidence. Similar examples could be given from the south basin. So for perch it is clear that a very abundant year class can dominate the population for several years.

Pike year classes have shown more stability than those of perch, and no one year class has dominated the pike population. Figure 2 shows the age distributions of male pike in the south basin in 1953 and 1963 ; they are much less variable than the perch.


Fig. 2. Age distributions of male pike in the south basin of Windermere in 1953 and 1963 , expressed as percentage of the estimated male population.

The estimated year class strengths of pike hatched in each year from I942 to 1964 in the north and south basins of Windermere are shown in figure 3. The main picture is the same in each basin, with strong year


Frg. 3. Estimated year class strengths of pike (1942-1964) and perch (1941-1964) in the north and south basins of Windermere.
classes in 1947, 1949, 1955, 1959 and 1963, and weak year classes in 1945, I946, I948, I953, 1954 and Ig61, and no failure in any year. What explanations can be put forward to account for these variations?

During his work on perch growth Mr Le Cren devised an index of temperature conditions in the lake during the summer (Le Cren 1958). It is a cumulative total of daily readings of the number of degrees by which the surface water temperature exceeds $14^{\circ} \mathrm{C}$. For example, if a reading for a certain day is $18^{\circ} \mathrm{C}$, this scores 4. The surface water temperature usually exceeds $I 4^{\circ} \mathrm{C}$ from the end of May to the end of September. The


Fig. 4. Year class strengths of pike and perch in the north and south basins of Windermere plotted against temperature index.
cumulative totals have ranged from 126 in 1946, the coolest year, to 515 in 1959, the warmest. Growth was found to be closely correlated with the cumulative totals which may also therefore be regarded as an index of growth and associated factors.

Year class strengths of pike have been plotted against this index in the year of hatch (Fig. 4), A definite association can be seen between low temperatures and weak year classes, and between high temperatures and strong year classes. The correlation cocfficients for the north and south
basins were both very significant. A comparison of the two basins shows that the 1949 and 1955 pike year classes were extremely successful in the the south basin, but less successful in the north basin. In both basins the pike year classes 1945 and 1953 were bolow expectation: in 1945 netting continued into the spawning season and in 1953 the combination of a warm May and cold June may have affected survival.

Other factors besides temperature were also considered, including estimates of the number of adult pike at the time of the hatch of the year class, and estimates of the biomass of the mature female pike which laid the eggs from which the year class was derived. In each case the corrclation with year class strength was not significant.

It therefore appears that the major part of the variation in pike year class strengths from 1942 to 1964 can be accounted for by variation in temperature conditions in the lake in the first fow months of life. Growth is suggested as a possible controlling factor. Cannibalism on young-of-the-year pike by pike a year older is mainly concentrated on pike which are smaller than 200 mm at the end of their first summer: in a warm year with good growth many more pike would exceed this critical length than in a cool year with poor growth.

The estimated year class strengths of perch hatched in each year from I94I to 1964 in the north and south basins of Windermere are shown in figure 3. The results differ from those for the pike mainly because there are many years of almost complete failure of perch year classes.

Ycar class strengths of perch have been plotted against the temperature index in the year of hatch (Fig. 4). It can be seen that there was some association, but not so close as that for pike. The rank correlation coefficients were very significant for the north basin, and significant for the south basin. However when the extremes of temperature, the four highest and four lowest values of the index, were omitted, the correlations were not significant. It is clear that when temperatures were low year classes were weak, and that very strong year classes occurred only when temperatures were very high, but that there were failures at all temperature levels. The 1947 year class was a comparative failure in both basins, and also the I949 and 1955 year classes in the north basin, despite high temperatures in those years.

Consideration of the biomass of the mature female perch which laid the eggs from which the year class was derived, and also of the total biomass of perch (aged more than one year old) in each basin at the time of hatch, showed that the strongest year classes occurred when biomass was low, and when biomass was high the year classes were weak. This suggests that shortage of eggs cannot have been a factor in controlling the population. Occasional cannibalism has been observed among perch, and this might have been a significant factor in reducing the survival of a year class when the biomass of perch in the lake was already high.

So far, therefore, it appears that extreme temperature conditions have affected perch year class strengths, and that strong year classes are un-
likely to occur when perch biomass in the lake is already high. These factors however are not adequate to account for the many years of total failure of perch year classes.

The possibility that predation by pike was an important factor was therefore considered. Perch are the main food of pike, and a significant part of this consists of perch of less than 550 mm in length, both adult and juvenile, described here as 'small perch'. Estimatcs of numbers of small adult perch suggest that by 1947 in the north basin there were not enough of these for the pike's food requirements, and that the pike would therefore have been eating juvenile perch; if so, this could account for the failure in the north basin of the perch year classes from 1946 to 1954 (with the partial exception of 1949). The shortage of small adult perch was partly due to the decline in population numbers, partly to changes in the age distribution, and partly to the increased growth of perch which took them more quickly beyond the critical length of 150 mm . In the north basin in 1943 more than $90 \%$ of the catch of adult percla was small, in I953 only $2 \%$. The same situation did not occur in the south basin at this time: there the reduction in perch numbers had been less drastic. By the early 1960 's, however, when the r 959 year class of perch had grown beyond 150 mm , there was a shortage of small adult perch in both the north and south basins, and this almost certainly contributed to the failure of perch year classes from 196I to 1964.

Many other factors are probably involved in determining perch year class strengths. I will mention just two: ice cover the previous winter, and predation by mergansers (Mergus serrator L.) The lake was frozen in the early months of 1947 and 1963, and the perch year classes hatched in these years were either complete failures or below expectation. Mergansers became abundant on the lake in the early Ig6o's; their diet is fish, and calculations suggest that in those years they could have eaten a weight of several tons of small fish each year (Atkinson and Bagenal, personal communication).

Figure 5 is an attempt to sum up the findings about year class strengths of perch. It brings in the temperature index, the biomass of perch already present, predation by pike and mergansers, and ice cover the previous winter. The year classes 1948, I949 and I950 in the south basin can be taken as examples. In 1948 the temperature index was below 150, the resulting year class a failure. In 1949 the index was over 400, biomass was low, predation was low and there was no ice cover the previous winter; the resulting year class was successful. In 1950 the temperature index was 255 , the biomass of perch already present was low, there was no ice cover the previous winter, but predation was high; the resulting year class was a failure.

To sum up, pike year class strengths have been found to be closely correlated with temperature conditions during the first few months of life, but perch year class strengths have been more variable. For success, a perch year class requires the presence of several positive
conditions and the absence of the many adverse conditions which could cause failure; a favourable combination of circumstances rarely occurs. These conclusions refer only to Windermere from 1941 to 1964.


Fig. 5. Diagram summarizing conclusions on perch year class strengths.
$\mathrm{T}-$ temperature index
$\mathrm{B}-$ biomass of perch already present
$\mathrm{P}-$ predation by pike and mergansers

I - ice cover the previous winter.

This article is concerned with year class strengths. This is only one aspect of the work on perch and pike which has been in progress for over thirty years. The investigation was initiated by Dr. E. B. Worthington when he was director of the FBA, and Dr W. E. Frost, Mr E. D. Le Cren, Miss J. C. McCormack, Mrs J. Pollard and Mr K. Shepherd have all been closely involved.

## References

Bagenal, T. B. (1970). An historical review of the fish and fisheries investigations of the Freshwater Biological Association, mainly at the Windermere Laboratory. J. Fish Biol., 2, 83-ror.
Kipling, C. \& Frost, W. E. (I970). A study of the mortality, population numbers, ycar class strengths, production and food comsumption of pike, Esox lucius, in Windermere from 1944 to 1962. J. Anim. Ecol., 39, 1×5-57.
Le Cren, E. D. (1955). Year to year variations in the year-class strength of Perca fluviatilis. Verh. int. Verein. theor. angew. Limnol., 12, 187-92.
Le Gren, E. D. (1958). Observations on the growth of perch (Perca fuwiatilis) over twenty-two years with special reference to the effects of temperature and changes in population density. J. Anim. Ecol., 27, 287-334.
Worthington, E. B. ( $\mathbf{9 5 0}$ ). An experiment with populations of fish in Windermere 1939-1948. Proc. zool. Soc. Lond., 120, ir3-49.

