THE LENGTH-WEIGHT RELATIONSHIP AND SEASONAL CYCLE IN GONAD WEIGHT AND CONDITION IN THE PERCH

(PERCA FLUVIATILIS)

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(With 8 Figures in the Text)

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1. INTRODUCTION

The present paper is an account of some of the investigations on the biology of the perch (Perca fluviatilis Linn.) in Windermere, which are being conducted in connexion with a trap-fishery experiment (Worthington, 1950). This experiment is mainly a study of populations, but it has been necessary simultaneously to investigate the general biology of the perch, particularly the growth and related aspects. The computation of a formula to express the length-weight relationship and provide a means of interconverting measurements of length and weight revealed the relative complexity of the interrelationships of length, weight and condition. Condition in turn was found to be correlated with the seasonal changes in gonad development and growth, and the importance of the effect of stomach contents on weight had also to be assessed. It was decided, therefore, to combine these separate but interrelated aspects in one paper.

The main part of the paper is devoted to the questions of length-weight relationship and condition. A brief review of the fundamental bases for the concepts of length-weight relationship and condition and of some of the methods of analysis of length-weight data precedes an account of the application of the chosen methods to the present material and its results. This is followed by an account of seasonal changes in gonad weights.

A brief account is then given of the rather scanty data available on the weight of stomach contents. The seasonal changes in condition are then described and, finally, some of the results are summarized, combined and discussed as a picture of the seasonal cycle in the Windermere perch.

In the statistical analysis of the length-weight relationship the data for only one group of fish are given in full (Tables 1 and 2) as an example of the method of computation used for all the groups. Again, in the section on seasonal changes in gonad weight and condition Figs. 2–7 are based partly on tables of data which are not published. The full tables have been deposited with the Freshwater Biological Association, from whom copies can be obtained.

2. THE ANALYSIS OF LENGTH-WEIGHT RELATIONSHIP AND CONDITION

Data on the lengths and weights of fish have commonly been analysed to yield biological information. One or other form of such analysis has, in fact, become one of the standard methods employed in fishery biology. Often, however, the examination of length-weight data has become so stereotyped that confused thinking on its aims, the methods employed and the results obtained has resulted. It is not proposed to enter here into a discussion of the
literature, but only to present an outline of the
principal methods that can be used in the analysis
of length-weight data before describing the applica-
tion of some of these methods in the present
work.

The analysis of length-weight data has usually
been directed towards two rather different objects. First, towards describing mathematically the rela-
tion between length and weight, primarily so
that one may be converted into the other. Secondly,
to measure the variation from the expected weight
for length of individual fish or relevant groups of
individuals as indications of fatness, general ‘well-
being’, gonad development, etc. Throughout this
discussion the term length-weight relationship is
applied rigorously to the first category, while the
term condition is applied as a rigorous but general
term for length-weight analyses of the second
category.

The length of a fish is often more rapidly and
accurately measured than the weight. Moreover,
back-calculations of past growth from scales, etc.,
usually yield data on length alone. Thus it is very
convenient to be able to determine a weight where
length only is known, and occasionally it may be
useful to reverse this process. It has been found
that the length-weight relationship of most fish can
adequately be described by a formula of the type:

\[ W = a L^n, \]  

(1)

where \( W \) = weight, \( L \) = length, \( a \) is a constant and
\( n \) an exponent usually lying between 2.5 and 4.0
(Hile, 1936; Martin, 1949). For an ideal fish which
maintains the same shape, \( n = 3 \), and this has
occasionally been observed (Allen, 1938). In the
vast majority of instances where length-weight
relationships have been calculated, however, it has
been found that the cube law is not obeyed and \( n \neq 3 \).
Further, most species of fish do change their shape as
they grow (e.g. Martin, 1949) and so a cube relation-
ship between length and weight would hardly be ex-
pected. It is, therefore, more logical as a general
basis for investigation to assume that probably
\( n \neq 3 \). It has also been found that while \( n \) may be
different for fish from different localities, of
different sexes, or for larval, immature and mature
fish (different ‘growth stanzas’) it is often constant
for fish similar in these respects. The length-weight
relationship may thus be a character for the differ-
etiation of small taxonomic units, like any other
morphometric relationship. It may also change
with metamorphosis or the onset of maturity, as
has been shown for other relative growth ratios
(Frost, 1945; Huxley, 1932). Further, the exponent
\( n \) is the ratio of the logarithmic growth-rates for
length and weight, the increment in log weight for
any period of time (of reasonable length) being
\( n \) times the increment in log length for the same
period of time. Thus the length-weight relationship
formula (1), besides providing a means for calculat-
ing weight from length, and a direct way of con-
verting logarithmic growth rates calculated on
lengths into growth-rates for weight, may also give
indications of taxonomic differences and events in
the life history such as metamorphosis and the onset
of maturity.

The length-weight relationship may be expressed
graphically by plotting the observed lengths and
weights as a dot diagram on double logarithmic
graph paper. The points for fish having the same
length-weight relationship will lie on a straight line
with some scatter due to individual variation. This
line represents the logarithmic form of equation (1)

\[ \log W = \log a + n \log L, \]  

(2)

where \( n \) represents the slope of the line, and \( \log a \) its
position. Changes in the value of \( n \) can usually be
readily observed as changes in slope. If the scatter
is not too great, a line can be fitted by eye to each
range in length having the points on a straight line,
and its slope measured. It is usually possible in this
way to judge the value of \( n \) to one decimal place, an
accuracy adequate for a preliminary investigation.
An accurate line can be computed from the same
data by the regression method of least squares. Any
one line should be fitted only to that range of size
over which it is apparent that the fish have the same
length-weight relationship. This range, and the
accuracy of the fits, can usually be more easily
judged by straight line graphs on logarithmic paper
than by drawing curves on arithmetic paper. It is
also important that the data from which the length-
weight relationship is calculated should not have
been subjected to any selection for weight against
length. For example, gill-nets may select the fatter
among short fish and the thinner among long fish,
and thus lower the value for \( n \), even though the
means of length and weight may be unaffected
(Kipling & Le Cren, unpublished data).

Individual variations from the general length-
weight relationship have usually been considered
more interesting than the length-weight relationship
itself, and have been frequently studied under the
general name of ‘condition’. In some cases the
specific gravity of the fish may not be unity, and
variations in the specific gravity of the flesh of fish
have been shown to occur (Tester, 1949) and their
importance in studies on condition has been dis-
cussed by Kesteven (1947). Usually, however, in
all but completely demersal fishes the density of the
fish as a whole is maintained the same as that of the
surrounding water by the swim bladder, and there-
fore changes in weight for length are due to changes
in form or volume and not specific gravity.
Such changes in condition have usually been analysed by means of a condition factor (or 'coefficient of condition', 'ponderal index', etc. (Thompson, 1942; Hile, 1936). This is calculated as a ratio between the observed weight and that expected from the observed length. The basis of the expected weight is that for an ideal fish in whose length-weight relationship formula weight is that for an ideal fish in whose length-weight relationship formula

\[ W = cL^3, \]  

(3) 

therefore 

\[ c = \frac{W}{L^3}. \]  

(4) 

As, however, \( c \) when so calculated is often an awkward decimal number, the average value of \( c \) found by trial from formula (3) was incorporated into the formula, and a new condition factor \( K \) found that would vary about unity 

\[ K = \frac{W}{cL^3}, \]  

(5) 

for example 

\[ K = \frac{W}{0.000427L^3} \quad \text{(Menzies, 1920).} \]  

(6) 

The value of \( c \) depends partly on the units used for weighing and measuring the fish; in formula (6) these are pounds and inches. In instances where the original value of \( c \) chosen was found to have only limited application, and \( K \) was found to average about some value approximating to \( c \), it has been further altered to a convenient round number and often changed into its reciprocal 

\[ K = \frac{CW}{L^3}, \]  

(7) 

for example 

\[ K = \frac{100W}{L^3} \quad \text{(Hile, 1936)} \]  

(8) 

(\( L \) is in centimetres and \( W \) in grams). In this formula, which is widely used, \( c \) has ceased to be equivalent to \( a \) in formula (1) and no attempt is made to make \( K \) on average. All these formulae are based on comparison with an ideal fish, whose \( W = cL^3 \), and in subsequent discussion the term condition factor and its symbol \( K \) are applied only to measurements of condition so derived.

Differences in condition factor have been interpreted as measuring various biological features such as, fatness, suitability of environment or gonad development. The number of variables that can affect the value of \( K \) is however considerable, and some of them will now be briefly discussed. They fall into three main groups.

First, there are those factors correlated with length which affect the condition factor because the fish does not in fact obey the cube law in its length-weight relationship. The condition factor will vary with length itself according to the expression 

\[ K \propto L^{n-3}. \]  

(9) 

Thus length itself and any correlated factor will affect the values of \( K \). This means that, except in the rare instances where \( n = 3 \), the condition factors of fish of different lengths cannot be directly attributed to features other than length. Further, factors such as age, sex or maturity which may affect the value of \( n \), may in turn affect the values of \( K \). Differences in mean \( K \) for fish from different environments may be due to the fish exhibiting racial differences in form, which will affect \( n \) and through it, \( K \). Thus differences in \( K \) attributed to environmental factors may in fact be genotypic.

Secondly, the values of \( K \) may be affected by selection in sampling. The effect of gill-nets on the computation of length-weight relationships has already been mentioned, they may also be selective for condition factor (Farran, 1936; Deason & Hile, 1947).

Thirdly, there are those features usually associated with \( K \). General, long-term, features such as environment, food supply and degree of parasitization may affect the fish's condition directly, or where \( K \) is correlated with length, via the growth-rate and average size. Seasonal changes have frequently been studied with the aid of condition factors, which have been shown to be correlated with gonad cycles, rate of feeding, etc. Short-term cycles of alternating growth in weight and growth in length have also been revealed by the use of condition factors (Brown, 1946).

In view of this list of widely different factors that can affect the condition factor, it is not surprising that the interpretation of \( K \) is difficult and often leads to erroneous results. As an example a hypothetical instance will be discussed. The population of a fish species is being studied for comparison in two lakes. It is only possible to fish each lake on one occasion, and gill-nets are used. Lake A is fished in June and most of the fish are caught in a gill-net of 2 in. mesh, and average 20 cm. in length. Lake B is fished in August and most of the fish, which average about 30 cm. are caught in a gill-net of 3 in. mesh. Condition factors are calculated for each fish (according to formula (5)) and averaged for each lake. For lake A, \( K = 0.95 \), for lake B, \( K = 1.03 \). It is then concluded that lake B is a more suitable environment for the particular species. Actually the higher average condition factor in lake B could just as easily be due to: (1) slight racial differences in shape between the fish of the two lakes, (2) the
greater mean length (due to growth-rate or mortality-rate), (3) the fact that in August the fish are in better condition after a summer of feeding than soon after spawning in June, and (4) selection by the gill-nets.

In this hypothetical case further information on morphometric measurements, average size, growth-rate, time of spawning, etc., might have ruled out many of the possible causes for the difference in \( K \), but probably would not have made it possible to attribute this difference to any one cause. It is thus clear that in using the condition factor great care must be exercised to decide for exactly what purpose the information on condition is required, and whether the condition factor will yield this information and give results undisturbed by the effect of variables other than those being studied. Where other variables affecting \( K \) can be controlled or eliminated, or where a biological feature can be shown to be highly correlated directly with \( K \), the use of the condition factor may be valuable. There are, however, alternative methods of analysing condition which may be more suitable.

It is relatively easy to eliminate the effect on \( K \) of length and correlated factors by calculating a 'condition factor' based not on the 'ideal' length-weight relationship

\[
W = cL^3, \quad (3)
\]

but on an empirical, calculated length-weight relationship

\[
W = aL^n. \quad (1)
\]

The 'condition factor', in this case called the relative condition factor and designated by \( K_n \) to distinguish it from the condition factor \( K \) based on the cube-law, is calculated from the formula

\[
K_n = \frac{W}{aL^n}. \quad (10)
\]

In practice the length-weight relationship would first be calculated as the logarithmic formula (2), and smoothed mean weights, \( \bar{W} \), for each length-group computed from this log formula or read off an accurate graph. The relative condition factors would then be calculated from the formula

\[
K_n = \frac{W}{\bar{W}}. \quad (11)
\]

The difference between \( K_n \) and \( K \) is that the former is measuring the deviation of an individual from the average weight for length, while the latter is measuring the deviation from a hypothetical ideal fish. The choice of which condition factor to use must be based to some extent on which of these two comparisons is the more relevant. Hile (1936) argues that a condition factor calculated from an empirical formula (of type (1)) fails to measure any change in form associated with change in length. This is true, but the change in form or condition associated with length is succinctly and accurately described by the value of exponent \( n \), and, as Hile points out, the relationship between condition as measured by \( K \) and length is given by the expression

\[
K \propto L^{n-3}, \quad (9)
\]

With the relative condition factor, therefore, it is possible to distinguish between and measure separately the influences on condition of length and other factors; whereas these are not readily separated when the ordinary condition factor is used.

For a more accurate analysis of condition, where the data are adequate, use may be made of the length-weight relationship formula itself. It has usually been considered that the empirical length-weight relationship formula of type (1) can provide little information on condition (Hile, 1936). Unless the value of \( n \) in equation (1) is identical for the groups of fish whose condition is being compared, the value of \( a \) in this equation gives no measure of their relative condition, and is not comparable to \( c \) in equation (4). Usually, as Hile (1936) points out, there is a negative correlation between the values of \( a \) and \( n \). Where, however, it can be shown that \( n \) is the same for two groups of fish, the values of \( a \) obtained in separate length-weight relationship formulae calculated for each group will be a direct measure of their condition relative to each other.

If it is expected that a large group of fish, containing a number of smaller groups the condition of which latter it is desired to compare, is suspected of being homogeneous in its length-weight relationship (a logarithmic graph of the length-weight data showing for instance one straight, but rather broad line of dots) then a length-weight relationship formula (2) can be calculated for each subgroup. The values of \( n \) determined are tested for homogeneity, and if as was expected there is no significant difference between them, a pooled regression can be calculated for the whole group combined and the values of \( a \) adjusted for this pooled length-weight relationship. These adjusted values of \( a \) are accurate measures of the relative condition of the subgroups, and the significance of the differences between them can be subjected to accurate statistical test (e.g. Snedecor, 1946; Goulden, 1939; Mather, 1943).

The computational labour involved in such an analysis of covariance is fairly large, but it is probably not much greater than that needed to calculate by formulae (7) or (8) a \( K \) for each fish and then find the mean value of \( K \) for each subgroup. Further analysis, within the subgroups, can be carried out by means of the relative condition factor, calculated.
from the pooled value of $n$ and the value of $a$ for each subgroup.

The use of both the relative condition factor and the analysis of covariance of the length-weight relationship as methods of directly comparing condition is confined to comparisons between fish which are homogeneous for $n$ in their length-weight relationship formulae. Comparisons between fish which have different length-weight relationships will normally have little relevance. If they differ in size, differences between relative or ordinary condition factors will be difficult to interpret; if they are of the same length the weights themselves can be compared. Comparisons between such groups of fish can perhaps best be expressed by graphs of lines on logarithmic scales representing their respective length-weight relationships.

To sum up this review, it may be concluded that the expression of length-weight relationship and the measurement of changes in condition are two rather different but interconnected aims in the analysis of length-weight data. The length-weight relationship can best be expressed by a formula of the type $W = aL^n$ (1), and is most conveniently calculated and graphed in its logarithmic form (2). The condition factor $K$, where $K = w/L^a$ (7) being based on the cube-law, which rarely holds, is affected by length as well as many other factors. This makes its interpretation difficult. The effect of length may be eliminated by using a relative condition factor based on an empirical length-weight relationship. The analysis of covariance in the log length-weight relationship may also be used for abundant data, where there is homogeneity of the exponent $n$ in the length-weight relationship. In any analysis, exact ideas as to the aims are required, and the method of analysis should be chosen so as to yield the maximum unequivocal biological information.

3. THE LENGTH-WEIGHT RELATIONSHIP

(a) Sources of material and methods of collection

The data used for length-weight analysis were obtained from fish collected primarily for other purposes. These fish were collected in the years 1943-6, and were all caught in the north basin of Windermere. They were collected mostly in traps (Worthington, 1950) and seines, but also by angling and a few of the very large fish were caught in gill-nets. These latter are the only gill-netted fish that have been included in the determinations of length-weight relationship, though some fish gill-netted in 1948 have been included in the seasonal samples used for determining relative condition factors. No samples likely to have been selected for weight relative to length have been included in the calculations of the regressions of weight on length.

Length was measured from the tip of the pre-maxilla to the tip of the longest caudal fin ray stretched out posteriorly. Length measurements were usually made to the millimetre below, but occasionally to the $\frac{1}{4}$ cm. below. Age was determined from the opercular bone or from the length frequency distribution for fish in their first two years (Le Cren, 1947). Age has been designated by the number of completed years of life, but with the birthday moved to 1 January. Thus a fish hatched in June 1945 will belong to the O group till 1 January 1946, then to the I group till 1 January 1947, and so on. The sex and state of gonad was determined by internal macroscopic examination, for all but running fish. This was usually easy for fish in their second year and older, though in early summer it was sometimes difficult to distinguish between immature and recovered spent fish.

As the weights of the perch varied from 1 mg. to 1450 g., several balances were used in an attempt to weigh each fish to approximately the same relative accuracy. The smallest fish were weighed in batches of ten or more on an analytical balance to the nearest milligram. It was found impossible to obtain a wet weight for these larval fish exactly comparable with the wet weight for larger fish, owing to the relatively large weight of any surface water, and the speed with which this water and then the fish themselves dried up. In practice surface water was removed with blotting-paper and the fish then weighed before they had time to dry up. Fish weighing between 0.2 and 10 g. were weighed on an ordinary chemical balance to 0.001 g.; fish between 10 and 200 g. were weighed on a 'Butchart' swinging arm balance to the nearest gram and for the largest fish a pan balance accurate to approximately 1 g. was used. In all cases the fish were weighed intact with gonads and stomachs, and damp with surface moisture, but wiped clean of any adhering dirt.

(b) Analysis of data

When a fairly large number of weighings from different sizes of fish and different seasons had been collected, they were divided into a series of groups according to age, sex and maturity of the fish, and the time of year, and were then plotted as a series of 'dot diagrams' on double logarithmic graph paper. These graphs revealed that the fish could be divided up into a series of sex, age and maturity groups, in each of which the length-weight relationship could then be described by a formula of type

$$\log W = \log a + n \log L. \quad (2)$$

Further, it seemed probable that the constant $n$ in the formula differed from one age, sex and maturity
Condition in the perch

group to another, but that it was the same for fish of the same group caught at different times of the year. The constant \( a \), however, varied with the season of capture.

It was then decided to analyse the data with accurate statistical methods and the fish were therefore classified first into groups according to age, sex, maturity, and then into subgroups according to the time of year. The list of groups and seasonal subgroups is as follows:

1. Larvae
2. O and I
3. Female immature II
4. Female immature III and older
5. Female mature
6. Male mature

For each of these subgroups a regression was calculated for the logarithm of weight on the logarithm of length, by the method of least squares. The lengths were grouped in 2 mm. groups for the smaller fish and 5 mm. groups for the larger, while the weights were grouped in equal-sized logarithmic groups, varying from 0.06 to 144 g. in size. Frequency distributions of lengths, and even more of weights, from fish tend to the Galton-MacAlister distribution rather than the normal, although the lengths are usually very near the normal. Thus the logarithms of the weights are approximately normally distributed.

When this series of regressions had been calculated, it was clear that in general the results agreed with the approximations obtained graphically. The data were then analysed further for covariance (Snedecor, 1946, pp. 318–29; Goulden, 1939, pp. 253–9; Mather, 1943, pp. 119–28). The regressions for each group of subgroups were tabulated with their sums of squares and regressions; and then the sums of squares were calculated for: (1) the 'pooled' regression within subgroups, (2) the means of subgroups, and (3) the total for the whole group. As an example of these calculations the skeleton data for the mature female group are shown in Table 1. The series of data obtained for each group by this analysis of covariance provided a set of statistical tests of significance.

The constant \( a \) for the 'within subgroups' regression coefficient was calculated from the residual sums of squares and used to calculate 95% confidence limits and in a 't' test of the significance of the difference of the regression coefficient from 3. The residual sums of squares for the 'within subgroups' regression were used in a test of the homogeneity of the subgroup regression coefficients. The regression for the means of the subgroups does not have much value in this instance as the mean lengths were affected by arbitrary factors. The residual sums of squares for the means regression has, however, been used as a test of the significance of the difference between the subgroup means, when they have been adjusted for the general regression. This test is therefore a test of the significance of subgroup differences in weight corresponding to the grand mean length, or in fact a test of seasonal variations in relative condition. Two further tests are possible relative to the means regression. One tests the significance of the difference between the pooled regression coefficient and the means regression coefficient, and the other tests the significance of the deviation of the subgroup means from their own regression. As the means of the subgroups are affected by arbitrary selection of the length of fish caught in the samples from different times of the year these tests have little meaning in this analysis of length-weight relationship. A summary of the tests of significance for the female fish is set out in Table 2, as an example of the tests carried out for each group. In each case Bartlett's test of homoscedasticity was also carried out to verify the validity of the 'F' tests.

When the analysis of covariance had been completed for each group, the values of the adjusted means for each subgroup were calculated. This gave for fish of the grand mean length the smoothed mean weight at each season of the year and was thus an accurate measure of seasonal change in relative condition. The significance of these differences between the adjusted means had already been tested as described above.

Further, accurate graphs were drawn on double logarithmic paper for each group of fish using the regression coefficient \( b \) for 'within subgroups' and the adjusted value of \( a \) for the subgroup with the maximum value of \( a \). From these graphs smoothed mean weights \( \tilde{W} \) could be read off for any length. In certain cases these smoothed mean weights were
Table 1. Data for regressions of log weight (y) on log length (x) for mature females, showing method of computation and analysis of sums of squares (s.s.) and degrees of freedom

<table>
<thead>
<tr>
<th>Subgroup</th>
<th>s.s. x</th>
<th>s.s. y</th>
<th>s. products xy</th>
<th>Regression coefficient b</th>
<th>s.s. due to regression</th>
<th>Residual s.s.</th>
<th>Degrees of freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>1.06099</td>
<td>12.62806</td>
<td>3.64674</td>
<td>3.43711</td>
<td>12.53425</td>
<td>0.09181</td>
<td>93</td>
</tr>
<tr>
<td>April–May</td>
<td>1.08443</td>
<td>13.40003</td>
<td>3.71861</td>
<td>3.42099</td>
<td>12.75145</td>
<td>0.64858</td>
<td>392</td>
</tr>
<tr>
<td>Spent</td>
<td>1.26846</td>
<td>15.39107</td>
<td>4.33807</td>
<td>3.41995</td>
<td>14.83598</td>
<td>0.55509</td>
<td>257</td>
</tr>
<tr>
<td>Late June</td>
<td>0.37000</td>
<td>4.31748</td>
<td>1.24122</td>
<td>3.35465</td>
<td>4.16386</td>
<td>0.15362</td>
<td>119</td>
</tr>
<tr>
<td>July</td>
<td>0.20429</td>
<td>2.43482</td>
<td>0.69505</td>
<td>3.40227</td>
<td>2.36475</td>
<td>0.07007</td>
<td>51</td>
</tr>
<tr>
<td>August</td>
<td>0.4923</td>
<td>4.67813</td>
<td>1.35927</td>
<td>3.32153</td>
<td>4.51486</td>
<td>0.16327</td>
<td>122</td>
</tr>
<tr>
<td>September</td>
<td>0.41593</td>
<td>4.66059</td>
<td>1.37450</td>
<td>3.30484</td>
<td>4.54223</td>
<td>0.11836</td>
<td>104</td>
</tr>
<tr>
<td>Autumn</td>
<td>2.87077</td>
<td>33.59050</td>
<td>9.74773</td>
<td>3.39553</td>
<td>33.09871</td>
<td>0.49179</td>
<td>358</td>
</tr>
<tr>
<td>Total within subgroups</td>
<td>7.68410</td>
<td>91.10668</td>
<td>26.12119</td>
<td>3.39393</td>
<td>88.79585</td>
<td>2.30483</td>
<td>1503</td>
</tr>
<tr>
<td>Total between means of subgroups</td>
<td>1.10438</td>
<td>9.46914</td>
<td>3.08322</td>
<td>2.79181</td>
<td>8.60776</td>
<td>0.86138</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>8.78848</td>
<td>100.56982</td>
<td>29.20441</td>
<td>3.32303</td>
<td>97.04713</td>
<td>3.52269</td>
<td>1510</td>
</tr>
</tbody>
</table>

Table 2. Analysis of variance for data in Table 1

<table>
<thead>
<tr>
<th>Source</th>
<th>Sums of squares</th>
<th>Degrees of freedom</th>
<th>Variance</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Due to total regression</td>
<td>97.04713</td>
<td>1</td>
<td>97.04713</td>
<td>63,000</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Between regression coefficients within subgroups</td>
<td>0.01024</td>
<td>7</td>
<td>0.00147</td>
<td>0.95</td>
<td>&gt; 0.05</td>
</tr>
<tr>
<td>Difference between 'pooled within subgroups' and 'means' regressions</td>
<td>0.35648</td>
<td>1</td>
<td>0.35648</td>
<td>233</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Deviation of means from means regression</td>
<td>0.86138</td>
<td>6</td>
<td>0.14356</td>
<td>94</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Residual</td>
<td>2.29459</td>
<td>1496</td>
<td>0.00153</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Total</td>
<td>100.56982</td>
<td>1511</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

used to calculate relative condition factors, (Kc) by formula (11). Mean relative condition factors were then calculated for small samples of fish caught at different dates especially in the 'spring' and 'autumn' when the adjusted mean weights for the subgroups for the whole season were inadequate to trace detailed changes in condition.

(c) Results

The results of the analysis of the length-weight data will be presented group by group followed by a summary of the combined data.

Larvae. The graphical plotting of the data revealed that the few points for weights of larval perch lay off the line taken by the young fish of between 3 and 14 cm. in length and formed a fairly distinct larval length-weight regression. A regression was therefore calculated for all the lengths and weights of fish from hatching till they were 3.0 cm. long. The regression formula found was

$$\log W = 0.68969 + 3.59163 \log L.$$  

The length of newly hatched fry was found to average 6 mm., and although accurate weighing was very difficult, several batches gave an average weight of 1 mg. per fish. The regression calculated for the larvae, because of the difficulty of weighing and the bulk weighing of the fish is not based on data quite comparable to the regressions calculated for older fish. It will be seen, however, from Table 3 that the regression coefficient of 3.59163 for the larvae is significantly greater than that obtained for any other group, and is significantly different from 3.0.

O and I. Between the time they reached a length of 3.0 cm. at an age of about 2 months, till the end
of their second growing season, the perch seemed to form a homogeneous group with their weight varying with approximately the cube of the length. Regressions were calculated for O group fish in August and September, and I group fish in the spring, July, August, September and October. These regression coefficients varied from $2.59831$ to $3.18333$ though most of them were very near $3.0$, and the differences between them were not significant. The pooled regression coefficient was $3.0117$, and it was not significantly different from $3.0$. The adjusted subgroup means differed significantly from each other, thus showing that there were significant seasonal changes in relative condition. The adjusted means and mean dates of collection for each subgroup are set out in Table 4.

**Immature females.** At first all immature female fish were grouped together, but the trial plotting indicated that most of the 2-year-old females probably had a distinct length-weight relationship from those that were older. The immature females were thus divided into two groups by their age.

The I+ and II+ females had a pooled regression coefficient of $3.19506$. The regression coefficients for the subgroups April and May were considerably heterogeneous. The adjusted means were very significantly different from each other (Table 5). After August, when they began to develop their ovaries in preparation for their first spawning the next spring, the maturing II females were classed with the mature females.

Some older females were found to remain immature. Some of these may be fish which mature late, others may never mature. However, they were treated as a separate group. The pooled regression coefficient is $3.05292$, and this is not significantly different from either $3.0$ or the regression coefficient of $3.19506$ obtained for 2-year-old immature females, but it is significantly different from that for mature females. There was no significant difference

---

Table 3. Summary of regressions of log weight on log length for each group of fish, and the combined total

<table>
<thead>
<tr>
<th>Group</th>
<th>No. of fish</th>
<th>Range in length (cm.)</th>
<th>Range in weight (g.)</th>
<th>Regression slope, $b$</th>
<th>Homogeneity of regression within group</th>
<th>$b$ significantly different from 3</th>
<th>Significant difference between adjusted means</th>
</tr>
</thead>
<tbody>
<tr>
<td>O and I</td>
<td>667</td>
<td>3.0-14.0</td>
<td>0.22-28</td>
<td>3.012</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>$\frac{1}{2}$ immature II</td>
<td>462</td>
<td>9.5-15.5</td>
<td>7-40</td>
<td>3.195</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>and older</td>
<td>131</td>
<td>11.0-18.5</td>
<td>11-70</td>
<td>3.553</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>$\frac{1}{2}$ mature</td>
<td>1512</td>
<td>11.5-43.5</td>
<td>11-1250</td>
<td>3.390</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>$\frac{1}{2}$ mature</td>
<td>640</td>
<td>10.0-44.5</td>
<td>7-1450</td>
<td>3.281</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Total</td>
<td>3412</td>
<td>3.0-44.5</td>
<td>0.22-1450</td>
<td>3.165</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Larvae</td>
<td>323</td>
<td>0.65-2.95</td>
<td>0.001-0.25</td>
<td>3.592</td>
<td>—</td>
<td>Yes</td>
<td>—</td>
</tr>
<tr>
<td>$\frac{1}{2}$ immature</td>
<td>35</td>
<td>8.5-26.5</td>
<td>5-180</td>
<td>3.243</td>
<td>—</td>
<td>Yes</td>
<td>—</td>
</tr>
</tbody>
</table>

Table 4. Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of O and I fish

<table>
<thead>
<tr>
<th>Subgroup</th>
<th>Average date</th>
<th>No. of fish</th>
<th>Adjusted mean weight</th>
<th>Percentage of maximum weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>O, Aug.</td>
<td>11 Aug.</td>
<td>85</td>
<td>3.536</td>
<td>97.1</td>
</tr>
<tr>
<td>O, Sept.</td>
<td>5 Sept.</td>
<td>91</td>
<td>3.642</td>
<td>100.0</td>
</tr>
<tr>
<td>I, Spring</td>
<td>18 Apr.</td>
<td>209</td>
<td>3.084</td>
<td>84.7</td>
</tr>
<tr>
<td>I, July</td>
<td>21 July</td>
<td>190</td>
<td>3.468</td>
<td>95.2</td>
</tr>
<tr>
<td>I, Aug.</td>
<td>11 Aug.</td>
<td>209</td>
<td>3.538</td>
<td>97.1</td>
</tr>
<tr>
<td>I, Sept.</td>
<td>11 Sept.</td>
<td>135</td>
<td>3.493</td>
<td>95.9</td>
</tr>
<tr>
<td>I, Oct.</td>
<td>26 Oct.</td>
<td>12</td>
<td>3.347</td>
<td>91.4</td>
</tr>
<tr>
<td>Total</td>
<td>—</td>
<td>667</td>
<td>3.379</td>
<td>92.8</td>
</tr>
</tbody>
</table>
between the subgroup regression coefficients, but the adjusted means varied significantly (Table 6).

Mature females. This was the largest group, and details of the analysis of its length-weight relationship have already been discussed as illustrating the method of analysis, and set out in Tables 1 and 2. The pooled regression coefficient was 3.3958; this is significantly different from 3.0 and from all the other groups. There was some difference between subgroup regression coefficients, they ranged from 3.30464 to 3.43711 but these differences were not significant. The whole group shows significant heteroscedasticity with Bartlett's test, but when the 'spent' subgroup is omitted the result loses its significance. The spent fish were rather variable owing to the inclusion of many fish that were part recovered and some only just spent. The adjusted mean weights show considerable and significant variation (Table 7).

Mature males. The pooled regression coefficient is 3.2863 which is significantly different from 3.0 and from the other groups except for the 2-year-old females. There was no great variation among the subgroup regression coefficients except for August which was 2.95847 and the spring which was 3.48383 but based on only ten fish. The whole series were significantly heterogeneous ($P < 0.01$), but when August is omitted the remainder are homogeneous. The data for August consist of only a few samples over a very limited range and thus may be atypical. The heterogeneity has been ignored in the further analysis of the results. The significant variation among the adjusted mean weights is very similar to that found for mature females (Table 7).

Immature males. The lengths and weights were recorded for thirty-five immature male perch of 2 years old or older. They gave a regression coefficient of 3.24253 which is not significantly different from that for mature males.

(d) Discussion and conclusions

Kesteven (1947) discussed the possibility of using the analysis of covariance in the treatment of length-weight data from fish, but the present work was started before his paper was published. As no other use of the method so far appears to have been made, the present analysis functions to some extent as a trial of the method. It has revealed information which would not have been shown if ordinary condition factors or a single length-weight relationship regression had been used. It is clear from the results described above, that no single regression will adequately describe the length-weight relationship for the perch. The fact that the length-weight relationship coefficient $n$ was considerably greater than the cube would also have complicated the analysis of seasonal changes in condition by means of the ordinary condition factor. It might have been possible to split up the groups still further and carry out a more detailed analysis of covariance, but it is probable that the data that were available would not have warranted the extra computational labour involved.

The length-weight regressions for the various age, sex and maturity groups are shown as lines on a logarithmic graph in Fig. 1, and the successive changes in slope will be noticed in this figure. The regression coefficient for the older immature females is very similar to, and not significantly different from, that for the young immature females of both sexes. This suggests that the change from this relationship to that of the mature fish is correlated with maturation rather than age. The older immature females may retain the length-weight relationship of the young fish because their gonads have not matured.

A detailed comparison of the length-weight relationship of perch from different lakes is not possible as different authors have used different methods of measurement and analysis. Perch, on the whole, would appear however to have a length-weight coefficient greater than the cube, although this is not invariably the case (e.g. $P. flavescens$ Mitchell in Lake Michigan (Hile & Jobes, 1942). Alm (1946) discusses the condition of perch from different lakes, and although there appears to be quite a number of exceptions there is apparently a tendency for the faster growing populations of perch to have a higher average condition. The Windermere perch would seem to be intermediate in condition to the Swedish examples Alm quotes, but perhaps to have a higher value for the length-weight coefficient $n$.

4. THE SEASONAL CYCLE IN GONAD WEIGHT AND CONDITION

(a) Gonad weight

The total weight of the perch as recorded included the weight of the gonads. As these change in size with the season, and when ripe may constitute a considerable fraction of the total weight, records were made at different seasons of the gonad weights of small samples of fish. It was also hoped that these weights would provide evidence of the season cycle in gonad development.

The perch were opened ventrally and the single ovary or both testes dissected out, an operation that could usually be accomplished in a few seconds. The gonads were then weighed complete. At first a rough chemical balance was used, and the gonads were weighed to the nearest 0.1 g., later a more accurate chain type balance was used and weights were recorded to 0.01 g. For the largest fish the
### Condition in the perch

Table 5. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of II immature females*

<table>
<thead>
<tr>
<th>Subgroup</th>
<th>Average date</th>
<th>No. of fish</th>
<th>Adjusted mean weight</th>
<th>Percentage of maximum weight of August</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr.</td>
<td>23 Apr.</td>
<td>46</td>
<td>14.9</td>
<td>81.9</td>
</tr>
<tr>
<td>May</td>
<td>20 May</td>
<td>70</td>
<td>16.1</td>
<td>88.5</td>
</tr>
<tr>
<td>June</td>
<td>21 June</td>
<td>55</td>
<td>18.2</td>
<td>100.0</td>
</tr>
<tr>
<td>July</td>
<td>20 July</td>
<td>116</td>
<td>16.9</td>
<td>92.9</td>
</tr>
<tr>
<td>Aug.</td>
<td>11 Aug.</td>
<td>175</td>
<td>17.5</td>
<td>96.2</td>
</tr>
<tr>
<td>Total</td>
<td>—</td>
<td>462</td>
<td>16.9</td>
<td>92.9</td>
</tr>
</tbody>
</table>

Table 6. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of III and older immature females*

<table>
<thead>
<tr>
<th>Subgroup</th>
<th>Average date</th>
<th>No. of fish</th>
<th>Adjusted mean weight</th>
<th>Percentage of maximum weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr.</td>
<td>21 Apr.</td>
<td>36</td>
<td>25.4</td>
<td>86.1</td>
</tr>
<tr>
<td>May</td>
<td>18 May</td>
<td>50</td>
<td>26.0</td>
<td>88.1</td>
</tr>
<tr>
<td>June</td>
<td>21 June</td>
<td>24</td>
<td>29.2</td>
<td>99.0</td>
</tr>
<tr>
<td>Late summer</td>
<td>5 Sept.</td>
<td>21</td>
<td>29.5</td>
<td>100.0</td>
</tr>
<tr>
<td>Total</td>
<td>—</td>
<td>131</td>
<td>27.0</td>
<td>91.5</td>
</tr>
</tbody>
</table>

Table 7. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of mature females*

<table>
<thead>
<tr>
<th>Subgroup</th>
<th>Average date</th>
<th>No. of fish</th>
<th>Adjusted mean weight</th>
<th>Percentage of maximum weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>21 Feb.</td>
<td>95</td>
<td>50.6</td>
<td>88.5</td>
</tr>
<tr>
<td>Apr. and May</td>
<td>21 Apr.</td>
<td>394</td>
<td>55.4</td>
<td>96.9</td>
</tr>
<tr>
<td>Spent</td>
<td>22 May</td>
<td>259</td>
<td>46.5</td>
<td>81.0</td>
</tr>
<tr>
<td>Late June</td>
<td>21 June</td>
<td>231</td>
<td>52.0</td>
<td>90.9</td>
</tr>
<tr>
<td>July</td>
<td>22 July</td>
<td>53</td>
<td>55.9</td>
<td>97.7</td>
</tr>
<tr>
<td>Aug.</td>
<td>8 Aug.</td>
<td>124</td>
<td>56.5</td>
<td>98.8</td>
</tr>
<tr>
<td>Sept.</td>
<td>14 Sept.</td>
<td>106</td>
<td>57.2</td>
<td>100.0</td>
</tr>
<tr>
<td>Autumn</td>
<td>25 Oct.</td>
<td>360</td>
<td>53.0</td>
<td>92.7</td>
</tr>
<tr>
<td>Total</td>
<td>—</td>
<td>1512</td>
<td>52.85</td>
<td>92.4</td>
</tr>
</tbody>
</table>

Table 8. *Average dates of collection, numbers of fish and adjusted mean weights for seasonal subgroups of mature males*

<table>
<thead>
<tr>
<th>Subgroup</th>
<th>Average date</th>
<th>No. of fish</th>
<th>Adjusted mean weight</th>
<th>Percentage of maximum weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>5 Feb.</td>
<td>10</td>
<td>18.9</td>
<td>86.3</td>
</tr>
<tr>
<td>Apr.</td>
<td>22 Apr.</td>
<td>161</td>
<td>19.2</td>
<td>87.6</td>
</tr>
<tr>
<td>Spent</td>
<td>25 May</td>
<td>46</td>
<td>18.5</td>
<td>84.4</td>
</tr>
<tr>
<td>Late June</td>
<td>21 June</td>
<td>82</td>
<td>21.0</td>
<td>95.8</td>
</tr>
<tr>
<td>July</td>
<td>20 July</td>
<td>112</td>
<td>21.0</td>
<td>95.8</td>
</tr>
<tr>
<td>Aug.</td>
<td>12 Aug.</td>
<td>153</td>
<td>21.7</td>
<td>99.0</td>
</tr>
<tr>
<td>Sept.</td>
<td>8 Sept.</td>
<td>56</td>
<td>21.9</td>
<td>100.0</td>
</tr>
<tr>
<td>Autumn</td>
<td>23 Oct.</td>
<td>20</td>
<td>21.6</td>
<td>98.6</td>
</tr>
<tr>
<td>Total</td>
<td>—</td>
<td>640</td>
<td>20.6</td>
<td>94.0</td>
</tr>
</tbody>
</table>
gonads were weighed on a ‘Butchart’ balance to the nearest gram. In every case an accuracy of at least 5% was obtained. In the case of the smallest immature fish, however, an accurate dissection and weighing of the minute gonads was not attempted.

First, for each fish whose gonads had been weighed a gonad:body-weight ratio was calculated and expressed as a percentage. It was then decided to determine whether this ratio altered with the size of the fish. Accordingly ‘dot diagrams’ were constructed of the logarithm of the gonad:body-weight ratio plotted against body weight. Graphs of this type were drawn for adequate samples of fish from different seasons. The data for mature females in February and October each gave a horizontal band of points on the graph. The points for very large fish weighing about 1 kg. also lay on the same horizontal band. The data for both ripe and spent fish in May in each case also showed no definite tendency for an increase or decrease in gonad:body-weight ratio with weight of fish. Data for other months, and for immature females, were less extensive and less conclusive. In the case of male fish, data for February, April, August and September were plotted, and in each case were not inconsistent with the conclusion that the gonad:body-weight ratio is constant at any one season for any size of fish. It can therefore be concluded, that although there is some individual variation in the gonad:body-weight ratio, it tends to be constant at any one season for all sizes of fish of the same sex and state of maturity.

Once it was clear that the gonad:body-weight ratio did not alter with size of fish, mean gonad:body-weight ratios of samples of fish that varied in size could be used to trace the seasonal changes in this ratio. The data for mature fish are plotted in Fig. 2. It will be seen that the ovary has a minimum size in mid-summer when it is quiescent. In August, however, it begins to increase in size, and this increase proceeds regularly through the winter and spring till the spawning time in May. At this time the gonad averages about 20% of the body weight. The freshly spent fish have empty ovaries weighing about 3% of the body weight. By the middle of June these ovaries have shrunk to about 1% of the body weight, at which ratio they remain till August. There is considerable variation among the different samples in the average gonad:body-weight ratio, especially in the spring, but this is almost certainly due to phenological differences from one season to the next. In 1947 in particular, after an unusually severe and late winter, the ratios in May were approximately equivalent to those for April in other years.

The mature male fish differ from the females in several ways. Development of the testes starts in August, but by October the testes have reached their maximum size, weighing about 8% of the body weight. They then remain this size through the autumn, winter and spring, till April. The average gonad weight then decreases through April and May till it is only 1–2% of the body weight. Quantitative data for the summer are nearly non-existent, but from visual observation it can be concluded that the testes remain small and quiescent through June, July and most of August. As the testes begin to be ripe early in April, the apparent fall in their weight from the beginning of April may
be due mainly to inevitable loss of milt with handling in capture and examination. These data on seasonal changes in the testes weight are very similar to those obtained for *Perca flavescens* Mitchill in America by Turner (1919), who also studied the histological changes in some detail.

The data for immature fish are very limited, but suggest that the gonad:body-weight ratio is relatively constant at about 0.5% for immature females and does not change with size or season. This ratio of 0.5% is approximately equivalent to that of the quiescent mid-summer ovaries of mature females. Although the evidence is not sufficient to be conclusive it suggests that this ratio begins to increase in normal females in their third August at the same time as the mature females begin to develop for spawning next spring, but remains constant throughout life in those females that still remain immature.

(b) The weight of stomach contents

In order to determine how much of the individual and seasonal variation in relative condition might be due to the weight of food in the stomach, the stomach contents of a few samples of perch seined in the summer of 1948 were weighed. The percentages of the total body weight contributed by the stomach contents were determined for each fish. The average stomach content:body-weight ratio for all the forty-eight fish was 0.52%. Individual ratios varied from 0.0 to 2.1%; there did not seem to be any significant difference between the mean ratios for samples from June, August or September; or any correlation between the ratio and the size of the fish, though the data available are not really adequate to determine these features. The perch in Windermere are known to feed more heavily in summer than in winter (Allen, 1935), but even if they did not feed at all in winter, these figures are adequate to show that, relative to the seasonal changes and individual variation in total weight, the weight of food in the stomach is not important. The weight of material in the remainder of the alimentary canal may nevertheless have some significant influence on the total weight, but visual observations suggest that the weight of the intestinal contents would tend to vary rather less than that of the stomach contents.

(c) Condition

The seasonal changes in relative condition are given in outline by the adjusted mean weights for the seasonal subgroup regressions for weight on length. These are presented in Tables 4–8. These data have been amplified by calculating relative condition factors for individual fish and finding the mean of these for each sample of fish from the two

---

*Fig. 2.* Seasonal changes in the gonad weight as a percentage of the total body weight. The larger symbols are the means for samples of five or more fish with the vertical lines indicating 95% confidence limits. The smaller symbols represent the means of samples of less than five fish.
years 1945 and 1948. These years were chosen to give a comparison between one year and another, and because they provided the most ample sources of data, but a few additional samples for the three spring and three autumn months from other years are also included. These means are plotted (with their 95% confidence limits) in Figs. 3–7.

For the O and I group fish data from the adjusted mean weights of the regression only are available. It will be seen from Fig. 3 that the O group fish have a somewhat higher relative condition in September than the I group fish a year later. There is a considerable gap in the data between September and the following spring, but the low value of 84.7% for the middle of April indicates that there must be a considerable fall in condition over the winter. A subsequent rise in the early summer is indicated by the higher values in July and August, but the detail of this increase cannot be followed without further material. As in the other groups the condition falls again in October, and presumably decreases throughout the autumn and winter.

In the case of the II group immature females the adjusted mean weight for June was thought to be unexpectedly high, and as it was based nearly entirely on one sample of fish, it was ignored, and the value for August taken as the basis (of 100%) for calculating the relative condition factors. The points for the adjusted regression means in April and May and the sample means for that period, show that the relative condition is low at the beginning of April but then rises rapidly through May. The July adjusted regression mean may be aberrantly low, and the relative condition probably increases slowly through June, July and August. After August the II group immature females begin to develop their ovaries and join the mature female group.

Relative condition factors for the few females that remain immature though three or more years old are plotted in Fig. 5. Data are somewhat scanty, except for April and May, but it will be seen that these fish follow a similar pattern to the II group females. Condition probably falls slowly through January, February and March, but rises in May and June. In summer the maximum is probably reached early in September followed by a fall through the autumn.

For the mature females the data are more adequate and are shown in Fig. 6. The condition is fairly constant with perhaps a slight fall through January, February and March. In April it rises sharply, and at the beginning of May some samples of ripe fish have a mean relative condition factor of nearly 100%. The ripe fish from later on in May, however, have much lower mean condition factors. Samples of newly spent fish have mean relative conditions of about 78–80%. By 20 June the condition of the spent fish has increased considerably and this increase is continued through July, till by August the relative condition is about 99% of the maximum in September. After the middle of September it falls sharply and by the middle of November it has reached an average value of about 91%. It then continues to fall slowly through the winter and early spring.

The mature males present a picture similar to the mature females, except that the loss of relative condition on spawning is not so great (Fig. 7). There is evidence that the fall in condition from December to March is somewhat steeper than in the females. There appears to be a similar sharp rise in April followed by a general decrease through the latter part of April and most of May as the male fish spawn. This spawning process appears to take several days for an individual male fish, unlike the females who probably lay all their eggs in one spawning act. After spawning the males increase in condition rapidly and then more slowly throughout the summer to a maximum in September. The autumnal fall in condition does not begin until late in October.

(d) Individual variations in relative condition and gonad weight

The data on relative condition and gonad weight that have just been discussed have been based on mean values obtained for a number of fish. There is, however, considerable individual variation in both relative condition and percentage gonad weight. As a measure of this individual variation the coefficient of variation has been calculated for a few representative samples. For relative condition factors the values obtained varied between 6 and 17%; while for ovary weight as a percentage of body weight the coefficient of variation ranged between 10 and 28% and for testis weight from 8 to 36%. The higher values were obtained at the spawning time or in the autumn when both the relative condition factor and the gonad weight were undergoing rapid change. As might be expected the greater individual variation shown at such times is probably due more to individual differences in the time of spawning or development of gonads than to inherent individual variations in condition or gonad weight maintained throughout the season, though the latter does occur to some extent. This greater variation at times of change is also shown by the greater range of the 95% confidence limits for mean condition factors in April, May, June and October than at other times as illustrated in Figs. 4–7.

The individual relative condition factors for a number of large samples from August, September and October, the latter part of the growing season,
Fig. 3. Group I females

Fig. 4. Group II females

Fig. 5. Group III + immature females
Figs. 3-7. Seasonal changes in relative condition expressed as a percentage of the maximum. The adjusted means for regression subgroups and the means of samples with their 95% confidence limits are given. A curve has been drawn by eye through these points.
were also examined for correlation between condition and growth in length. It was suspected that those fish that were growing slowly in length as indicated by a small 'plus' growth for the current season, might also be growing slowly in weight and so be in poor condition. Further, those fish that were making the maximum increment in length might be doing so at the expense of weight and also be in poor condition. On examining the data, however, it was found that although one or two samples showed a very slight suggestion that such a correlation existed, the overall picture gave no indication that there was any correlation between growth increment in length and relative condition factor.

(e) Discussion of the seasonal cycle

It is to be expected that there will be a seasonal cycle in condition with a high level of condition during the late summer and a low level at the end of the winter. The immature fish (O and I group, II females, and III and older immature females) show this cycle with a minimum in March and April, a rapid increase in May and June, a maximum in August and September and a rapid fall in October and November.

These groups, and the mature males but not the mature females, also show a high value for condition in June and low in July, relative to the expected trend. This may be because most of the data for these 2 months comes from a few samples mainly collected in one year (1945) and may thus be aberrant. On the other hand, the younger fish were probably feeding mainly on zooplankton (Allen, 1935) and Smyly (unpublished data), studying the food and growth of O group perch in Windermere, has found that in some years there may be a shortage of littoral zooplankton about the middle of July. Thus the apparent July fall in condition might possibly be due to a temporary shortage of food for the smaller, plankton-feeding fish.

The effect of the actual weight of the gonads on the relative condition and its seasonal changes can be seen in Fig. 8, where the seasonal curve for condition is plotted with and without the percentage gonad weight subtracted. For convenience the lower curve may be termed the 'condition-minus-gonads', although it has been calculated indirectly from the data for average condition, and gonad weight as an average percentage of body weight, and not from calculating the condition of fish weighed after the removal of their gonads.

It will be seen from Fig. 8 that the curve for the mature females minus gonads is very similar to that for the immature females 3 years old and older, but that the seasonal fluctuation is rather greater. Again the curve for the mature males minus gonads is similar. It appears therefore that nearly all the difference between the seasonal curves for condition for mature and immature fish is due to the gonad-weight cycle in the former. For example, in the mature females the nearly constant level of condition through the winter, as contrasted with the continued fall in the condition of immature fish, is due to the increase in ovary size offsetting the fall in body weight. The rise in condition in April is further due to the continued increase in ovary weight concurrently with a slight increase in body weight.

This slight, and unexpected, rise in body-minus-gonad-weight in April before spawning has been examined in rather more detail by calculating condition-minus-gonads for a series of samples from 1944 and 1947. They confirm the suggestion from the general Fig. 8 that there is a slight rise in condition-minus-gonads in April followed by a slight fall, possibly due to the final increase in gonad weight just before spawning being made at the expense of body weight. A similar tendency is apparent in the males as well as the females. As, however, there is considerable individual variation it is doubtful how significant these relatively small changes are. It is impossible with the present data to elucidate them fully.

It appears then that the loss of weight on spawning is almost but perhaps not quite entirely due to loss of ova or milt and not general 'condition'. That some sacrifice in general body weight is made towards the build up of the ova is, however, indicated by the high rate of fall and subsequent low level of the condition-minus-gonads through the winter. It is significant that all the groups of fish, except the II group females, have their lowest level of condition-minus-gonads about the middle of April and the spring increase in condition starts at about the same time. In the II group females, however, it seems to start at about 3 weeks earlier.

In the mature males the development of the mass of the testes takes place in about 6 weeks between the middle of August and the middle of October. The curve for condition-minus-gonads of the males falls off steeply earlier than in the other groups, but the condition with gonads is maintained at a high level for longer into October than is the case for the females. Thus the development of both the testes and the ovary is made partly by maintaining a total body weight for length higher than normal and partly at the expense of the condition of the rest of the fish. It is significant that a large proportion of the food available for growth, and the growth potential of the mature fish, particularly the females, must be devoted each year to the annual production of gonad products.

It is hoped to provide some detailed evidence of the season when growth in length takes place in
Fig. 8. Diagrammatic seasonal curves for relative condition with and without gonads. The solid black represents the gonad weight; the upper edge of the black the condition with gonads and the lower edge the condition-minus-gonads.
a later paper. It would seem, however, that the immature fish grow in length from early in May until early in October, but that growth is most rapid in June, July and August. The mature fish do not begin to grow in length until after the spawning season; probably about the middle of June and when the relative condition has reached 90–95%. If the start of the growing season for length is correlated with some stage of the spring increase in condition, it would then be expected that the annual growth of immature fish, as compared with mature, might benefit from the longer growing season of the former. The females do grow more in their second year than the males, but the older immature females grow at about the same rate as mature females of the same age. These older immature females have in fact a spring increase in condition at about the same time as the mature females. It cannot be concluded however, from the evidence at present available, that the seasonal changes in condition are the sole factors controlling the growing season for length, although it would seem reasonable to suggest that a fish would recover the weight lost over the winter and in spawning before starting again to grow in length.

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6. SUMMARY

1. The methods of analysing length-weight data from fish are reviewed. Emphasis is laid on empirical formulae of the type \( W = aL^n \), and the limitations of the conventional condition factor.

2. The length-weight relationship of perch of all sizes was determined from a series of regressions of log weight on log length, and an analysis of covariance. Relative condition factors were calculated for individual fish from smoothed mean weights obtained from the regression lines.

3. In length-weight relationship it was found that the perch could be divided into a series of six groups corresponding with age, sex and maturity. Each group was generally homogeneous within itself throughout the seasons, but usually differed significantly from the other groups. Relative condition was found to vary significantly with the season.

4. At any one season the gonad weight is a constant percentage of the body weight for fish of all sizes. The seasonal changes in gonad weight are described and differ somewhat for the two sexes. Stomach contents weigh up to 2% of the body weight in summer.

5. There is a regular seasonal cycle in condition which is at its maximum in September and minimum in early spring. The different seasonal changes in condition between mature and immature fish can largely be accounted for by the cycle in gonad weight of the former.

REFERENCES


