

The Body/Scale Relationship in Atlantic Salmon (*Salmo salar* L.) A Preliminary Report

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Introduction

Scale-reading in fishes may consist of mere age determination or be extended to studies of growth history. The prerequisites, necessary for growth history determinations in fishes, are (1) time marks in the scale (or other body part used), (2) a known body/scale (body/body part) relationship for the scale dimension measured at the time of the year when the time marks are laid down.

It is a remarkable fact that the Atlantic salmon since its early appearance in the history of scale reading (JOHNSTON, 1905; DAHL, 1910) has gained comparatively little interest in basic scale studies. No detailed investigation on its body/scale relationship seems to have been published. (See, however, LINDSAY and THOMPSON, 1932; KERR, 1961.)

Material and Methods

The material treated in this preliminary report is derived from wild and hatchery parr and commercial catches of adult fish in the rivers and open waters of the Baltic Sea. The fundamental curves for the body/scale relationship are drawn on data from:—

Salmon parr (pond reared)	73 specimens
Young post-smolt (wild, in the sea)	5 specimens
Adult fish (Baltic Sea)	282 specimens
The dimensions measured are, in the fish:—	
Maximum length	L_m
Head length	C
Scalated length	L_{sc}
Girth	G
In the scale:—	
Maximum length	l
Maximum anterior radius	r
Height (or width)	h

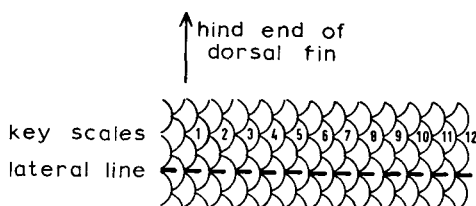


Figure 1. Position of key scales on the salmon.

Scale measurements are, if otherwise not stated, made on key scales the position of which is made clear in Figure 1. Numerical values for scale dimensions are means of 5–20 measured key scales from each specimen. All measurements are given in mm.

Results

Special part

The combined material (Fig. 2) agrees fairly well with a rectilinear body/scale relationship for scale radius and height expressed by the equations

$$L_m = 163r \quad \text{and} \quad L_m = 114h$$

The plotted data, however, strongly suggest different relationships for different stages of the life cycle of the salmon.

Parr data (Fig. 3) give a better fit for the following equations

$$L_m = 10 + 65l, \quad L_m = 18 + 121r, \quad \text{and} \quad L_m = 10 + 106h$$

or better, for scale height, the power equation

$$L_m = 116h^{0.9}$$

The few measurements of smolt taken in the sea are significantly different ($P < 0.001$) from those of the large parr and are better fits to adult fish curves.

Adult fish data give for scale length

$$L_m = 103l - 77$$

For the other dimensions the above formulae may be used. The data suggest that for routine work on Atlantic salmon a proportionality method of back-calculation may be satisfactory using the anterior radius.

For computations of adult size the validity of direct proportionality, proposed by DAHL (1910), has been corroborated by LINDSAY and THOMPSON (1932)¹. A correction for variations in individual scale size can be made by substituting the direct proportionality equation $L_x = \frac{L_c r_x}{r_c}$ for the above $L_m = 163r$. (L_c and r_c are body length and scale radius at capture.)

The first post-smolt period of life in the sea probably conforms to the same

¹) Recently KERR (1961) published his investigation on scale to length ratio in Atlantic salmon giving the equation $L = 2.40 + 12.90r + 1.22r^2$.

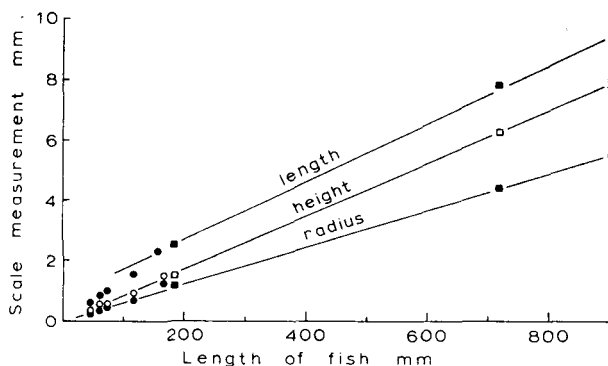


Figure 2. Body/scale relationship in Atlantic salmon. Mean values of subsamples. Circles: parr. Squares: post-smolt and adults. Lines drawn by eye.

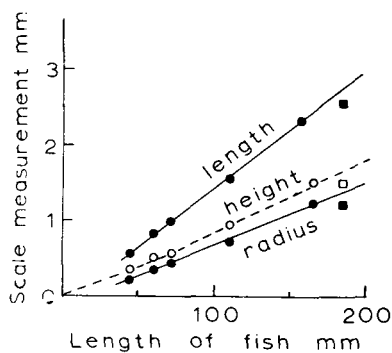


Figure 3. Body/scale relationship in salmon parr. Squares: post-smolt. Straight lines freely drawn. Curve for scale height:
 $L_m = 116 \times h^{0.9}$.

regression but it is doubtful whether it is valid for the exact time when the mark is laid down, that is at the change from river to sea growth.

For parr growth, parr scales may be used with a correction term in the direct proportion formula

$$L_x = 18 + \frac{(L_c - 18)r_x}{r_c}$$

Adult scales, however, are not suitable for computing parr size by means of direct proportion on account of the break of the curve at the smolt transition stage. Either a calculated apparent size at the last parr annulus must be corrected to a true size and this size used in the above parr formula, or regression methods must be used.

The formulae for adult and parr scale growth make it possible to calculate the correction for estimating the true parr size. The correction varies with size of the fish at the last parr annulus and the present data warrant no precise

The following example will make the procedure clear:—

Age	Scale radius, mm	adult, mm	Fish length	parr, mm
3·2 +	5·50	897	—	—
3·2	4·00	$\frac{897 \times 4·00}{5·50} = 652$	—	—
3·1	2·50	$\frac{897 \times 2·50}{5·50} = 408$	—	—
3	1·20	$\left(\frac{897 \times 1·20}{5·50} = 196\right)$	$196 \times 0·85 = 167$	$= 167$
2	0·65	$\left(\frac{897 \times 0·65}{5·50} = 106\right)$	$18 + \frac{(167 - 18) 0·65}{1·20} = 99$	$= 99$
1	0·20	$\left(\frac{897 \times 0·20}{5·50} = 33\right)$	$18 + \frac{(167 - 18) 0·20}{1·20} = 43$	$= 43$

calculation of numerical corrections. Pending further work, however, a correction of apparent size of large parr by the factor 0·85 could be used¹.

Parr lengths calculated by means of the adult fish formula are given in parantheses.

Finally, it may be pointed out that in many investigations of comparative nature absolute values of fish size can be dispensed with and replaced by relative scale measurements. For the present this seems recommendable for parr when the material consists of adult scales.

General part

Even by using key scales, as in this study, a considerable variation between the measurements of individual fish is apparent. A closer examination of the sources of variance seems necessary from two points of view. (1) To judge the validity of the back-calculation methods which are based in part upon unverified suppositions concerning the proportionate growth of scales, (2) to investigate the scale growth determining factors and the possibility of obtaining more information on the growth history of fish from the scale reading. An examination with these objects in view is in progress along the following lines.

1. General trend of the body/scale relationship

Scale growth in fishes, as a special case of relative growth of body parts, cannot be presupposed to be isometric. Allometry in fishes is a well known phenomenon. Reference is here made only to the excellent paper by MARTIN (1949).

General body form, expressed as a length/weight relationship, changes and there seems to be a common tendency among fish for an increase in relative weight (KEYS, 1928; HUXLEY, 1932; MARTIN, 1949; and others) or girth (MOTTLEY, 1936) with size and for changes in relative head size (DAHL, 1922; MOTTLEY, 1936; and others). These changes influence the relative size of the growing scalated body surface in relation to the different fish length measurements which are ordinarily used in scientific work to denote fish size. As scale growth, both functionally and causally, must be related to the growth of the scalated area, though not necessarily isometrically, it follows that measure-

¹) The formulae give, apparent parr size 140 mm, true parr size 122 mm, factor 0·87
 apparent parr size 160 mm, true parr size 137 mm, factor 0·86
 apparent parr size 180 mm, true parr size 152 mm, factor 0·85
 apparent parr size 200 mm, true parr size 166 mm, factor 0·83

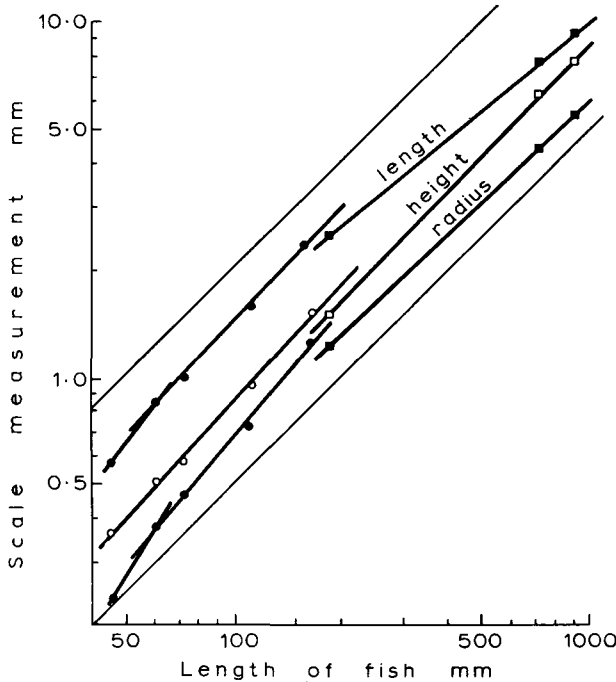


Figure 4. Logarithmic plot of body/scale relationships.
Narrow lines: slope of isometric growth.

ments of this area would be desirable in theoretical scale growth studies (cf. DAHL, 1922).

From this starting point it would certainly be worth while to compare changes in form in the growing fish with changes in size and form in the scale. The general observation of a positive heterauxesis¹ in fish weight, included in and partly obscured by the concept of 'condition' (LEE, 1913; VAN OOSTEN, 1929; LE CREN, 1951) may have something to do with the not uncommon phenomenon of positive heterauxesis in fish scale dimensions.

The present data on general body/scale relationship in Atlantic salmon (Fig. 4) support the advantage of regarding body parts as growing through different growth stanzas (MARTIN, 1949). On the whole, all dimensions of the parr scale show a slight tachyauexesis which in the adult fish is maintained only in the vertical dimension (height) whereas the longitudinal dimensions turn to bradyauexesis. Adjacent scales in vertical rows border on each other without vertical overlapping. This may cause the scales to be closer bound to body size in vertical direction (cf. MASTERMAN, 1913; VAN OOSTEN, 1923; CREASER, 1926; VERNON and MCMYNN, 1957) than in longitudinal direction where overlapping may occur to varying degrees (see below and VAN OOSTEN, 1929). In this case the longitudinal dimensions, most commonly measured in

¹) HUXLEY, NEEDHAM, and LERNER (1941) have defined these terms. Heterauxesis refers to a changing relation between the growth rate of part of a developing organism and the growth rate of the whole or of another part. Isauxesis, tachyauexesis and bradyauexesis denote cases where the growth of the part is at the same rate, or faster, or slower than that of the whole body.

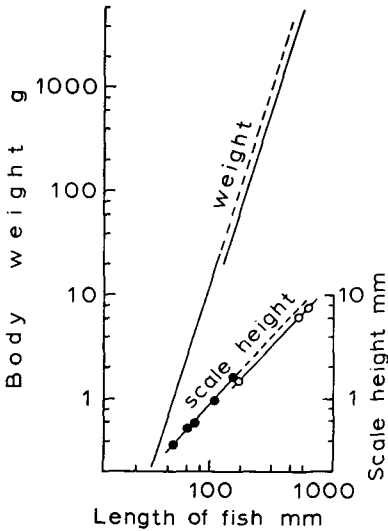


Figure 5. Body length/weight (data from HOAR, 1939 redrawn by MARTIN, 1949) and body length/scale height in parr and adult salmon.

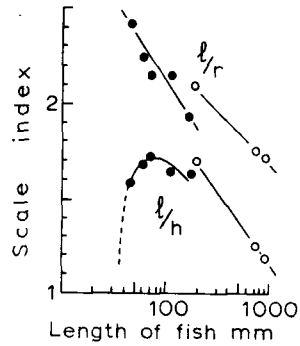


Figure 6. Change in scale form with body size. Scale indices: length/height and length/radius.

scale work, may be correlated to scale height in specific ways in different fish species giving rise to varying allometry in radius and length as to species under study, independent of possible tachyauexis in girth, weight, and scale height.

For Atlantic salmon this probable connection between body-form changes and scale-form changes is of special interest. The observation of a body-form change at smoltification has been investigated (HOAR, 1939; MARTIN, 1949) and the more slender form of the smolt corresponds to the transition, mentioned in the special part above, from parr scale curve to post-smolt scale curve implying relatively smaller and longer scales (Figs. 3 and 5). The suggested connection between girth and scale height is strengthened by this agreement.

Comparisons between different scale dimensions often show changes in scale form during growth. Early observers noted a 'displacement' of the scale nucleus, i.e. unequal growth of anterior and posterior scale margin (VAN OOSTEN, 1923; MONASTYRSKY, 1924, 1930; CREASER, 1926; EINSELE, 1942; and others). Also in the present investigation a relative lengthening of the anterior radius is obvious, from a length/radius index of about 2.4 in very small parr to 1.7 in large adult fish. Smoltification seems to bring about a transition from a parr index curve to an adult scale curve (Fig. 6).

The outer form of the salmon scale, represented by the scale length/height index, shifts from the fairly circular shape of the first papilla (PAGET, 1920) to a maximum value of about 1.7 at a parr size of 60–70 mm only to sink again close to 1.0 in large fish (Fig. 6, cf. MASTERMAN, 1913). In fact the body/scale curve indicates an inflection at a parr length of 60–70 mm. Before this size of the fish, scale length and radius show a pronounced tachyauexis, after this size the tachyauexis is less pronounced (Fig. 4). A change from parr scale form to a relatively longer smolt scale form is indicated and plausible.

As scale height grows approximately proportionate to the fish, the relative

length and, consequently, the degree of longitudinal overlapping, decreases in the growing salmon.

Another general problem is that of the origin of the scale curve. A very common feature in scale studies is a positive intercept on the body-length axis of the extrapolated curve in arithmetical plots. The old and surviving idea that this intercept corresponds to fish length at time of scale formation must be abandoned. SMITH (1955) has demonstrated the very rapid scale growth in a first strongly tachyauxic growth stanza until the more isauxic scale curve is attained (see also VAN OOSTEN; KIPLING, 1962; and others), and every regenerated scale shows the same property (cf. REEVE and HUXLEY, 1945).

The partitioning of the scale growth into successive growth stanzas may be a satisfactory explanation of the phenomenon. In case of the salmon, the data of parr scale height fit a power equation curve through the origin down to very small size which the data of scale length and radius do not (see above) even when referred to scalated body length; yet another indication of the significance of the vertical dimension.

Another explanation of a positive intercept on the body axis or, in this case more correct, a negative intercept on the scale axis, would be the existence of constant vertical interspaces between scales. Preliminary measurements of vertical interspaces seem not to corroborate this hypothesis, however.

2. Variability in relative scale size

All methods of back-calculation of fish size by means of scale-reading are founded upon the supposition that the individual scale during the life of the fish specimen, or at least at all reference times (time at capture and times at completion of annuli), maintains its size position in relation to a standard body/scale curve, i.e. that a curve based on mean values for the population can be made valid for every single scale by simple transformation methods. This, however, "has probably never been shown" (LE CREN, 1947; HILE, 1941), and a survey of sources of variance must consider this question particularly.

A. Within fish specimen

1. Within time.

(a) Within scale, between scale dimensions.

The fish scale does not grow isometrically in different dimensions (see above and VAN OOSTEN, 1923; and others). As the dimension most suitable for use is chosen for standard curves or equations and their subsequent use in scale-reading this source of variation has no practical importance.

(b) Between scales.

Disregarding the variation normal in biological data, there exist systematic differences in size between scales of different position on the body (ESDAILE, 1912; DANNEVIG and HØST, 1931; for salmon). For the first years of life this corresponds with differing times of scale formation (KELEZ, 1932; PARROT, 1934; CLUTTER and WHITESEL, 1956; cf. NEAVE, 1943, as between species) exhibiting characteristic patterns in the fish species. Badly growing salmonid parr will not always be definitely scalated in the first year (COOPER, 1951; BROWN and BAILEY, 1952; ANON., 1959), which is missing in the scales from some body parts leading to considerable errors in age and growth determina-

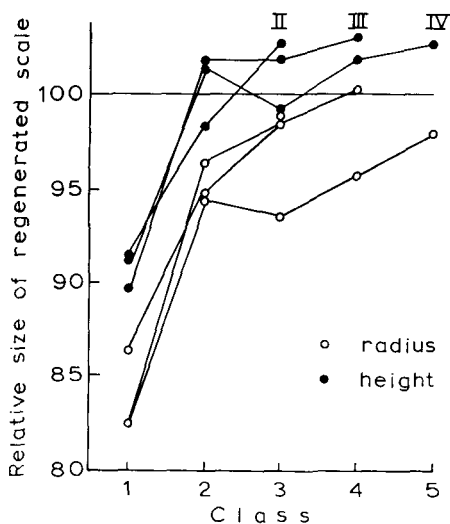


Figure 7. Relative size of regenerated parr scales in % of normal scales. II–IV: normal scales with 2–4 growth periods. Classes indicate age of regenerate estimated from the number of circuli. IV:1 means a young regenerate, with only 1–8 circuli outside the enlarged nucleus, in a 3+ parr; III:3 means a regenerate with 2 growth periods outside the regenerated nucleus in a 2+ parr.

tions (missing annuli in older fish are reported by ALVORD, 1954; for eel, see FROST, 1945).

The variation between scales from different body parts is overcome, when necessary, by the use of key or standard scales. This is not always feasible in field work or in scale sampling by commercial fishermen.

(c) Abnormal scales.

Regenerated scales grow to about normal size if the dermis is not too heavily damaged (NEAVE, 1940; BLAIR, 1942; MÜLLER, 1953; THOMSON, 1957). Regenerated scale height may even exceed the normal value significantly (as in salmon, see Fig. 7) probably a sign of retarded growth in vertical neighbour scales (cf. LEA, 1919; BLAIR, 1942; CLUTTER and WHITESEL, 1956; cf. CREASER, 1926; NEAVE, 1940; who report enlarging of surrounding scales). Whereas it is easy to weed out regenerated scales, it is impossible in ordinary work to avoid scales whose neighbours were regenerated. The occurrence and magnitude of this source of error ought to be investigated.

Scales with resorbed margins and spawning marks are often avoided in back-calculation work. However, maximum radius and even other dimensions are suitable for use in Atlantic salmon.

2. Between times.

(a) Within scale.

If external factors modify relative scale size; if such factors that control the growth of fish during its life, as light, temperature, and food, affect the relative scale size in the individual fish causing seasonal or random time variations, this would mean that the individual scale size during growth takes varying positions in relation to mean scale growth curves obtained on a large amount of material and would be a serious drawback in growth calculations. It should

be possible to study this with new scale marking methods (see FRY *et al.*, 1960). As, however, my own contribution to this problem is derived from between-fish comparisons the discussion will be postponed to a following section.

The observation of the failure of scale growth in trout during its spring growth increase is of particular interest in this connection (see PYEFINCH, 1958).

(b) Between scales.

There exists a normal variation in growth curves between the scales. Salmon parr scale samples from every other horizontal row from the key scale row (Fig. 1) upwards, six rows in all, in some instances failed to reveal significant differences between rows but sometimes such differences occurred in respect of relative size of the first annulus. Other investigations on salmon (ESDAILE, 1912; DANNEVIG and HØST, 1931) and other fish (THOMPSON, 1922; KAGANOVSKAYA, 1937; PHILLIPS, 1948; COOPER, 1951; BROWN and BAILEY, 1952) extended over larger parts of the fish body indicate systematic differences¹. The use of key scales minimizes this type of error.

B. *Between fish* (of the same population)

1. Within time.

(a) Within year-class.

Samples of fish of the same age show body/body part and body/scale relationships of the same general type as mixed material. Deviations from sample regression may be due to genetically fixed or modificatory causes. Environmental variations (temperature) during earlier growth stanzas are known to affect meristic characters (see SEYMOUR, 1959; and others) and thereby scale number in lateral line (MOTTLEY, 1934; and others) and probably also in other directions. Scale number influences scale size in whitefish, *Coregonus* (VAN OOSTEN, 1929), and preliminary inspection of the present data suggests this to be true also in salmon.

Relative size of other body parts not dependent upon myomere number may also be influenced by the previous history during past growth stanzas. Variation of body size at time of inflection to a new growth stanza — be the variations of genetical or environmental origin — results in varying relative body part size for the stanza to follow. MARTIN (1949) exemplifies this and gives experimental data on rainbow trout to prove that higher temperature at early development gives greater relative size of head, depth, and width after a growth inflection at about 30 mm body length, a size sector apparently critical in juvenile salmonids (see also SMITH, 1955) just as is the smoltification period in the anadromous Atlantic salmon. Obviously the same mechanism may be applicable to relative scale size, for instance when slow-growing salmon parr tends to migrate as the largest (oldest) smolt. An influence of smolt size on relative scale size seems possible. To this type of variation belongs the influence of fish size at time of scalation which is known to affect the number of circuli and size of scale (CLUTTER and WHITESEL, 1956; NICHOLLS, 1957).

Fish length variation in within-time (age) samples is tantamount to a variation in growth rate. It is important to consider this fact as it implies that the slope in body/scale regression of within-age samples may deviate from the slope of

¹) Note the agreement between the area of early scalation in salmonids (PAGET, 1920; NEAVE, 1940; and others) and the area of largest apparent computed yearling size in salmon (DANNEVIG and HØST, 1931).

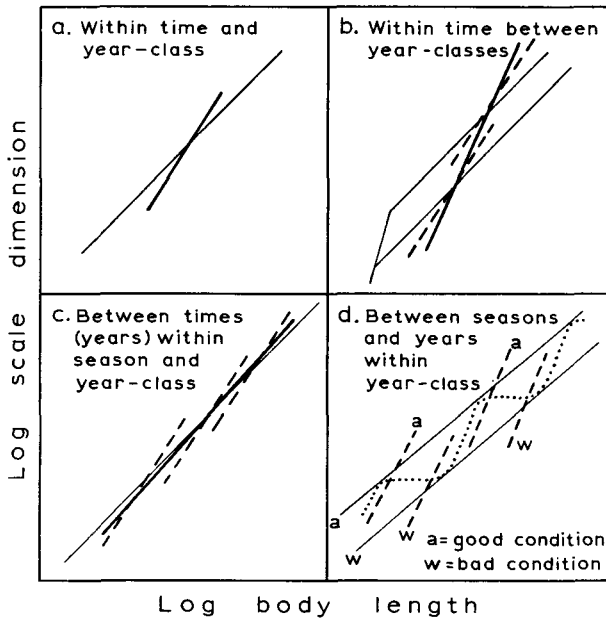


Figure 8. Schematical illustration of possible interrelations between, on the one hand, body/scale relationships based on samples of different origin (a-d) and supposed to be rectilinear in the logarithmic plot, and, on the other hand, 'true' relationships or growth curves.

- total sample regression.
- - - - - subsample regression (subsample within time and year-class as in 'a').
- supposed true relationship for the actual season or state of 'condition'.
- supposed true scale growth curve through seasons.

between-age samples of the same population and year-class if growth rate affects relative scale growth, that is; within-age curves are not true growth curves (see Fig. 8a). With reference to the discussion below it may be pointed out that within-time differences in growth rate does not *per se* mean difference in condition (MARTIN, 1949; LE CREN, 1951).

(b) Between year-classes.

Modificatory differences may be supposed to exist between year-classes. If the relative size of scales is affected to any degree, the year-classes may follow different scale growth curves and data from simultaneous subsamples of different year-classes may give misleading curves (see Fig. 8b).

2. Between times.

(a) Within season.

True growth curves will be obtained only by sampling the same year-class repeatedly. This has very seldom been done (VAN OOSTEN, 1923). Thus, existing body/scale curves may contain errors derived from imperfect agreement in slope between (1) within-age samples, (2) between year-class samples on the one hand, and the true growth curve on the other hand.

The influence of growth rate on relative body part growth has been studied (see MARTIN, 1949). WHITE (1936) found larger eyes in slowly growing popula-

tions of salmon parr. The adult salmon in the present material indicate differences in relative head size (and, consequently, in scalated length) with growth rate. Growth rate as affecting relative scale size has been touched upon by several workers though, unfortunately, not submitted to a closer analysis. *JOBES* (1952), *JOERIS* (1957), and *THOMSON* (1957) found no scale size variation due to age, season, etc. between individuals of the same size whereas *CREASER* (1926) and *LEA* (1933) report relatively smaller scales in slow-growing fish. *MOLANDER* (1920), *LEE* (1920), *BELDING* (1934), *OTTESTAD* (1938), *VAN OOSTEN* (1942), and *NICHOLLS* (1957) are in favour of the opposite view (cf. *KIPLING*, 1962; as between populations). This diversity of opinion is not surprising as the mechanics of growth of body parts as discussed by *MARTIN* may allow of both cases.

Growth rate and condition varies with the season. Investigations in the dependence of relative size on age has to eliminate the effect of season, for instance, by restricting the selection of data to one season of the year. This may be equally true of relative scale size with the result that comparisons between years and year-classes but within season give only the relative size of scales attained annually at that particular season but no true growth curves (Fig. 8c).

(b) Between seasons.

Growth in fishes displays cycles where the time curves for increase in length do not seem to coincide with the curves for weight increase (*BROWN*, 1946) from which it follows that form changes occur continually (*COOPER*, 1953). By far most pronounced is the seasonal growth cycle. Whereas growth-rate differences treated above are within time (or season), between individuals and probably not affecting condition (see above), the seasonal variations are between seasons, within individuals, and affecting condition (form).

An experimentally induced depression of growth rate (*MARTIN*, 1949) resulted in larger relative head size and decreasing depth, width and weight measurements within the growth stanza. This may be regarded as a model of seasonal (or other) variations in condition in wild fishes. The conclusions as far as scale structure is concerned (circuli, annuli and checks) have been studied by several workers (experimentally by *BHATIA* (1931a, b; 1932) in several papers). But little attention has been paid to the very likely effect on scale size and form.

The present material of adult salmon from the winter (January) and autumn (October) 1958, that is periods of slow and rapid growth respectively, displays interesting features. Relative head size and relative girth measurements (condition) are larger in autumn as is relative scale height (significance of difference in height in Figure 9, $P < 0.001$). Relative scale length and radius, in contrast, are smaller or unchanged.

Thus, to the seasonal form changes in the fish (body length/girth) correspond form changes in the scale (scale length/height); to the relatively lengthening body in the winter fish corresponds the winter growth of the scale when incomplete circuli are added mainly along the anterior margin adjusting the scale to a more elongated form (cf. *MASTERMAN*, 1913; *CREASER*, 1926; *BAYRAKCI*, 1936)¹. The data strongly suggest seasonal fluctuations in the fish scale

¹) In some tropical fishes the seasonal decrease in scale height is brought about by resorption of upper and lower margin during the dry season followed by the addition of very widely spaced circuli in the growth period (*JOHNELS*, 1952, 1954).

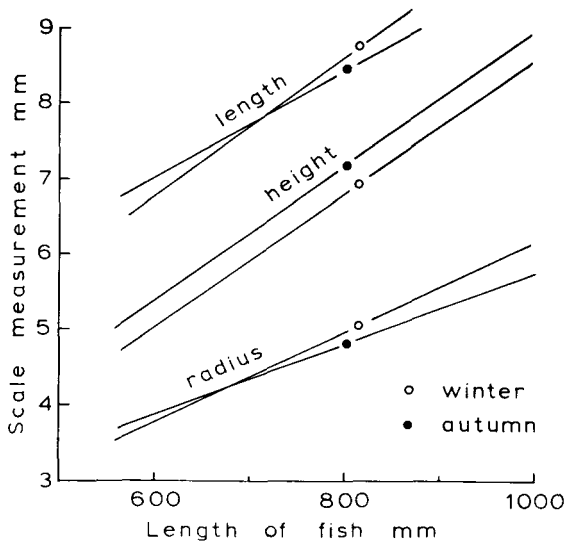


Figure 9. Body/scale regression lines in adult salmon from the Baltic Sea caught in January and October 1958.

form and relative size of fish scale dimensions in conformity with fluctuations in body form, one more evidence of the plasticity of the scales adapting themselves to the scalated area.

The data condensed in Figure 9 are derived from different year-classes and ages and contain probably a mixture of river populations. It is thought, however, that this fact does not invalidate the conclusions made above. At least the growth curve of vertical scale dimensions (height) in relation to body length seems to have an undulatory course in salmon (see Fig. 8d). Probably the same is true of other species and of longitudinal dimensions but the definite statement ought to await further studies.

C. Between populations

As stressed by many authors (HILE, 1941; CARLANDER, 1950; LAAKSO, 1956; JOERIS, 1957; KIPLING, 1962; and others) the same body/scale relationship cannot be presupposed to be valid for different populations of a species. This question is not dealt with in the present study.

Discussion

The analysis made above of the general trend of the body/scale relationship in fishes and of the sources of variance in relative scale size data has as its main object to serve as a survey of pertinent problems. In some cases the data preliminarily presented here have contributed substantially to the discussion.

As stated above, the back-calculation technique demands a detailed knowledge of scale growth in relation to body growth. Some doubt is thrown upon the validity of ordinary body/scale curves as an expression for scale growth. Disregarding errors which may be avoided by adequate sampling and treatment technique, there remains the suspicion that scale growth is fluctuating with

the seasonal growth rate (condition) an effect obscured by the treatment of data. Most scale work is done on samples from the summer half of the year or commercial catch seasons. If the body/scale curves are constructed from samples of fish with a growth rate (condition) deviating from that of the season for annulus formation the danger exists of using a curve which does not express the body/scale relation at time of annulus formation. The existence of fluctuating scale growth and the size of errors should be investigated.

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Summary

1. Data are presented on the body/scale relationship of parr, post-smolt and adults of Atlantic salmon.

- (a) Back-calculation of adult size can be made by direct proportion.
- (b) Back-calculation of parr size from parr scales can be made in the same way after the introduction of a correction term.
- (c) Back-calculation of parr size from adult scales is complicated by the transition from the adult to parr scale curve. A provisional method for overcoming the difficulty is indicated.

2. The general trend of body/scale relationships in fishes and the sources of variance in relative scale size data are discussed. The connection between scale form and body form is stressed and this is of special interest in the salmon where the transition from parr form to adult body form at smoltification is accompanied by a corresponding change in scale form.

Variations in relative scale dimensions within and between fish, within and between times and season are surveyed and their effects on body/scale curves discussed. The present data indicate changes in scale form and relative scale dimensions with the growth rate (condition) of the fish which imply fluctuations of relative scale growth. If further work corroborate this finding the theoretical foundations of back-calculation by means of scales will have to be reconsidered. The practical significance may, however, be of minor importance.

References

- ALVORD, W., 1954. "Validity of age determinations from scales of brown trout, rainbow trout, and brook trout". *Trans. Amer. Fish. Soc.*, **83**: 91-103.
- ANON., 1959. *Progr. Fish-Cult.*, **21**: 193.
- BACKMAN, G., 1932. "Das Wachstum der Wirbeltiere. Die abnormen Schuppen beim Lachs". *Verh. Anat. Ges., Vers. Lund*, **41**: 59-63.
- BAYRAKCI, J. K., 1936. "Die Schuppenentwicklung bei Süßwasserfischen und ihre örtliche Verschiedenheiten". *Int. Rev. Hydrobiol.*, **33**: 73-155.
- BECKMAN, W. C., 1942. "Annulus formation on the scales of certain Michigan game fishes". *Mich. Acad. Sci., Arts Lett.*, **28**: 281-312.
- BELDING, D. L., 1934. "Improved technical methods for determining the annual growth of salmon parr by scale measurements". *Trans. Amer. Fish. Soc.*, **64**: 103-06.
- BHATIA, D., 1931a. "A critical study of the scales of two specimens of starved and excessively fed trout - *Salmo irideus*". *J. Cons. int. Explor. Mer.*, **6**: 266-72.
- BHATIA, D., 1931b. "On the production of annual zones in the scales of the rainbow trout (*Salmo irideus*)". *J. exp. Zool.*, **59**: 45-59.

- BHATIA, D., 1932. "Factors involved in the production of annual zones of the scales of the rainbow trout (*Salmo irideus*)". J. exp. Biol., 9: 6-11.
- BLAIR, A. A., 1937. "The validity of age determinations from the scales of landlocked salmon". Science, 86: 519-20.
- BLAIR, A. A., 1938. "Scales of Lake Ontario salmon indicate a landlocked form". Copeia 1938, No. 4: 206.
- BLAIR, A. A., 1942. "Regeneration of the scales of Atlantic salmon". J. Fish. Res. Bd Can., 5: 440-47.
- BROWN, C. D. J., & BAILEY, J. E., 1952. "Time and pattern of scale formation in Yellowstone cutthroat trout, *Salmo clarkii lewisii*". Trans. Amer. Fish. Soc., 71: 120-24.
- BROWN, M. E., 1946. "The growth of brown trout (*Salmo trutta* L.) II. The growth of two-year-old trout at a constant temperature of 11.5°C". J. exp. Biol., 22: 130-44.
- CARLANDER, K. D., 1950. "Some considerations in the use of fish growth data based upon scale studies". Trans. Amer. Fish. Soc., 79: 187-94.
- CLUTTER, R. I., & WHITESEL, L. E., 1956. "Collection and interpretation of sockeye salmon scales". Bull. int. Pacif. Salm. Fish. Comm., 9: 159 pp.
- COOPER, E. L., 1951. "Validation of the use of scales of brook trout, *Salvelinus fontinalis*, for age determination". Copeia 1951, No. 2: 141-48.
- COOPER, E. L., 1953. "Periodicity of growth and change of condition of brook trout (*Salvelinus fontinalis*) in three Michigan trout streams". Copeia 1953, No. 1: 107-14.
- CREASER, C. W., 1926. "The structure and growth of the scales of fishes in relation to the interpretation of their life-history, with reference to the sunfish, *Eupomotis gibbosus*". Univ. Mich. Mus. Zool., Misc. Publ., No. 17: 1-82.
- LE CREN, E. D., 1947. "The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone". J. anim. Ecol., 16: 188-209.
- LE CREN, E. D., 1951. "The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*)". J. anim. Ecol., 20: 201-19.
- DAHL, K., 1910. "Alder og vekst hos laks og ørret belyst ved studiet av deres skjæld". Ber. Landbruksdept., 115 pp.
- DAHL, K., 1922. "Bemerkninger om skjældmetodens feilkilder". Svensk Fiskeritidskr., 31: 84-92.
- DANNEVIG, A., 1928. "Om dannelsen av årringer i lakseungernes skjell". Norsk Jæg.- og FiskForen. Tidsskr., 57: 301-09.
- DANNEVIG, A., & HØST, P., 1931. "Sources of error in computing I_1-I_2 etc. from scales taken from different parts of the fish". J. Cons. int. Explor. Mer, 6: 64-93.
- EINSELE, W., 1942. "Über das Wachstum der Coregonen im Voralpengebiet insbesondere über das Verhältnis von Schuppen- und Längenwachstum". Z. Fisch., 41: 23-45.
- ELSON, P. F., 1939. "Order of appearance of scales in speckled trout". J. Fish. Res. Bd Can., 4: 302-08.
- ESDAILE, P., 1912. "Intensive study of the scales of three specimens of *Salmo salar*". Manchr. Lit. Philos. Soc., Mem. Proc., 56 (3): 1-22.
- FROST, W. E., 1945. "The age and growth of eels (*Anguilla anguilla*) from the Windermere catchment area". J. anim. Ecol., 14: 106-24.
- FRY, F. E. J., 1943. "A method for the calculation of the growth of fishes from scale measurements". Univ. Toronto Stud. Biol. Ser., 51: 5-18.
- FRY, F. E. J., CUCIN, D., KENNEDY, J. C., & PAPSON, A., 1960. "The use of lead versenate to place a time mark on fish scales". Trans. Amer. Fish. Soc., 89: 149-53.
- HILE, R., 1941. "Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin". Trans. Wis. Acad. Sci., Arts Lett., 33: 189-337.
- HOAR, W. S., 1939. "The weight-length relationship of the Atlantic salmon". J. Fish. Res. Bd Can., 4: 441-60.
- HUNTSMAN, A. G., 1918. "The scale method of calculating the rate of growth in fishes". Trans. Roy. Soc. Can., Ser. 3, 12: 47-52.
- HUXLEY, J. S., 1932. "Problems of relative growth". Methuen & Co. Ltd., London. 276 pp.
- HUXLEY, J. S., NEEDHAM, J., & LERNER, J. M., 1941. "Terminology of relative growth rates". Nature, Lond., 148: 225.
- JÄRVI, T. H., & MENZIES, W. J. M., 1934. "The position on the body of the fish from which scales for examination should be taken". Rapp. Cons. Explor. Mer, 91: 5.
- JOBES, F. W., 1952. "Age, growth and production of yellow perch in Lake Erie". Fish. Bull. U.S., 70: 205-66.
- JOERIS, L. S., 1957. "Structure and growth of scales of yellow perch of Green Bay". Trans. Amer. Fish. Soc., 86: 169-94.

- JOHNELS, A. G., 1952. "Notes on the scale-rings and growth of tropical fishes from the Gambia river". Ark. Zool., 3: 363-66.
- JOHNELS, A. G., 1954. "Notes on fishes from the Gambia river". Ark. Zool., 6: 327-411.
- JOHNSTON, H. W., 1905. "The scales of Tay salmon as indicative of age, growth and spawning habits". Rep. Fish. Bd Scot., 1904: 63-79.
- KAGANOVSKAYA, S. M., 1937. "On the authenticity of calculations on length and rate of growth based on scales from various parts of Jvarsi (*Sardinops melanosticta*)". Bull. Pacif. Sci. Inst. Fish. Oceanogr. Vladivostok, 12: 115-24.
- KELEZ, G. B., 1932. "Variability in the size of scales of an individual red salmon (*Oncorhynchus nerka* Walbaum)". M. A. Thesis, Univ. Stanford. (Unpubl.)
- KERR, B. B., 1961. "Scale to length ratio, age and growth of Atlantic salmon in Miramichi fisheries". J. Fish. Res. Bd Can., 18: 117-24.
- KEYS, A. B., 1928. "The weight-length relation in fishes". Proc. Nat. Acad. Sci., 14: 922-25.
- KIPLING, Charlotte, 1962. "The use of scales of the brown trout (*Salmo trutta* L.) for the back-calculation of growth". J. Cons. int. Explor. Mer, 27: 304-15.
- LAAKSO, M., 1956. "Body-scale regressions in juvenile cutthroat trout from Yellowstone Lake". Proc. Utah Acad. Sci., Arts Lett., 33: 107-11.
- LEA, E., 1919. Report on "Age and growth of the herring in Canadian waters". Dep. Naval Serv. Can., Fish. Exped. 1914-1915: 77-164.
- LEA, E., 1933. "Connected frequency distributions". Rep. Norweg. Fish. Invest., 4 (2): 1-12.
- LEA, E., 1938. "A modification of the formula for calculation of the growth of herring". Rapp. Cons. Explor. Mer, 108 (1): 13-22.
- LEE, R. M., 1913. "A comparison of the rod and net fishery statistics of the Wye". Fish. Invest. Lond., Ser. 1, 1: 80-108.
- LEE, R. M., 1920. "A review of the methods of age and growth determination in fishes by means of scales". Fish. Invest. Lond., Ser. 2, 4 (2): 1-32.
- LINDSAY, S., & THOMPSON, H., 1932. "Biology of the salmon (*Salmo salar* L.) taken in Newfoundland waters in 1931". Rep. Newfoundland Fish. Comm., 1 (2): 1-80.
- MARR, J. C., 1955. "The use of morphometric data in systematic, racial and relative growth studies in fishes". Copeia 1955, No. 1: 25-31.
- MARTIN, W. R., 1949. "The mechanics of environmental control of body form in fishes". Univ. Toronto Stud. Biol. Ser., 58; Publ. Ont. Fish. Res. Lab., 70, 81 pp.
- MASTERMAN, A. T., 1913. "Investigations upon the salmon with special reference to age determination by study of scales". Fish. Invest. Lond., Ser. 1, 1 (1): 79 pp.
- MENZIES, W. J. M., 1934. "Standardization of method of reading salmon scales with special regard to the spawning and winter marks". Rapp. Cons. Explor. Mer, 91: 6-7.
- MOLANDER, A., 1920. "Studies in the growth of the herring, especially with regard to the examination of the scales for determining its growth". Sv. hydro.-biol. Komm. Skr., 6: 16 pp.
- MONASTYRSKY, G., 1924. "Die Beschreibung des abgeänderten Apparates von Einar LEA". Rep. Sci. Inst. Fish. (Moscow), 5 (1): 128-38.
- MONASTYRSKY, G., 1930. "Über Methoden zur Bestimmung des linearen Wachstums der Fische nach der Schuppe". Rep. Sci. Inst. Fish. (Moscow), 5 (4): 5-44.
- MOTTLEY, C. McC., 1934. "The effect of temperature during development on the number of scales in the Kamloops trout, *Salmo kamloops* Jordan". Contr. Can. Biol. Fish., N.S., 8: 252-63.
- MÜLLER, K., 1953. "Die Schuppenmissbildung bei der Forelle, *Salmo trutta* L., und eine Deutung dieser Erscheinung". Rep. Inst. Freshw. Res. Drottningh., 34: 78-89.
- NEAVE, F., 1936. "The development of the scales of *Salmo*". Trans. Roy. Soc. Can., 30: 55-72.
- NEAVE, F., 1940. "On the histology and regeneration of the teleost scale". Quart. J. micr. Sci., N.S., 81: 541-68.
- NEAVE, F., 1943. "Scale pattern and scale counting methods in relation to certain trout and other salmonids". Trans. Roy. Soc. Can., 37: 79-91.
- NICHOLLS, A. G., 1957. "The Tasmanian trout fishery. 1. Sources of information and treatment of data". Austr. J. Mar. Freshw. Res., 8: 451-75.
- OOSTEN, J. VAN, 1923. "The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages". Zoologica N.Y., 2: 381-412.
- OOSTEN, J. VAN, 1929. "Life history of the lake herring (*Leucichthys artedi* le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method". Bull. Fish. U.S., 44: 265-428.

- OOSTEN, J. VAN, 1942. "The age and growth of the Lake Erie white bass, *Lepibema chrysops* (Rafinesque)". Mich. Acad. Sci., Arts Lett., **27**: 307-34.
- OTTESTAD, P., 1938. "On the relation between the growth of the fish and the growth of the scales". Rapp. Cons. Explor. Mer, **108**: 23-31.
- PAGET, G. W., 1920. "Report on the scales of some teleostean fish with special reference to their method of growth". Fish. Invest. Lond., Ser. 2, **4** (3): 24 pp.
- PARROT, A. E., 1934. "The variability and growth of the scales of the brown trout (*Salmo trutta*) in New Zealand". Trans. Proc. N.Z. Inst., **63**: 497-516.
- PHILLIPS, J. B., 1948. "Comparison of calculated fish lengths based on scales from different body areas of the sardine, *Sardinops caerulea*". Copeia 1948, No. 1: 99-106.
- PYEFINCH, K. A., 1958. "Report of the officer-in-charge of the Freshwater Fisheries Laboratory on Brown Trout Research". Sci. Invest. Freshwat. Fish. Scot., No. 21: 5-13.
- REEVE, E. C. R., & HUXLEY, J. S., 1945. "Some problems in the study of allometric growth". Essays in Growth & Form, Clarendon Press, Oxford: 121-56.
- SCHUCK, H. A., 1949. "Problems in calculating size of fish at various ages from proportional measurement of fish and scale sizes". J. Wildlife Mgmt., **13**: 298-303.
- SEGERSTRÅLE, S., 1933. "Scalimetriscche Methoden zur Bestimmung des linearen Wachstums bei Fischen". Acta Zool. fenn., **15**: 168 pp.
- SEYMOUR, A., 1959. "Effects of temperature upon the formation of vertebrae and fin rays in young chinook salmon". Trans. Amer. Fish. Soc., **88**: 58-69.
- SMITH, S. B., 1955. "The relation between scale diameter and body length of Kamloops trout, *Salmo gairdneri kamloops*". J. Fish. Res. Bd Can., **12**: 742-53.
- THOMPSON, H., 1922. "Problems of haddock biology with special reference to the validity and utilization of the scale theory". Scot. Sci. Invest., Fish., No. 5: 78 pp.
- THOMSON, J. M., 1957. "Interpretation of the scales of the yellow-eye mullet, *Aldrichetta forsteri* (Cuvier and Valenciennes) (Mugilidae)". Austr. J. Mar. Freshw. Res., **8**: 14-28.
- VERNON, E. H., & MCMYNN, R. G., 1957. "Scale characteristics of yearling coastal cutthroat and steelhead trout". J. Fish. Res. Bd Can., **14**: 203-12.
- WHITE, H. S., 1936. "Age determination of salmon parr by effect of rate of growth on body proportions". J. Biol. Bd Can., **2**: 379-82.
- WHITNEY, R. R., & CARLANDER, K. D., 1956. "Interpretations of body/scale regression for computing body length of fish". J. Wildlife Mgmt., **20**: 22-27.