The Determination of the Age and Growth of Pike *(Esox lucius* L.*)* from Scales and Opercular Bones

By

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Introduction

In fishery biology the annual "rings", "checks", or "annuli" on certain structures of the fish, such as the scales, opercular bones, otoliths, vertebrae, fin rays etc., are used to determine the age and sometimes, the growth of a fish. For the pike, *Esox lucius* L., scales have been used for this purpose by both European and American workers, but in a study of this species in Windermere opercular bones have been used as well as scales. This is apparently the first time that these bones have been used to determine the age and growth of the pike. Both the scales and opercular bones of the pike of Windermere presented difficulties and early results obtained from "readings" of them were unsatisfactory and inconsistent. Therefore the use of scales and bones has been critically examined in the hope that a satisfactory method of determining the age and growth of the pike from one or both of these structures might be evolved and this paper deals with the methods and results of the examination and the conclusions derived therefrom. Throughout this paper, which is essentially concerned with technique, only growth in length is considered and no reference is made to weight.

Materials

Material from Windermere, which includes scales and opercular bones, has been collected from 1944 to 1957. Most of the pike (about 5,000) have been taken in gill nets (mesh size 2½″ [6·3 cm] bar) set in the lake each year from October to March, and from these fish scales and operculars have been taken. In addition, samples of scales have been collected from about 2,000 pike caught in perch traps (mid-April to mid-June) and about 250 opercular bones have been taken from these fish. Pike from standard monthly seines have also provided some 300 scales and about 150 operculars. About 250 specimens of small pike, 0+ fish, were taken by seine and angling and hand net. As no serious attempt was made to rear pike in aquaria or ponds there is (with the exception of one fish) no material of known age available. Since 1949 over 1500 pike, mostly taken in perch traps, have been tagged with individually numbered tags on the upper jaw (maxilla) or on the opercular bone (the majority on the former), and released in the lake. By December 1957, more than a third of these tagged fish had been recaptured in perch traps, gill nets, seines, and by anglers. Scales were taken at the time of tagging and at recapture, and in addition the operculars were taken off those recaptured fish which were killed.

Methods

Measurements

All fish were measured from the snout to fork of the caudal fin (for a few specimens, covering a representative size range from 5 to 103 cm, length to the distal end of the longest caudal fin ray was also taken, i.e., the total length. The mean ratio of total length to fork length for these 157 fish was 1:1·06. The ratios did not vary with the size of the fish). Fish caught in gill nets from 1944 to 1952 were measured to the centimetre below and the necessary correction of 0·5 cm added to the means, thereafter the fish were measured to the millimetre below. All tagged pike were measured to the nearest millimetre, as were specimens caught by seine, angling, and hand net. The sex and condition of the gonad of the fish was determined by internal examination. The age of the pike is recorded so that fish in their first year of life belong to age-group 0, those in their second year of life to age-group I, in their third year to age-group II and so on, whereas fish which have completed their first year of life are recorded as age 1 and so on.

Treatment of scales and operculars

From experience the following technique has been adopted. The left opercular bone is removed with a scalpel and if immediately put into hot water for a few minutes it can be cleaned easily with a cloth between thumb and finger. When it is dry the rings on the bone are visible and these are much clearer after some months of storage of the bones. They are numbered and then stored in envelopes or jars, properly protected from predation by mice, insects, or fungi!

The scales are scraped off the pike from an area just above the lateral line and about midway along the body length. Here scales are first laid down (p. 323), moreover it was found that in this region there was a greater number of scales of typical form and large size than in samples from other parts of the body. Scales are stored in envelopes and when needed three or four with good centres are soaked in 4% NaOH solution overnight and then cleaned with a brush. They are mounted dry between two glass microscope slides.

Technique for reading opercular bones and scales

The rings on the opercular can be seen with the naked eye but a more reliable count of them can be made under a low power binocular microscope by reflected light on a dark background (Plate 2a). A scale projecting apparatus, with its greater magnification and transmitted light, gives the best and most

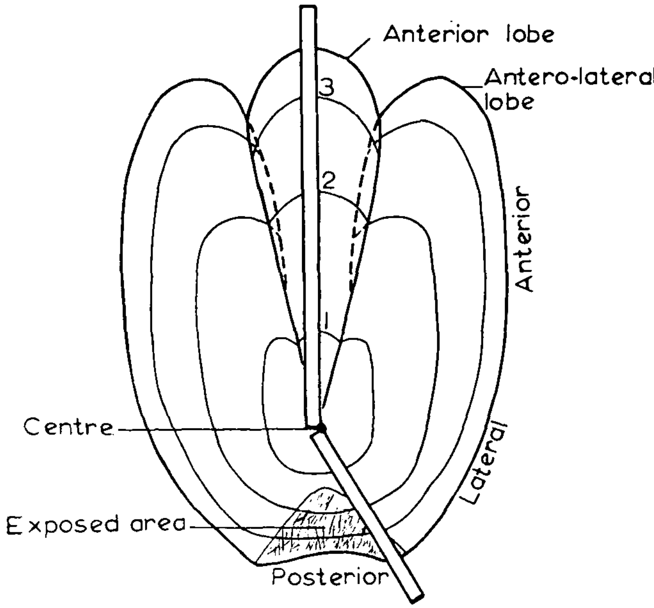

Figure 1. Diagram of pike scale showing position of cardboard strips used for back-calculation.

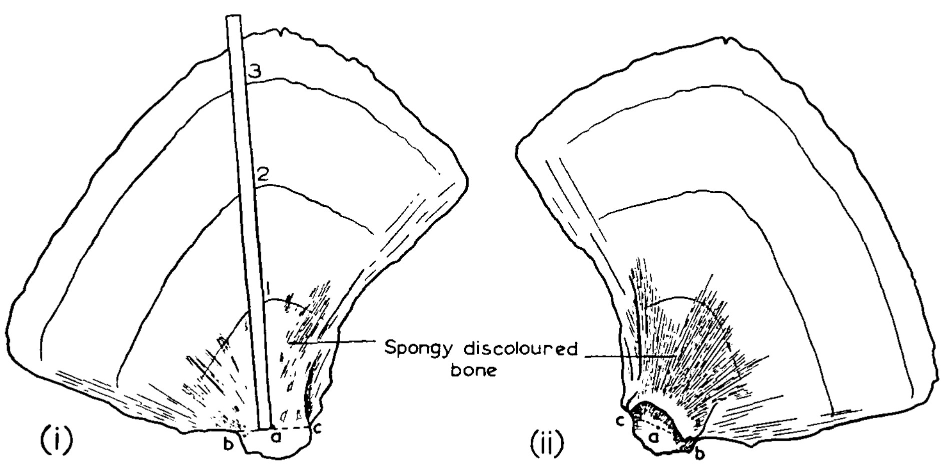

Figure 2. Diagram of pike opercular bone.
(i) Convex (outer) side, showing position of cardboard strip used for back-calculation on projected bone.
(ii) Concave (inner) side showing articulating surface of bone.
a = chosen centre of growth of bone.
b and c = indentations seen on outline of projected bone.

reliable results and is essential for accurate measurement of the rings (back-calculation (Plate 2b). The apparatus used magnifies the bone 5·3 times natural size. It was usual when projecting the bone to rest it on a glass plate but it was found that if the bone were in a glass dish of xylol instead of on the plate a much clearer image was obtained, and that this particularly applied to the thicker bones. This technique is now used for all the bones. The bone is slightly curved but it was found that measurements of the rings were much the same whether the concave or convex side of the bone received the light. In practice the convex (outer) side is placed on the stage of the projector so that the concave faces the source of artificial light.

The same projector is used for reading the scale but set up to give a higher magnification, namely 20 times natural size.

The image of both scales and bones is cast downwards on to a sheet of white paper on the table beneath the projector. To back-calculate growth a narrow strip of cardboard is laid on the image and on this the position of the rings is marked off with a pencil. The edge of the cardboard strip is placed at the centre of the scale and set on the long axis on the anterior part of the scale and at an angle on the posterior part as shown in Figure 1, on the opercular the strip is set at right angles to the line used in locating the chosen centre of the bone (p. 330). This centre is taken to be the point where a line drawn from the opposite indentations of the articulating "nub" is bisected. (Fig. 2(i)).

Ford-Walford plots

The graphic method described by Walford (1946) and summarized by Rounsefell and Everhart (1953) for determining age and growth has been found most useful in studying the age and growth of pike, and has proved essential to the use of operculars for this purpose. The formula on which this graphic method is based is essentially the same as that given by Ford (1933) and assumes that the successive yearly increments added to length decrease in magnitude in geometric progression, until a limiting value of total length (ultimate length) is approached. This pattern of growth is similar to that described by the equation of organic growth which has been derived by von Bertalanffy (1957).

Walford changes the form of the growth curve by plotting "length at age n" against "length at age $n + 1$", which gives a straight line relationship when the above assumptions are fulfilled, much simplifying the application of the method. A theoretical example is shown in Figure 3(a). The first year length is given by the intercept on the y axis (length at $0 + 1$), and the ultimate length at the intercept with the diagonal. The ultimate length is that length to which the growth pattern is directed, individual fish which come near to this length will continue to grow but probably at a different rate.

To plot the data thus, the age of the fish need not be known, a fact obviously of great importance when there is the possibility of missing annuli. Information on the length in two successive years (derived from tagged fish, or back-calculations) gives one point on the line, in three successive years two points etc., or knowledge of past catches from the same environment can supply information on the probable ultimate length, or, with more chance of error, first year length. Once any two points are fixed the line can be drawn, and the growth throughout life found by successive estimates. Length at age 1, see Figure 3(a),

p. 319, is found on the x axis and the corresponding value on the line read off from the y axis for length at age 2, and so on, or the estimates can be made in the opposite direction starting from any point on the line plotted at the end of any year's growth and working back to length at age 1. In this case a check can be made, as length at age 1 on the x axis must agree with the intercept on the y axis.

Growth thus determined cannot, of course, take into account variations caused by a good or bad growth season or individual irregularities. It is implied in the assumptions that the type of growth throughout life is fixed in the first year: once a fast grower always a fast grower and vice versa. In general the growth of pike in Windermere has been found to follow a linear relationship when plotted in the above manner, both for individual fish and means of various samples (Fig. 3), which makes it possible to use this technique for age and growth determinations.

Results

Determination of age and growth from the scales

Determination of age. On the scales of a fish are fine rings or circuli, the pattern of these rings is not uniform but shows interruptions or checks. When these are established as of annual occurrence then their number corresponds to the number of years of the fish's life. The check often consists of a number of narrowly spaced circuli, but the detailed appearance of it differs with the species of fish.

The shape of the pike scale is shown in Figure 1. The anterior part of the scale, which is the buried portion, is usually tricuspid, the posterior and protruding part, which comprises less than a third of the scale area, is rounded. Both parts of the scale have fine rings or circuli. These are not uniformly spaced but are arranged in alternate groups of widely and narrowly spaced circuli, a grouping which is much better defined on the anterior than the posterior part of the scale. Usually, but not always, one or two fragmented or irregular circuli occur among or at the anterior edge of the group of narrowly spaced circuli. On the anterior lobes of the scale this fragmentation produces a disrupted or "beaded" look, and at the sides a thin interrupted white line effect which cuts over into the circuli, the whole giving the check or annulus on the anterior part of the scale. On the posterior part of the scale fragmentation is more or less replaced by an absence of circuli and the hyaline layer so exposed gives a white line, which gives the check or annulus on the posterior part of the scale (Plate 1a and b),

The curious pattern, a chain-like deposition of the circuli, which WILLIAMS (1955) found anteriorly immediately after the first annulus on some pike scales from Michigan, U.S.A., was not found on the scales of Windermere pike.

To justify age determination of the pike from these checks on the scales it must be established that they are of annual occurrence. There are several methods of doing this, including that used by WILLIAMS (1955) who demonstrated the yearly occurrence of the annuli by examination of scales of pike of known age sampled over three years. Three attempts to rear pike for this purpose were made with Windermere specimens but only one fish survived more than one growing season. This specimen, which measured 5·5 cm when 0+ in June 1949, registered one annulus on the scale (Plate 1c) when it died

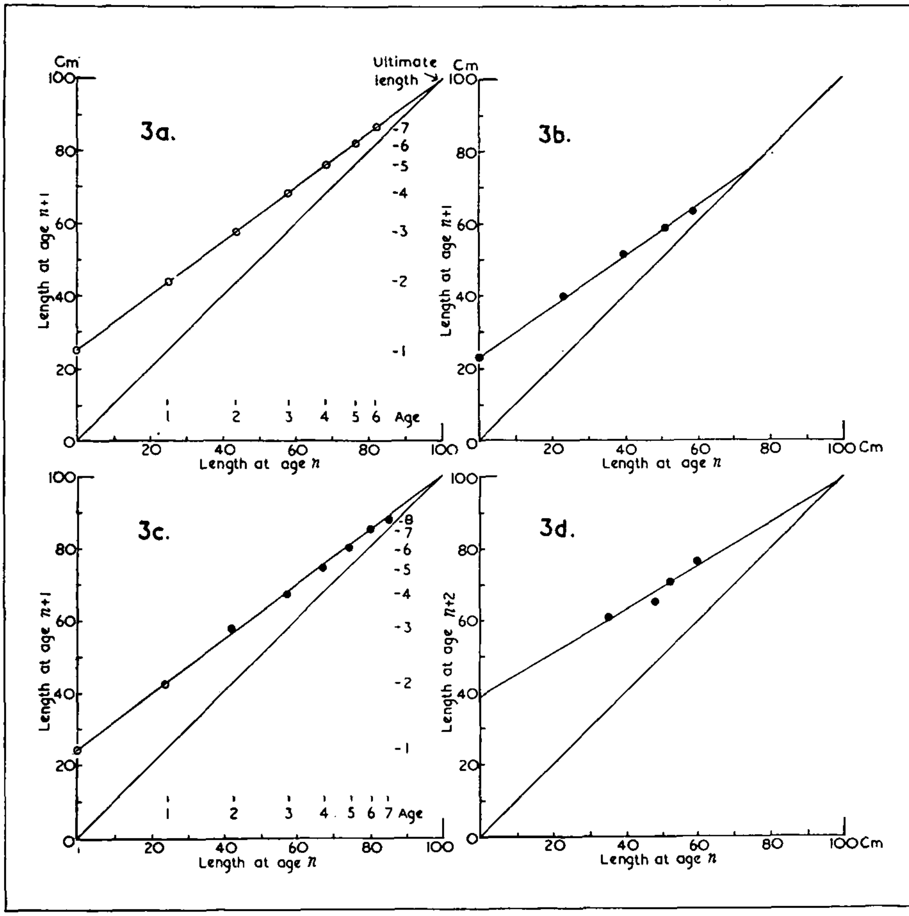

Figure 3. Walford plots of pike growth. On each plot the lower line is the diagonal. Open circles denote theoretical growth derived from the plots.

(a) Theoretical growth. This plot is based on two assumptions, that length at age 1 = 25 cm and that ultimate length = 100 cm. (These figures correspond to the growth of fast growing female pike in Windermere, see Table 3.) From the line joining 25 cm on the *y* axis to 100 cm on the diagonal theoretical growth for the first seven years has been derived, as described on page 317.

(b) Mean back-calculated growth. This plot shows the mean lengths at ages 1 to 5 of 54 male pike caught in gill nets 1946–1947 when aged 5 and over. The lengths were back-calculated from the opercular bones, using estimates for missing early annuli when necessary. To derive theoretical growth the line joining 23 cm on the *y* axis to 75 cm on the diagonal has been used. It agrees closely with the back-calculated growth. See Table 7.

(c) Individual back-calculated growth and example of missing first annulus. The black circles on this plot show the growth back-calculated from the opercular bone of a female pike (log number P 118(7)). The length of this fish back-calculated to the innermost visible annulus was 42·4 cm. To estimate its length at age 1 a line has been drawn by eye from 100 cm on the diagonal to fit the black circles as closely as possible. This line cuts the *y* axis at 24 cm, which therefore gives the estimate of length of this fish at age 1. Taking 24 cm as "Length at age *n* (= 1)", "Length at age *n* + 1 (= 2)" is seen from the line to be

42·5 cm. The innermost visible annulus, which was read to 42·4 cm, is therefore the second annulus, and the fish is aged 8.

(d) Estimation of length at age 2. These four points are plotted from the observed measurements of 4 female pike which were absent exactly two years between tagging and recapture. The line of best fit has been calculated by the method of least squares. It cuts the y axis at 38·9 cm, which therefore gives the estimate of length at age 2, two years having elapsed between each pair of measurements. It cuts the diagonal at 98·3 cm, thus further confirming the choice of 100 cm as the ultimate length for females.

November 1950 at 16·2 cm, and this annulus gave a back-calculated length (corrected) of 12·5 cm.

For the pike of Windermere the main proof of the annual occurrence of the checks is provided by the study of the scales of recaptured tagged fish. Scales were taken off each pike when it was tagged and also when it was recaptured, which might be any time from a few days to three years later. The number of annuli recorded on the scales of the returned fish agreed with the known years of absence since the fish was marked. This proof is best illustrated by photographs of scales taken at the time of tagging and on recapture as shown in Plate 1d and e. The evidence from returned tagged fish that the check or annulus was of annual occurrence has been accepted as sufficient proof of this phenomenon so that further evidence from other methods used in fishery practice was deemed unnecessary.

That the annuli are annual in occurrence justifies a count of them to find the age of the pike. But certain difficulties in reading the age from scales have been encountered. On some scales it is difficult to identify the first true annulus, on both anterior and posterior parts of the scale, because there may be an abrupt change of growth during the first year which results in a check (Plate 1b). Back-calculation of growth to this "first" annulus reveals that it is false, for such growth will be much below that expected for the first year. WILLIAMS (1955), who also found this false annulus, suggests that it is associated with a change from insect to a fish diet during the first year of life, which explanation could also apply to Windermere material (FROST, 1954).

In subsequent years false annuli or summer checks may occur on scales and they are difficult to detect because in pattern they may closely resemble the true annuli. If a scale shows two annuli unexpectedly close together it is reasonable to suspect that one of them is false, a suspicion which would be increased if, in addition, there was a discrepancy with the age and growth readings as obtained from the opercular bone of the fish (p. 330). (It may be noted here that false annuli are much easier to detect on the bone than on the scale; p. 328.) On the other hand, it is possible to make a mistake because there have been instances when a true check has been accepted as a false annulus. The false annulus does differ slightly in pattern from the true annulus, for although the fragmented look of the circuli which characterizes the true annulus is present, to some extent, on the anterior part and there is also a suggestion of the white line at the sides of the scale, posteriorly this latter often fades out. WILLIAMS (1955) has made a most detailed study of the "mid-summer false annulus", particularly of its form and methods of identifying it, based largely on scales from pike of known age. He finds that "the false check may consist of a hyaline line on the scale or of an abrupt crowding of the circuli either followed by the wider spacing of more rapid growth or a continuation of the closely-approximated circuli". The false check "may pass entirely round the scale as does an annulus

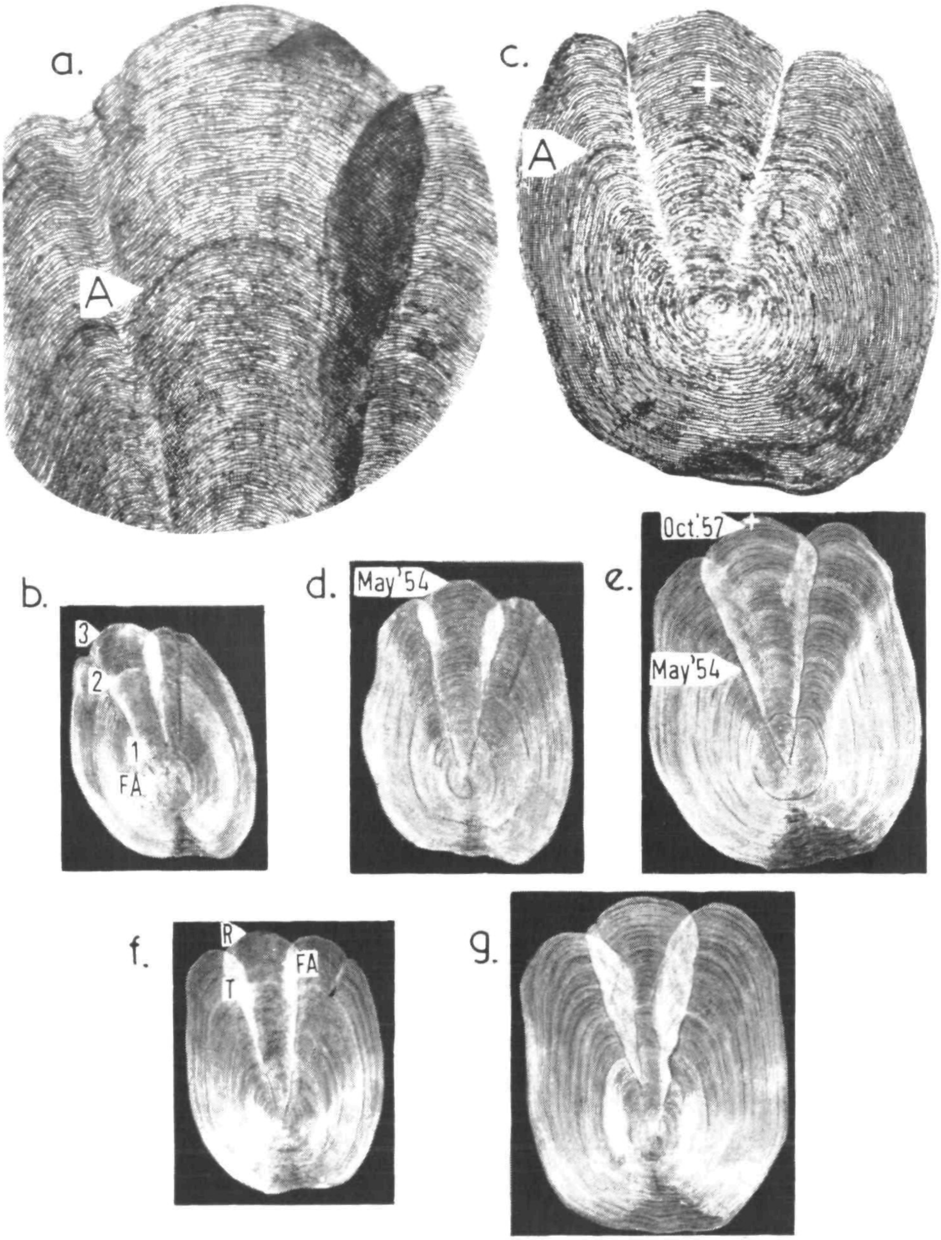

Plate 1. Pike scales.
See explanation, page 321.

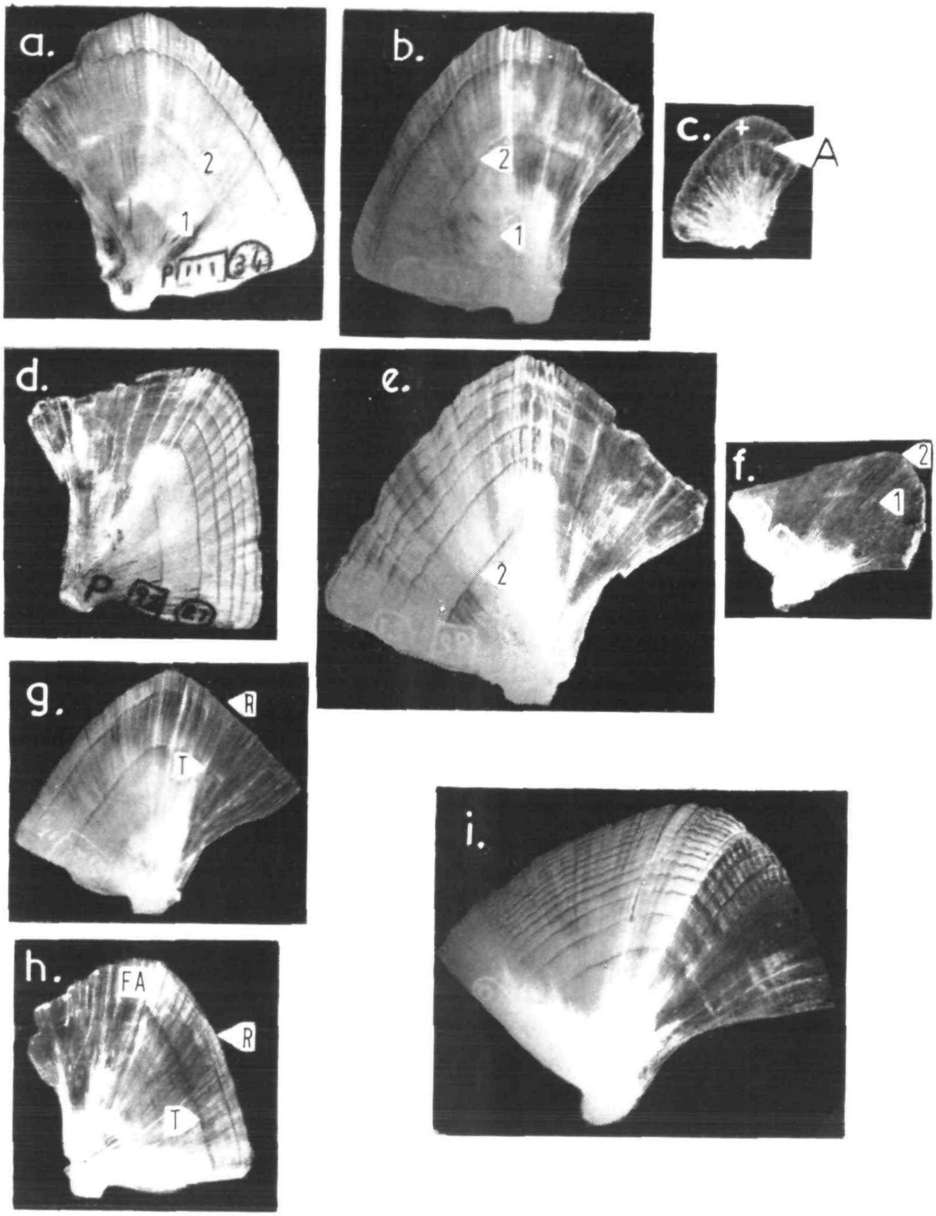

Plate 2. Operculars.

Explanation of Plate 1.

(a) Enlargement of part of scale (b) to show detail of the annulus, A, note narrowly spaced and fragmented circuli.
(b) Scale from 54·0 cm pike, well defined annuli anteriorly and posteriorly, age 3 years, last on edge: false annulus seen in first year.
(c) Scale from 16·2 cm pike reared 1½ years in aquarium showing one annulus, A, and plus growth: opercular of same fish, Plate 2 (c).
(d) Scale from 42·8 cm pike taken at time of tagging, May 1954, age 2 years.
(e) Scale from same fish (d), but lower magnification, at recapture 80·3 cm October 1957 3+ years later, showing 3 additional annuli and plus growth. (This fish a notably fast grower.)
(f) Scale from 61·0 cm returned tagged pike away one year, T tag, R return, showing an intermediate annulus which must therefore be false, FA. Opercular same fish, Plate 2 (h).
(g) Scale from 100 cm female, annuli not clear, possibly 12 anteriorly, compare opercular of same fish (Plate 2 (i)) which has 14 annuli, last on edge, clearly seen; the first missing.

Explanation of Plate 2.

(a) Opercular from 64·5 cm pike seen by reflected light, first annulus visible, female age 4 years, last on edge.
(b) Same opercular (a) when projected for reading by transmitted light, the standard practice.
(c) Opercular from 16·2 cm pike reared 1½ years in aquarium showing one annulus, A, and plus growth: scale of same fish, Plate 1 (c).
(d) Opercular from 64·5 cm pike seen by reflected light, first annulus missing, male age 8 years, i.e. 1 missing and 7 visible, last on edge.
(e) Same (d) but different magnification, seen by transmitted light.
(f) Opercular from 27·0 cm pike, age 2 years, showing first annulus visible, this usual in young fish.
(g) Opercular from 58·0 cm returned tagged pike (T, tag May 1955, R, return Aug. 1956). Fish away 1 year 3 months. Length back-calculated to annulus next but one to edge corresponds to known length at time of tagging, proving annulus is annual.
(h) Opercular from 61·0 cm returned tagged pike away one year showing an intermediate annulus which must therefore be false. Scale same fish, Plate 1 (f).
(i) Opercular from 100 cm female age 15 years, i.e., 14 visible and 1 missing annuli, showing that in big fish annuli much clearer on bone than on the scale, Plate 1 (g).

or it may be present only on a part, most often it is present from the anterolateral region to the posterolateral region of the scale. It is usually not present on the extreme anterior lobe nor is it usually pronounced at the extreme high anterolateral region of the scale, i. e., the inner portion of the two outer lobes". From which he concludes that "a good criterion for recognising a false annulus in many cases is its absence at the anterior or high anterolateral fields since annuli usually are distinct here whereas the false annuli are not". As a more precise method of determining a check as false or true "counts [of the circuli] were made from the annulus to the most distant point at the anterolateral margin and (on the same side of the scale) from the annulus to the posterolateral margin as near to the beginning of the exposed posterior section as possible". Then if "the number of anterolateral circuli is more than twice the number of posterolateral circuli, the mark is likely to be a false check", conversely if less than twice the number then the mark is likely to be a true annulus. False annuli on the scales of pike of Windermere were suspected as such from their form (on the criteria mentioned earlier in this paragraph) and usually proved so by relating the growth increment involved with comparable increments as obtained from other sources. On the scales of returned tagged fish the presence of false annuli is certain when more annuli are seen than the known years of absence

Table 1

Examples of back-calculations of length (cm) from difficult scales and operculars of individual fish. Both fish have the first annulus missing on the opercular and other annuli have been missed on the scales. The opercular readings have been accepted from age 2 (37·0 and 45·0 cm) upwards

Male Log No. P 182 (12)		Female Log No. P 182 (11)	
Scales	Opercular	Scales	Opercular
16·9	37·0	26·6	45·0
36·8	50·0	46·6	59·9
52·5	56·5	65·8	67·0
60·0	59·8	74·2	73·9
64·4	62·9	79·9	80·6
67·4	65·5	86·8	85·8
69·7	68·2	92·2	90·0
72·1	69·9	95·6	93·2
74·3	71·7	98·2	95·8
75·0	73·3	100·0	98·4
–	75·0	–	100·0

(Plate 1 f). Finally false annuli may be suspected (justifiably or not) when the age as determined from the scale differs appreciably from that obtained from the opercular bone, for although false annuli are also found on the bone they appear to occur less often and moreover are usually much easier to identify than those on the scale.

Comparison of the age as determined from the anterior part of the scale and from the opercular bone indicates that, in some older fish, annuli on the anterior part of the scale have been missed (Plate 1 g). Two examples from individual fish are shown in Table 1. In both these and in most other cases after comparison of increments of growth the opercular reading has been accepted in preference to the scale. The main reason for the differences seems to be that in the middle years of the fish's life "true" annuli on the scale have been considered to be "false" and have been omitted.

The annulus on the anterior part of the scale can pass round, but with a different pattern, to the posterior part (p. 318). This usually makes it possible to confirm the age, i.e., the number of anterior annuli, by a count of the posterior annuli, particularly as on some scales the white hyaline line which is the check on the posterior part is clearer than the narrow and fragmented annuli that give the check on the anterior part. The age of 85 fish ranging from 12 to 102 cm was read from both anterior and posterior annuli on the scale. On fish of up to about five years the number of annuli seen anteriorly and posteriorly was the same but with increasing age there was a discrepancy, sometimes amounting to three years, between the two readings, and in most but not all cases the anterior part gave the higher number. When this was so the discrepancy may be explained by the inclusion of false annuli in the anterior count since these false checks may have no counterpart on the posterior part of the scale (page 320). Alternatively if the posterior part has the higher number it may be due to omission of true annuli on the anterior part because they were mistaken for false ones. In older pike the annuli on the posterior part of the scale, particularly those near the edge, can be congested and ill defined. This makes it difficult to relate the anterior and posterior part of the same annulus, with the result that the two parts can be counted as different annuli so that the ages as read from the anterior and posterior part of the scale differ. In addition, if the age of a large (and old fish) is read from the posterior part of the scale only there is a likelihood of an error because the congestion of the annuli here often makes it difficult to dissociate one annulus from another.

To find out when scales are laid down some specimens of 0-group fish, young-of-the-year, were examined. Those of 3·4 cm and less had no scales. The smallest specimen with scales was 3·6 cm, a fish caught in June, but as it already showed three circuli the platelet was probably laid down when the fish was a little smaller; another June-caught pike of 3·9 cm had similar scales. A specimen of 4·0 cm, caught in mid-July, had scales with 5 and 6 circuli. On this and similar evidence it may be accepted that the pike puts on scales when it is about 3·5 cm long and that in Windermere this length is usually attained sometime in June. It was noted that the scales first appeared just above and below the lateral line and practically simultaneously along the whole body length. A fish of 3·8 cm caught in late June had still no scales on the back or belly.

The exact time of year when the annulus is formed on the scale is not easy to determine as it is difficult to detect it at the edge of the scale until some plus growth has also been laid down, moreover the ill defined boundary of the annulus adds to this difficulty. The pattern at the edge of the scales taken from fish of different sizes and caught from February to July has been examined and recorded as "annulus not yet formed", "annulus forming", and "plus growth present". On Figure 4 these records are plotted for date against length of the fish. The figure shows that from mid-February to mid-May the annulus may be in process of forming. As almost all the fish examined in late April and early May have the annulus forming or already formed (the latter evident from the new (plus) growth outside the annulus) we may take it that the time of annulus formation on the scales of pike of Windermere is, in general, the first half of May. HARTLEY (1947) notes that "In East Anglia the late summer is the season of formation of checks on the scales", and WILLIAMS (1955) found that in the southern latitude of Michigan, U.S.A., the time of annulus formation ranges from early March to 1. June, and in the middle and northern latitudes of the State from late March to late June.

On the evidence from Windermere and because many recently hatched pike have been found in early and mid-May the conventional birthday of pike of Windermere is taken as 1. May.

Determination of growth. The "back-calculation" of growth of a fish from its scales has been applied to many species. The method is based on the annual character of the check and on there being a proportional relationship between the growth of the fish and its scales.

In age and growth studies of the pike back-calculation of growth (also often referred to as "estimated growth" but *not* used in this sense in this paper) has been used by several workers including ALM (1919, 1921), NILSSON (1921), HAAKH (1929), VAN ENGEL (1940), MILLER and KENNEDY (1948), HEALY (1955), OLIVA (1956), and MUNRO (1957); of these MILLER and KENNEDY, HEALY, and OLIVA, justify in different ways the calculation of growth of the fish, although none of them presents proof of the validity of the method and in some published tables LEE's phenomenon is apparent but unexplained.

Early in the present investigation attempts were made to back-calculate the annual increments in length from checks on the scales.

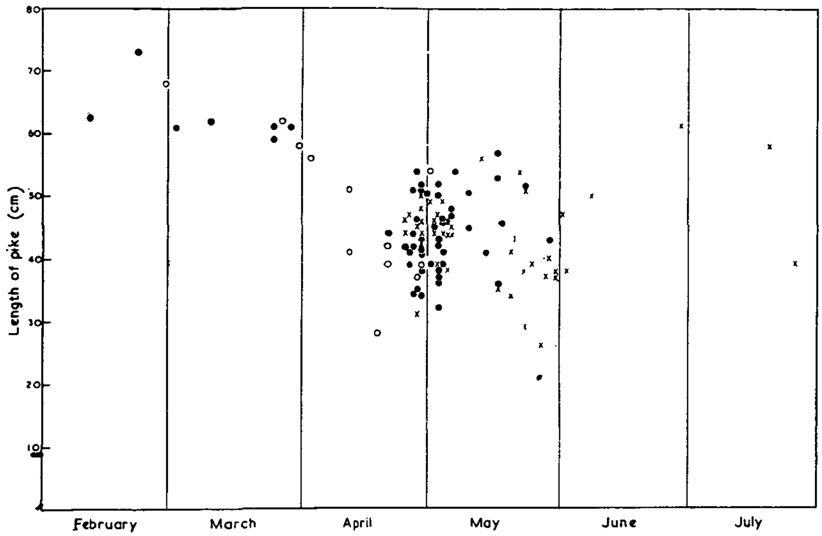

Figure 4. Time of annulus formation on scales.
Open circles = annulus not yet formed; black circles = annulus forming; crosses = plus growth present.

At first these calculations were made from the annuli on the anterior part of the scale (the usual fishery practice) later they were also made from the annuli on the posterior part (Fig. 1); no calculations were made laterally on the scale, although it was learned later that this was the technique of MILLER and KENNEDY (1948) and OLIVA (1956), who were the only workers who did not read the anterior lobe of the scale.

Throughout the present investigation it was found that, for purposes of back-calculation, it was difficult to "pin-point" the limits of the annulus, and it was soon realized that this was definitely one of the reasons for the inconsistencies which marked the results obtained from back-calculation. Under low power magnification the annulus, both anterior and posterior, appears to be reasonably well defined, but when the scale is projected for back-calculation the outer edge or boundary of the annulus, particularly on the anterior part and more especially in older fish, is often difficult to locate precisely with the result that growth as calculated from the measurement made on the scale may differ, sometimes markedly, from the growth actually made.

It was thought unlikely, however, that such a technical fault provided the whole explanation of the discrepancies which characterized growth as calculated from scales, for it was found that: —

(1) Growth as back-calculated from the anterior part of the scale of a fish which had been tagged and recovered later showed poor agreement between the measured length of the fish when it was tagged and the length at that time as back-calculated on subsequent recapture; such calculations from the posterior part of the scale sometimes showed closer agreement.

(2) Lengths back-calculated from the anterior and from the posterior parts of the same scale and for the same year of life, did not always agree. For a few fish there was good agreement between the readings from the two sources,

notably for fish of up to three years old, but for the majority there were discrepancies (often a difference of 5 or 6 cm) between calculated lengths as made to the anterior and posterior annuli.

(3) Growth as back-calculated from the anterior part of the scale did not agree with that back-calculated from the opercular bone, although there was sometimes quite good agreement between back-calculations from the bone and the posterior part of the scale.

In view of these anomalies the possibility that the growth in length of the pike and the growth of its scales were not in direct proportion was therefore examined. To do this the length of the scales as recorded on the cardboard strips used for back-calculation were measured; these measurements, made for both the anterior and posterior parts of the scale, were plotted against the lengths of the individual fish from which they were taken. (Fig. 5(a)). The figure shows that the points for the anterior part of the scale lie on a curve, which indicates that growth of the anterior part of the scale and the growth of the body of the pike is allometric. On the other hand the points for the posterior part of the scale lie on a straight line, which indicates that the growth of the posterior part of the scale and of the body of the pike is isometric. This latter line cuts the x axis at 3·5 cm which gives the length at which scales were laid down (coinciding with the length found by observation, p. 323). Therefore direct proportion could be used for back-calculation from the annuli on the posterior part of the scale, provided that allowance is made for the length of the fish when the scale was laid down. However, although the posterior annuli appear to be reasonably well defined, it can be difficult, especially in older fish, to locate precisely the boundary of the annulus, consequently growth estimates obtained from these back-calculations are liable to error, and as the distance between individual annuli is so small (particularly in older fish) exact "pin-pointing" of the annulus is essential. These errors on the posterior part are relatively more important than on the anterior part, because the total length of the posterior part of the scale is so much shorter, so that the errors will be of greater account when the measurements on the scale are expressed in terms of fish length. Therefore the posterior annuli have been rejected as the main method of growth determination, although they are sometimes a useful adjunct to age determinations from the anterior part of the scale.

To use the anterior part of the scale for growth determination it is necessary to provide a method of correction for the allometry and for the length of the fish when the scale was laid down. A logarithmic regression equation was therefore calculated using measurements of fish length and length of the projected image of the anterior part of the scale of 77 fish ranging from 10 to 106 cm. This provides correction for both the above factors. The resulting equation was:—

$$\log_{10}F = 0{\cdot}836 + 0{\cdot}749 \log_{10}S$$

where F is the length of the fish and S the length of the projected image of the scale. A curve for correcting for allometry the back-calculations made from the anterior part of the scale was drawn from this equation. Using this curve a simple apparatus was constructed (Fig. 6) (LE CREN, 1947) and this has been found most useful in enabling rapid determinations to be made of the necessary corrections, which can be of considerable size. For example, if back-calculation by direct proportion of the rings on the anterior part of the scale of a fish of

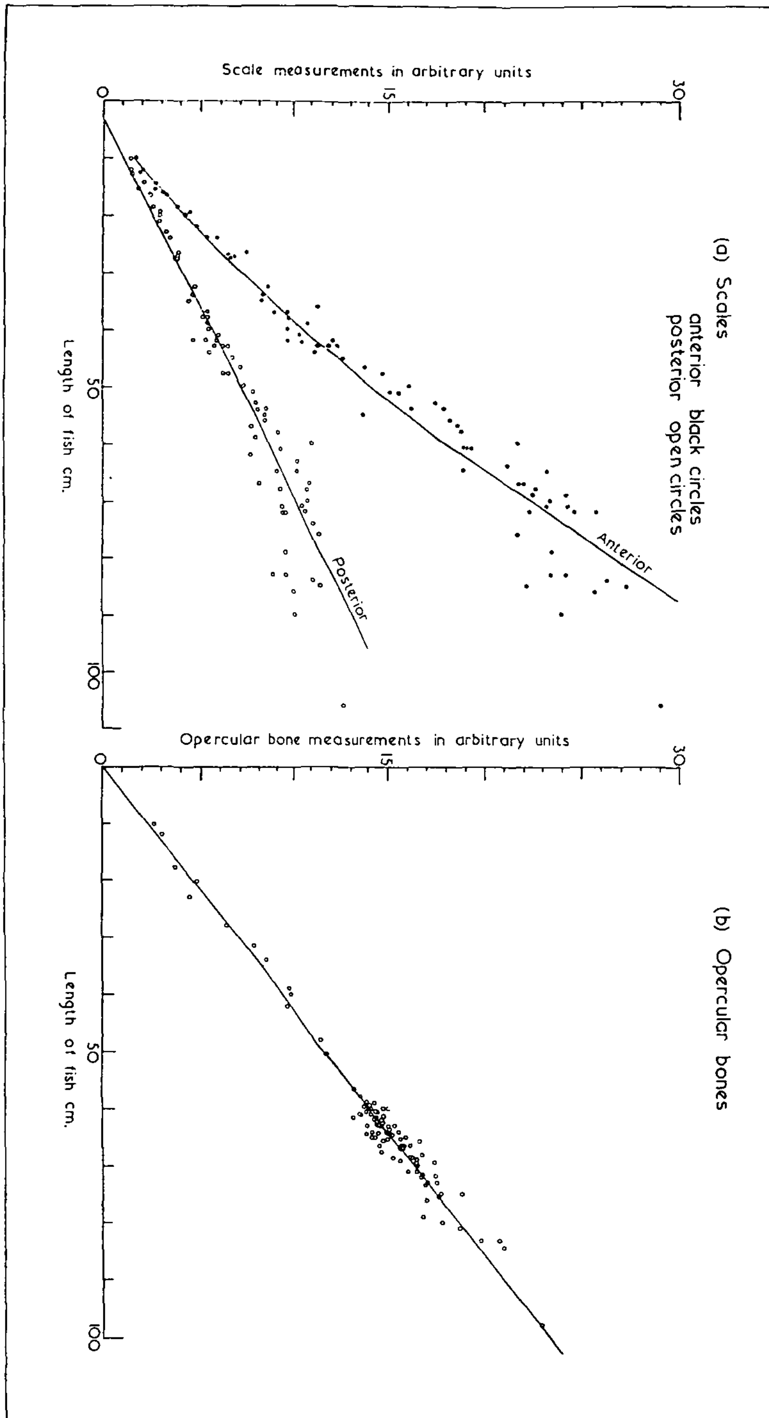

Figure 5. Tests for allometry.

(a) Scales. The plotted points for the anterior part (black circles) lie on a curve, for the posterior part (open circles) they lie on a straight line cutting the x axis at 3·5 cm.

(b) Opercular bones. The points lie on a straight line which passes through the origin.

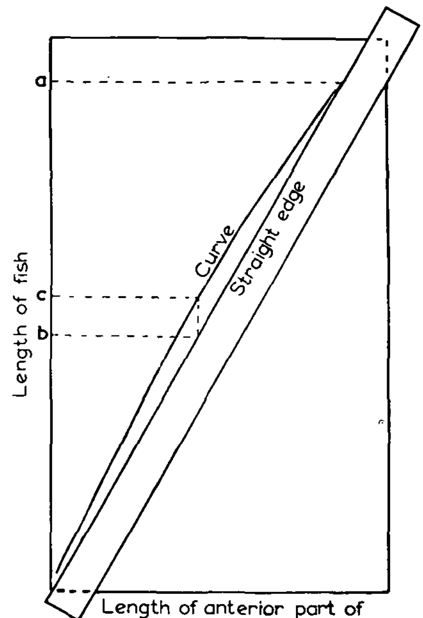

Figure 6. Diagram showing the method of correcting back-calculations for allometric growth.
a = final length of fish; b = recorded back-calculated length by direct proportion; c = correct back-calculated length.

90 cm showed the first year length to be 14 cm and second 28 cm, then the corrected values would be 22 cm and 38 cm, differences of 8 and 10 cm. All back-calculations from measurements of the anterior part of the scale have subsequently been corrected for allometry, *and all further references to scale readings automatically include correction for allometry unless the contrary is stated.*

Thus when correction for allometry has been made for readings from the anterior part of the scale, a moderately satisfactory method for determining the age and growth of the pike from its scales is available. However, as previously mentioned, there are difficulties in the use of the scale for this purpose.

Determination of age and growth from the opercular bones

Early in his study of the age and growth of perch (*Perca fluviatilis*) in Windermere, LE CREN (1947) found that opercular bones were much more satisfactory for age determinations than were scales. In view of this opercular bones as well as scales were taken from the pike of Windermere and have proved invaluable in the age and growth determination of this fish.

Determination of age and growth. On the opercular bone of fish such as perch and pike, there are "bands" which stand out because they have a different degree of whiteness from the rest of the bone (Plate 2). If these checks in the general bone structure are established as annual they give the number of years of the fish's life.

The shape of the opercular of the pike is shown in Figure 2. The bone is slightly curved, the convex and concave surfaces being the outer and inner sides of the bone respectively when it is attached to the pike. The point of attachment of the bone to the skull is seen on the concave view (Figure 2 (ii)). At this point, the centre of the bone, the opercular is thick and this thickness fans out into a spongy tissue which often becomes orange-brown and glutinous. (This rough and dense part of the bone caused much trouble since it often covered the first and sometimes the second years annuli and so obscured them, page 331). The bone shows an alternation of pattern which coincides with different types of growth. Seen by reflected light on a dark ground the opercular bone shows a broad opaque white zone (grading outwards from a milky white "line" to a more watery white area) corresponding to the rapid summer growth which passes into a narrow transparent dark zone, the winter growth, which ends abruptly with a sharp line of discontinuity between it and the next opaque zone (Plate 2a). This sharp line marking the end of the winter's growth is taken as the end of a year's growth and accepted as the annulus. In practice the bone is magnified and read by transmitted artificial light (which alters the "colour" of the two zones) (Plate 2b). These conditions make it easier to locate the boundary of the annulus precisely, although this, under any circumstances, is usually much better defined on the bone than on the scale.

Evidence that the zones of different growth pattern are annual is available from four sources: —

(1) Small fish. The opercular bones of small pike of less than 20 cm caught in Windermere between May and November in no case had an annulus. Evidence will be presented later (page 331) that such fish are almost certainly under one year-old. Therefore if any of them *had* shown a ring the annual character of such a check would be disproved.

(2) The opercular bone of the one pike reared in an aquarium (Plate 2c) and known to be 1+ years showed one annulus on the bone (and some plus growth).

(3) The growing edge of the opercular bones taken at different seasons of the year was examined. Those taken in summer and autumn had an opaque white zone at the edge whereas in winter and spring (until April-May) there was a transparent dark zone on the edge. This alternation of the two types completed the annual cycle.

For testing the annual character of the checks on the opercular data were used from those fish tagged in early spring, (thus avoiding the complication of plus growth) and recaptured after exactly one or two years absence. The lengths of all tagged pike were recorded at the time of tagging and again on recovery. If the length obtained from back-calculation to the outermost ring on the bone (i.e., that nearest to the edge) or the next but one for two years absence, tallies with the measurement of the fish when tagged, it may be concluded that the check is of annual occurrence (Plate 2g). This has been found to be so (Table 2) for it can be seen that for each fish the relevant reading from the opercular agrees reasonably well with the actual measurement at time of tagging.

Operculars, like scales, may show false annuli (Plate 2h). These are usually recognizable because they show as an abrupt instead of a gradual change or fading out from the opaque to the thin transparent zone. This characteristic is easier to pick out in the early years with their rapid growth than in the later years of slow growth so that recent false annuli are less likely to be detected

Table 2

Comparison of actual measurements and back-calculated lengths (cm) for seven tagged pike recaptured after (a) one year's absence (b) two years' absence

(a) One year's absence

Fish Log No.	P 210 (97)			P 223 (23)			P 238 (10)			P 217 (137)			
Age	1	2	3	1	2	3	1	2	3	1	2	3	4
Actual measurements on tagging and recapture	–	43·4	53·7	–	42·2	53·3	–	44·1	51·4	–	–	49·0	54·6
Back-calculated from opercular	(26)	42·8	–	25·3	43·5	–	26·0	44·5	–	19·7	34·3	48·9	–
Corrected back-calculation from scales:—													
collected on tagging	24·6	–	–	24·5	–	–	27·2	–	–	21·5	35·4	–	–
collected on recapture	23·0	42·8	–	27·8	44·0	–	27·5	44·2	–	22·7	36·0	50·5	–
Uncorrected back-calculation from scales:—													
collected on tagging	20·0	–	–	20·3	–	–	22·9	–	–	16·1	31·6	–	–
collected on recapture	17·0	39·1	–	22·2	41·0	–	22·2	42·1	–	16·8	31·0	48·7	–

Fish Log No.	P 237 (133)						P 237 (157)						
Age	1	2	3	4	5	6	1	2	3	4	5	6	7
Actual measurements on tagging and recapture	–	–	–	–	63·5	67·2	–	–	–	–	–	66·6	68·3
Back-calculated from opercular	(21)	(36)	47·0	57·3	62·0	–	(22)	35·8	52·3	58·8	63·2	66·8	–
Corrected back-calculation from scales:—													
collected on tagging	19·5	36·4	49·5	60·5	–	–	22·0	36·0	51·7	59·0	63·0	–	–
collected on recapture	19·5	38·8	52·8	61·5	64·0	–	19·8	35·2	52·2	59·6	63·0	67·0	–
Uncorrected back-calculation from scales:—													
collected on tagging	13·0	30·0	45·8	59·1	–	–	15·5	29·2	47·7	57·0	61·7	–	–
collected on recapture	12·8	32·0	48·7	59·5	63·2	–	13·0	28·0	47·8	56·8	61·9	66·3	–

(b) Two years absence

Fish Log No.	P 237 (75)							
Age	1	2	3	4	5	6	7	8
Actual measurements on tagging and recapture (twice)	–	–	–	–	–	62·5	65·0	66·0
Back-calculated from opercular	(19)	33·4	45·7	52·8	58·5	62·2	63·8	–
Corrected back-calculation from scales:—								
collected on tagging	21·2	34·7	46·5	53·4	60·0	–	–	–
collected on 1st recapture	21·8	36·0	47·0	55·0	60·5	64·0	–	–
collected on 2nd (final) recapture	22·5	35·2	46·5	54·3	60·6	63·6	65·0	–
Uncorrected back-calculation from scales:—								
collected on tagging	14·7	28·1	42·2	51·0	59·0	–	–	–
collected on 1st recapture	15·0	29·8	42·6	52·3	59·0	63·4	–	–
collected on 2nd (final) recapture	15·8	28·5	41·5	50·9	59·0	62·8	64·4	–

Figures in parentheses are estimates from the theoretical growth table.

in older fish. As with scales a false check may be suspected on the bone if a growth increment is markedly different from that found in similar fish.

From examination of the character of the edge of the opercular bone it is difficult to determine the exact date of annulus formation because the annulus is a line of discontinuity between winter and summer growth (p. 328) and is therefore not apparent until some summer growth (plus growth) is registered on the edge of the bone. The operculars from some fish ranging in size from 15 to 65 cm, caught from March to June, were examined for the character of the edge of the bone which was noted as being with or without the new (plus) growth. It was found that plus growth (but only very little) was present on some of the pike caught in mid-April but on none caught earlier, and that some fish caught in mid-May had no plus growth although others caught at the same time showed a little; from mid-May onwards almost all the operculars had plus growth at the edge. These observations indicate that the annulus on the opercular is probably formed in early May, at much the same time as on the scales (p. 323).

Determination of growth. To use the operculars for back-calculation of length it was necessary to decide on the correct centre or origin of growth of the bone from which to measure these annual increments. Unlike the bone of the perch (LE CREN, 1947) that of the pike has no "hole" near its articulating surface to help to fix the origin of growth, so that an arbitrary point which appeared to be the origin of growth was chosen. On looking at the concave (the inner) face of the bone the articulating concavity can be seen (Fig. 2 (ii)) and the centre of this was taken to be the origin of growth. But because of the thickness of the articulating surface this centre is hidden when the bone is projected therefore its position has to be determined indirectly thus:— The projected bone has an outline as in Figure 2 (i) and it was found that the mid-point of a line drawn from the indentations 'b' and 'c' on this outline coincided with the accepted origin of growth of the bone, 'a' on Figure 2 (ii) on the articulating surface. The good agreement found between back-calculations as measured from this point and the observed measurements obtained from recaptured tagged fish justifies this arbitrarily chosen point as a satisfactory centre for measurement of the annual increments in growth.

Before it is justifiable to back-calculate the growth of the pike from the opercular it is also necessary, as it was with scales, to find the true proportional relationship between the growth of the opercular and the fish throughout their life. The projected images of the operculars from fish ranging in size from 10 to 98 cm were measured on the back-calculation cardboard strips. The measurement was made from the chosen centre to the posterior edge of the bone, along the line shown in Figure 2 (i). When these measurements were plotted against the lengths of the individual fish from which they were taken it was found, by eye, that the points lay on a straight line passing through the origin, showing that the bone grows in direct proportion to the fish throughout life (Figure 5 (b)). As a further check a regression line was calculated on the same data and it gave the same results. It follows that the growth made by the fish can be calculated directly from measurements made to the annual rings on the bone without any correction for allometry or for the length of the fish when the bone was formed. The main support for the foregoing conclusions concerning the annual character of the check, the choice of the centre of the bone, the isometry of growth and length of fish when the bone was formed, is the incontravertible evidence from many returned marked pike, for they

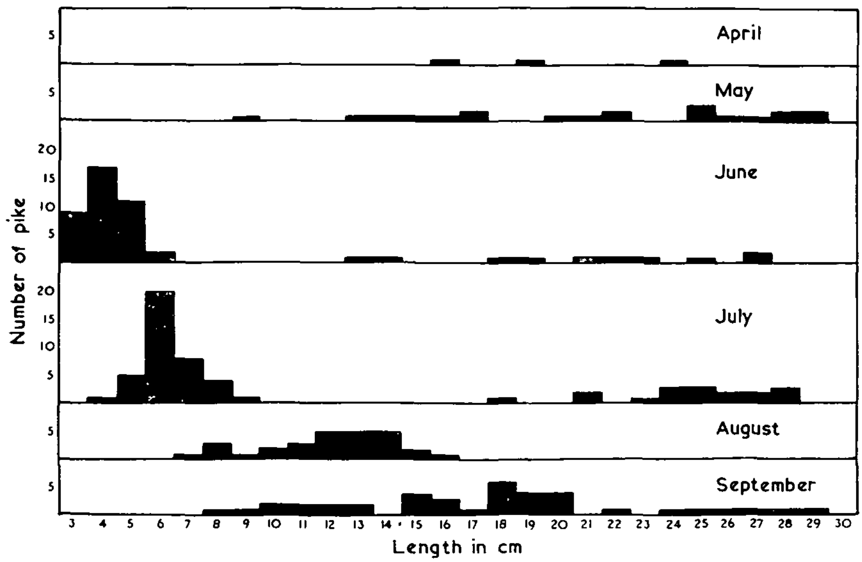

Figure 7. Length-frequency distributions of young pike of Windermere.

showed good agreement between the observed increments and those back-calculated from the operculars.

Thus the evidence given in the foregoing paragraphs justifies the use of opercular bones for determination of age and growth of the pike. But this usage still presents problems. The operculars of some fish of over about 65 cm are rather thickened throughout so that it is difficult to find the annuli, particularly those near the edge of such bones, so that an error in the ageing of the fish can be made. But the main problem associated with reading operculars is the difficulty which arises from the thickening and discolouration at the base of the bone since this can obliterate the early annuli. This presents the problem of the "missing first years". Of the hundreds of opercular bones collected from pike of Windermere about a quarter come from smaller fish. On the whole the operculars of these smaller pike (10–45 cm) are reasonably easy to read because the tissue at the base of the bone is not so dense and discoloured as to obscure the first annulus (Plate 2f). The majority of the pike, however, are larger specimens from 50–110 cm. These larger fish usually, but not always, have the base of the bone so much thickened that the first annulus (at least) is obscured so that the age read may be incorrect. Apart from this difficulty of missing first years the opercular bone presents a more satisfactory structure than the scale for reading the age of the pike and it is especially so for back-calculation of growth because the boundary of the annulus is much clearer, and therefore can be more accurately "pin-pointed", on the bone than on the scale (p. 324).

For estimating whether early rings are missing a knowledge of the length distribution of pike in Windermere at the end of the first and second year's growth is obviously essential. That wide variations can be expected is apparent from the work of CARBINE (1945) on growth potential of northern pike (*Esox lucius*) in America. Three different methods have been used in an attempt to find these length distributions:—

(a) Direct observation of small fish. For several successive years small pike

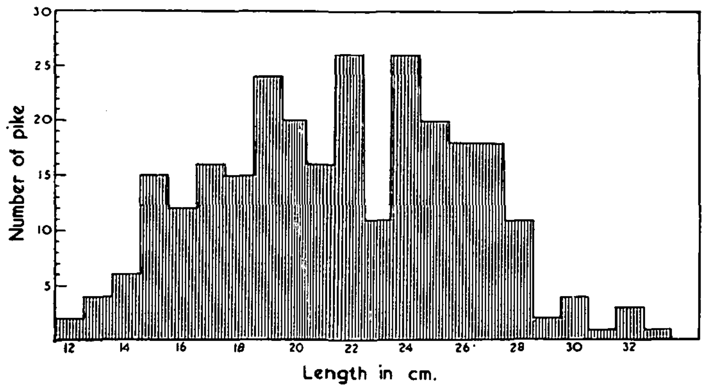

Figure 8. Frequency distribution of lengths at age 1 back-calculated from the scales of 271 pike.

were caught in weed beds and shallow bays of Windermere from April onwards. The monthly length distributions of these fish are given in Figure 7. It is possible that these samples give an underestimate of the mean length of all the fish in their first year as the quicker growing larger fish may quit the shallow waters before the end of the summer leaving mainly the smaller specimens in the area sampled. The growth of the 0+ age-group can be clearly followed from June through the early months of life, and by September the distribution has a mode of 18 cm, though, as stated above, this may be an underestimate and also some further growth may occur before they are age 1 in the next spring. The slowest growth of the fish-of-the-year here recorded is that of a fish of 8 cm caught in September, though there is no reason to suppose that this was necessarily the smallest of this age-group.

(b) Length-frequency distribution of back-calculations from scales (Figure 8). A length-frequency distribution of 271 first year lengths was derived from back-calculations from scales. The fish were caught over several years and by several methods, and males and females have not been separated. The largest was 33 cm, the smallest 12 cm, and the mean 21·6 cm (standard deviation 4·4 cm).

(c) Walford plots (p. 317) on data from tagged returned fish. Actual measurements of tagged pike recaptured after intervals of exactly one year were used. (It may be noted that for this purpose it does not matter at what time of year the fish were taken, provided the interval between the measurements was exactly one year.) These data were plotted in the manner described on p. 317 for 36 males and 21 females separately. The points for each lay approximately on straight lines cutting the diagonals at 75 and 100 cm, respectively. When these lines were projected to cut the y axis for estimates of length at age 1 the result for males was 20 cm and for females 21 cm. From the plots the fastest growing fish were estimated to have reached about 35 cm by the end of the first year.

These three different methods, two of them based entirely on actual measurements, yield very similar estimates of the mean length attained by pike in Windermere at the end of the first year of life. The lengths approximately range from 11 cm to 35 cm with a mean of about 21 cm.

The length distribution at the end of the second year's growth has also been

Table 3

Theoretical growth of Windermere pike

Calculated from Ford's formula assuming:—

1. Ultimate lengths .... females .... 100 cm
   males .... 75 cm
2. Lengths at end of first year .... slow growers .... 15 cm
   medium growers .... 20 cm
   fast growers .... 25 cm
   very fast growers........ 30 cm

Age	Length in cm				Increment in cm			
	Slow	Medium	Fast	Very fast	Slow	Medium	Fast	Very fast
Females								
1...........	15	20	25	30	15	20	25	30
2...........	28	36	44	51	13	16	19	21
3...........	39	49	58	66	11	13	14	15
4...........	48	59	68	76	9	10	10	10
5...........	56	67	76	83	8	8	8	7
6...........	62	74	82	88	6	7	6	5
7...........	68	79	87	92	6	5	5	4
Males								
1...........	15	20	25	30	15	20	25	30
2...........	27	35	42	48	12	15	17	18
3...........	37	45	53	59	10	10	11	11
4...........	44	53	60	65	7	8	7	6
5...........	50	59	65	69	6	6	5	4
6...........	55	63	68	72	5	4	3	3
7...........	59	66	71	73	4	3	3	1

calculated by methods (b) and (c). For the Walford plots data were used from tagged fish which had been absent exactly two years. (Figure 3 (d)). The two methods both gave a mean length of about 38 cm and a range of about 25 cm to 50 cm.

From these results it is plain that there must be some overlap of age-group I and II in particular between 25 cm to 35 cm and occasionally down to about 20 cm, that is some fish will be age 1 and some age 2 between these lengths. This was confirmed by ageing, from both scales and operculars, 18 fish of lengths 24–30 cm caught in perch traps in early spring, 12 of these were aged 1 and 6 aged 2. Therefore it is not possible to say with certainty to which age-group a particular fish belongs between these lengths, for example if back-calculation to the first visible annulus of the opercular gives a length of 30 cm this might be either the first or second annulus depending on whether the fish was a fast or slow grower, in other words, for such fish age cannot be determined without reference to growth. A simple statement of a limit below which all fish can be expected to be age 1 is therefore not possible. It should here be stressed that it is the older fish which are likely to have missing early rings but their growth increments in the later years can be back-calculated, although the age will not be known owing to doubt about the early years. If from these later increments it is possible to find out whether the fish is a fast (or medium, or slow) grower, then it would be possible to estimate the number of the missing early rings with greater accuracy. To make use of later increments to give this greater accuracy theoretical growth tables for pike of Windermere have been calculated from FORD's formula, they could also have been derived from Walford plots, (Fig. 3 (a)). The results are shown in Table 3. These tables have been derived from the basic assumptions of "length at age 1" and "ultimate length". They have been calculated for slow, medium, fast, and very fast growers, males and females separately. From the results obtained on p. 332 fish which reached 15 cm, 20 cm, 25 cm, and 30 cm at the end of their first year were arbitrarily considered to be slow, medium, fast, and very fast growers respectively. After inspection of many Walford plots and study of the length distributions of fish caught in the past the ultimate length of males was taken to be 75 cm and of females 100 cm. These lengths are based on pike caught in Windermere in the last fifteen years, and must not be assumed to apply to other environments. These tables are therefore not necessarily valid for other waters.

The method evolved for determining age and growth from opercular bones using the theoretical growth tables is as follows. The bones are read and back-calculations made in the usual manner. Then as it is known that the first or more annuli may have been missed owing to the thickening of the bone at the centre, particularly in older fish, the growth as calculated for each individual fish is compared with the theoretical tables and a decision made as to which category the fish belongs. For example a female pike, whose innermost visible annulus on the opercular gave a back-calculated length of 48 cm, could have been at this length an exceptionally fast growing 2 year-old, or a medium 3 year-old, or a slow 4 year-old. If during the following year it had put on an increment of 10 cm from 48 to 58 cm it was probably a fish of medium growth, and therefore had the first two annuli missing on the bone. Alternatively if its increment had been 15 cm and it grew from 48 to 63 cm it was probably a fast grower and therefore only one annulus had been missed. In all cases confirmation would be sought by finding out whether slow or fast growth had been maintained throughout the rest of its life. Identical results could of course be obtained by making Walford plots for each individual fish; the theoretical tables merely provide a quicker and more convenient method of dealing with large numbers of fish. When theoretical tables are not available the procedure for Walford plots is as follows for each individual fish. The back-calculated lengths are plotted in pairs (length at age n, length at age $n+1$) as described on p. 317. A line is fitted by eye to the plotted points and extended to cut the y axis: the intercept gives the length at age 1. If this corresponds to the smallest back-calculated length obtained then no annuli have been missed. If not, then length at age 2 ($= n+1$) is found from the plot using the length at age 1 just found from the y axis intercept. If this length at age 2 corresponds with the smallest back-calculated length then one annulus has been missed (Figure 3 (c)). Again if not, then length at age 3 can be found from the plot, if this corresponds with the smallest back-calculated length then two annuli have been missed.

Obviously this individual plotting takes much time if many fish are involved. If there are more than about fifty it would probably be worth while to calculate theoretical growth tables for the particular water.

When the number (if any) of missing annuli has been found then the missing lengths attained at these annuli can be estimated from theoretical tables or from the individual Walford plots, although it is obvious that these estimates will be liable to some error, owing to the assumptions on which they are based. In the above example the estimates of the missing first and second year lengths, if it were a fish of medium growth, would be 20 and 35 cm. If it is intended to calculate mean growth from a collection of operculars then those

Table 4

Comparison of means of back-calculations of length (cm) made from the scales and operculars of 47 male pike, mean length at capture 57·7 cm

	Age 1			Age 2	Age 3
	Annulus visible on opercular	Annulus missing on opercular	Total	Annulus visible on opercular	Annulus visible on opercular
	35 fish	12 fish	47 fish	47 fish	47 fish
Uncorrected scales . .	17·5	14·9	16·8	35·3	49·6
Corrected scales	23·5	21·0	22·9	39·9	51·8
Opercular	23·1	20·9[1])	22·5	39·1	51·3

[1]) Mean of individual estimates from theoretical growth table.

The differences between the means derived from corrected scale readings and the means derived from operculars are in no case significant. Fish with early annuli visible are faster growing than those with annuli missing.

Table 5

Comparison of means of back-calculated lengths (cm) of fish with annuli visible and annuli missing on the opercular, based on pike aged 5 years and over caught in gill nets 1946–1947

	Age 1			Age 2		
	Annulus visible	Annulus missing	Total	Annulus visible	Annulus missing	Total
	27 fish	27 fish	54 fish	50 fish	4 fish	54 fish
Males	24·4	21·6[1])	23·0	40·2	31·8[1])	39·6
	13 fish	49 fish	62 fish	56 fish	6 fish	62 fish
Females	25·6	21·2[1])	22·1	39·0	35·4[1])	38·7

[1]) Mean of individual estimates from theoretical growth table.

Fish with early annuli visible are faster growing than those with early annuli missing.

bones with missing annuli must not be ignored (just because they are difficult) for their omission would produce a definitely biased mean since it is the slower growing fish which are more likely to have the missing annuli (Tables 4 and 5). It has been found that few fish under the age of 4 have missing annuli while over the age of 7 almost all have at least one missing. Two is the maximum number of missing annuli so far discovered.

The theoretical tables or individual Walford plots can also be used as a guide to check for possible false annuli (p. 328). If the back-calculated lengths do not reasonably relate to the lengths deduced theoretically it is possible that there might have been an error in reading either the age or the increments and a further check, perhaps using scales, is advisable. We have found for the pike of Windermere that this is not likely to be necessary for fish of less than 65 cm.

Tests of Validity of Methods

The validity of these methods of determining age and growth from scales and operculars of pike has been tested in various ways and the results are here briefly summarized.

(a) Agreement was in general good between observed measurements of fish at the time of tagging and lengths back-calculated to this time from operculars

Table 6

Mean back-calculated lengths (cm) at the end of each year of life of 74 male and 116 female pike caught in gill nets, 1946–1947

	Age at capture	Number of fish		Age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Number of theoretical estimates Age 1	Age 2
Males	2	1		29·4	44·5															
	3	1		19·0	40·6	51·5														
	4	18		23·2	41·0	54·6	60·1												4	
	5	21		24·1	41·3	52·7	60·8	64·4											10	
	6	20		22·7	39·9	51·5	58·7	64·2	66·6										8	1
	7	5		21·0	36·4	48·5	55·4	60·7	64·5	66·3									4	1
	8	4		25·0	38·5	51·4	56·4	61·0	64·3	67·5	69·3								1	
	11	1		20·1	35·2	44·5	53·4	59·9	64·3	67·4	71·0	73·8	76·5	77·5					1	1
	12	2		19·1	33·2	44·8	54·4	58·9	61·9	64·4	66·4	67·9	69·4	71·0	72·5				2	1
	15	1		21·1	36·7	47·3	52·2	55·2	57·9	59·9	62·2	64·4	66·6	68·2	69·9	71·3	72·5	73·5	1	
		74	Mean	23·1	40·0	52·1	59·1	63·3	65·4	66·0	68·0	68·4	70·4	72·0	71·5	71·3	72·5	73·5	31	4
Females	2	1		27·1	47·5															
	3	9		29·2	49·3	61·3													1	
	4	44		22·3	39·3	56·4	66·0												26	
	5	30		21·7	38·0	53·6	63·6	69·3											23	
	6	12		21·8	37·9	53·0	63·2	70·8	76·2										9	1
	7	3		20·1	36·2	50·4	58·7	65·1	70·2	73·8									3	1
	8	6		25·3	43·2	56·8	65·2	71·7	76·9	81·3	84·3								4	
	10	3		23·4	41·5	56·3	66·0	72·7	78·4	82·4	85·7	88·8	90·8						3	1
	11	2		21·1	38·7	51·8	61·8	68·8	73·9	77·4	80·9	83·4	85·9	87·5					2	
	12	5		23·3	39·8	53·1	61·7	69·3	75·8	80·6	85·0	88·2	91·1	93·9	95·5				4	2
	14	1		21·1	37·2	49·8	62·3	69·3	75·8	80·4	85·4	91·3	94·7	97·5	100·4	101·7	102·5		1	1
		116	Mean	22·7	39·9	55·3	64·4	69·8	75·7	79·7	84·4	87·8	90·4	92·8	96·3	101·7	102·5		76	6

Table 7

Comparison of back-calculated growth from operculars and theoretical growth

	Length (cm) at age				
	1	2	3	4	5
Males					
Back-calculated growth of 54 male pike aged 5 and over caught in gill nets 1946–47	23·0	39·6	51·2	58·6	63·3
Theoretical growth of fish reaching 23 cm in the first year assuming an ultimate length of 75 cm..........	(23)	38·9	50·0	57·7	63·0
Females					
Back-calculated growth of 62 female pike aged 5 and over caught in gill nets 1946–47	22·1	38·7	53·6	63·4	69·8
Theoretical growth of fish reaching 22 cm in the first year assuming an ultimate length of 100 cm.........	(22)	39·2	52·5	63·0	71·1

and scales (corrected for allometry) taken when the fish was recaptured subsequently. For 42 fish which had been tagged and recaptured the differences between observed mean and the means back-calculated both from opercular and scale were not significant. (Observed mean at time of tagging 47·0 cm, mean back-calculated from scales (corrected) 47·8 cm, from operculars 46·2 cm. Observed mean at time of recapture 64·1 cm.) For individual differences (absolute values i. e., ignoring sign) between observed and calculated lengths the mean was 1·5 cm for scale readings (corrected) and 1·0 cm for opercular readings. The maximum difference for an individual fish was 4·4 cm for scale readings (corrected) and 3·3 cm for opercular readings. Table 2 gives full details of those 7 of the 42 fish which were recaught after exactly one or two years and had been tagged in early spring at the end of a year's growth. It can be seen that the observed measurements on tagging agree well with back-calculations to that time, for example P 210 (97) measured 43·4 cm at time of tagging, and back-calculation from both opercular and scales (corrected) showed 42·8 cm.

(b) Agreement was good between the means of scale readings (corrected) and opercular readings; none of the differences between these values shown in Table 4 is significant. Although the means are satisfactory, individual differences between scale readings (corrected) and opercular readings can be considerable. For example in Table 2 the length of P 237 (133) at age 3 back-calculated from the opercular was 47·0 cm and back-calculated from the scale (corrected) taken at recapture was 52·8 cm.

(c) Scale readings uncorrected for allometry were unsatisfactory, (Tables 2 and 4).

(d) Those fish which had the early annuli visible on the opercular were faster growing than those which had missing annuli, (Tables 4 and 5). It follows that omission of those with missing annuli would give a biased estimate of the growth of the population.

(e) Agreement was very good between theoretical growth and growth back-calculated from operculars, (Table 7 and Fig. 3 (c)). Therefore it appears that at least in the early years of life the method of calculating theoretical growth is adequate to describe actual growth, assuming always that the environment remains reasonably constant.

(f) When operculars were read more than once the separate results agreed closely. The second reading was in some cases made three years after the first, and in some cases by a different person.

(g) The back-calculated mean lengths at ages 1 and 2 shown in Tables 2, 4, 5, and 6 are in general agreement with those found by Walford plots using observed measurements of returned tagged fish, and also with directly observed measurements of young fish (p. 331 and Figures 7 and 8).

(h) Table 6 shows the calculated mean lengths at the end of each year of life of all the pike caught in gill nets during the season 1946–1947. The results are consistent. The back-calculated mean lengths of those age-groups containing more than six fish provide some evidence of Lee's phenomenon, which is almost certainly due to gill-net selection of those particular age-groups.

We conclude that opercular bones can be used to determine the age and growth of pike satisfactorily, and that they are preferable to scales for this purpose. Therefore it is our present practice to use the opercular bones and to turn to scales only when the opercular bone readings are difficult to interpret.

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Summary

1. The use of scales and opercular bones to determine the age and growth of the pike (*Esox lucius*) has been critically examined and the use of operculars for this purpose is described for the first time.

2. It was found that age can be determined from the annuli on both the anterior and posterior parts of the scale, but care is needed to identify and reject false annuli.

3. Correction for allometry was found to be necessary for back-calculation of growth from annuli on the anterior part of the scale. It is not necessary for the posterior part of the scale.

4. The length of the fish when the scales are laid down was found to be about 3·5 cm and correction for this is required for all the back-calculations from scales.

5. An equation describing the relationship between the length of the fish and the length of the anterior part of the scale is given for the pike of Windermere and has been used for correcting back-calculations from the anterior part of the scale both for allometry and for the length of the fish when the scales were laid down.

6. The use of scales for the back-calculation of the growth of *individual* fish was found in general to be unsatisfactory, primarily on account of the ill-defined boundary of many of the annuli. On the posterior part, in older fish, the annuli in addition may be so crowded that accurate back-calculation is impossible. Therefore readings from the annuli on the anterior part of the

scale and corrected as described above have been used in preference to readings from the posterior part, and, for *large numbers* of fish, the means of such readings agree well with means obtained by other methods.

7. The rings or annuli on the opercular bones have been found to be annual, and therefore can be used to determine age, despite the fact that early annuli may be missed owing to the thick and discoloured base of some bones, particularly of older fish. False annuli may also be present, but they are easier to identify than those on the scales.

8. Growth of the opercular bone and the fish is isometric, and also no correction is needed for the length of the fish when the bone is formed. Therefore direct proportion can be used to determine growth from the annuli on the bone. The method of finding an arbitrary "origin of growth" of the bone from which to make the back-calculations is described.

9. To overcome the difficulty of the missing early annuli on the operculars a method has been evolved using either Walford plots or calculated theoretical growth tables, which enables estimates to be made of the number of missing annuli and the lengths at these times. (Walford plots are for individual fish; identical results are obtained from the tables, which, however, provide a quicker method of dealing with many fish.)

10. Tests of validity of the methods are described, some of them based on comparisons with records of returned tagged fish.

11. It is concluded that the opercular bone provides a valid method of determining the age and growth (but not the age without the growth) of pike, and that although the scales can be satisfactory for the determination of age they are not recommended for the determination of growth.

Zusammenfassung

1. Die Verwendung der Schuppen und des Operculum für die Bestimmung des Alters und Wachstums des Hechtes (*Esox lucius*) wurde kritisch geprüft. Die Verwendung des Operculum für diesen Zweck wird zum erstenmal beschrieben.

2. Es wurde gefunden, dass das Alter sowohl nach den Ringen im vorderen wie im hinteren Abschnitt der Schuppe bestimmt werden kann, dass aber darauf geachtet werden muss, dass falsche Ringe erkannt und ausgeschieden werden.

3. Mit Rücksicht auf die Allometrie wurde für die Rückberechnung des Wachstums nach Ringen auf dem vorderen Abschnitt der Schuppe eine Korrektur für notwendig befunden; für den hinteren Abschnitt der Schuppe ist eine solche Korrektur nicht notwendig.

4. Wenn die Schuppen auftreten, hat der Fisch bereits eine Länge von 3·5 cm erreicht. Bei allen Rückberechnungen von Schuppen muss daher auch dafür eine Korrektur angewendet werden.

5. Für den Windermere-Hecht wird eine Gleichung für die Beziehung zwischen der Länge des Fisches und der Länge des Vorderabschnittes der Schuppe aufgestellt. Durch die Verwendung dieser Gleichung nach der Rückberechnung aus dem Vorderabschnitt der Schuppe ist sowohl die Allometrie wie die Fischlänge beim Auftreten der Schuppen korrigiert.

6. Die Verwendung der Schuppen zur Rückberechnung des Wachstums des *einzelnen* Fisches wurde im allgemeinen unbefriedigend gefunden, vor allem

wegen der unklaren Begrenzung der Ringe. Im hinteren Abschnitt der Schuppen stehen ausserdem die Ringe bei älteren Fischen oft so eng, dass eine sichere Rückberechnung nicht möglich ist. Deshalb wurde es vorgezogen, die Ringe des vorderen Abschnittes unter Berücksichtigung der oben erwähnten Korrektur zu verwenden. Die Mittelwerte solcher Berechnungen stimmen mit den Mittelwerten aus anderen Methoden gut überein, wenn sie von einer *grossen Anzahl* von Fischen gewonnen werden.

7. Die Ringe auf dem Operculum haben sich als Jahresringe erwiesen und können daher für die Altersbestimmung verwendet werden, wenn auch die ersten Ringe wegen der dicken und verfärbten Basis mancher Opercula besonders älterer Fische fehlen können. Es können auch auf dem Operculum falsche Ringe vorhanden sein, aber sie sind hier leichter als solche zu erkennen als bei den Schuppen.

8. Das Wachstum des Operculum und des Fisches ist isometrisch. Eine Korrektur der Fischlänge beim Auftreten des Operculum ist nicht nötig. Daher kann das Wachstum nach dem Operculum direkt berechnet werden. Es wird eine Methode beschrieben, einen "Beginn des Wachstums" des Operculum für die Rückberechnung des Wachstums willkürlich festzulegen.

9. Um die Schwierigkeit des häufigen Fehlens der ersten Ringe auf dem Operculum zu überwinden, wurde unter Verwendung von Walford-Diagrammen oder theoretisch berechneten Wachstumstabellen eine Methode entwickelt, die die Schätzung der Zahl der fehlenden Ringe und der ihnen entsprechenden Längen ermöglicht. (Das Walford-Diagramm ist für Einzelfische gut anwendbar. Die Tabellen bringen dieselben Resultate, ermöglichen aber die schnellere Bearbeitung einer grösseren Anzahl von Fischen)

10. Es werden Tests auf die Genauigkeit der Methoden beschrieben, die zum Teil auf den Vergleich mit Ergebnissen von markierten Fischen basiert sind.

11. Aus den Ergebnissen der vorliegenden Untersuchungen wird geschlossen, dass das Operculum eine gute Methode für die Bestimmung des Alters und Wachstums des Hechtes bietet (nicht aber des Alters ohne Wachstum!) und dass die Schuppen, obwohl sie für die Altersbestimmung befriedigende Resultate liefern, für die Bestimmung des Wachstums nicht empfohlen werden können.

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