ABSTRACT OF THESIS

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Title of Thesis

A Comparison of Seasonal Growth in the Scales, Otoliths and Branchiostegal Rays of a Population of Young Trout Salmo trutta Linn.

The aim of this work was to study for one complete year marginal activity on scales, otoliths and branchiostegal rays obtained from young trout of known maximum age. Special attention was to be paid to the relationship between the length of the branchiostegal ray and length of fish with a view to estimating its suitability as a back up method to scales in the study of a fish's past growth pattern. The time and form of annulus formation was to be fixed.

With this view in mind four trout were caught every two weeks from November 1964 till November 1965. The scales, otoliths and rays were extracted mounted and measured after the fish had been weighed and measured. It was found that indistinct marks on the rays could be seen more clearly if the bones were viewed between two strips of polaroid placed at extinction.

As a parallel sample from an entirely different source, a deep cold Loch as against a shallow fertile stream, eight samples were obtained from Loch Earn from March till October, 1965.

From a study of the scale margins it was shown that Linlithgow trout commenced fast growth in March/April and sustained this growth till September/October. From November till February there seemed to be little marginal activity. Loch Earn fish commenced their growth in April/May and continued this growth till September/October when sampling ceased in this area. It was shown that this pattern conforms closely to that found by workers from other sources.

A study of the branchiostegal rays showed that rapid growth began in March/April in Linlithgow and April/May in Loch Earn and continued until September/October in both Linlithgow and Loch Earn. This fast growth was denoted by the appearance of an opaque zone following a clear "winter" zone. This zone was milky white shading to a watery white in late Summer then into the transparent "inter" zone. This opaqueness was found to be due to aggregation of cells which appeared after a ripple on the edge of the bone. A true annulus was found to continue round the outer margin of the ray to the hinge.

An analysis of the relationship between ray length and fish length yielded the following results. Linlithgow fish: correlation coefficient 0.9105 Loch Earn: 0.917. This marked similarity from two such diverse habitats suggest a uniformity of relationship. It was found that the best fit regression lines for the two samples had similar slopes but were of significant difference in form.

Use other side if necessary.
Linlithgow \[ y = 5.632x - 2.01 \]
Loch Earn \[ y = 5.044x - 1.316 \]

where \[ x \] = desired fish length
\[ y \] = bone length

A graph of head length/body length for both samples showed a similar picture and it was suggested that Loch Earn fish had smaller heads than Linlithgow fish for the same body length. Correlations for these results were very high as one would expect. Linlithgow 0.9786, Loch Earn 0.9709.

The branchiostegal ray was shown to fit the criteria laid down by McConnell (Sulkley 1960) if it was to be used in growth studies. It is suggested that this bone would be a useful instrument in trout study.

The otoliths were found to be disappointing as sources of information as structures were indistinct and several otoliths were calcareous and opaque. From the results obtained Linlithgow otoliths appeared to lay down an opaque layer from March to August and in Loch Earn from April/May till August. With a translucent margin throughout the rest of the year.

The three structures under observation were shown to have markedly similar growth patterns with new growth beginning in Spring and early Summer and continuing until late Summer early Autumn. All three objects had a slow growth period from late Autumn until early Spring.
A Comparison of Seasonal Growth in the Scales, Otoliths and Branchiostegal Rays of a Population of Young Trout Salmo trutta Linn.

By

William S. Gentleman

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CONTENTS

Summary
Acknowledgements
Introduction

Review: Time and place of origin and subsequent growth of scales, Otoliths and Branchiostegal rays.

Scales 2
Otoliths 8
Bones 11

Material and Methods

Sampling areas and methods of sampling 19
Fish preparation and measuring 20
Scale mounting and measuring 21
Otolith extraction and measuring 22
Branchiostegal ray preparation and measurement 22

Results
Scale development - Linlithgow 24
Scale development - Loch Earn 26
Otolith development - Linlithgow 26
Otolith development - Loch Earn 27
Branchiostegal ray development - Linlithgow 28
Branchiostegal ray development - Loch Earn 30
Branchiostegal ray and its use as an age determinant 30

Indicator in trout.
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discussion</td>
<td>36</td>
</tr>
<tr>
<td>Part 1</td>
<td></td>
</tr>
<tr>
<td>Material and Methods</td>
<td>38</td>
</tr>
<tr>
<td>Part 2</td>
<td></td>
</tr>
<tr>
<td>Scale Development</td>
<td>40</td>
</tr>
<tr>
<td>Part 3</td>
<td></td>
</tr>
<tr>
<td>Otolith Development</td>
<td>43</td>
</tr>
<tr>
<td>Part 4</td>
<td></td>
</tr>
<tr>
<td>Branchiostegal Ray Development</td>
<td>46</td>
</tr>
<tr>
<td>Part 5</td>
<td></td>
</tr>
<tr>
<td>Comparison of growth of Scales, Otoliths and Branchiostegal Rays</td>
<td>50</td>
</tr>
<tr>
<td>References</td>
<td></td>
</tr>
<tr>
<td>Appendix</td>
<td>53</td>
</tr>
</tbody>
</table>
SUMMARY

Review

A brief review has been made of the historical development of the present state of knowledge relating to the use of scales, otoliths and bones of various types in the study of fish growth and development.

Material and Methods

The suitability of the material used has been discussed with special reference to sample sizes, the methods of sampling and the method of examining and measuring the branchiostegal ray.

Scales

The development of trout scales has been followed in one denoted area for one complete year and the times of fast growth and slow growth fixed as follows: fast growth - March/April to October/November and slow growth - November to February.

The development of trout from samples caught in Loch Earn from March to October 1965 has been followed and the times of fast growth fixed at April/May to October and slow growth is suggested from October/November until March/April.

These growth cycles have been shown to conform to those recorded by various other workers.

Otoliths

The development of the sagittal otolith in trout in Linlithgow has been followed for one complete year and for Loch Earn for the eight months
March to October 1965. The formation of the opaque region has been tentatively fixed at March/April to August/September for Linlithgow and April/May to August/September for Loch Earn. The translucent zone has been tentatively fixed at forming from August/September onwards for the Linlithgow fish and similarly for the Loch Earn fish.

The difficulty involved in obtaining readings from trout otoliths compared to seafish otoliths and some other freshwater fish otoliths has been discussed as a possible drawback to their being used as a means of ageing trout and studying their earlier development.

Branchiostegdal Rays

The branchiostegdal ray was studied from Linlithgow and Loch Earn fish for the periods stated above for both scales and otoliths. It was noted that the Winter period of growth appeared to be represented by a clear area on the bone's margin where there were very few or no bone cells. There was a change in appearance of the margin in March/April for Linlithgow and April/May for Loch Earn. As this new area increased in size there was a corresponding increase in the number of cells associated with it. The cell density was noted as falling away throughout September/October, the months taken as the other limit of good growth, to give the characteristic clear appearance at the edge of the ray for the Winter months.

The branchiostegdal ray was shown to satisfy the criteria laid down by McConnell (see Bulkley 1960) expanded from Freidenfelt 1922, if it was to be of any value as an age indicator and record of previous growth. There was found to be a high correlation between the ray length and the fish
length, *0.9105* for Linlithgow and *0.917* for Loch Earn. The importance of this in determining the usefulness of this bone as a method back calculation has been discussed. The correlation between head length and fish length was also calculated with the following results - Linlithgow *0.9786* and Loch Earn *0.9709*. These were used as a comparison and cross check of the ray length/fish length correlations.

Linear regression formulae were established for both areas:

- **Linlithgow**
  \[ x = 5.632y - 2.01 \]

- **Loch Earn**
  \[ x = 5.044y - 1.316 \]

where \( x \) is the fish length to be found and \( y \) is the known ray length.

It was noted that the lines of best fit for these samples had similar slopes but were significantly different. A suggested explanation for this was put forward i.e. that the Loch Earn fish had smaller heads for the same overall size than the Linlithgow fish.

### Comparison of Growth

It has been shown that the three structures under examination have periods of rapid growth which fall within the same section of their yearly cycle, namely from late Spring to early Autumn.

The period of slow or non-growth extends from late Autumn to early Spring. Therefore all three structures exhibit a marked similarity in their seasonal growth patterns.
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Outwith the department my thanks must go to the Forth Federation of Anglers for allowing me to take samples from their rearing areas.
Introduction

It has been felt for some time that, while scales have proven their worth as sources of information for the estimation of a fish's age and growth patterns, a parallel system to cross check results would be a useful tool in the hands of the researchers. While otoliths are of known value in work on sea fish such as Cod and Plaice, they do not appear to have much potential as sources of information in fresh water salmonids. A variety of structures such as Perch opercular bones (Le Cren 1947) and Dogfish spines (Holden and Meadows 1962) have also been studied but have all been found to have some drawbacks.

The author's attention was caught by paper relating to work done on the branchiostegal rays of the Longnose gar (Netsch and Witt 1962) and Lake Trout (Bulkley 1960) as a potential source of information on the fish's development. An opportunity arose to continue sampling a population of known maximum age trout, *Salmo trutta*, in an outlet stream from rearing ponds (author Honors. thesis 1964). The offer was accepted with the aim in mind of comparing the times of appearance of the various structures on the scales, otoliths and branchiostegal rays, with special attention being paid to the branchiostegal ray and its relationship to fish length and development.
Fig. 1. S - stria, H - hyalodentine layer, F.P. - Fibrillary plates and G is the growing region.

Fig. 2, showing the pattern of appearance of the scales on trout fry. (a) is the area of first appearance, (b) shows rapid spread in the posterior region and (c) an almost completely scaled fish.
Trout scales are typical two layer Teleost scale. The surface layer being composed of hyalodentine material and the lower layer being fibrous in composition. Fig. 1. The upper layer, which contains calcium salts, increases in area but not in thickness during its development. The lower layer which is only partly calcified, increases in thickness by the deposition of successively larger layers each subsequent layer being composed of fibres laid down at an angle to the immediately preceding layer.

Trout scales are not present when the trout hatches but first appear when the trout is 3-5 cms. in length (Neave). The appearance of the scales appears to be closely linked to the development of the lateral line system. The first scale papillae appear in close connection with neuromasts along the lateral line. Fig. 2a. Once the scales begin to appear further development takes place in an anterior direction and outwards in all directions until the fish is completely scaled. The scales spread in a dorso-ventral direction with the farthest spread being in the direction of the adipose fin (Paget from Neave). Fig. 2b. This scale development occurs along lines which cross the myocommata at an angle towards the head there being usually two lines of scales to one myotome. Paget has shown that due to this pattern of development, one may find, on the same fish i.e. a trout of 5-6 cms. in length, fully developed scales on the median posterior region while on the shoulder and lower sides of the fish they are still in the papillar stage. On the ventral surface of this fish they have not even reached the papillae stage. Fig. 2c. This stepped development makes the site of sampling of greatest importance to the researcher and to ensure that the oldest scales are used, it is the
accepted procedure to take the scales from the region bounded by the dorsal fin and the lateral line. Fig. 7.

The structures of greatest importance to the scale reader are the striae or circuli which appear on the upper surface of the hyalodentine layer. There are several theories regarding the origin of these circuli. Setna (from Neave) has suggested that the upper layer produces calcifying salts at a steady rate while the scale pocket exhibits discontinuous growth. In the periods when the scale pocket is not growing he suggests that the upper layer comes in contact with the sides of the pocket. While contact is maintained the upper layer cannot grow and the organic salts are deposited in the form of a ridge or circulus. Wallin, however, also believes in the discontinuous growth phenomenon of the scale pocket but suggests that when the upper layer is in contact it continues to grow. This growth produces a compression factor which is relieved by buckling occurring along the edge of the scale. This buckled region of the scale is then calcified to form a circulus. Regenerated scales, i.e. those laid down to replace those dislodged from their pockets lay down no circuli until the regenerating scale reaches the margin of the pocket. This could, however, be explained by either of the above theories and would appear to shed no light on the problem. Neave has shown by staining that the upper layer of the scale appears first and grows faster than the underlying fibrillary plate. There may be a margin containing several circuli outside the periphery of the fibrillary plate (Crichton 1935 from Neave). This would appear to dispose of the old idea that the surface ridges were surface manifestations of the underlying fibrillary plates.
The scale reader, while interested in this early development, especially the time and position of appearance of the scales, is more interested in the growth patterns shown in the arrangement of the circuli on the scale surface and in any factors which may bring about changes in the growth pattern. He is especially interested in the times when these changes occur. Hoffbauer in 1899 noted that the scales of the carp he was rearing seemed to have more space between their summer circuli than their winter circuli. The scales also exhibited a pattern of radial lines which increased in number with each successive year. Much work has been done since then on examining the appearance of countless scales and cataloguing the results until the scale has now become of prime importance in ageing many species of fish.

These checks which appear on the scales are now thought to be due to a number of interacting factors. Bhatia (1 & 2) showed that checks could be produced at constant temperatures by starving fish. Gray and Setna fed fish continually throughout the year and found no evidence of checks on their scales. They fed another group with an abundance of food and found widely spaced circuli even in the winter months, while a third group fed with a limited diet developed abnormally narrow spaces. This would seem to confirm that ring width is closely linked to growth rate. Bhatia, Gray and Setna concluded that the production of narrow spaces was not linked to any inherent rhythm but was directly linked to food availability. Brown, however, working with 2 years old trout showed that under conditions of constant temperature and food availability will produce checks in September. If these fish are kept a further year another check will appear at the same time in the year. These 3 years old fish were examined and their gonads were found to be ripe, suggesting that the check was linked with gonadal development. Van Someren working in Kenya with fish taken from rivers with very little
Fig. 3 showing a scale with three Winter rings checks \( \text{III} - \text{III} \) and one Summer check of two rings, F, with no preceding narrowing down of the Summer rings. The line along which all intercirculi distances are measured is also shown.
fluctuation in temperature or food supply showed the presence of checks on the scales of these fish when they were running upstream to spawn. This evidence would appear to bear out Brown's findings. It should be remembered that trout spawning occurs in late autumn or early winter when food is also decreasing in availability and that there is every likelihood of an interaction of both the above factors in producing a check on trout scales.

Ball and Jones (1960) in their work on Llyn Tegid trout gave the following definitions of ring types and checks. It was decided to apply these definitions to the scales in the samples being studied.

**Ring Types**

(a) wide spaced rings are called Summer rings or open growth rings. When these appear on the scale margin the scale is called an open margin scale or a wide margin scale.

(b) closely spaced rings are generally called narrow rings, Winter rings or closed rings and when they appear on the scale margin the scale is called a closed or narrow margin scale.

When there are wide rings alternating with narrow rings they are called Summer and Winter bands respectively and Seasonal bands on joint reference.

Summer rings are of two main types:-

(1) wide Summer rings at the beginning of the Summer band.

(2) narrow Summer rings outside these.

There is a progressive narrowing of wide Summer rings through narrow Summer rings into Winter rings. Fig.3. This process is not always distinguishable in the first Summer but is nearly always recognisable in subsequent summer bands.
Recognition features of Winter rings:

1. much closer together than any Summer rings
2. they look less well developed than Summer rings
3. they are irregular and broken
4. they rarely extend far round the anterolateral shoulder of the scale.

Winter checks

A good pointer to check recognition is the cutting over on the scale shoulder of Winter rings, which do not extend past this region, by the first Summer ring. Fig. 3.

Using three distinct scale types Ball and Jones (1960) split their Winter fish into three groups as follows:

(A) 1-5 wide rings on the margin. These fish formed 20-30% of the sample. It was suggested that these fish laid down their Winter rings in September/October then resumed rapid growth for a few rings then ceased growth for the rest of the Winter. They reported an increased number in the March sample but it was thought that these were C type fish resuming rapid growth earlier than usual.

(B) 10 or more wide rings on the margin. These represented 10% of the sample and it was suggested that these fish had ceased growth in October without laying down any narrow rings. These fish were named late growers.

(C) closed margin with less than 5 narrow rings. These fish represented 70% of the sample. These slow growers represented a constant percentage of the sample from September to March suggesting that there was no marginal growth after the Winter band had formed and
there was evidence in support of this which had been obtained from tagged and recaptured fish.

**Summer or False checks**

The existence of False checks is one of the hazards faced by the scale reader in determining the age of a fish. These checks manifest themselves in the form of a narrow band of narrow rings in the middle of the Summer band of the second and subsequent Summers, although they are not always present. This check is characterised by the rings being regular and unbroken, continuing round the shoulder of the scale with the absence of any preceding intermediate width rings. This band of narrow rings is positioned between two bands of Summer rings, each band being narrower than the normal Summer band. Fig. 3. Brown, studying the effects of different temperatures on the growth of two year old trout, came to the conclusion that there were two maxima of growth involved, one between 7 and 9°C and the other between 16 and 19°C and that growth was low above and below these temperatures. It may be suggested therefore, that when the water reaches 6–9°C in summer, that maximum growth has been reached and that, as the temperature climbs above this level that the growth rate decreases giving rise to the Summer check and that when the temperature falls back down to this level in the early autumn there will be a growth spurt before the steady decline in growth into the Winter check.

Ball and Jones (1960) report that these Summer or False checks are reported by most workers on fish scales. It will be shown later that False checks are a phenomenon not exclusive to scales.
Plate 1 Showing a dorsal X-ray of a trout’s head. The position of the sagittal otolith is marked O. The lines of incision are also marked.
Fig. 4.

A.V.C. anterior vertical canal
P.V.C. posterior vertical canal
H.C. horizontal canal

C.C. crus commune
U. Utriculus with lapillus
S. Sacculus with sagitta
L. Lagena with asteriscus

From Brown, Physiology of Fishes II.

Fig. 5.

Diagrammatic otolith with opaque growth, O, shaded and translucent growth, T, unshaded, this fish would be in its year of growth.
Otoliths

For one reason or another it is not possible to determine the ages of some fish from their scales. In the case of an eel for example, scales from different parts of the body give widely varying ages e.g. 5-13 years (Frost). In the case of the Stickleback there are no scales present at all (Jones). In some fish such as the Cod the early years are clearly recorded on the scales but in older fish the picture becomes confused. It is clear in these cases, that another source of information has to be found. One of the earliest alternatives studied were the otoliths, more especially the sagittal otolith.

Otoliths are to be found in close connection with the semi-circular canals. There are three otoliths connected to each set of semi-circular canals on each side of the fish's head. Fig.4 and Plate 1. The anterior or Lapillue otolith is the smallest of the three. The posterior or Asteriscus otolith is intermediate in size and there seems to be some evidence that in trout at least, that this otolith may be connected to the middle and largest Sagittal otolith at an early stage in its development by a bridge structure (Gentleman).

Most work on the early development of otoliths has been done on sea fish, probably because of their economic importance. Wimpenny working with plaice reported that the otoliths first made their appearance as tiny crystals in the ear vesicles of plaice of one to two days old. Cod otoliths were reported by Trout not to make their appearance until the cod was 2-3cms long. Gentleman, using very fine grain X-ray film obtained X-ray images of what appeared to be radio-opaque material in the correct region of the heads of trout allevins which were killed by placing in alcohol as soon as they left their egg cases. The specimens were embedded in wax, which was
then thinned down above and below the heads of the specimens to afford less resistance to the rays. The appearance on the X-rays of these crystals would seem to confirm the sightings reported by Kille (personal communication) of crystals in the ear vesicle of trout shortly after their formation. Trout otoliths would seem to be present from the moment the fish hatch and therefore record a full pattern of the fish's development.

Otoliths have been analysed to determine their composition. Dannevig gives the contents of cod otoliths as follows: CaCO₃ 76.3%; CaO 11.4%; H₂O and organic material 11.4%; other compounds 0.6%. The organic material consists of a range of proteins, 14 to 15 amino acids being found by chromatography. Decalcification with chromic acid left a series of membranous sacs corresponding in number to the number of opaque zones on the otolith.

By sampling fish over a period of time Cunningham 1905, Wallace 1905, Dannevig 1933, Frost 1945, Jones and Hynes 1950, Trout 1953, Dannevig, Eva H. 1955 and Christensen 1963 to quote only a few of the many workers involved in this field all arrived at the same conclusion namely that there were two zones laid down in the sagittal otolith in the course of one year's development. These zones were characterised by being opaque and translucent in transmitted light and white and dark respectively when viewed on a dark background in incident light. Fig.5.

The main point of contention among all the papers is the actual time of appearance of the zones mentioned. Both Dannevigs, working with cod from Norwegian coastal waters, came to the conclusion that the opaque zone developed during the months of December to July inclusive and the transparent zone during the months of August to November inclusive. Trout, working with
Barent Sea Cod, came to the conclusion that the opaque zone was laid down in late July and August merging into a clear winter ring. Cunningham and Wallace held the view that the opaque zone was laid down in the summer and the clear zone in the winter. Christensen analysed the peripheries of ten otoliths from sole in each quarter of the year to determine the presence or absence of organic material. Dannevig Eva H. had already shown by decalcification as stated above, that there were a series of membranous sacs present in the makeup of an otolith corresponding in position to the opaque zone of the otolith. Christensen burned each otolith for 10 to 30 seconds in a spirit flame then broke the otolith open and showed that the organic material had carbonized leaving a black zone. From his results he came to the conclusion that the organic material was being laid down sometime from April to June with the inorganic material being deposited from July to September. From September to March there appeared to be no change in the width of the zone on the periphery of the otolith and this was taken as being indicative of no growth occurring. This burning technique was tried out by Friend and Gentleman 1964 using trout otoliths but with no success.

These above results all deal with sea fish on which the vastly greater amount of work has been done. Frost working with eels in the Windermere catchment area and quoting other eel workers found that in Anguilla anguilla the white opaque band was laid down from August to November and the dark, translucent band was formed in winter. Jones and Hynes working with Sticklebacks, also in the Windermere area, showed that these fish laid down a transparent ring in June/July followed by an opaque zone laid down sometime between July and the following June. Sometimes the opaque zone was not visible until as late as September. Smyly in his study of the stone loaches
of the Windermere region came to the conclusion the otoliths showed annual markings of the opaque zone, translucent zone type. His studies led him to the conclusion that the opaque zone in these otoliths was laid down between April and September and the translucent band sometime during the other months of the year. In his later studies on the Bullhead or Miller's Thumb, from the same region, he used the otoliths to determine age but not growth as they were too irregular in outline for this purpose. The structure used in this case appeared to form from April to June but at no other time.

From the diversity of results with regard to times of appearance of the structures, it is obvious that the rings on an otolith may be called annual rings but should not be called Winter and Summer rings.

**Bones**

A second alternative to scales presents itself in the form of the bony skeleton of the teleost fish the many parts of which present themselves for examination by the simple method of boiling the fish when fresh and rubbing off the boiled flesh. Menon 1949 provides a very useful review of work done up to that time on various bones from a variety of fishes. In his survey of the literature Menon notes that Heinoke and his associates in 1904 were first to utilise the annual zones appearing on the bony skeleton of several food fishes in which the otoliths were unsuitable. Heinoke found that the growth in the bones was periodic, with the annual growth being marked in definite layers. He noted that there were two clearly recognised zones one white and opaque and the other dark but translucent when viewed with transmitted light. Heinoke noted that the slowing down of growth in winter was marked by the white layer but that any intervening boundary was of varying sharpness. Heinoke lists the concavities of the vertebral centra, the opercular bones
especially the sub- and inter-opercula, certain parts of the girdles especially the coracoid and scapula, the urostyle, the epural, the hypural and the hyomandibular as being the regions displaying the age zones most clearly.

Cunningham 1905 examined these bones and came to the conclusion that while he admitted that several of them had markings which could be called annual, for him, the otolith was to be preferred.

In 1908 Hiinoke elaborated on his earlier work giving more concise times of appearance of the various structures. The opaque zone was noted as appearing in late spring and early summer and the clear zone in late summer and early autumn with a sharp line marking the cessation of growth in winter. He noted that bones were especially useful in determining the age of older fish as each year was clearly marked, which was not the case with scales or otoliths. He conceded that the earlier years in plaice were clearer in the otoliths but that the bones were to be preferred for the later years.

Haempel (1910) compared the opercula, vertebrae and upper jaw bones to scales and otoliths from the Danube salmon. He claimed that the number of clear and dark rings on the bones corresponded exactly with those on the scales and otoliths with the vertebrae giving the best practical results. He noted the occurrence of false rings but claimed that they could be easily recognised by their discontinuous nature.

Tereschenko (1913) using the cleithrum of Rutilus rutilus also noted the presence of false rings which he claimed were temporary growth checks and easily recognised by their weak and discontinuous nature when compared to the true rings. He noted that the winter zone only became apparent in April/May although formed in winter and that it appeared earlier in younger fish.
Tereschenko also noted that the ratio length of fish to length of cleithrum decreased with age. However in later work (1917) done on bream he found that for them the ratio was constant.

Nilsson (1914) found good agreement between the vertebrae, scales and otoliths of mackerel but preferred to use scales and otoliths in his work as he found that the vertebrae gave a higher proportion of ambiguous results. In his 1916 work on perch using the operculum, he found considerable agreement between the readings from the operculum and the scales.

Later workers such as Chugunov (1925) working on sturgeon, Scofield (1931) on bass opercula, Waganowskaia (1933) and Holden and Meadows (1962) on dogfish spines, Roper (1936) on perch opercula and scales Boyko (1946) on fin rays, Le Cren (1947) on perch opercula and Menon (1950) using the supra-occipital crests of Gadus minutus have all strengthened the claims of different parts of the skeleton of fish to be used in age and growth studies.

One of the best vindications of the use of bones in age and growth comes from the work done by Le Cren on the Windermere perch mentioned above. The bone chosen by Le Cren for his especial attention was the operculum. He found that the longer the bones were left stored in a dry condition the clearer the rings became. Using a vertical projector and polarised light he magnified the image of the bones by a factor of five times normal. He found false rings easily distinguished by the abrupt change in appearance of the bone both before and after their appearance as compared to a more gradual change in normal checks. Le Cren examined a number of scales from the same fish but found a great prevalence of false rings in them and discarded them. His main task was to establish the validity of his method of back calculating the lengths of fish from their opercular markings. At
Fig. 6 shows a diagrammatic representation of a branchiostegal ray from the right side of the head. Three years growth are shown, I - III, with one false check, F. The false check is easily recognised as its lateral extension is not developed all the way round to the hinge, unlike the lateral extension of a true check.
Plate 2 Showing a Branchiostegal ray projected with normal light.
Plate 3 Showing the same ray projected between crossed polaroid strips.

A = Summer growth  
B = Winter growth  
C = Lateral extension of annulus to hinge  
D = Hinge

The line of measurement is also shown marked: ---
first some discrepancies were observed but these were held to be due to allometric growth of the bones coupled with differential mortality and selective sampling. By introducing a regression coefficient into the formula which then became:

\[
F_x = \frac{F_y}{0.9202} \frac{B_x}{0.9202}
\]

where 0.9202 is the regression coefficient Fx is the desired fish length, Fy is the observed fish length, By is the present bone length and Bx is the bone length at the previous age for which the fish length is required, the discrepancies were reduced.

By comparing the mean length of a sample of the population with the means of the back-calculated lengths from samples caught later in the year; by rearing Perch in aquaria and by marking Le Cren tested the accuracy of his modified formula. These tests showed that the adjusted formula was satisfactory. These results were fairly definite proof that the opercular bone could be used in the determination of fish's age and also for back-calculation of the fish's size at any previous age.

One of the more recently studied bones is the one under review in this work namely the branchiostegal ray. Branchiostegal rays are dermal bones found attached anteriorly by a hinge, Fig.6. Plate 2., to the hyoid bones their main function being to support the branchiostegal membrane. Their number and attachment vary in different groups of fishes (Lagler, Bardach and Miller). There are from nine to thirteen branchiostegals in the Salmonidae (Ox) and a count shows the number in *Salmo trutta* to be eleven.
Bulkley in his work on lake trout, *Salvelinus namayoush* (Walbaum), states that he chose this bone because of its easy accessability and because its marking seemed to show all the characteristics of annual markings suitable for use in age determination. Also, one ray could be removed from a tagged fish without inflicting a mortal wound. On recapturing the fish the corresponding ray from the other side of the head could be used to determine what changes in the rays' structure had occurred since the fish had been released. The last ray on each side was selected since it was the largest and most ossified. Both rays were taken to cover the eventuality of one ray being damaged or malformed. The rays were cleaned by boiling and removing the flesh. Bulkley noted that the rays were marked by a series of white, opaque bands separated by thin transparent bands that ran parallel to the edge of the ray. Fig. 6. These lines were noted as giving the appearance of having been at one time on the margin of the ray. The lines which extended from the posterior end of the ray along the full length of the ray were postulated as being annuli. The narrow transparent lines being assumed to be winter growth and the opaque band summer growth.

One drawback of the opercular bone is that there is considerable thickening near the focus of the bone. This thickening very often obscures the first annulus. The branchiostegal ray is a much thinner bone than the opercular and this thickening does not occur to the same extent leaving the first annulus much more visible. Most annuli could be read easily with the naked eye or a hand lens, but in older fish, where the annuli were bunched closely together on the scale margin, Bulkley found it a help to project the bones from a slide projector when the annuli could then be easily separated.
The accuracy of the ageing technique was tested by using known age fish. Bulkley's paper gives an expanded version of the criteria suggested by Freidenfelt 1922 (from Menon) which must be satisfied if a structure is to be considered of value as an age determinant indicator. The criteria are as follows:

1. There must be a good correlation between the size of the structure used for age determination and the size of the fish.

2. The number of annuli on the structure must increase with the size of the fish.

3. The outer margin of the structure must grow outwards from the annulus as the growing season progresses.

4. Paired or similar structures from the same fish must have the same number of annuli present.

5. Calculated lengths by the method proposed should agree with the empirical lengths of younger fish.

6. Age determined by the method should agree with age determined by other methods.

Bulkley found that the branchiostegal ray in lake trout satisfied almost all these criteria, with only slight discrepancies in older groups where there were fewer examples. There was found to be some disagreement between the back calculated lengths of younger fish and the expected lengths. Bulkley's samples however, contained an unknown number of hatchery reared fish which he suggests would be larger than the normal wild stock of the same age and would therefore lead to a bias towards a higher
figure in the estimated lengths. This was thought to be a likely explanation as the calculated lengths of older fish came much closer to the expected size and well within acceptable limits. Since most of the material came from fishermen there was also the possibility of bias towards larger fish being kept by them which would also affect the results.

Using known age fish Bulkley found 30 out of 37 readings from the rays agreed with the known age of the fish. The other 7 were explained by their time of capture, February to early May which is prior to the principal growing season as detailed by Cable (1956). These seven fish were assumed to have the missing annulus on the margin of the ray with insufficient new growth to make it visible. Using this assumption all assigned ages agreed with the known ages.

Bulkley suggests that the branchiostegal ray can be used to determine the age of lake trout but that the ray/body length relationship should be examined more closely. Difficulty in determining the exact position of the annulus led to some discrepancy in estimated lengths as did the possibly falsely high sizes obtained from hatchery fish in the sample.

Netsch and Witt (1962) also used the branchiostegal ray, but not in trout. The fish they examined was the Longnose Gar from the Central Missouri area. Once again false annuli are reported as lines which do not extend the full length of the ray. Fig.6. In fish of over 15.7 inches long the body/ray relationship was found to be linear but it was suggested that below this length the relationship would be curvilinear. This phenomenon may in part be explained by the remarkable daily increase in length attributed to these fish in Netsch and Witt's paper of an average of just over 2.8 millimetres per day which is almost six times the increments attributed to thicker bodied fish.
The branchiostegal ray is also known to have been used as an aid in ageing trout from Loch Leven, Scotland by Dr. Witcomb of Salford University (personal communication) but, unfortunately, no further information regarding this work has been obtained.

Fig. 6 shows a diagrammatic drawing of a branchiostegal ray from a trout Salmo trutta Linn. The ray shows three annuli extending from the posterior of the ray parallel to the margin all the way round to the point of attachment, or hinge, and one false annulus which is not developed in this fashion. The shaded areas represent the opaque regions of the ray and the grading in the shading is an attempt to represent the lessening the ray's opacity until the translucent zone is reached. It is an attempt to fix chronologically for trout in the area studied, the appearance and further development of the opaque and translucent zones described above which is one of the main aims of this work.
MATERIAL AND METHODS

Sampling Areas and Method of Sampling

The material worked with consisted of Brown Trout, Salmo trutta, from two sources. The larger, and more important, sample came from the exit stream of two small storage tanks near Linlithgow, about 17½ miles West of Edinburgh. The second, and smaller, sample came from a small area of Loch Earn, near Locheearnhead, Perthshire.

The Linlithgow ponds, since filled in, were fed by small drains from the surrounding fields and the exits to the stream were blocked by sluices, netting and perforated zinc plates. In April 1963, these ponds which had previously held only some three spined sticklebacks as a fish population, were stocked with several thousand trout fry for rearing purposes. This population was studied from August 1963 until March 1964 with regard to their scale and otolith development (Gentleman 1964). In the Spring of 1964 the bulk of the fish were removed by netting, transferred to Linlithgow Loch and replaced with a further stock of fry. Further permission to take samples was obtained in October 1964 and these fish in the exit stream, into which they had escaped from the ponds, were sampled at the rate of four fish every second Saturday for one complete year until November 1965 by which time 27 samples had been obtained. This gave a total catch of 108 fish. These fish were all caught using a rod line and baited hook.

The Loch Earn sample, totalling 31 fish, was obtained during the course of normal angling outings at four weekly intervals from March 1965 until October 1965. All the fish were taken within a few hundred yards of the mouth of a feeder stream which enters Loch Earn at its North West corner flowing after down Glen Ogle. Loch Earn is a narrow, deep loch reaching over 250 feet
Figure 7  Showing the position, A, of the branchiostegal rays. Also illustrated if the method of measuring a fish's head length using a ruler and two pins. One, B, fixed in the ruler and the other, C, movable. The area of scale sampling is also shown, marked D.
at its deepest part. The bed of the loch tends to shelve steeply round most of its perimeter, giving very few shallow feeding areas.

Fish Preparation and Measuring

After the fish had been caught and killed they were left for 24 hours to allow excess mucus to be secreted before being washed. The fish were then weighed to the nearest half gramme. The Hippural Standard Length, which is the length from the tip of the snout to the distal end of the vertebral column where the urostyle starts to bend dorsally and from which the major hypural elements fork (Ricker and Merriman), was measured to the nearest millimetre. This was done by inserting a mounted needle through the fish's tail sticking it into the zero mark on a ruler and allowing the fish to hang down the ruler. The point of insertion is found by bending the fish's tail while holding it close to the base. A fold appears across the end of the vertebral column on the inside curve of the bend and the needle can be inserted through this fold.

The head length was measured by inserting a pin in the region indicated in Fig. 7. The site of insertion is found by probing with a pin held at right angles to the fish until no resistance is met with and the pin may be pushed firmly home. A second pin is inserted at right angles into the zero mark of a ruler which is then slid along the fish's back until the second fin touches the fish's snout, with the pins parallel. The measurement was taken as the distance between the two pins.
Scale Mounting and Measuring

The mucus was wiped off and a scale sample taken from the region between the dorsal fin and the lateral line, Fig. 7. The scales, which were first washed by being shaken in water in a test tube with gauze over the end, were then mounted on a slide. If possible six good, that is non regenerated, scales were transferred to a second slide where they were carefully mounted in two rows. In the case of some fish one had to be content with fewer than six scales because of the large number of damaged scales in the sample. The scales were then secured under a cover slip held in place with gummed paper bands on which the sample numbers were written. All that was necessary for scale examination at a later date was the introduction of a drop of water under the cover slip. This water film cut out reflection from the scale surface and allowed the surface features to be more clearly seen.

The scales were then carefully examined and the one showing least malformation was measured along its long axis using a lens graticule and its length recorded in arbitrary units. The width of the spaces between the rings was then measured along the anterior-lateral field, Fig. 3., as the rings were of solidest formation in this region. These measurements were then transferred to centimetre graph paper where one millimetre was taken to represent one unit of measurement as shown in Figs. 8 and 9 (see results). All checks or suspected checks in growth and spawning marks were noted in their relevant positions. A clearer impression of ring arrangement with regard to closures is obtained if the Figs. 8 and 9 are viewed from the inside margin of the page at a shallow angle along their length.
Otolith Extraction and Measurement

The otoliths were extracted by making a deep incision along the lines marked in the X-ray photograph, Plate 1. The flap of bone was folded forward and when the brain was displaced first to one side then the other the otoliths were easily reached and removed. The otoliths were rubbed between finger and thumb to remove any adherent membrane. They were measured along their long axis using the same microscope and graticule as was used for scale measurement with the otoliths in direct light on a dark background. It was found that clearing with xylol helped in most cases except in those where the fish had been kept in formalin for some time before being studied in which cases the otoliths had assumed a chalky opaqueness. Any variations in the appearance of the otolithe periphery were noted as were the number of rings, if any. Sketches were made where appropriate. The otoliths were then transferred to little glass bottles, one bottle per fish and a little water added to prevent, or at least cut down damage to the otoliths when the bottles were being handled.

Branchiostegal Ray Preparation and Measurement

The posterior branchiostegal ray on either side of the fish's head was removed completely, using a fine scalpel, and immediately immersed in boiling water for one to two minutes to soften adhering tissue. This tissue is easily removed by drawing the bone, hinge first, between the first finger and thumb of one's hand. The bones were mounted flat between two slides which were then bound together with gummed strips with the sample numbers written on them.

After the bones had dried out their image was projected onto a sheet of
photographic paper using a 35 mm enlarger set at $2\frac{1}{2}$ x magnification. The paper was then developed and the image produced, Plate 2 and 3, closely resembled the picture seen when a bone is viewed under direct illumination on a dark background. The length from the centre of the hinge D to the farthest limit of bone growth was measured using a small flexible ruler which followed the curve of the bone, Fig.6, Plate 3. If a strip of polaroid was inserted above the slide and another rotated underneath it was often possible to detect structures not readily visible using normal light; as shown in Fig.6. Growth checks are taken as the lines which continue from the distal edge of the bone to the hinge while false checks are taken as those lines which do not continue to the hinge. A quick age determination can be carried out if the slide is held up to the light between two pieces of Polaroid when faint checks become more readily visible.
The centre of each scale is situated on the left edge of the figures and the margin on the right edge.
Fig. 8a-f Showing diagramatic representation of rings on scales from Linlithgow trout. Special attention should be paid to the last few rings on each scale.
RESULTS

Scale Development

Linlithgow Fish. This sample is the more important one representing, as it does, a complete season's development as seen at fortnightly intervals.

From an examination of Fig. 8 it is noted quite clearly that only one fish, M4, has not laid down any narrow winter rings. This would suggest that for most of these fish the winter band is laid down sometime before the middle of November.

In the December sample, however, while five of the fish have closed margins, D1 has an open margin and D2 and D3 appear to have laid down a few wider rings after laying down their winter band. These results would seem to put D1 in the (B) category described above as late growers and D2 and D3 in the (A) category.

The first January sample appears to have one category (B) late grower, J2, and three category (C) slow growers J1, 3 and 4. In the second sample, however, there are two fish J5 and J8 which seem to fit the (C) category although their margins are not markedly closed, and two, J6 and J7 where their margins would appear to be quite open categorising them as group (B). The J9 - J12 fish would all appear to fit the category (B) classification, which seems most unusual and may be due to their juvenile state.

In the February sample, F1 would also appear to belong to the (B) group of fish, while F's 2, 3 and 4 have some suggestion of closure on the margin indicative of weak winter banding. In the second February sample, the F5 fish has some suggestion of narrowing 7 - 9 rings in from an open margin, which, if so, would classify it as a possible group (B) fish. F6 appears to have two to three wide rings outside a winter band suggesting that either it
belongs to the group (A) classification, or has begun new growth early. The 
P7 fish has a well defined closed margin while the P8 fish appears to have laid 
down one wide ring on its scale margin.

In March the M1, 3 and 4 fish all have narrow bands on, or close to, the 
scale margin although in the case of the M4 fish there are three wider rings on 
the scale margin suggesting renewed activity. M2, however, has an open margin 
of over 10 rings which would seem to classify it as a late grower. M5, 6 and 
8 have commenced new growth while M7 still has a closed margin.

In April the A1, 2 and 3 fish have all laid some wide rings while A4 has 
retained its closed margin. The A5, 6 and 8 fish have all laid down 1 or 2 
wide rings on their margins outside a narrow band. The A7 fish, however, has 
at least ten broad rings on its margin (category B7) making it difficult to 
assess if new growth has actually commenced.

From April through May, June, July and into August, there is seen to be an 
increasing number of broad Summer rings on the scale margins, Figs.8c to e. 
There is, however, some suggestion of a closing in of rings on the peripheries 
of scales A9 and A10.

In September, Fig.8e this closing in is to be found in scales 31 and 35 
while all the other fish seem to be maintaining good growth. This growth 
would seem to be maintained in October save for the 01, 06 and possibly 05 
fish where there is seen to be some narrowing on the margin.

The November sample caught at the end of the year under review has two 
fairly definite sets of narrow rings on the margins of scales from the N2 and 
N4 fish and some suggestion of narrowing on the M1 and N3 scales.

All in all it would seem that for this stream in Linlithgow, the fish 
form their Winter band in October/November with very little winter growth, and
Fig. 9a-b  Showing diagrammatic representation of rings on scales from Loch Earn trout. As in Linlithgow scales the last few rings should be examined carefully.
commence new growth in March/April.

Loch Earn

From the Fig. 9a it is obvious that apart from N3 and N2 all the fish have closed margins. Even the J1 fish show this closed margin but the J2 and J3 fish appear to have laid down 2–3 wide rings outside a winter band. These broad marginal rings are seen in increasing numbers throughout the July, August and September (9b) samples. In the September sample, however, the S1, S2 and S3 fish give a vague impression of narrowing in of rings towards the scale margin.

In the October sample caught right at the beginning of the month (on the night of the 2nd-3rd October) the O1, 2, 4 and 5 fish show a reasonably obvious narrowing on the scale margin while the 3 and 6 fish still have open margins. This would seem to suggest that the growing season in Loch Earn is from April/May until September/October.

Otolith Development

Linlithgow Fish. The otoliths proved more difficult to work with than either scales or branchiostegal rays with the following results.

As shown in Fig. 10 a from November 1965, N, until March/April 1966 M/A there appeared to be a translucent band on the edge of the otoliths. This had already been recorded from this area, Gentleman 1964. From March/April Fig. 10a, until July/August 1966 M/A, Fig. 10b, an increasingly broader band of opaque material made its appearance. During this time the edge of the otolith had a jagged appearance usually taken as an indication of fast growth. By late August, A8 Fig. 10b, the margin was appearing more translucent and
Fig. 10a-b  One otolith per month from the Linlithgow trout.

Particular attention should be paid to the appearance of the edge of the otolith in the sketches. Where there was doubt as to the state of the margin this is signified by a ?.
Fig. 11 Sketches of otoliths from Loch Earn trout. As in the Linlithgow otoliths the margin of the otolith is the most important part of the otolith.
from September, S, onwards this translucent margin became increasingly obvious e.g. October, O and November, N (1965).

In some of the otoliths from the youngest fish it was often difficult to decide what was actually taking place and, to add to the difficulty, after storage some of the otoliths went completely opaque. In conjunction with Mr. Friend burning of the otoliths was attempted after Christensen (1964) but the results we obtained were disappointing compared with the results he had obtained with sea fish otoliths.

Otolith growth in Linlithgow fish would seem to fall into two divisions, with opaque growth occurring from late March/April until August/September and translucent growth from August/September until March.

**Loch Earn.** The Loch Earn otoliths were, on average, from slightly older fish than the Linlithgow otoliths and were slightly more easily worked with. The March and April otoliths L.E. M and L.E. A, Fig.11, had translucent margins. By May, L.E. M Fig.11, an opaque band was beginning to develop.

This band is seen to develop through June L.E. J, Fig.11 into July L.E. J and August L.E. A Fig.11. By September L.E. S a translucent zone has appeared and is increasingly obvious in October L.E. O when sampling in this area ceased.

For Loch Earn therefore, the division of growth would appear to be the development of an opaque zone from May until August followed by the development of an opaque zone between September and April. The second part is, of course, an estimation as fish were not obtained for a complete year from this area for reasons stated earlier (see Sampling).
Points of interest are marked with arrows on the scales and with supplementary line drawings for the bones.
Plate 4 a November scale with closed margin.
   b November branchiostegal ray with clear margin.

Plate 5 a December scale with closed margin.
   b December branchiostegal ray with clear margin.
Plate 6  
a. January with some closure in lateral field.  
b. January branchiostegale ray with clear margin.

Plate 7  
a. February scale suggestion of closure on scale shoulder. 
b. February branchiostegale ray with clear margin.
Plate 8 a March scale one ring outside check.
   b March branchiostegal ray with clear margin.

Plate 9 a April scale with two rings outside check.
   b April branchiostegal ray with slight marginal activity.
Plate 10 a May scale with three rings outside check.
    b May branchiostegal ray with annulus more visible.

Plate 11 a June scale with six rings outside check.
    b June ray showing increasing opacity and lateral growth
Plate 12 a. July scale with eight rings outside check.
   b. July ray showing broad marginal growth.

Plate 13 a. August 5 fish showing thirteen rings outside check.
   b. August ray obscure due to immersion in formalin.
Plate 14 a August 9 scale showing some narrowing to margin.
   b August 9 ray margin clearing at tip.
   Gonads ripe.

Plate 15 a September scale narrowing at margin.
   b September ray obvious marginal clearance.
   Gonads ripe.
Plate 16 a October scale **open margin**.

b October ray thinning towards margin.
Gonads ripening

Plate 17 a November 1965 scale **closed margin**.

b November 1965 ray clear margin.
Gonads ripe
Plate 18  a March scale closed margin.
   b March ray clear margin.

Plate 19  a April scale with two rings outside check.
   b April ray clear margin.
Plate 20 a May scale with three rings outside check.
   b May ray showing annulus forming.

Plate 21 a June scale with six rings outside check.
   b June ray showing broader marginal development.
Plate 22

a July scale with five rings outside check.

b July ray showing good marginal development.

Plate 23

a August scale with six rings outside check.

b August ray obscure due to immersion in formalin.
Plate 24

a September scale with nine rings outside check.
b September ray thinning towards margin.

Plate 25

a October scale showing narrowing on scale shoulder.
b October ray with clear margin developing.
Branchiostegal Ray Development

Linlithgow Fish. The bones were carefully examined with special emphasis being placed on the appearance of the area including the tip of the bone at the opposite end from the hinge as this is the region where most growth would be expected to occur. From the November 1964 sample to the March 1965 sample, Plates 4-8, this area was found to be clear with no associated cells. In March, however, there was seen to be a narrow margin arising from a fold in the ray. This margin was broadest at the tip and narrowed considerably round the periphery of the ray. In the first March sample only the narrow marginal band was visible with no associated cells. In the second sample M5 to M8 the band was slightly broader and there were a very few scattered cells making themselves visible in this region with some beginning to arrange themselves along a line roughly parallel to the edge of the bone.

As the samples progressed through April, Plate 9, the cell density increased with an increasing alignment of cells along a fold visible to a greater or less degree on all the bones. The line where the cells begin to appear varied from two to eight units from the end of the bone and the distance appeared to depend on the overall size of the bone, being greater in the larger bones. In the M5, Plate 10, fish which is taken as being a two year old fish there is an aggregation of cells along a line 4-5 units from the bone margin then very few cells are seen until 18 units from the bone margin. This distant aggregation of cells is taken as being the mark laid down in Spring 1964.

From the June sample, Plate 11, onwards the most noticeable development was an increase in the width of the clear marginal area on all bones examined associated with an increase in the number of cells in the area
where they first appeared. It is very obvious from Plates 11 to 17 that the cell density drops off rapidly towards the edge of the bone with only very few near the margin at all. This development is seen in all the samples right through until November 1965 when sampling ceased. The fish in November 1965 bear a marked resemblance to the fish in November 1964 regarding the appearance of the area under observation.

While this tip area was developing as described above there was a similar development but on a lesser scale along the margin of the bone leading along the outer edge of the bone to the hinge, Plate 15. The photographs and drawings Plates 10 to 15 of this area show quite well the gradual broadening of this band from a fold with an associated deposition of cells arranged along the line of the fold. It is this fold which distinguishes a false annulus, in which it is not present, from a true annual mark in which it is present.

From the above observations it would appear that the seasonal development of the branchiostegal ray in the Linlithgow fish follows this pattern:— in March/April there is a surge of growth around the edge of the bone being greatest at the tip farthest from the hinge. Following the first surge of growth there is a gradual thickening of the bone in this area signified by an increase in the number of cells seen in this area. In April/May the growth is continued in a longitudinal direction but, by September the cells appear to have reached the limit of their spread as denoted by the increasingly broader clear margin seen throughout this month and the succeeding months although there may be localised increases in cell density.

These aggregations of cells are found on examination, to correspond to the areas which appear white when viewed under incident light and also appear white
when photographed by the method described above. The clear margin appears to broaden until October/November when there appears to be a great slackening off in growth until the March/April surge. The annulus is therefore taken as being the line shown in Fig. 6 and Plates 2 and 3 where there is a sharp increase in the number of cells in the bone, these cells being arranged in a line roughly corresponding to the end of the ray. The second annulus appears to be more distinctly marked than the first, see Plates 14 and 15, and great care should be taken when reading the bones not to overlook the first annulus.

Loch Earn Fish. In the Loch Earn fish there is only a faint suggestion of growth in the March sample. The April sample, plate 19, is at a stage roughly parallel to the March sample from Linlithgow, and it is not until the May sample, Plate 20, that cells appear in association with the fold between the old and new growth. From June onwards, Plate 21, the pattern of development parallels that of the Linlithgow fish with an increasingly broader margin and an increase in the number of cells associated with the new growth. By the October sample, Plate 25, the familiar pattern had developed of a dense aggregation of cells along the fold line with a reduction in numbers towards the ray margin and a broad marginal band with very few, if any, cells in it.

The Loch Earn growth pattern for this bone would appear to parallel that of the Linlithgow fish but lag behind it by about a month. This agrees with times of appearance of new growth on the scales from the respective areas.

Age and Length Determination

The results obtained by examining and measuring the bones were examined in the light of the criteria suggested by McConnell, described earlier above.
Fig. 12 Average monthly fish length and average monthly ray length plotted against time. The spread of the sample is also shown for each month. Note the close similarity in shape and the steady upward rise in sample size.

Fig. 13 Average monthly fish length and average monthly ray length plotted against time. The spread of the sample size is also shown for each month. Note the close similarity in shape and the low Summer average size.
**Fig. 14** Showing a plot of ray length against fish length.
Note the close grouping round the lines of best fit which have been inserted for both Linlithgow and Loch Earn fish.

**Fig. 15** Showing a plot of head length against body length.
Note the very close grouping and also the similar arrangement of Loch Earn results below the Linlithgow results.
Ray and Body Length

In order for the branchiostegal rays to be good indicators of age they must be closely related with body size. The correlation between ray and body length was calculated separately for the Linlithgow and Loch Earn samples and for the joint sample. For the Linlithgow sample the correlation was 0.9105. For the Loch Earn sample the correlation was 0.917 and for the joint sample, using all the figures as one large sample, the correlation was 0.9795. All these correlations are of a very acceptable high value and agree closely with the figure of 0.961 obtained from Lake Trout, Bulkley (1960) and 0.9408 from Longnose gar, Netsch and Witt (1962). The closeness of the correlations from the Linlithgow and Loch Earn samples would appear to strengthen the case of using this bone as a growth indicator in a diversity of habitats. The graphs of average ray length and fish length to time Figs.12 and 13 show a marked similarity in the shape of the lines, especially in the case of the Linlithgow fish where a steady increase in average fish size is closely paralleled by a steady increase in ray length. In the Loch Earn fish a slight decrease in fish size followed by a slight increase in the September/October samples is reflected in a similar pattern of ray development.

The relationship between ray length and body length is seen displayed on the graph in Fig.14. The narrow spread would appear to bear out the close correlations found above. It should be noticed that there appears to be a marked separation between the lines of best fit for the Linlithgow sample and for the Loch Earn sample although their respective gradients are very similar. Linear regression formulae were derived for the Linlithgow, Loch Earn and joint samples with the following results.
\[ y = mx + c \]

- \( x = \) fish length
- \( y = \) bone length
- \( c = \) constant

Linlithgow:
\[ y = 5.632x - 2.01 \]

Loch Earn:
\[ y = 5.044x + 1.316 \]

Linlithgow and Loch Earn joint samples:
\[ y = 5.817x - 2.169 \]

The relationship between the Linlithgow and Loch Earn lines was analysed with the following results: The Loch Earn fish were found to be significantly more variable than the Linlithgow fish, possibly due to their wider age range. The slopes were not found to be significantly different although the lines themselves were significantly different. The Linlithgow fish appeared to have higher values in ray length for the same length of fish than the Loch Earn fish. The relationship of head length/body length was also plotted, Fig.15 and shows a similar distribution of results to the ray length/body length graph with a much tighter grouping of results. The correlation coefficients were calculated as before for each sample independently and for the joint figures with the following results: Linlithgow fish 0.9786; Loch Earn 0.9709 and the joint sample 0.9727. These results bear out what one would reasonably expect, that is, that there is a closer relationship between
head and body length than between a single bone length and the body length. The comparative positions of the majority of the results for the Linlithgow and Loch Earn fish would seem to suggest that the Linlithgow fish have larger heads in proportion to the overall body length than the Loch Earn fish. This state of affairs would appear to lend support to the above suggestion that the Linlithgow fish had longer rays for the same body length than the Loch Earn fish.

**Annuli number and body length**

The number of annuli increased with size of the fish. This was more clearly seen in the Loch Earn fish where there were a number of fish older than the maximum of two years for the Linlithgow sample.

**New growth on rays**

There must be a constant increase in marginal growth during the growing season. This growth was found to occur and has been described above with reference to the plates quoted earlier.

**Similarity of rays on the same fish**

The two rays from opposite sides of the fish were compared to determine whether there were the same number of annuli on each ray. The rays were found to be very similar and the number of annuli was always the same on either side in each pair examined. Sometimes it was found that the annuli were more clearly marked on one side than the other especially near the base of the ray, but a closer examination, especially using the polaroid strip method described above, almost invariably led to the location of the faint annulus.
Calculated versus empirical length of fish

The Standard errors for all three samples were calculated with the following results:

<table>
<thead>
<tr>
<th>Location</th>
<th>Sx</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linlithgow</td>
<td>1.384</td>
</tr>
<tr>
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Several randomly chosen ray lengths were used to calculate fish lengths using the regression formulae described above and it was found that the calculated lengths came within one to one and a half times the standard error of known fish lengths for these ray lengths. In the absence of large amounts of data giving the size frequency for each age group for the fish under observation this rather oblique method has been used. It is suggested that, since the randomly calculated length is close to a known length for each ray size, the calculated lengths would be reasonably representative of the fish at given ray lengths in the back calculation of fish sizes for the juvenile stages of older fish. Bulkley (1960) discovered that the calculated lengths were fairly consistent with mean lengths at capture for age groups up to year V but tended to be larger in age group VI and upwards. He suggested that this may have been due to the presence of hatchery fish in the younger samples which would affect the mean length. He also suggests that since samples were mostly obtained from fishermen that there was selection as to the size of fish kept with a bias towards larger fish.
Branchiostegal rays versus Scales

Age determined by the rays should agree with age determined from the scales of the same fish. Bulkley (1960) found a 24% agreement on age between the two methods. An examination of the data (appendix) will show an agreement of approximately 80% but it should be noted that most of the disagreement appears between the time of formation of the winter rings on the scale in late autumn and the appearance of new growth on the ray in early spring. If we take the clear margin on the bone as being equivalent to the closed rings on the scale margin then most of the disagreement disappears. Therefore a knowledge of the time of capture of the fish whose rays and scales are being compared is of greatest importance to the reader.

Bulkley also found the assigned age from scale reading in older fish was lower from the scales than from the rays because of the difficulty in separating the checks on the scale margin compared to those on the ray margin.
Material and Methods

The situation at Linlithgow was thought to be suitable as it approximated very closely to a natural habitat. The artificial stream and ponds had been in existence for in excess of 50 years and, in this time, the stream bed had become overlaid with a thick deposit (from the surrounding fields) in which various plants had become established. The banks of the stream were overgrown with long grass and a few trees, giving it a natural appearance. Also in its favour was the fact that the fish were subjected to all climatic variations and were not artificially fed.

It was not considered wise to take more than four fish every second week as the stock would have been very quickly depleted. Fish did escape over the barrier at the common exit from the ponds in time of high water. It was considered that sampling combined with the escape of fish over the barrier which separated this stream from its lower reaches, probably combined to keep the number constant. To obtain samples of a larger size it would become necessary to resort to netting a larger stream or loch or to depend upon the goodwill of enlightened anglers who would be willing to note down the length of their fish and supply this information complete with the head and a scale scraping.

Since much of the earlier work done, was done on fish caught by anglers and net fishermen there seemed to be no objection to catching the fish by rod and line. The very small fish which could have been caught by netting would have been too young to have developed any annual markings. Possibly the only drawback which this method has, and which must be borne in mind, is that there is a possibility of a bias towards larger fish in the same age group.
being caught. This bias would lead to an untrue picture of the mean fish size at any one age.

The steadily increasing average sample length Fig.12 shows that the fish were maintaining a steady growth rate. This is not seen in the Loch Earn fish Fig.13 but over several years angling on Loch Earn the author has found the average fish size higher in the Spring, late Summer and Autumn months than in the mid-summer months when there was a falling off in both catch numbers and quality. This may be due to the larger fish spreading out from the sampling area at the mouth of the spawning stream during the summer months then returning to this area later in the year in readiness for an ascent of the stream to the spawning beds.

The preparation of the material for study was fairly standard procedure except for the use of polarised light also described by Le Cren (1947) and the method of projecting the image of the bone directly onto photographic paper for the purpose of measuring and for later study. As noted above the photographic image produced is very similar to that seen when the bone is viewed in direct light on a dark background. This method has the advantage that enlargements are obtained relatively quickly and easily in a permanent form. A medium definition paper was found to be quite suitable. The bones being relatively thick material, the exposure time had to be fairly long, in the region of 10-15 seconds with normal light and 25-30 seconds with polarised light.

The Hippurial Standard Length used is perhaps not the most popular length to measure due to the difficulty noted in measuring it in the field and the possibility of damaging the fish, if it is to be released, while using the method described above. About its only claim over other methods is that it
is useful if the tail fins have been damaged during handling. However, Carlanier and Smith (1945) showed that all methods of measuring the fish's length gave very similar results when used to calculate fish weights therefore the main factor in the choice of method would seem to be one of convenience as long the method used is clearly defined.

DISCUSSION PART 2

Scale development

The range of development in the scales with the Linlithgow fish appearing to commence Spring growth in March/April and the Loch Earn fish in April/May through to a check formation dated October/November for Linlithgow and September/October for Loch Earn fits in very well with the results noted by other workers. Ball and Jones working on Llyn Tegid trout fixed the time of appearance of wide rings as Feb/March and the formation of narrow rings as September/October with approximately 70% of the fish showing no growth after the formation of the winter rings until the appearance of the wide Summer rings. Johnston (Fish. Invest. 2 1928-29) working with salmon parr and smolts puts rapid growth as occurring from April to September with very little growth between October and March. Cooper (1951) in his work on Salvelinus fontinalis reported very little change in the appearance of the scales from the formation of a check in September/October till the following Spring when the pattern of new growth appeared.

It would seem to be the case, therefore, that the Linlithgow and Loch
Finnish fish appear to fit into the accepted growth pattern with slight variations due possibly to latitude and differing environmental conditions. The month's delay in the Loch Earn fish may be due in part to the area being much colder in early Spring and in part to the Loch Earn early samples being comprised of older fish as younger fish have been noted as starting their Summer growth earlier than older fish, McFadden (1959).

The relatively large number of fish with fairly open Winter margins may be due in part to their age and size as small young fish are thought to continue their growth throughout the winter months to a greater extent than larger older fish, Ball and Jones (1960).

The Linlithgow fish appear to have grown much faster, show greater growth on their scales, for their age than trout from other waters as described by Mills et al (1972) in their findings with regard to Tweed trout. This may be due to the very rich feeding and relatively low density of the fish in the Linlithgow area when compared to the higher density and poorer feeding in the feeder streams in the Tweed basin.

Allen (1951) in his study of a New Zealand trout stream, which was admittedly of considerably greater size than the Linlithgow stream, ranging from a mountain stretch to a tidal stretch covering several miles, used scales for age and back calculation of growth. Allen found that in areas of high food availability beside the sea there was no Winter banding in the fishes' first Winter. Higher up the stream in an area of harsher conditions, some of the scales did show Winter banding. This area in New Zealand probably has a milder climate than the Linlithgow or Loch Earn areas. This would help to explain the high incidence of Winter banding in the Linlithgow fish where there was a reasonably plentiful food supply. Conditions at Linlithgow could be harsh and
one sample was actually taken when the ponds above the stream were ice covered.

Taking these differences into consideration the Spring growth surge following the Winter check and the Autumn slowing down in both areas would appear to point to the Linlithgow fish conforming to the normally accepted pattern of growth sequences for trout with regard to the appearance of broad and narrow rings on their scales.

**DISCUSSION PART 3**

**Otolith development**

As has been mentioned earlier the state of knowledge of otolith development as far as trout are concerned is far from clear. Dr. Swan (personal communication from a wealth of experience covering many years and many hundreds of fish, stated that he always found trout otoliths difficult to read and always preferred to use scales. Dr. D. H. Mills (personal communication) also states that he and his fellow workers have found trout otoliths difficult to work with even compared to salmon although he found eel otoliths very useful.

One of the major difficulties found when examining the otoliths was that of determining the time of first appearance on the otolith edge of new structures. One could never be sure whether there was a change or whether the apparent change was due to trapped or reflected light, or, in fact the thinness of the margin. Rotating the otolith sometimes helped in the first two cases as did
altering the angle of illumination. This meant that any change was well advanced before it could be readily identified, therefore the timing of the earliest appearance of the changes could be out by up to one month.

The development of the opaque region has been tied to the warm season by several workers. Poinsard and Troaede (1966) on West African Croakers and Wallace (1905) working with plaice, placed the occurrence of the opaque zone as late Spring and early Summer and the translucent zone as Autumn and Winter. Cunningham (1905) examining otoliths from plaice, cod and whiting found the opaque zone was formed during Summer and the translucent zone during Autumn and Winter. Gambell and Messtorff (1964) in their work on whiting otoliths found that the opaque zone was formed in Summer with 100% of the July sample having opaque margins.

The time of opaque zone formation would appear to agree closely with the time of formation of densest growth of bone in the branchiostegal ray (see results) and is presumably tied in with the availability of material. Hickling (1931) and Miller (1961) both suggest that the availability of organic material for otolith formation is tied to the breeding season. Miller (1961) showed that in the Rock Goby the translucent zone reached its greatest sample frequency in May when the Goby spawns. Since trout spawn in late Autumn and early Winter this would correspond to the time of appearance of the translucent zone noted above.

Jones and Hynes (1950) had no option but to use otoliths when studying sticklebacks as these fish have no scales. Regular monthly samples were taken over one year and it was found that the translucent zone appeared on the otoliths edge during the months of June and July, shortly after the finish of the fishes' breeding season. The opaque zone persisted on the edge of the otolith from July until the following June. In some fish,
however, the opaque zone did not become apparent until as late as September.

In a study of the Stone Loach however, Smyly (1955) found an opaque zone on the edge of the otoliths from May until September which appears to closely parallel the results obtained from the trout samples under consideration here. Smyly (1957) also reports on finding opaque/translucent zones in the otoliths of Bullheads but unfortunately omits to detail which one is at the margin at which time. He reports a distinctive feature from April to June but does not say whether it is opaque on translucent.

It would seem therefore as has already been stated above, it is incorrect to label the opaque and translucent zones as Summer and Winter bands but justifiable to name them seasonal rings from the weight of evidence to justify the title especially from sea fish studies. The opaque zone on trout otoliths would appear to be related to a time of high food availability in Spring and Summer and the translucent zone connected in some way with the lower food availability in Autumn and Winter and with the maturation of the gonads. There is some precedence for this assumption as Swift (1961) found changes in the growth pattern on trout scales as the fish approached sexual maturity under optimum food conditions when no change in the growth rate would normally be expected.

A tentative start was made to establish the relationship between otolith length and fish length. Quite a reasonable relationship was appearing, although not as closely grouped as that of the ray length fish length relationship. The difficulty involved in establishing a fish's age from these otoliths was proving so great that it was decided that this extra line would be too time consuming and unprofitable so it was discontinued. It may well be however, that a sample containing many much older fish may prove more profitable as the Loch Earn otoliths from older fish proved to be clearer than those of the younger Linlithgow fish.
DISCUSSION PART A

Branchiostegal ray development

As described in the results the time of greatest growth in the Linlithgow fish appear to lie between March/April and October and between April/June and October for the Loch Earn fish. This time of appearance of the annulus appears to fit in quite well with the times given by Netsch and Witt (1962) working with Longnose gar branchiostegal rays i.e. May/June; Bulkley (1960) on Lake Trout, May/June; April/May for the opercular bone in Esox lucius, Frost and Kipling (1959) and May for the Perch operculars, Le Cren (1947). All the above named workers described a clear band appearing in September/October as being the Winter band.

The zones of the rays are much more easily seen without as much preparation as that needed to examine the otoliths and may be seen with the naked eye as described in Methods. This is an advantage over both scales and otoliths. Unfortunately, no really old fish were included in the samples. It is in these older fish that workers such as Le Cren (1947) and Bulkley (1960) found the bones of most use as the annual markings on the scales were often compressed on the scale edge of where erosion had often destroyed them.

The annulus is described by the above workers as the point on the bone where the clear area gives way to an opaque zone. This transitional area is also marked by a distinct ripple on the surface of the bone. This description of the annulus by these workers matches very closely the observations on the changes noted in trout branchiostegal rays in the early Spring, from both Linlithgow and Loch Earn. It was also noted that the true annulus appeared to be marked by an extension of this clear/opaque zone round the periphery of the bone to the hinge. This is also recorded for the branchiostegals rays
under observation. As shown in the results Plates 9 to 14, the development of this area is quite easily seen.

A closer examination of the opaque zone shows it to be composed of a dense aggregation of cells while the lessening in opacity towards the clear zone is shown to be caused by a gradual reduction in cell density as one moves away from the fold line.

As fish were sampled for only one year it is difficult to state categorically that the markings noted of the ray are annual markings. It would also be erroneous to claim the times of appearance noted for the various structures as the exact times as these might vary with varying winter conditions. The winter of 1964-1965 was one in a series of very mild winters and may have affected the results. To back up this pilot study fish would have to be caught for several winters in possibly larger numbers than here and the rays examined closely for the appearance of the structures described above.

As described above, the branchiostegals ray appears to satisfy the requirements needed before it can be considered as being of use in studying the earlier growth of trout. There are several provisos which must be made regarding its use. It has already been stated that more work needs to be done on larger samples to confirm the description of the noted structures as annual markings. The same also holds true for its use as an indicator of previous lengths using the formulae described earlier. Because of the low sample numbers at any one age it is impossible to compare calculated lengths against mean empirical lengths for any one age group. It would therefore be necessary to catch large numbers of fish, split them into year groups then compare the calculated lengths for any one
age, with the mean lengths of the corresponding age group as described by Bulkley. Previous workers such as Bulkley appear to have carried out this part of the necessary work by collecting large numbers of fish, producing suitable formulae and testing them against the suitable age group as described above without actually following the bone throughout the fish's entire yearly cycle. Le Cren went some way towards this goal by comparing the back calculated lengths from Perch caught late in the year with the actual lengths of those caught earlier in the same year.

Larger sample numbers including many older fish are also necessary to determine whether the apparent straight line formed when comparing ray length and fish length has, perhaps, a curved upper region as the fish ages. As quite a few of the samples used here were below one year old it would appear from the lower of the graph of ray length/bone length that the relationship appears to be linear at least in the fish's early years.

Capture-recapture experiments could be carried out using the branchiostegal ray first from one side of the head then from the other. One danger would be that the shock the fish might get when the ray was being removed would interrupt its growth cycle and cause discrepancies to appear on the ray markings. Scales could also be taken at the same time as indicators of any change in growth pattern as they are reasonably sensitive barometers of any such changes. One other difficulty is the possibility of one bone being deformed in which case the result from that fish would be lost, also only one reading and one follow up reading could be taken as the use of other rays from the same fish might produce false lengths of bone when compared to the length of the last ray on each side.
Bearing these difficulties in mind the branchiostegal ray still appears to have some future as a possible back up in determining the age and growth patterns of trout. In view of the reported allometry of scale growth, and consequent difficulties associated with their use (Kipling 1962).

**DISCUSSION PART 5**

Comparison of growth of Scales, Otoliths and Branchiostegal rays.

From the above results it is obvious that these three structures show a marked similarity in their growth patterns. They all exhibited poor development from late Autumn to early Spring except in the case of the scales of some small young fish, an explanation for which has already been suggested. It is suggested that all three structures produce an annual mark such as had been shown in the scales, otoliths and vertebrae of the Danube salmon by Haempl 1910 (Fish. Invest. 1928-29). The band of narrow rings taken as a Winter check is formed in September/December, with older fish with maturing gonads producing a check in the earlier part of this time and younger fish in the later. The clear "Winter" band on the ray is formed from September onwards but does not become obvious until the formation of the new opaque growth in the following Spring. An examination of the Plates 4-17 for Linlithgow and 18-25 for Loch Earn in conjunction with the sketches of the otoliths Fig.10a-b for Linlithgow and Fig.11 for Loch Earn show quite clearly
the parallel development of these three structures.

Freidenfelt (1922 from Menon) studying Lucioperca compared the growth of scales and vertebrae from these fish. He found that there was a good correlation between these two structures although there was some time difference in the appearance of the annual markings especially in younger fish, as has been found above for trout.

As suggested earlier this pilot survey could be backed up by taking larger samples over the course of two to three years in an attempt to compensate for any discrepancies caused by exceptionally mild or severe winters. Such a survey it is hoped would give a mean time of appearance while any extremes of weather conditions would give the limits of the times of appearance of the markings.

It is also interesting to note the similarity obtained in the results from fish obtained in two very marked habitats as described earlier. The Loch Earn fish are smaller in size than their contemporaries with regard to age from Linlithgow. Some of the Linlithgow fish of just over two years were as large as the five year old Loch Earn fish and later angling returns from Linlithgow Loch into which the stream flows have shown fish of a maximum of five years from time of stocking to be over six pounds in weight showing the excellent fertility of this area.

The closeness in the regression formulae for Linlithgow and Loch Earn would appear to suggest that if fish were taken from a very wide variety of sources it might be possible to produce a blanket formula which could be used in conjunction with ray lengths from almost any trout to calculate early growth without having to develop a specific formula for that area. Any such formula would of necessity have to work within broad limits. It may possibly
be that these limits would have to be so broad that the results obtained using 
the formula would be of little value above giving a general impression of the 
fish's past history. If the limits were not too broad however, it would 
mean that a worker could take a much smaller sample size to study a water 
thus preserving what might in some cases be a fairly small fish stock.

Even if such a formula as described was not workable the branchiostegyal 
ray would appear to hold some place in the study of trout, perhaps not such a 
high place as scales but probably a higher place than otoliths.
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APPENDIX

Tables 1 - 13  Linlithgow fish
Tables 14 - 16  Loch Earn fish
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